

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 Huggins (1989) and Alho (1990) 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 accom-

plish this using a method related to classical “data augmentation” from the statistics literature Tanner and Wong (e.g., 1987)). This is a general concept in statistics but, in the context of capture-recapture models where N is unknown, it has a consistent implementation across classes of capture-recapture models and one that is really convenient from the standpoint of doing MCMC (Royle et al., 2007). We use data augmentation throughout this book and thus emphasize its conceptual and technical origins and demonstrate applications to closed population models. We refer the reader to Kery and Schaub (2011, ch. 6) for an accessible and complimentary development of ordinary closed population models.

3.1 The Simplest Closed Population Model: Model M0

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

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

for every individual in the population. This is a remarkably simple model that forms the cornerstone of almost all of classical capture-recapture models, including most spatial capture-recapture models discussed throughout this book. Evidently, the basic capture-recapture model structure is precisely a simplistic version of a logistic-regression model with only an intercept term ($\text{logit}(p) = \text{constant}$). To say that all capture-recapture models are just logistic regressions is only slightly inaccurate. In fact, we are proceeding here “conditional on N ”, i.e., as if we knew N . In practice we don’t, of course, and that is kind of the point of capture-recapture models as estimating N is the central objective. But, by proceeding conditional on N , we can specify a simple model and then deal with the fact that N is unknown using standard methods that 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 Illian (2008, 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 Royle and Dorazio, 2008, 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 (Sanathanan, 1972).

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

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.

capture-recapture models based on the (1) binomial model for the joint or un-
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 augmen-
tation (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 Tanner and Wong (1987) but see also Liu
and Wu (1999). 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 Royle et al. (2007), and has
subsequently been applied to a number of different contexts including individ-
ual covariate models (Royle, 2009), open population models (Royle and Dorazio,
2008, 2010; Gardner et al., 2010), spatial capture-recapture models (Royle and
Young, 2008; Royle, 2010; Gardner, 2009), 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

¹RC: 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 .

models following Royle and Dorazio (2008, sec. xyz).

In occupancy models (MacKenzie et al., 2002; Tyre et al., 2003) the sampling situation is that M sites, or patches, are sampled multiple times to assess whether a species occurs at each site. This yields encounter data such as that illustrated in the left panel of Table 3.3. The important problem is that a species may occur at a site, but go undetected, yielding the “all-zero” encounter histories which are observed. However, some of the all-zeros may well correspond to sites where the species in fact *does not* occur. Thus, while the zeros are observed, there are too many of them and, in a sense, the inference problem is to allocate the zeros into “structural” (fixed) and “sampling” (or stochastic) zeros. More formally, inference is focused on the parameter ψ , the probability that a site is occupied. In contrast, in classical closed population studies, we observe a data set as in the middle panel of Table 3.3 where *no* zeros are observed. The inference problem is, essentially, to estimate how many sampling zeros there are - or should be - in a “complete” data set. The inference objective (how many sampling zeros?) is precisely the same for both types of problems if an upper limit M is specified for the closed population model. The only distinction being that, in occupancy models, M is set by design (i.e., the number of sites to visit) whereas a natural choice of M for capture-recapture models may not be obvious. However, by assuming a uniform prior for N on the integers $[0, M]$, this upper bound is induced (Royle et al., 2007). Then, one can analyze capture-recapture models by adding $M - n$ all-zero encounter histories to the data set and regarding the augmented data set, essentially, as a site-occupancy data set.

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

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

218 set of assumptions:

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

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

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

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

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

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

226 Which can be maximized directly to obtain the MLEs of the structural param-
 227 eters ψ and p or those of other more complex models (e.g., see Royle, 2006). We
 228 could estimate these parameters and then use them to obtain an estimator of
 229 N using the so-called “Best unbiased predictor” (see Royle and Dorazio, 2011).

230 3.2.2 Model M_0 in BUGS

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

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

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

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

237 Thus, if $z_i = 0$ then the success probability of the binomial distribution is
 238 identically 0 whereas, if $z_i = 1$, then the success probability is p . This is useful
 239 in describing the model in the **BUGS** language, as shown below. Note the last
 240 line of the model specification here provides the expression for computing N
 241 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

```

242 p ~ dunif(0,1)
243 psi~dunif(0,1)
244
245 # nind = number of individuals captured at least once
246 # nz = number of uncaptured individuals added for PX-DA
247 for(i in 1:(nind+nz)) {
248   z[i]~dbern(psi)
249   mu[i]<-z[i]*p
250   y[i]~dbin(mu[i],K)
251 }
252
253 N<-sum(z[1:(nind+nz)])

```

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

```

258 for(i in 1:(nind+nz)) {
259   z[i]~dbern(psi)
260   for(k in 1:K){
261     mu[i,k]<-z[i]*p
262     y[i,k]~dbin(mu[i,k],1)
263   }
264 }

```

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

267 3.2.3 Formal development of data augmentation

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

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

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

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

279 This arises by removing N from Eq. multinomial XYZ by integrating over the
 280 binomial prior distribution for N . Thus, the models we analyze under data
 281 augmentation arise formally by removing the parameter N from the ordinary
 282 model - the model conditional on N - by integrating over a binomial prior
 283 distribution for N .

284 Note that the $M - n$ unobserved individuals in the augmented data set
 285 have probability $\psi\pi(0) + (1 - \psi)$, indicating that these unobserved individuals
 286 are a mixture of individuals that are sampling zeros ($\psi\pi_0$, and belong to the
 287 population of size N) and others that are “structural zeros” (occurring in the
 288 augmented data set with probability $1 - \psi$). In Eq. 3.4 N has been eliminated as
 289 a formal parameter of the model by marginalization (integration) and replaced
 290 with the new parameter ψ , which we will call the “data augmentation param-
 291 eter.” However, the full likelihood containing both N and ψ can be analyzed
 292 (see Royle et al., 2007).

293 3.2.4 Remarks on Data Augmentation

294 Data augmentation may seem like a strange and mysterious black-box, and
 295 likely it is unfamiliar to most people even those with extensive experience with
 296 capture-recapture models. However, it really is a formal reparameterization of
 297 capture-recapture models in which N is removed from the ordinary (conditional-
 298 on- N) model by integration. In the case of Model M0, data augmentation pro-
 299 duces the zero-inflated binomial which is distinct from the original observation
 300 model, but only in the sense that it embodies, explicitly, the $\text{Unif}(0, M)$ prior
 301 for N . Choice of M might be cause for some concern related to potential sen-
 302 sitivity to choice of M . The guiding principle is that it should be chosen large
 303 enough so that the posterior for N is not truncated, but no larger because large
 304 values entail more computational burden. It seems likely that the properties of
 305 the Markov chains should be affected by M and so some optimality might exist
 306 (Gopalaswamy, 2012), as in occupancy models (Mackenzie and Royle, 2005).
 307 Formal analysis of this is required.

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

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

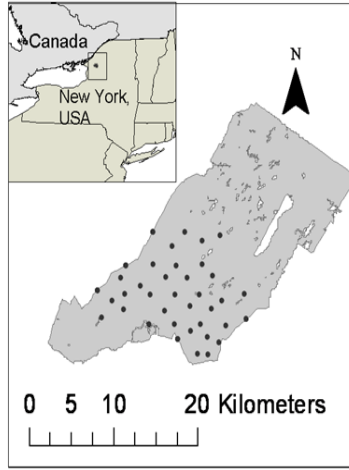


Figure 3.1: Fort Drum study area and hair snare locations.

algorithms² (Durbin and Elston, 2012; King, missing; Schofield and Barker, missing). 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 (Converse and Royle, 2010; ?) 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 Gardner (2009); Gardner et al. (2010), and Wegan (missing). 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.

²Look these citations up in Royle-Dorazio EURING paper

```

345 ## Good idea. This will be done in final draft
346 trapmat<-read.csv("FDtrapmat.csv")
347 bearArray<-source("FDbeararray.R")$value
348 nind<-dim(bearArray)[1]
349 K<-dim(bearArray)[3]
350 ntraps<-dim(bearArray)[2]
351
352 M=175
353 nz<-M-nind
354
355 Xaug <- array(0, dim=c(M,ntraps,K))
356 Xaug[1:nind,,]<-bearArray
357 y<- apply(Xaug,c(1,3),sum)
358 y[y>1]<-1
359 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:

```

366 set.seed(2013) # to obtain the same results each time
367 data0<-list(y=y,M=M,K=K)
368 params0<-list('psi','p','N')
369 zst=c(rep(1,nind),rbinom(M-nind, 1, .5))
370 inits = function() {list(z=zst, psi=runif(1), p=runif(1)) }
371
372 cat("
373 model {
374
375   psi~dunif(0, 1)
376   p~dunif(0,1)
377
378   for (i in 1:M){
379     z[i]~dbern(psi)
380     for(k in 1:K){
381       tmp[i,k]<-p*z[i]
382       y[i,k]~dbin(tmp[i,k],1)
383     }
384   }
385   N<-sum(z[1:M])
386 }
387 ",file="modelM0.txt")
388
389 fit0 = bugs(data0, inits, params0, model.file="modelM0.txt",
390            n.chains=3, n.iter=2000, n.burnin=1000, n.thin=1,
391            debug=TRUE,working.directory=getwd())

```

The posterior summary statistics from this analysis are as follows:


```

393 > print(fit0,digits=2)
394 Inference for Bugs model at "modelM0.txt", fit using WinBUGS,
395 3 chains, each with 2000 iterations (first 1000 discarded)
396 n.sims = 3000 iterations saved
397      mean      sd   2.5%    25%    50%    75%   97.5% Rhat n.eff
398 psi      0.29  0.04   0.22   0.26   0.29   0.31   0.36    1  3000
399 p        0.30  0.03   0.25   0.28   0.30   0.32   0.35    1  3000
400 N        49.94 1.99  47.00  48.00  50.00  51.00  54.00    1  3000
401 deviance 489.05 11.28 471.00 480.45 488.80 495.40 513.70    1  3000
402
403 [... 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 (Dice, 1938) 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 (Bales et al., 2005) 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:

```

423 library("rgeos")
424
425 bcharea<-function(buff,traplocs){
426   p1<-Polygon(rbind(traplocs,traplocs[1,]))
427   p2<-Polygons(list(p1=p1),ID=1)
428   p3<-SpatialPolygons(list(p2=p2))
429   p1ch<-gConvexHull(p3)
430   bp1<-gBuffer(p1ch, width=buff)
431   plot(bp1, col='gray')
432   plot(p1ch, border='black', lwd=2, add=TRUE)
433   gArea(bp1)
434 }

```

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

⁴BETH: Why?

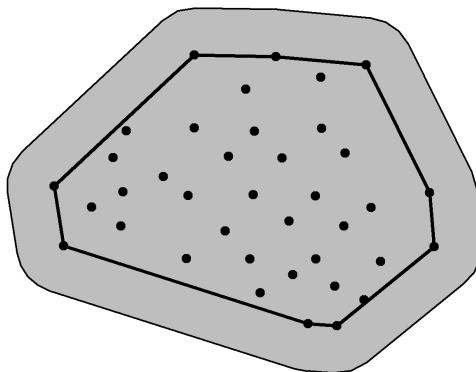


Figure 3.2: buffered convex hull of the bear hair snare array

435

436 `bcharea(2.19,traplocs=trapmat)`

437

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

438

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

439

440 `> summary(fit0$sims.list$N/277.011)`

441

	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
	0.1697	0.1733	0.1805	0.1803	0.1841	0.2130

442

443

444 `> quantile(fit0$sims.list$N/277.011,c(0.025,0.975))`

445

	2.5%	97.5%
	0.1696684	0.1949381

446

447

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

448

449

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

450

451

452

453

454

455

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 (Kéry et al., 2010; Gardner et al., 2010). 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 Yang and Chao (2005) 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 (Burnham and Overton, 1978; Norris III and Pollock, 1996; Pledger,

2000). One important practical matter is that estimates of N can be extremely sensitive to the choice of heterogeneity model (Fienberg et al., 1999; Dorazio and Royle, 2003; Link, 2003). Indeed, Link (2003) 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 Royle and Dorazio (2008, chapt. 6) and Kery and Schaub (2011, chapt. 6).

Model M_h has important historical relevance to spatial capture-recapture situations (Karanth, 1995) 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 Royle and Young (2008)). 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 (Royle and Young, 2008; ?). 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 (Chandler et al., 2011). This system describes, precisely, that of "random temporary emigration" (Kendall, 1997) 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

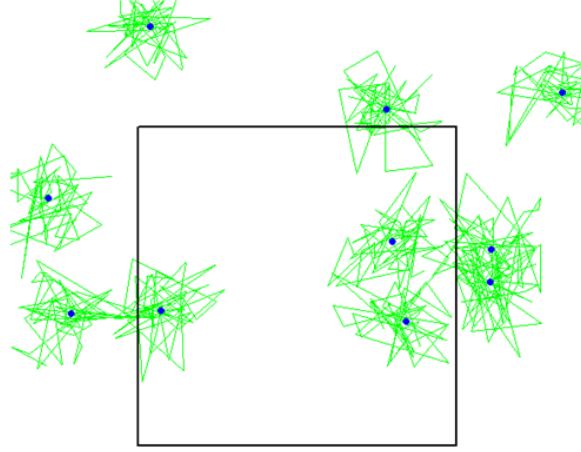


Figure 3.3: A quadrat searched for lizards and the locations of each lizard over some period of time.

of individual i is

$$p_i = p_0 \phi_i$$

so we see clearly that individual heterogeneity in encounter probability is induced as a result of the juxtaposition of individuals (i.e., their home ranges) with the sample apparatus and the movement of individuals about their home range.

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

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

where

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

We could as well write

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

This “logit-normal mixture” was analyzed by Coull and Agresti (1999) and elsewhere. It is a natural extension of the basic model with constant p , as a mixed GLMM, and similar models occur throughout statistics. It is also natural to consider a beta prior distribution for p_i (Dorazio and Royle, 2003) and so-called “finite-mixture” models are also popular (Norris III and Pollock, 1996; Pledger, 2000).

3.4.1 Analysis of Model Mh

If N is known, it is worth taking note of the essential simplicity of Model M_h 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 (Laird and Ware, 1982; Berger et al., 1999) 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 (Royle, 2006) and more traditional analysis of model M_h based on integrated likelihood, without using data augmentation, has been considered by Coull and Agresti (1999), Dorazio and Royle (2003), 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 $M = 500$

599 individuals. We ran the model using **JAGS** with the instructions given as
 600 follows⁵.

```

601 [... get data as before ....]
602
603 set.seed(2013)
604
605 cat("
606 model{
607   p0 ~ dunif(0,1)          # prior distributions
608   mup<- log(p0/(1-p0))
609   taup~dgamma(.1,.1)
610   sigmap<-sqrt(1/taup)
611   psi~dunif(0,1)
612
613   for(i in 1:(nind+nz)){
614     z[i]~dbern(psi)        # zero inflation variables
615     lp[i] ~ dnorm(mup,taup) # individual effect
616     logit(p[i])<-lp[i]
617     mu[i]<-z[i]*p[i]
618     y[i]~dbin(mu[i],K)    # observation model
619   }
620
621   N<-sum(z[1:(nind+nz)])
622 }
623 ",file="modelMh.txt")
624
625 library("rjags")
626 jm<- jags.model("modelMh.txt", data=data1, inits=inits, n.chains=4,
627                n.adapt=1000)
628 jout<- coda.samples(jm, params1, n.iter=50000, thin=1)
629
630 CHANGE THIS TO RUN SIGMA  DUNIF(0,5) PRIOR INSTEAD OF
631 TAUY
632
633 ANDY IS WORKING THIS SECTION RIGHT NOW. KEY IS-
634 SUE IS THAT BEAR DATA HAVE VERY LONG RIGHT TAIL.
635 POSSIBLY NOT EVEN IDENTIFIABLE FOR LOGIT-NORMAL MODEL.
636 NEED TO RUN WINBUGS AND JAGS FOR M=500 AND RUN
637 A 200K RUN AND THEN MAYBE A 500K RUN TO SEE HOW
638 THINGS LOOK. THEN RUN MY R CODE BELOW FOR 5 MIL-
639 LION ITERS OR SOME bs like that. I'm not sure if this is a teaching
640 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:

```

641 > summary(jout)
642 Iterations = 1001:201000
643 Thinning interval = 1

```

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

```

644 Number of chains = 4
645 Sample size per chain = 2e+05
646
647 1. Empirical mean and standard deviation for each variable,
648    plus standard error of the mean:
649
650           Mean          SD Naive SE Time-series SE
651 N      108.63259 52.53176 5.873e-02      2.077726
652 p0       0.08615  0.05919 6.618e-05      0.001950
653 psi      0.21841  0.10615 1.187e-04      0.004141
654 sigmap   1.94096  0.51014 5.703e-04      0.018244
655
656 2. Quantiles for each variable:
657
658           2.5%      25%      50%      75%      97.5%
659 N      59.00000 77.00000 93.00000 121.0000 261.0000
660 p0       0.00418  0.03852  0.07657  0.1240  0.2210
661 psi      0.11230  0.15373  0.18920  0.2457  0.5241
662 sigmap   1.11906  1.57643  1.87752  2.2386  3.1166

```

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

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

The posterior mode compares well with the MLE which we obtained using the R code contained in Panel 6.1 of Royle and Dorazio (2008). The MLE of $\log(n_0)$, the logarithm of the number of uncaptured individuals, is $\log(n_0) = 3.86$ and therefore the MLE is $\hat{N} = \exp(3.86) + 47 = 94.47$ consistent with the apparent mode in Figure XYZ.⁶ To convert this to density we use the buffered area as computed above (255.3 km^2)⁷ and perform the required summary analysis on the posterior samples of N , which results in about 0.37 individuals/ km^2 . The reader should carry out this analysis to confirm the estimates, and also obtain the 95% confidence interval.

3.4.3 Building your own MCMC algorithm

For fun, we construct our own MCMC algorithm using a Metropolized Gibbs sampler for Model M_h . In chapter 7 we devise MCMC algorithms for spatial

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 #

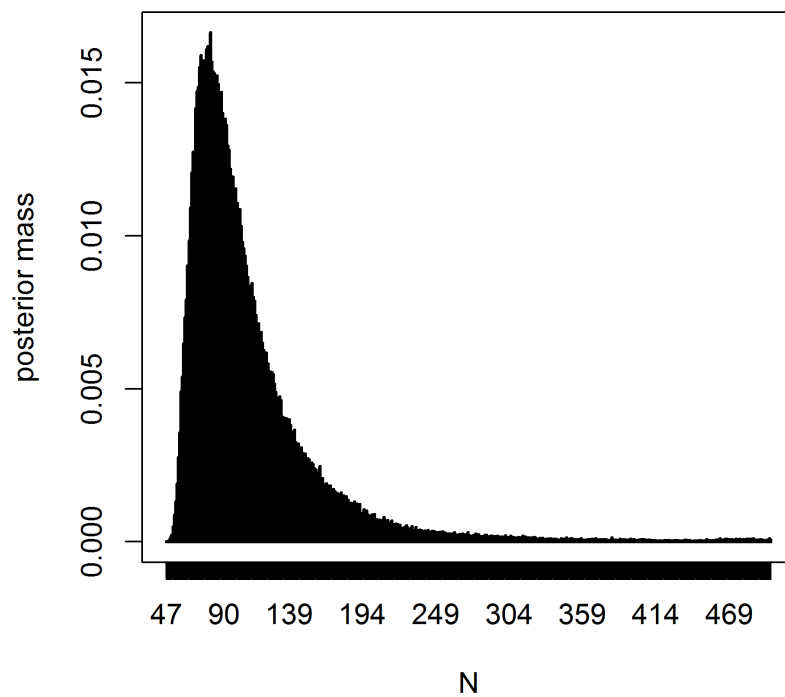


Figure 3.4: Posterior of N for Fort Drum bear study data under the logit-normal version of model M_h . From WinBUGS output. 200k samples.

capture-recapture models and the basic conceptual and technical considerations are entirely analogous to Model M_h .

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

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

(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.

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.

```

713
714 ## obtain the bear data by executing the previous data grabbing
715 ## function
716
717 temp<-getdata()
718 M<-temp$M
719 K<-temp$K
720 ytot<-temp$ytot
721
722
723 ###
724 ### MCMC algorithm for Model Mh
725
726 out<-matrix(NA,nrow=100000,ncol=4)
727 dimnames(out)<-list(NULL,c("mu","sigma","psi","N"))
728 lp<- rnorm(M,-1,1)
729 p<-expit(lp)
730 mu<- -1
731 p0<-exp(mu)/(1+exp(mu))
732 sigma<- 1
733 psi<- .5
734 z<-rbinom(M,1,psi)
735 z[ytot>0]<-1
736
737 for(i in 1:100000){
738
739   ### update the logit(p) parameters
740   lpc<- rnorm(M,lp,1) # 0.5 is a tuning parameter
741   pc<-expit(lpc)
742   lik.curr<-log(dbinom(ytot,K,z*p)*dnorm(lp,mu,sigma))
743   lik.cand<-log(dbinom(ytot,K,z*pc)*dnorm(lpc,mu,sigma))
744   kp<- runif(M) < exp(lik.cand-lik.curr)
745   p[kp]<-pc[kp]
746   lp[kp]<-lpc[kp]
747
748   p0c<- rnorm(1,p0,.05)
749   if(p0c>0 & p0c<1){
750     muc<-log(p0c/(1-p0c))
751     lik.curr<-sum(dnorm(lp,mu,sigma,log=TRUE))
752     lik.cand<-sum(dnorm(lp,muc,sigma,log=TRUE))
753     if(runif(1)<exp(lik.cand-lik.curr)) {
754       mu<-muc
755       p0<-p0c
756     }
757   }
758

```

```

759 sigmac<-rnorm(1,sigma,.5)
760 if(sigmac>0){
761   lik.curr<-sum(dnorm(lp,mu,sigma,log=TRUE))
762   lik.cand<-sum(dnorm(lp,mu,sigmac,log=TRUE))
763   if(runif(1)<exp(lik.cand-lik.curr))
764     sigma<-sigmac
765 }
766
767 ### update the z[i] variables
768 zc<- ifelse(z==1,0,1) # candidate is 0 if current = 1, etc..
769 lik.curr<- dbinom(ytot,K,z*p)*dbinom(z,1,psi)
770 lik.cand<- dbinom(ytot,K,zc*p)*dbinom(zc,1,psi)
771 kp<- runif(M) < (lik.cand/lik.curr)
772 z[kp]<- zc[kp]
773
774 psi<-rbeta(1, sum(z) + 1, M-sum(z) + 1)
775
776 out[i,]<- c(mu,sigma,psi,sum(z))
777 }

```

778 `plot(out[,4])` `mean(out[,4])` [1] 107.4009 `plot(table(out[,4]) +)`
779 `as.mcmc.list(out)` Error in `mcmc.list(x)` : Arguments must be mcmc objects
780 `mean(out[,4])` [1] 107.4009 `sqrt(var(out[,4]))` [1] 39.30742 `median(out[,4])` [1]
781 98 `dim(out)` [1] 501000 4

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

3.4.4 Exercises related to model Mh

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

3.5 Individual Covariate Models: Toward Spatial Capture-Recapture

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 (Royle and Dorazio, 2008, 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” (Royle, 2008, 2009; Langtimm, 2010).

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 Huggins (1989) and Alho (1990). 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 (Royle, 2009). Classical likelihood analysis of

the so-called “full likelihood” is covered in some detail by Borchers et al. (2002). 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 Boulanger and McLellan (2001) (see also Ivan (2012)), 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 Boulanger and McLellan (2001). 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])
```

```

908 Cy<-mean(trapmat[,2])
909 avg.s<-rbind(avg.s,matrix(NA,nrow=nz,ncol=2))
910 xcent<- sqrt( (avg.s[,1]-Cx)^2 + (avg.s[,2]-Cy)^2)

```

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

```

913 minx<- min(trapmat[,1]-Cx)
914 maxx<-max(trapmat[,1]-Cx)
915 miny<- min(trapmat[,2]-Cy)
916 maxy<- max(trapmat[,2]-Cy)
917 # most extreme point determines maxD
918 ul<- c(minx,maxy)
919 maxD<- sqrt( (ul[1]-0)^2 + (ul[2]-0)^2)

```

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

```

924 cat("
925 model{
926   p0 ~ dunif(0,1)          # prior distributions
927   mup<- log(p0/(1-p0))
928   psi~dunif(0,1)
929   beta~dnorm(0,.01)
930
931   for(i in 1:(nind+nz)){
932     xcent[i]~dunif(0,maxD)
933     z[i]~dbern(psi)        # DA variables
934     lp[i] <- mup + beta*xcent[i] # individual effect
935     logit(p[i])<-lp[i]
936     mu[i]<-z[i]*p[i]
937     y[i]~dbin(mu[i],K)    # observation model
938   }
939   N<-sum(z[1:(nind+nz)])
940 }
941 ",file="modelMcov.txt")
942 data2<-list(y=ytot,nz=nz,nind=nind,K=T,xcent=xcent,maxD=11.5)
943 params2<-list('p0','psi','N','beta')
944 inits = function() {list(z=z, psi=psi, p0=runif(1),beta=rnorm(1) ) }
945 fit2 = bugs(data2, inits, params2, model.file="modelMcov.txt",working.directory=getwd(),
946             debug=T, n.chains=3, n.iter=4000, n.burnin=1000, n.thin=4)

```

947 Posterior summaries are given in Table ?? XYZ, and the posterior distribu-
 948 tion of N is given in Figure XYZ. It might be perplexing that the estimated N

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

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. Moreover, importantly, using our new model, *the estimated N applies to an explicit area which is defined by our prescribed value of maxD*. 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 maxD from the centroid of the trap array. As such, the implied “effective trap area”⁹ for any maxD is that of a circle with radius maxD.

```

%% Not sure whether this should be a table or verbatim print-out
\begin{table}
\tabular{cccccccc}
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 maxD 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 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

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

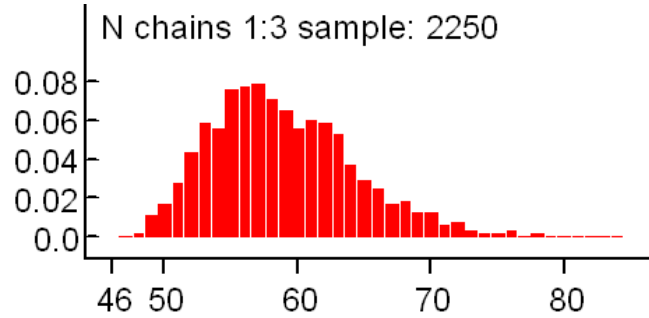


Figure 3.5: Needs a caption

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 $F(x) = \Pr(X < x) = \pi i * x * x / \pi i * \text{maxD} * \text{maxD}$. Then, $f(x) = dF/dx = 2 * x / (\text{maxD} * \text{maxD})$. 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:

```

> u<-runif(10000,-1,1)
> v<-runif(10000,-1,1)
> d<- sqrt(u*u+v*v)
> hist(d[d<1])
> hist(d[d<1],100)
> hist(d[d<1],100,probability=TRUE)
> 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 $2 * x$. 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 $p[i] = 2 * xm[i] * \delta / (D_{\text{max}} * D_{\text{max}})$, 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

1020 be used as described previously. The new variable labeled `xround` is actually
 1021 then the integer category label in units of δ from 0. Thus, to convert back
 1022 to distance in the expression for $lp[i]$, `xround[i]` has to be multiplied by δ .

```

1023 delta<-.2
1024 xround<-xcent%%delta + 1
1025 Dgrid<- seq(delta,maxD,delta)
1026 xprobs<- delta*(2*Dgrid/(maxD*maxD))
1027 xprobs<-xprobs/sum(xprobs)
1028
1029 cat("
1030 model{
1031   p0 ~ dunif(0,1)          # prior distributions
1032   mup<- log(p0/(1-p0))
1033   psi~dunif(0,1)
1034   beta~dnorm(0,.01)
1035
1036   for(i in 1:(nind+nz)){
1037     xround[i]~dcat(xprobs[])
1038     z[i]~dbern(psi)          # zero inflation variables
1039     lp[i] <- mup + beta*xround[i]*delta # individual effect
1040     logit(p[i])<-lp[i]
1041     mu[i]<-z[i]*p[i]
1042     y[i]~dbin(mu[i],K)      # observation model
1043   }
1044
1045   N<-sum(z[1:(nind+nz)])
1046 }
1047 ",file="modelMcov.txt")

```

1048 To fit the model we do this - keeping in mind that the data objects required
 1049 below have been defined in previous analyses of this chapter:

```

1050 data2<-list(y=ytot,nz=nz,nind=nind,K=T,xround=xround,xprobs=xprobs,delta=delta)
1051 params2<-list('p0','psi','N','beta')
1052 inits = function() {list(z=z, psi=psi, p0=runif(1),beta=rnorm(1) ) }
1053 fit = bugs(data2, inits, params2, model.file="modelMcov.txt",working.directory=getwd(),
1054           debug=FALSE, n.chains=3, n.iter=11000, n.burnin=1000, n.thin=2)

```

1055 This is a useful model because it induces a clear definition of area in which
 1056 the population of N individuals reside. Under this model, that area is defined
 1057 by specification of $\max D$. We can apply the model for different values of $\max D$
 1058 and observe that the estimated N varies with $\max D$. Fortunately, we see empirically,
 1059 that while N seems highly sensitive to the prescribed value of $\max D$,
 1060 density seems to be invariant to $\max D$ as long as it is chosen to be sufficiently
 1061 large. We fit the model for $\max D = 12$ (points in close proximity to the trap
 1062 arra) to 20 for and the results are given in Table ??.

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’

$\max D$	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
----------	------	------	------	----	-------	-------	------	----	-------	-------	------	----	-------	-------	------	----	-------	-------	------	----	-------

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 km^2 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 $\max D$

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 $\max D$ in this case), we expect that density estimators should be invariant to this area. In the model used above, we note that $\text{Area}(\max D) = \pi * \max D * \max D$ and $E[N(\max D)] = \lambda * A(\max D)$ and thus $E[\text{Density}(\max D)] = \lambda$ 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 $\max D$ is prescribed to be. As we verified empirically above, the posterior density is also invariant if $\max D$ as long as the implied area (implied by $\max D$) is large enough so that the data no longer provide information about density (i.e., “far away”), then our estimator of density should

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.

1098 become insensitive.

1099 3.5.4 Toward Fully Spatial Capture-recapture Models

1100 We developed this model for the average observed location and equated it to
 1101 home range center s_i . Intuitively, taking the average encounter location as an
 1102 estimate of home range center makes sense but more so when the trapping grid is
 1103 dense and expansive relative to typical home range sizes. However, our approach
 1104 also ignored the variable precision with which each $s[i]$ is estimated and also, as
 1105 noted previously, estimates of $s[i]$ around the “edge” (however we define that)
 1106 are biased because the observations are truncated (we can only observe locations
 1107 within the trap array). In the next Chapter we provide a further extension of
 1108 this individual covariate model that definitively resolves the ad hoc nature of
 1109 the individual covariate approach we took here. In that model we build a model
 1110 in which $s[i]$ are regarded as latent variables and the observation locations (i.e.,
 1111 trap specific encounters) are linked to those latent variables with an explicit
 1112 model. We note that the model fitted previously could be adapted easily to
 1113 deal with s_i as a latent variable, simply by adding a prior distribution for s_i .
 1114 The reader should contemplate how to do this in WinBUGS.

1115 3.6 DISTANCE SAMPLING: A primitive Spatial 1116 Capture-Recapture Model

1117 Distance sampling is one of the most popular methods for estimating animal
 1118 abundance. One of the great benefits of distance sampling is that it provides
 1119 explicit estimates of *density*. The distance sampling model is a special case of a
 1120 closed population model with a covariate. The covariate in this case, x_i , is the
 1121 distance between an individual’s location “ u ” and the observation location or
 1122 transect. In fact, the model underlying distance sampling is precisely the same
 1123 model as that which applies to the individual-covariate models, except that ob-
 1124 servations are made at only $K = 1$ sampling occasion. In a sense, distance
 1125 sampling is a spatial capture-recapture model, but without the “recapture.”
 1126 This first and most basic spatial capture-recapture model has been used rou-
 1127 tinely for decades and, formally, it is a spatially-explicit model in the sense that
 1128 it describes, explicitly, the spatial organization of individual locations (although
 1129 this is not always stated explicitly) and, as a result, somewhat general models
 1130 of how individuals are distributed in space can be specified (Royle, 2004; John-
 1131 son, 2010; Sillett, 2011). As before, the distance sampling model, under data
 1132 augmentation, includes a set of M zero-inflation variables z_i and the binomial
 1133 model expressed conditional on z (binomial for $z = 1$, and fixed zeros for $z = 0$).
 1134 In distance sampling we pay for having only a single sample (i.e., $K = 1$) by
 1135 requiring constraints on the model of detection probability. A standard model
 1136 is

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

1137 for $b < 0$, where x_i denotes the distance at which the i th individual is detected
 1138 relative to some reference location where perfect detectability ($p = 1$) is as-
 1139 sumed. This function corresponds to the “half-normal” detection function (i.e.,
 1140 with $b = 1/\sigma^2$). If $K > 1$ then the intercept α is identifiable and such mod-
 1141 els are usually called “capture-recapture distance sampling” (Borchers, missing)
 1142 and others XYZ????).

1143 As with previous examples, we require a distribution for the individual co-
 1144 variate x_i . The customary choice is

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

1145 wherein $B > 0$ is a known constant, being the upper limit of data recording by
 1146 the observer (i.e., the point count radius, or transect half-width). In practice,
 1147 this is sometimes asserted to be infinity, but in such cases the distance data are
 1148 usually truncated. Specification of this distance sampling model in the BUGS
 1149 language is shown in Panel 3.1. Royle and Dorazio (2008), p. xyz provide a
 1150 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” detec-
 tion function.

1151 As with the individual covariate model in the previous section, the distance
 1152 sampling model can be equivalently specified by putting a prior distribution on
 1153 individual *location* instead of distance between individual and observation point
 1154 (or transect). Thus we can write the general distance sampling model as

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

1155 Along with

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

1156 where x_0 is a fixed point (or line) and $u[i]$ is the individual’s location which is
 1157 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, missing)(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.

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

```

1195 library("R2WinBUGS")
1196 data<- read.csv("Muntjac.csv")
1197 nind<-nrow(data)
1198 y<-rep(1,nind)
1199 nz<-400
1200 y<-c(y,rep(0,nz))
1201 x<-data[,3]
1202 x<-c(x,rep(NA,nz))
1203 z<-y
1204 data<-list(y=y,x=x,nz=nz,nind=nind,B=150,striparea=708*.15*2)
1205
1206 cat("
1207 model{
1208   b~dunif(0,10)
1209   psi~dunif(0,1)
1210
1211   for(i in 1:(nind+nz)){
1212     z[i]~dbern(psi)      # DA Variables
1213     x[i]~dunif(0,B)      # B=strip width
1214     p[i]<-exp(logp[i])    # DETECTION MODEL
1215     logp[i]<- -((x[i]*x[i])*b)
1216     #logp[i]<- -b*log(x[i]+1)
1217     mu[i]<-z[i]*p[i]
1218     y[i]~dbern(mu[i])    # OBSERVATION MODEL
1219   }
1220   N<-sum(z[1:(nind+nz)])
1221   D<- N/striparea      # area of transects
1222 }
1223 ",file="dsamp.txt")

```

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

```

1226 params<-list('b','N','D','psi')
1227 inits = function() {list(z=z, psi=runif(1), b=runif(1,0,.02) )}
1228 fit = bugs(data, inits, params, model.file="dsamp.txt",
1229 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

```

1232 node mean sd MC error 2.5% median 97.5% start sample
1233 D 1.096 0.1694 0.009122 0.8098 1.078 1.474 501 4500
1234 N 232.8 35.99 1.938 172.0 229.0 313.0 501 4500

```

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


```

1235 b 5.678E-4 1.05E-4 4.129E-6 3.867E-4 5.616E-4 7.949E-4 501 4500
1236 deviance 681.2 16.72 0.7536 650.8 680.6 716.6 501 4500
1237 psi 0.5099 0.08238 0.004442 0.3681 0.5033 0.6918 501 4500

```

1238 3.7 Summary and Outlook

1239 Traditional closed population capture-recapture models are closely related to
 1240 binomial generalized linear models. Indeed, the only real distinction is that in
 1241 capture-recapture models, the population size parameter N (corresponding also
 1242 to the size of a hypothetical “complete” data set) is unknown. This requires
 1243 special consideration in the analysis of capture-recapture models. The classi-
 1244 cal approach to inference recognizes that the observations don’t have a stan-
 1245 dard binomial distribution but, rather, a truncated binomial (from which which
 1246 the so-called “conditional likelihood” derives) since we only have encounter fre-
 1247 quency data on observed individuals. If instead we analyze the models using
 1248 data augmentation, the observations can be modeled using a zero-inflated bino-
 1249 mial distribution. In short, when we deal with the unknown- N problem using
 1250 data augmentation then we are left with zero-inflated GLM and GLMMs in-
 1251 stead of ordinary GLM or GLMMs. The analysis of such zero-inflated models is
 1252 practically convenient, especially using the various Bayesian analysis packages
 1253 that use the BUGS language.

1254 Spatial capture-recapture models that we will consider in the rest of the
 1255 chapters of this book are closely related to what have been called individual co-
 1256 variate models. Heuristically, spatial capture-recapture models arise by defining
 1257 individual covariates based on observed locations of individuals – we can think of
 1258 using some function of mean encounter location as an individual covariate. We
 1259 did this in a novel way, by using distance to the centroid of the trapping array
 1260 as a covariate. We analyzed the “full likelihood” using data augmentation, and
 1261 placed a prior distribution on the individual covariate which was derived from
 1262 an assumption that individual locations are, a priori, uniformly distributed in
 1263 space. This assumption provides for invariance of the density estimator to the
 1264 choice of population size area (induced by maximum distance from the centroid
 1265 of the). The model addressed some important problems in the use of closed pop-
 1266 ulation models: it allows for heterogeneity in encounter probability due to the
 1267 spatial context of the problem and it also provides a direct estimate of density
 1268 because area is a feature of the model (via the prior on the individual covariate).
 1269 The model is still not completely general because the model does not make use
 1270 of the fully spatial encounter histories, which provide direct information about
 1271 the locations and density of individuals. A specific individual covariate model
 1272 that is in widespread use is classical “distance sampling.” The model underlying
 1273 distance sampling is precisely a special kind of SCR model - but one without
 1274 replicate samples. Understanding distance sampling and individual covariate
 1275 models more broadly provides a solid basis for understanding and analyzing
 1276 spatial capture-recapture models.

1277 **Chapter 4**

1278 **Fully Spatial**
1279 **Capture-Recapture Models**

1280 Chapter 5

1281 Other observation models

1282 Chapter 6

1283 Maximum likelihood 1284 estimation

1285 **Chapter 7**

1286 **MCMC details**

1287 Chapter 8

1288 Goodness of Fit and stuff

1289 Chapter 9

1290 Covariate models

1291 Chapter 10

1292 Inhomogeneous Point 1293 Process

1294 Chapter 11

1295 Open models

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