

1

2

Spatial Capture-Recapture Models

3

Hierarchical modeling of capture-recapture
data with auxiliary spatial information

4

5

The Four Horsemen (and women)

6

USGS Patuxent Wildlife Research Center
North Carolina State University

7

8

ACADEMIC PRESS

CONTENTS

9

10

11	1 Introduction	9
12	2 Introduction to Bayesian Analysis of GL(M)Ms Using R/WinBUGS	11
13		
14	2.1 Notation	12
15	2.2 GLMs and GLMMs	13
16	2.3 Bayesian Analysis	14
17	2.3.1 Bayes Rule	15
18	2.3.2 Bayesian Inference	16
19	2.3.3 Prior distributions	18
20	2.3.4 Posterior Inference	18
21	2.3.5 Small sample inference	19
22	2.4 Characterizing posterior distributions by MCMC simulation	20
23	2.5 What Goes on Under the MCMC Hood	21
24	2.5.1 Rules for constructing full conditional distributions	22
25	2.5.2 Metropolis-Hastings algorithm	23
26	2.6 Practical Bayesian Analysis and MCMC	24
27	2.6.1 Choice of prior distributions	24
28	2.6.2 Convergence and so-forth	25
29	2.6.3 Bayesian confidence intervals	26
30	2.6.4 Estimating functions of parameters	27
31	2.7 Bayesian Analysis using WinBUGS	27
32	2.7.1 Linear Regression in WinBUGS	27
33	2.7.2 Inference about functions of model parameters	30
34	2.8 Model Checking and Selection	30
35	2.8.1 Goodness-of-fit	31
36	2.8.2 Model Selection	32
37	2.9 Poisson GLMs	33
38	2.9.1 Important properties of the Poisson distribution	34
39	2.9.2 Example: Breeding Bird Survey Data	34
40	2.9.3 Doing it in WinBUGS	35
41	2.9.4 Constructing your own MCMC algorithm	38
42	2.10 Poisson GLM with Random Effects	43

43	2.11	Binomial GLMs	45
44	2.11.1	Binomial regression	45
45	2.11.2	Example: Waterfowl Banding Data	46
46	2.12	Summary and Outlook	48
47	3	Estimating the Size of a Closed Population	51
48	3.1	The Simplest Closed Population Model: Model M0	52
49	3.1.1	The Spatial Context of Capture-Recapture	54
50	3.1.2	Conditional likelihood	54
51	3.2	Data Augmentation	55
52	3.2.1	DA links occupancy models and closed population models . .	56
53	3.2.2	Model M_0 in BUGS	57
54	3.2.3	Formal development of data augmentation	59
55	3.2.4	Remarks on Data Augmentation	60
56	3.2.5	Example: Black Bear Study on Fort Drum	61
57	3.3	Temporally varying and behavioral effects	65
58	3.4	Models with individual heterogeneity	66
59	3.4.1	Analysis of Model Mh	69
60	3.4.2	Analysis of the Fort Drum data	70
61	3.4.3	Building your own MCMC algorithm	72
62	3.4.4	Exercises related to model Mh	76
63	3.5	Individual Covariate Models: Toward Spatial Capture-Recapture . .	76
64	3.5.1	Example: Location of capture as a covariate.	78
65	3.5.2	Extension of the Model	81
66	3.5.3	Invariance of density to maxD	84
67	3.5.4	Toward Fully Spatial Capture-recapture Models	85
68	3.6	DISTANCE SAMPLING: A primitive Spatial Capture-Recapture	
69		Model	85
70	3.6.1	Example: Muntjac deer survey from Nagarahole, India . . .	88
71	3.7	Summary and Outlook	89
72	4	Fully Spatial Capture-Recapture Models	91
73	4.1	Sampling Design and Data Structure	92
74	4.2	The binomial observation model	93
75	4.2.1	Distance as a latent variable	94
76	4.3	The Binomial Point-process Model	95
77	4.3.1	Definition of home range center	96
78	4.3.2	The state-space of the point process	97
79	4.3.3	Invariance and the State-space as a model assumption	98
80	4.3.4	Connection to Model Mh	99
81	4.3.5	Connection to Distance Sampling	100
82	4.4	Simulating SCR Data	100
83	4.4.1	Formatting and manipulating real data sets	102

84	4.5	Fitting an SCR Model in BUGS	102
85	4.6	Unknown N	105
86	4.6.1	Analysis using data augmentation in WinBUGS	106
87	4.6.2	Use of other BUGS engines: JAGS	109
88	4.7	Case Study: Wolverine Camera Trapping Study	110
89	4.7.1	Fitting the model in WinBUGS	113
90	4.7.2	Conclusion of Analysis	116
91	4.8	Constructing Density Maps	117
92	4.8.1	Example: Wolverine density map.	119
93	4.9	Discrete State-Space	119
94	4.9.1	Evaluation of Coarseness of Discrete Approximation	121
95	4.9.2	Analysis of the wolverine camera trapping data	123
96	4.9.3	SCR models as multi-state models	125
97	4.10	Summary and Outlook	125
98	5	Other observation models	129
99	6	Likelihood Analysis of Spatial Capture-Recapture Models	131
100	6.1	Likelihood analysis	132
101	6.1.1	Implementation (simulated data)	134
102	6.2	MLE when N is Unknown	137
103	6.2.1	Exercises	140
104	6.2.2	Integrated Likelihood using the model under data augmenta- tion	141
105	6.2.3	Extensions	141
106	6.3	Classical model selection and assessment	142
107	6.4	Likelihood analysis of the wolverine camera trapping data	142
108	6.4.1	Exercises	145
109	6.5	Program DENSITY and the R package secr	145
110	6.5.1	Analysis using the secr package	147
111	6.6	Summary and Outlook	149
112	7	MCMC Details	151
113	7.1	Introduction	151
114	7.1.1	Why build your own MCMC algorithm?	151
115	7.2	MCMC and posterior distributions	152
116	7.3	Types of MCMC sampling	155
117	7.3.1	Gibbs sampling	155
118	7.3.2	Metropolis-Hastings sampling	158
119	7.3.3	Metropolis-within-Gibbs	162
120	7.4	GLMMs Poisson regression with a random effect	162
121	7.4.1	Rejection sampling and slice sampling	166
122	7.5	MCMC for closed capture-recapture Model Mh	166
123			

124	7.6	MCMC algorithm for the basic spatial capture-recapture model . . .	167
125	7.6.1	SCR model with binomial encounter process	170
126	7.6.2	Looking at model output	171
127	7.6.3	Posterior density plots	174
128	7.6.4	Serial autocorrelation and effective sample size	174
129	7.6.5	Summary results	176
130	7.6.6	Other useful commands	178
131	7.7	Manipulating the state-space	178
132	7.8	MCMC software packages	181
133	7.8.1	WinBUGS	181
134	7.8.2	OpenBUGS	181
135	7.8.3	JAGS Just Another Gibbs Sampler	182
136	7.9	Summary and Outlook	183
137	8	Goodness of Fit and stuff	185
138	9	Covariate models	187
139	10	State-space Covariates	189
140	10.1	Homogeneous point process revisited	190
141	10.2	Inhomogeneous binomial point process	191
142	10.3	Examples	193
143	10.3.1	Simulation and analysis of inhomogeneous point processes . .	193
144	10.3.2	Fitting inhomogeneous point process SCR models	196
145	10.3.3	The jaguar data	200
146	10.4	Summary	201
147	10.5	Other ideas	202
148	11	Inhomogeneous Point Process	203
149	12	Open models	205
150	13	Spatial Capture-Recapture for Unmarked Populations	207
151	13.1	Data Requirements and Survey Designs	208
152	13.2	Encounter Histories as Latent Variables	208
153	13.3	Estimation by MCMC	210
154	13.4	Northern Parula Example	211
155	13.5	On (Im)precision	214
156	13.6	How Much Correlation Is Enough?	214
157	13.7	Mutants	214
158	13.7.1	Other observation models	214
159	13.7.2	Linear designs	214
160	13.8	Summary	214

161	13.8.1 <i>N</i> -mixture models	216
162	13.8.2 Alternative Observation Models	216
163	13.8.3 Spatial point process models	217
164	13.9 Conclusion	218
165	Bibliography	219

166
167
168

1

INTRODUCTION

2

INTRODUCTION TO BAYESIAN ANALYSIS OF GL(M)MS USING R/WINBUGS

A major theme of this book is that spatial capture-recapture models are, for the most part, just generalized linear models (GLMs) wherein the covariate, distance between trap and home range center, is partially or fully unobserved – and therefore regarded as a random effect. Such models are usually referred to as Generalized Linear Mixed Models (GLMMs) and, therefore, SCR models can be thought of as a specialized type of GLMM. Naturally then, we should consider analysis of these slightly simpler models in order to gain some experience and, hopefully, develop a better understanding of spatial capture-recapture models.

In this chapter, we consider classes of GLM models - Poisson and binomial (i.e., logistic regression) GLMs - that will prove to be enormously useful in the analysis of capture-recapture models of all kinds. Many readers are probably familiar with these models because they represent probably the most generally useful models in all of Ecology and, as such, have received considerable attention in many introductory and advanced texts. We focus on them here in order to introduce the readers to the analysis of such models in **R** and **WinBUGS**, which we will translate directly to the analysis of SCR models in subsequent chapters.

Bayesian analysis is convenient for analyzing GLMMs because it allows us to work directly with the conditional model – i.e., the model that is conditional on the random effects, using computational methods known as Markov chain Monte Carlo (MCMC). Learning how to do Bayesian analysis of GLMs and GLMMs in **WinBUGS** is, in part, the purpose of this chapter. While we use **WinBUGS** to do the Bayesian computations, we organize and summarize our data and execute

WinBUGS from within **R** using the useful package **R2WinBUGS** (Sturtz et al., 2005). Kéry (2010), and Kéry and Schaub (2011) provide excellent introductions to the basics of Bayesian analysis and GLMs at an accessible level. We don't want to be too redundant with those books and so we avoid a detailed treatment of Bayesian methodology - instead just providing a cursory overview so that we can move on and attack the problems we're most interested in related to spatial capture-recapture. In addition, there are a number of texts that provide general introductions to Bayesian analysis, MCMC, and their applications in Ecology including McCarthy (2007), Kéry (2010), Link and Barker (2009), and King (2009).

While this chapter is about Bayesian analysis of GLMMs, such models are routinely analyzed using likelihood methods too, as discussed by Royle and Dorazio (2008), and Kéry (2010). Indeed, likelihood analysis of such models is the primary focus of many applied statistics texts, a good one being Zuur et al. (2009). Later in this book, we will use likelihood methods to analyze SCR models but, for now, we concentrate on providing a basic introduction to Bayesian analysis because that is the approach we will use in a majority of cases in later chapters.

2.1 NOTATION

We will sometimes use conventional “bracket notation” to refer to probability distributions. If y is a random variable the $[y]$ indicates its distribution or its probability density/mass function (pdf, pmf) depending on context. If x is another random variable then $[y|x]$ is the conditional distribution of y given x , and $[y, x]$ is the joint distribution of y and x . To differentiate specific distributions in some contexts we might label them $g(y)$, $g(y|\theta)$, $f(x)$, or similar. We will also write $y \sim \text{Normal}(\mu, \sigma^2)$ to indicate that y “is distributed as” a normal random variable with parameters μ and σ^2 . The expected value or mean of a random variable is $E[y] = \mu$, and $\text{Var}[y] = \sigma^2$ is the variance of y . To indicate specific observations we'll use an index such as “ i ”. So, y_i for $i = 1, 2, \dots, n$ indicates observations for n individuals. Finally, we write $\text{Pr}(y)$ to indicate specific probabilities, i.e., of events “ y ” or similar.

To illustrate these concepts and notation, suppose z is a binary outcome (e.g., species occurrence) and we might assume the model: $z \sim \text{Bern}(p)$ for observations. Under this model $\text{Pr}(z = 1) = \psi$, which is also the expected value $E[z] = \psi$. The variance is $\text{Var}[z] = \psi * (1 - \psi)$ and the probability mass function (pmf) is $[z] = \psi^z (1 - \psi)^{1-z}$. Sometimes we write $[z|\psi]$ when it is important to emphasize the conditional dependence of z on ψ . As another example, suppose y is a random variable denoting whether or not a species is detected if an occupied site is surveyed. In this case it might be natural to express the pmf of the observations y *conditional* on z . That is, $[y|z]$. In this case, $[y|z = 1]$ is the conditional pmf of y given that a site is occupied, and it is natural to assume that $[y|z = 1] = \text{Bern}(p)$ where p is the “detection probability” - the probability that we detect the species, given that it is present. The model for the observations y is completely specified once we describe

the other conditional pmf $[y|z = 0]$. For this conditional distribution it is sometimes reasonable to assume $\Pr(y = 1|z = 0) = 0$ (MacKenzie et al. (2002); see also Royle and Link (2006)). That is, if the species is absent, the probability of detection is 0. This implies that $\Pr(y = 0|z = 0) = 1$. To allow for situations in which the true state z is unobserved, we assume that $[z]$ is Bernoulli with parameter ψ . In this case, the marginal distribution of y is

$$[y] = [y|z = 1]Pr(z = 1) + [y|z = 0]Pr(z = 0)$$

because $[y|z = 0]$ is a point mass at $y = 0$, by assumption, then

$$\Pr(y = 1) = p\psi$$

And

$$\Pr(y = 0) = (1 - p) * \psi + (1 - \psi)$$

2.2 GLMS AND GLMMS

We have asserted already that SCR models work out most of the time to be variations of GLMs and GLMMS. Some of you might therefore ask: What are GLMs and GLMMS, anyhow? These models are covered extensively in many very good applied statistics books and we refer the reader elsewhere for a detailed introduction. We think Kéry (2010), Kéry and Schaub (2011), and Zuur et al. (2009) are all accessible treatments of considerable merit. Here, we'll give the 1 minute treatment of GLMMS, not trying to be complete but rather only to preserve a coherent organization to the book.

The generalized linear model (GLM) is an extension of standard linear models by allowing the response variable to have some distribution from the exponential family of distributions (i.e., not just normal). This includes the normal distribution but also dozens of others such as the Poisson, binomial, gamma, exponential, and many more. In addition, GLMS allow the response variable to be related to the predictor variables (i.e., covariates) using a link function, which is usually nonlinear. Finally, GLMs typically accommodate a relationship between the mean and variance. The classical reference for GLMs is Nelder and Wedderburn (1972) and also McCullagh and Nelder (1989). The GLM consists of three components:

1. A probability distribution for the dependent variable y , from a class of probability distributions known as the exponential family.
2. A "linear predictor" $\eta = \mathbf{X}\beta$.
3. A link function g that relates $E[y]$ to the linear predictor, $E[y] = \mu = g^{-1}(\eta)$. Therefore $g(E[y]) = \eta$.

The dependent variable y is assumed to be an outcome from a distribution of the exponential family which includes many common distributions including the

normal, gamma, Poisson, binomial, and many others. The mean of the distribution of y is assumed to depend on predictor variables x according to

$$g(E[y]) = \mathbf{x}'\beta$$

where $E[y]$ is the expected value of y , and $\mathbf{x}'\beta$ is termed the *linear predictor*, i.e., a linear function of the predictor variables with unknown parameters β to be estimated. The function g is the link function. In standard GLMs, the variance of y is a function V of the mean of y : $Var(y) = V(\mu)$ (see below for examples).

A Poisson GLM posits that $y \sim \text{Poisson}(\lambda)$ with $E[y] = \lambda$ and usually the model for the mean is specified using the *log link function* by

$$\log(\lambda_i) = \beta_0 + \beta_1 * x_i$$

The variance function is $V(y_i) = \lambda_i$. The binomial GLM posits that $y_i \sim \text{Binomial}(K, p)$ where K is the fixed sample size parameter and $E[y_i] = K * p_i$. Usually the model for the mean is specified using the *logit link function* according to

$$\text{logit}(p_i) = \beta_0 + \beta_1 * x_i$$

Where $\text{logit}(u) = \log(u/(1-u))$. The inverse-logit function, g^{-1} , is a function we will refer to as “expit”, so that $\text{expit}(u) = \exp(u)/(1 + \exp(u))$.

A GLMM is the extension of GLMs to accommodate “random effects”. Often this involves adding a normal random effect to the linear predictor, and so a simple example is:

$$\log(\lambda_i) = \alpha_i + \beta_1 * x_i$$

where

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

2.3 BAYESIAN ANALYSIS

Bayesian analysis is unfamiliar to many ecological researchers because older cohorts of ecologists were largely educated in the classical statistical paradigm of frequentist inference. But advances in technology and increasing exposure to benefits of Bayesian analysis are fast making Bayesians out of people or at least making Bayesian analysis an acceptable, general, alternative to classical, frequentist inference.

Conceptually, the main thing about Bayesian inference is that it uses probability directly to characterize uncertainty about things we don’t know. “Things”, in this case, are parameters of models and, just as it is natural to characterize uncertain outcomes of stochastic processes using probability, it seems natural also to characterize information about unknown “parameters” using probability. At least this seems natural to us and, we think, most ecologists either explicitly adopt that view or tend to fall into that point of view naturally. Conversely, frequentists use

probability in many different ways, but never to characterize uncertainty about parameters¹ Instead, frequentists use probability to characterize the behavior of *procedures* such as estimators or confidence intervals (see below), which can lead to some inelegant or unnatural interpretations of things. It is paradoxical that people readily adopt a philosophy of statistical inference in which the things you don't know (i.e., parameters) should *not* be regarded as random variables, so that, as a consequence, one cannot use probability to characterize ones state of knowledge about them.

2.3.1 Bayes Rule

As its name suggests, Bayesian analysis makes use of Bayes' rule in order to make direct probability statements about model parameters. Given two random variables z and y , Bayes rule relates the two conditional probability distributions $[z|y]$ and $[y|z]$ by the relationship:

$$[z|y] = [y|z][z]/[y]$$

Bayes' rule itself is a mathematical fact and there is no debate in the statistical community as to its validity and relevance to many problems. Generally speaking, these distributions are characterized as follows: $[y|z]$ is the conditional probability distribution of y *given* z , $[z]$ is the marginal distribution of z and $[y]$ is the marginal distribution of y . In the context of Bayesian inference we usually associate specific meanings in which $[y|z]$ is thought of as "the likelihood", $[z]$ as the "prior" and so on. We leave this for later because here the focus is on this expression of Bayes rule as a basic fact of probability.

As an example of a simple application of Bayes rule, consider the problem of determining species presence at a sample location based on imperfect survey information. Let z be a binary random variable that denotes species presence ($z = 1$) or absence ($z = 0$), let $\Pr(z = 1) = \psi$ where ψ is usually called occurrence probability, "occupancy" (MacKenzie et al., 2002) or "prevalence". Let y be the *observed* presence ($y = 1$) or absence ($y = 0$), and let p be the probability that a species is detected in a single survey at a site given that it is present. Thus, $\Pr(y = 1|z = 1) = p$. The interpretation of this is that, if the species is present, we will only observe presence with probability p . In addition, we assume here that $\Pr(y = 1|z = 0) = 0$. That is, the species cannot be detected if it is not present which is a conventional view adopted in most biological sampling problems (but see Royle and Link (2006)). If we survey a site T times but never detect the species, then this clearly does not imply that the species is not present ($z = 0$) at this site. Rather, our degree of belief in $z = 0$ should be made with a probabilistic statement $\Pr(z = 1|y_1 = 0, \dots, y_T = 0)$. If the T surveys are independent so that we might regard y_t as *iid* Bernoulli trials, then the total number of detections, say y , is Binomial with probability p then we can use Bayes rule to compute the

¹To hear this will be shocking to some readers perhaps.

probability that it is present given that it is not detected in T samples. In words, the expression we seek is:

$$\Pr(\text{present}|\text{not detected}) = \frac{\Pr(\text{not detected}|\text{present}) \Pr(\text{present})}{\Pr(\text{detected})}$$

Mathematically, this is

$$\begin{aligned} \Pr(z = 1|y = 0) &= \Pr(y = 0|z = 1) \Pr(z = 1) / \Pr(y = 0) \\ &= [(1 - p)^T \psi] / [(1 - p)^T \psi + (1 - \psi)]. \end{aligned}$$

To apply this, suppose that $T = 2$ surveys are done at a wetland for a species of frog, and the species is not detected there. Suppose further that $\psi = .8$ and $p = .5$ are obtained from a prior study. Then the probability that the species is present at this site is $.25 * .8 / (.25 * .8 + .2) = 0.50$. That is, there seems to be about a 50/50 chance that the site is occupied despite the fact that the species wasn't observed there.

In summary, Bayes' rule provides a simple linkage between the conditional probabilities $[y|z]$ and $[z|y]$ which is useful whenever one needs to deduce one from the other. Bayes' rule as a basic fact of probability is not disputed.

2.3.2 Bayesian Inference

What is controversial to some is the scope and manner in which Bayes rule is applied by Bayesian analysts. Bayesian analysts assert that Bayes rule is relevant, in general, to all statistical problems by regarding all unknown quantities of a model as realizations of random variables - this includes "data", latent variables, and also "parameters". Classical (non-Bayesian) analysts sometimes object to regarding "parameters" as outcomes of random variables. Classically, parameters are thought of as "fixed but unknown" (using the terminology of classical statistics). Of course, in Bayesian analysis they are also unknown and, in fact, there is a single data-generating value and so they are also fixed. The difference is that this fixed but unknown value is regarded as having been generated from some probability distribution. Specification of that probability distribution is necessary to carryout Bayesian analysis, but it is not required in classical frequentist inference.

To see the general relevance of Bayes rule in the context of statistical inference, let y denote observations - i.e., "data" - and let $[y|\theta]$ be the observation model (often colloquially referred to as the "likelihood"). Suppose θ is a parameter of interest having (prior) probability distribution $[\theta]$. These are combined to obtain the posterior distribution using Bayes' rule, which is:

$$[\theta|y] = [y|\theta][\theta]/[y]$$

Asserting the general relevance of Bayes rule to all statistical problems, we can conclude that the two main features of Bayesian inference are that: (1) "parameters"

θ are regarded as realizations of a random variable and, as a result, (2) inference is based on the probability distribution of the parameters given the data, $[\theta|y]$, which is called the posterior distribution. This is the result of using Bayes rule to combine “the likelihood” and the prior distribution. The key concept is regarding parameters as realizations of a random variable because, once you admit this conceptual view, this leads directly to the posterior distribution, a very natural quantity upon which to base inference about things we don’t know - including parameters of statistical models. In particular, $[\theta|y]$ is a probability distribution for θ and therefore we can make direct probability statements to characterize uncertainty about θ .

The denominator of our invocation of Bayes rule, $[y]$, is the marginal distribution of the data y . We note without further remark right now that, in many practical problems, this can be an enormous pain to compute. The main reason that the Bayesian paradigm has become so popular in the last 20 years or so is because methods exist for characterizing the posterior distribution that do not require that we possess a mathematical understanding of $[y]$, i.e., we never have to compute it or know what it looks like, or know anything specific about it.

A common misunderstanding on the distinction between Bayesian and frequentist inference goes something like this “in frequentist inference parameters are fixed but unknown but in a Bayesian analysis parameters are random.” At best this is a sad caricature of the distinction and at worst it is downright wrong. What is true is that, to a Bayesian, parameters are random variables. However, a Bayesian assumes, just like a frequentist, that there was a single data-generating value of that parameter - a fixed, and unknown value that produced the given data set. The distinction between Bayesian and frequentist approaches is that Bayesians regard the parameter as a random variable, and its value as the outcome of a random value, on par with the observations. This allows Bayesians to use probability to make direct probability statements about parameters. Frequentist inference procedures do not permit direct probability statements to be made about parameter values - because parameters are not random variables!

While we can understand the conceptual basis of Bayesian inference merely by understanding Bayes rule - that’s really all there is to it - it is not so easy to understand the basis of classical “frequentist” inference which is mostly like² a “basket of methods” with little coherent organization. What is mostly coherent in frequentist inference is the manner in which items in this basket of methods are evaluated - the performance of a given procedure is evaluated by “averaging over” hypothetical realizations of y , regarding the *estimator* as a random variable. For example, if $\hat{\theta}$ is an estimator of θ then the frequentist is interested in $E_y[\hat{\theta}|y]$ which is used to characterize bias. If the expected value of $\hat{\theta}$, when averaged over realizations of y , is equal to θ , then $\hat{\theta}$ is unbiased.

The view of parameters as fixed constants and estimators as random variables leads to interpretations that are not so straightforward. For example confidence

²Characterization from Sims REF XYZ

intervals having the interpretation “95% probability that the interval contains the true value” and p-values being “the probability of observing an outcome as extreme or more than the one observed.” These are far from intuitive interpretations to most people. Moreover, this is conceptually problematic to some because the hypothetical realizations that characterize the performance of our procedure we will never get to observe.

While we do tend to favor Bayesian inference for the conceptual simplicity (parameters are random, posterior inference), we mostly advocate for a pragmatic non-partisanship approach to inference because, frankly, some of these “bucket of methods” are actually very convenient in certain situations as we will see in later chapters.

2.3.3 Prior distributions

The prior distribution $[\theta]$ is an important feature of Bayesian inference. As a conceptual matter, the prior distribution characterizes “prior beliefs” or “prior information” about a parameter. Indeed, an oft-touted benefit of Bayesian analysis is the ease with which prior information can be included in an analysis. However, more commonly, the prior is chosen to express a lack of prior information, even if previous studies have been done and even if the investigator does in fact know quite a bit about a parameter. This is because the manner in which prior information is embodied in a prior (and the amount of information) is usually very subjective and thus the result can wind up being very contentious, e.g., if different investigators might report different results based on subjective assessments of things. Thus it is usually better to “let the data speak” and use priors that reflect absence of information beyond the data set being analyzed.

But still the need occasionally arises to embody prior information or beliefs about a parameter formally into the estimation scheme. In SCR models we often have a parameter that is closely linked to “home range radius” and thus auxiliary information on the home range size of a species can be used as prior information (e.g., see Chandler and Royle (2012) ; also chapter XYZ).

XXXXXXXXX

noninformative prior on one scale is informative on another scale. e.g., flat prior on $\text{logit}(p)$ is very different from $\text{uniform}(0,1)$ on p ... show graphic.....

reference to non-invariance of prior distributions to transformation.....

XXXXXXXXX

2.3.4 Posterior Inference

In Bayesian inference, we are not focusing on estimating a single point or interval but rather on characterizing a whole distribution – the posterior distribution – from which one can report any summary of interest. A point estimate might be the posterior mean, median, mode, etc.. In many applications in this book, we will

compute 95% Bayesian intervals using the 2.5% and 97.5% quantiles of the posterior distribution. For such intervals, it is correct to say $\Pr(L < \theta < U) = 0.95$. That is, "the probability that θ is between L and U is 0.95". It is not a subtle thing that this cannot be said using frequentist methods - although people tend to say it anyway and not really understand why it is wrong or even that it is wrong. This is actually a failing of frequentist ideas and the inability of frequentists to get people to overcome their natural tendency to use probability - which is something that, as a frequentist, you simply cannot do in the manner that you would like to.

Posterior inference is the main practical element of Bayesian analysis. We get to make an inference conditional on the data that we actually observed - i.e., what we actually know. To us, this seems logical - to condition on what we know. Conversely, frequentist inference is based on considering average performance over hypothetical unobserved data sets (i.e., the "relative frequency" interpretation of probability). Frequentists know that their procedures work well when averaged over all hypothetical, unobserved, data sets but no one ever really knows how well they work for the specific data set analyzed. That seems like a relevant question to biologists who oftentimes only have their one, extremely valuable, data set. This distinction comes into play a lot in exposing philosophical biases in the peer review of statistical analyses in ecology in the sense that, despite these opposing conceptual views to inference (i.e. conditional on the data you have, or averaged over hypothetical realizations), those who conduct a Bayesian analysis are often (in ecology, almost always) required to provide a frequentist evaluation of their Bayesian procedure.

2.3.5 Small sample inference

Using Bayesian inference, we obtain an estimate of the posterior distribution which is an exhaustive summary of the state-of-knowledge about an unknown quantity. It is the posterior distribution - not an estimate of that thing. It is also not, usually, an approximation except to within Monte Carlo error (in cases where we use simulation to calculate it). One of the great virtues of Bayesian analysis which is not really appreciated is that it is completely valid for any particular sample size. i.e., it is $[\theta|y]$, as precise as we claim it to be based on our ability to do calculations, for the particular sample size and observations that we have even if we have only a single datum y . The same cannot be said for almost all frequentist procedures in which estimates or variances are very often (almost always in practice) based on "asymptotic approximations" to the procedure which is actually being employed.

There seems to be a prevailing view in statistical ecology that classical likelihood-based procedures are virtuous because of the availability of simple formulas and procedures for carrying out inference, such as calculating standard errors, doing model selection by AIC, and assessing goodness-of-fit. In large samples, this may be an important practical benefit, but the theoretical validity of these procedures cannot be asserted in most situations involving small samples. This is not a minor

issue because it is typical in many wildlife sampling problems - especially in surveys of carnivores or rare/endangered species - to wind up with a small, sometimes extremely small, data set. For example, a recent paper on the fossa (*Cryptoprocta ferox*), an endangered carnivore in Madagascar, estimated an adult density of 0.18 adults / km sq based on 20 animals captured over 3 years (Hawkins and Racey, 2005). A similar paper on the endangered southern river otter (*Lontra provocax*) estimated a density of 0.25 animals per river km based on 12 individuals captured over 3 years (Sepúlveda et al., 2007). Gardner et al. (2010) analyzed data from a study of the Pampas cat, a species for which very little is known, wherein only 22 individual cats were captured during the two year period. Trolle and Kéry (2005) reported only 9 individual ocelots captured and Jackson et al. (2006) captured 6 individual snow leopards using camera trapping. Thus, studies of rare and/or secretive carnivores necessarily and flagrantly violate one of Le Cam's Basic Principles, that of "If you need to use asymptotic arguments, do not forget to let your number of observations tend to infinity." (Le Cam, 1990).

The biologist thus faces a dilemma with such data. On one hand, these datasets, and the resulting inference, are often criticized as being poor and unreliable. Or, even worse³, "the data set is so small, this is a poor analysis." On the other hand, such data may be all that is available for species that are extraordinarily important for conservation and management. The Bayesian framework for inference provides a valid, rigorous, and flexible framework that is theoretically justifiable in arbitrary sample sizes. This is not to say that one will obtain precise estimates of density or other parameters, just that your inference is coherent and justifiable from a conceptual and technical statistical point of view. That is, we report the posterior probability $\Pr(D|data)$ which is easily interpretable and just what it is advertised to be and we don't need to do a simulation study to evaluate how well some approximate $\Pr(D|data)$ deviates from the actual $\Pr(D|data)$ because they are precisely the same quantity.

2.4 CHARACTERIZING POSTERIOR DISTRIBUTIONS BY MCMC SIMULATION

In practice, it is not really feasible to ever compute the marginal probability distribution $\Pr(y)$, the denominator resulting from application of Bayes' rule. For decades this impeded the adoption of Bayesian methods by practitioners. Or, the few Bayesian analyses done were based on asymptotic normal approximations to the posterior distribution. While this was useful stuff from a theoretical and technical standpoint and, practically, it allowed people to make the probability statements that they naturally would like to make, it was kind of a bad joke around the Bayesian water-cooler to, on one hand, criticize classical statistics for being, essentially, completely ad hoc in their approach to things but then, on the other hand,

³Actual quote from a referee

526 have to devise various approximations to what they were trying to characterize.
 527 The advent of Markov chain Monte Carlo (MCMC) methods has made it easier to
 528 calculate posterior distributions for just about any problem to arbitrary levels of
 529 precision.

530 Broadly speaking, MCMC is a class of methods for drawing random numbers
 531 (sampling or simulating) from the target posterior distribution. Thus, even though
 532 we might not recognize the posterior as a named distribution or be able to ana-
 533 lyze its features analytically, e.g., devise mathematical expressions for the mean
 534 and variance, we can use these MCMC methods to obtain a large sample from the
 535 posterior and then use that sample to characterize features of the posterior. What
 536 we do with the sample depends on our intentions – typically we obtain the mean or
 537 median for use as a point estimate, and take a confidence interval based on Monte
 538 Carlo estimates of the quantiles. These are estimates, but not like frequentist es-
 539 timates. Rather, they are Monte Carlo estimates with an associated Monte Carlo
 540 error which is largely determined arbitrarily by the analyst. They are not estimates
 541 qualified by a sampling distribution as in classical statistics. If we run our MCMC
 542 long enough then our reported value of $E[\theta|y]$ or any feature of the posterior dis-
 543 tribution is precisely what we say it is. There is no “sampling variation” in the
 544 frequentist sense of the word. In summary, the MCMC samples provide a Monte
 545 Carlo characterization of *the* posterior distribution.

2.5 WHAT GOES ON UNDER THE MCMC HOOD

546 We will develop and apply MCMC methods in some detail for spatial capture-
 547 recapture models in chapter ???. Here we provide a simple illustration of some basic
 548 ideas related to the practice of MCMC.

549 A type of MCMC method relevant to most problems is Gibbs sampling (REF
 550 XYZ XYZ), which is based on the idea of iterative simulation from the “full con-
 551 ditional” distributions (also called conditional posterior distributions). The full
 552 conditional distribution for an unknown quantity is the conditional distribution of
 553 that quantity given every other random variable in the model - the data and all other
 554 parameters. For example, for a normal regression model with $y \sim \text{Normal}(\alpha + \beta x, 1)$
 555 then the two full conditionals are, in symbolic terms,

$$[\alpha|y, \beta]$$

556 and

$$[\beta|y, \alpha].$$

557 We might use our knowledge of probability to identify these mathematically. In
 558 particular, by Bayes’ Rule, $[\alpha|y, \beta] = [y|\alpha, \beta][\alpha|\beta]/[y|\beta]$ and similarly for $[\beta|y, \alpha]$.
 559 For example, if we have priors for $[\alpha]$ and $[\beta]$ which are also normal distributions,
 560 some algebra reveals that XXXX COPY NOTATION FFROM CH. 6 XXXXX

$$[\alpha|y, \beta] = \text{Normal}(\text{ybar}, \dots \text{weightedvariancehere} \dots).$$

561 Similarly,

$$[\beta|y, \alpha] \text{isnormal}(\dots\dots)$$

562 The MCMC algorithm for this model has us simulate in succession, repeat-
 563 edly, from those two distributions. See Gelman et al. (2004) for more examples of
 564 Gibbs sampling for the normal model. A conceptual representation of the MCMC
 565 algorithm for this simple model is therefore: XXXX Check out ALGORITHM en-
 566 vironment XXXXX

567 **Algorithm**

```
568
569     0. Initialize  $\alpha$  and  $\beta$ 
570
571     Repeat{
572         1. Draw a new value of  $\alpha$  from Eq. \ref{xyz}
573
574         2. Draw a new value of  $\beta$  from Eq. \ref{xyz}
575     }
```

576 As we just saw for this simple “normal-normal” model it is sometimes possible
 577 to specify the full conditional distributions analytically. In general, when certain
 578 so-called conjugate prior distributions are chosen, the form of full conditional distri-
 579 butions is similar to that of the observation model. In this normal-normal case, the
 580 normal distribution for the mean parameters is the conjugate prior under the normal
 581 model, and thus the full-conditional distributions are also normal. This is conven-
 582 nient because, in such cases, we can simulate directly from them using standard
 583 methods (or **R** functions). But, in practice, we don’t really ever need to know such
 584 things because most of the time we can get by using a simple algorithm, called the
 585 Metropolis-Hastings (henceforth “MH”) algorithm, to obtain samples from these
 586 full conditional distributions without having to recognize them as specific, named,
 587 distributions. This gives us enormous freedom in developing models and analyzing
 588 them without having to resolve them mathematically because to implement the MH
 589 algorithm we need only identify the full conditional distribution up to a constant
 590 of proportionality, that being the marginal distribution in the denominator (e.g.,
 591 $[y|\beta]$ above).

592 We will talk about the Metropolis-Hastings algorithm shortly, and we will use
 593 it extensively in the analysis of SCR models (e.g., chapter ??).

594 2.5.1 Rules for constructing full conditional distributions

595 The basic strategy for constructing full-conditional distributions for devising MCMC
 596 algorithms can be reduced conceptually to a couple of basic steps summarized as
 597 follows:

598 (step 1) Collect all stochastic components of the model;

- 599 (step 2) Recognize and express the full conditional in question as proportional to
 600 the product of all components;
 601 (step 3) Remove the ones that don't have the focal parameter in them.
 602 (step 4) Do some algebra on the result in order to identify the resulting pdf or pmf.

603 Of the 4 steps, the last of those is the main step that requires quite a bit of statistical
 604 experience and intuition because various algebraic tricks can be used to reshape the
 605 mess into something noticeable - i.e., a standard, named distribution. But step 4
 606 is not necessary if we decide instead to use the Metropolis-Hastings algorithm as
 607 described below.

608 To illustrate for computing $[\alpha|y, \beta]$ we first apply step 1 and identify the model
 609 components as: $[y|\alpha, \beta]$, $[\alpha]$ and $[\beta]$. Step 2 has us write $[\alpha|y, \beta] \propto [y|\alpha, \beta][\alpha][\beta]$.
 610 Step 3: We note that $[\beta]$ is not a function of alpha and therefore we remove it to
 611 obtain $[\alpha|y, \beta] \propto [y|\alpha, \beta][\alpha]$. Similarly we obtain $[\beta|y, \alpha] \propto [y|\alpha, \beta][\beta]$. We apply
 612 step 4 and manipulate these algebraically to arrive at the result or, alternatively, we
 613 can sample them indirectly using the Metropolis-Hastings algorithm (see below).

614 2.5.2 Metropolis-Hastings algorithm

615 The Metropolis-Hastings (MH) algorithm is a completely generic method for sam-
 616 pling from any distribution, say $f(\theta)$. In our applications, $f(\theta)$ will typically be
 617 the full conditional distribution of θ . While we sometimes use Gibbs sampling,
 618 we seldom use “pure” Gibbs sampling because we might use MH to sample from
 619 one or more of the full conditional distributions. When the MH algorithm is used
 620 to sample from full conditional distributions of a Gibbs sampler the resulting hy-
 621 brid algorithm is called *Metropolized Gibbs sampling* or more commonly *Metropolis-*
 622 *within-Gibbs*. Shortly we will actually construct such an algorithm for a simple
 623 class of models.

624 The MH algorithm generates candidates from some proposal or candidate-
 625 generating distribution, that may be conditional on the current value of the pa-
 626 rameter, denoted by $h(\theta^*|\theta^t)$. Here, θ^* is the *candidate* or proposed value and θ^t is
 627 the current value, i.e., at iteration t of the MCMC algorithm. The proposed value
 628 is accepted with probability XXXX check notation with Rahel XXXXXX

$$r = \frac{f(\theta^*)h(\theta^t|\theta^*)}{f(\theta^t)h(\theta^*|\theta^t)}$$

629 which we call the MH acceptance probability. This ratio can sometimes be > 1 in
 630 which case we set it equal to 1. It is useful to note that $h()$ can be anything at all.
 631 Absolutely anything! You can generate candidate values from a *normal*(0,1) dis-
 632 tribution, from a *uniform*(-3455,3455) distribution, or anything of proper support.
 633 Note, however, that good choices of $h()$ are those that approximate the posterior
 634 distribution. Obviously if $h() = f(\theta|y)$ (i.e., the posterior) then you always accept
 635 the draw, and it stands to reason that proposals that are more similar to $f(\theta|y)$

will lead to higher acceptance probabilities. No matter the choice of $h()$, we can evaluate this ratio numerically because the marginal $f(y)$ cancels from both the numerator and denominator, which is the magic of the MH algorithm.

A special kind of $h()$ are those that are symmetric, which means that $h(a|b) = h(b|a)$ in which case $h(a|b)$ and $h(b|a)$ just cancel out from the MH acceptance probability and r is then just the ratio of the target density evaluated at the candidate value to that evaluated at the current value. A type of symmetric proposal useful in many situations is the so-called *random-walk* proposal distribution where candidate values are drawn from a normal distribution with mean equal to the current value and some standard deviation, say δ , which is prescribed by the user. For parameters that have support on the real line, e.g., α in our example above, the random walk proposal generator has us generate $\alpha^* \sim \text{Normal}(\alpha^t, \delta)$. If we set δ very small we have a high probability of accepting the proposal and vice versa. In practice, we “tune” delta to achieve a compromise between acceptance rate and efficient mixing of the Markov chains (see below for an example) normally assessed by autocorrelation. Low δ increases the acceptance rate but will tend to produce Markov chains with high autocorrelation, and vice versa.

Parameters with bounded support: Many models contain parameters that have bounded support. E.g., variance parameters live on $[0, \infty]$, parameters that represent probabilities live on $[0, 1]$, etc.. In that case it is sometimes convenient to use a random walk proposal distribution that can generate any real number (e.g., a normal random walk proposal). In that case, we can just reject parameters that are outside of the parameter space (XXXX REF FOR THIS XXXX).

2.6 PRACTICAL BAYESIAN ANALYSIS AND MCMC

There are a number of really important practical issues to be considered in any Bayesian analysis and we cover some of these briefly here.

2.6.1 Choice of prior distributions

**XXX integrate this material with previous section on prior distributions
XXXXXX**

Bayesian analysis requires that we choose prior distributions for all of the structural parameters of the model (we use the term structural parameter to mean all parameters that aren’t customary thought of as latent variables). We will strive to use priors that are meant to express little or no prior information - default or customary “non-informative” or diffuse priors. This will be $\text{Unif}(a, b)$ priors for parameters that have a natural bounded support and, for parameters that live on the real line we use either (1) diffuse normal priors; (2) “improper” uniform priors or (3) sometimes even a bounded $\text{Unif}(a, b)$ prior if that greatly improves the performance of **WinBUGS** or other software doing the MCMC for us. In **WinBUGS** a prior with low “precision”, τ , where $\tau = 1/\sigma^2$, such as $\text{Norm}(0, .01)$ will typically

be used. Of course $\tau = 0.01$ ($\sigma^2 = 100$) might be very informative for a regression parameter that has a high variance. Therefore, we recommend that predictor variables *always* be standardized. Clearly there are a lot of choices for ostensibly non-informative priors, and the degree of non-informativeness depends on the parameterization. For example, a natural non-informative prior for the intercept of a logistic regression

$$\text{logit}(p_i) = \alpha + \beta x_i$$

Would be $[\alpha] = \text{const}$ which is the same as saying $a \sim \text{Unif}(\infty, \text{infy})$, the customary improper uniform prior. However, we might also use a prior on the parameter $p_0 = \text{logit}^{-1}(a)$, which is $\text{Pr}(y = 1)$ for the value $x = 0$. Since p_0 is a probability a natural choice is $p_0 \sim \text{Unif}(0, 1)$. These two priors can affect results (see Chapter 3.XYZ), yet they are both sensible non-informative priors. Choice of priors and parameterization is very much problem-specific and often largely subjective. Moreover, it also affects the behavior of MCMC algorithms and therefore the analyst needs to pay some attention to this issue and possibly try different things out. XXX REFS on prior distributions XXXXX

2.6.2 Convergence and so-forth

Once we have carried-out an analysis by MCMC, there are many other practical issues that we have to confront. One of the most important is “have the chains converged?” Most MCMC algorithms only guarantee that, eventually, the samples being generated will be from the target posterior distribution. So-called “convergence” of the Markov chain is achieved when that happens. Typically a period of transience is observed in the early part of the MCMC algorithm, and this is usually discarded as the “burn-in” period.

The quick diagnostic to whether convergence has been achieved is that your Markov chains look “grassy” – see Fig. 2.5 below. Another way to check convergence is to update the parameters some more and see if the posterior changes. It is good to confirm convergence using the “R-hat” statistic (\hat{R}) or Brooks-Gelman-Rubin statistic (Gelman et al., 1996)) which should be close to 1 if the Markov chains have converged and sufficient posterior samples have been obtained. In practice, $\hat{R} = 1.2$ is probably good enough for some problems. For some models you can’t actually realize a low \hat{R} . E.g., if the posterior is a discrete mixture of distributions then you can be misled into thinking that your Markov chains have not converged when in fact the chains are just jumping back and forth in the posterior state-space. So, for example, using model selection methods (section XYZ) sometimes suggests non-convergence. Another situation is when one of the parameters is on the boundary of the parameter space which might appear to be very poor mixing, but all within some extreme region of the parameter space.⁴ This

⁴it would be nice if we could compile examples of this later in the book and reference back to this point

kind of stuff is normally ok and you need to think really hard about the context of the model and the problem before you conclude that your MCMC algorithm is ill-behaved.

Some models exhibit “poor mixing” of the Markov chains or what people might also say “have not covered” (or “slow convergence”) which is a term we would disagree with because the samples might well be from the posterior (i.e., the Markov chains have converged to the proper stationary distribution) but simply mix around the posterior rather slowly. Anyway, poor mixing can happen for a huge number of reasons – when parameters are highly correlated (even confounded), or barely identified from the data, or the algorithms are very terrible and probably many other reasons. Slow mixing equates to high autocorrelation in the Markov chain – the successive draws are highly correlated, and thus we need to run the MCMC algorithm much longer to get an effective sample size that is sufficient for estimation – or to reduce the MC error to a tolerable level. A strategy often used to reduce autocorrelation is “thinning” – i.e., keep every m^{th} value of the Markov chain output. However, thinning is necessarily inefficient from the stand point of inference – you can always get more precise posterior estimates by using all of the MCMC output regardless of the level of autocorrelation (MacEachern and Berliner, 1994). Practical considerations might necessitate thinning, even though it is statistically inefficient. For example, in models with many parameters or other unknowns being tabulated, the output files might be enormous and unwieldy to work with. In such cases, thinning is perfectly reasonable. In many cases, how well the Markov chains mix is strongly influenced by parameterization, standardization of covariates, and the prior distributions being used. Some things work better than others, and the investigator should experiment with different settings and remain calm when things don’t work out perfectly. MCMC is an art, and a science.

Is the posterior sample large enough? A good rule of thumb is that you should never report MCMC results to more than 2 decimal places – because they will always be different! Look at the MC error which is printed by default in summaries of BUGS output. You want that to be smallish relative to the magnitude of the parameter and this might depend on the purpose of the analysis. For a preliminary analysis you might settle for a few percent whereas for a final analysis then certainly less than 1% is called for, but you can run your MCMC algorithm as long as it takes. Note that MC error in summaries of the posterior is not the same as having an “approximate” solution in a standard likelihood analysis or similar. The approximate SE in likelihood inference is actually wrong in its actual value.... XYZ.

2.6.3 Bayesian confidence intervals

The 95% Bayesian interval based on percentiles of the posterior is not a unique interval – there are many of them – and the so-called “highest posterior density” (HPD) interval is the narrowest interval. We might compute that frequently because

it is easy to do with an integer parameter which N is (See the next chapter). The 95 % HPD is not often exactly 95% but usually slightly more conservative than nominal because it is the narrowest interval that contains at least 95% of the posterior mass.

2.6.4 Estimating functions of parameters

A benefit of analysis by MCMC is that we can seamlessly estimate functions of parameters by simply tabulating the desired function of the simulated posterior draws. For example, if θ is the parameter of interest and let $\theta^{(i)}$ for $i = 1, 2, \dots, M$ be the posterior samples of θ . Let $\eta = \exp(\theta)$, then a posterior sample of η can be obtained simply by computing $\exp(\theta^{(i)})$ for $i = 1, 2, \dots, M$. We give another example in section 2.7.2 below and throughout this book. Almost all SCR models in this book involve at least 1 derived parameter. For example, density D is a derived parameter, being a function of population size N and the area A of the underlying state-space of the point process (see chapter ??).

2.7 BAYESIAN ANALYSIS USING WINBUGS

We won't be too concerned with devising our own MCMC algorithms for every analysis although we will do that a few times for fun. More often, we will rely on the freely available software package **WinBUGS** or **JAGS** for doing this. We will always execute these **BUGS** engines from within **R** using the **R2WinBUGS** (REF XYZ XYZ) or **rjags** packages. **WinBUGS** and **JAGS** are MCMC black boxes that takes a pseudo-code description (i.e., written in the **BUGS** language) of all of the relevant stochastic and deterministic elements of a model and generates an MCMC algorithm for that model. But you never get to see the algorithm. Instead, **WinBUGS/JAGS** will run the algorithm and just return the Markov chain output - the posterior samples of model parameters.

The great thing about using the **BUGS** language is that it forces you to become intimate with your statistical model - you have to write each element of the model down, admit (explicitly) all of the various assumptions, understand what the actual probability assumptions are and how data relate to latent variables and data and latent variables relate to parameters, and how parameters relate to one another.

While we normally use **WinBUGS** or **JAGS** in this book, we note that **OpenBUGS** is the current active development tree of the **BUGS** language. See Kéry (2010, ch.xyz) and Kery and Schaub (2011, appendix xyz) for more on practical analysis in **WinBUGS**. That book should also be consulted for a more comprehensive introduction to using **WinBUGS**. In this example, we're going to accelerate pretty fast.

2.7.1 Linear Regression in WinBUGS

We provide a brief introductory example of a normal regression model using a small simulated data set. The following commands are executed from within your **R**

workspace, the command line being indicated by ‘>’. First, simulate a covariate x and observations y having prescribed intercept, slope and variance:

```
789 > x<-rnorm(10)
790 > mu<- -3.2+ 1.5*x
791 > y<-rnorm(10,mu,sd=4)
```

The **BUGS** model specification for a normal regression model is written within **R** as a character string input to the command `cat()` and then dumped to a text file named `normal.txt`:

```
797 > cat("
798 model {
799   for (i in 1:10){
800     y[i]~dnorm(mu[i],tau)      # the "likelihood"
801     mu[i]<- beta0 + beta1*x[i] # the linear predictor
802   }
803   beta0~dnorm(0,.01)          # prior distributions
804   beta1~dnorm(0,.01)
805   sigma~dunif(0,100)
806   tau<-1/(sigma*sigma)        # tau is a derived parameter
807 }
808 ",file="normal.txt")
```

Alternatively, you can write the model specifications directly within a text file and save it in your current working directory, but we do not usually take that approach in this book.

Remarks: 1. WinBUGS parameterizes the normal in terms of the mean and inverse-variance, called the precision. Thus, `dnorm(0,.01)` implies a variance of 100; **2.** We typically use diffuse normal priors for mean parameters, β_0 and β_1 in this case, but sometimes we might use uniform priors with suitable bounds $-B$ and $+B$. **3.** We typically use a `Unif(0, B)` prior on standard deviation parameters (Gelman XXX 2006 XXXX). But sometimes we might use a gamma prior on the precision parameter τ . **4.** In a **WinBUGS** model file, every variable referenced in the model description has to be either data, which will be input (see below), a random variable which must have a probability distribution associated with it using the “~”, or it has to be a derived parameter connected to variables and data using “<-”.

To fit the model, we need to describe various data objects to **WinBUGS**. In particular, we create an **R** list object called `data` which are the data objects identified in the BUGS model file. In the example, the data consist of two objects which exist as y and x in the **R** workspace and also in the **WinBUGS** model definition. We also have to create an **R** function that produces a list of starting values `inits` that get sent to **WinBUGS**. Finally, we identify the names of the parameters (labeled correspondingly in the **WinBUGS** model specification) that

we want **WinBUGS** to save the MCMC output for. In this example, we will “monitor” the parameters β_0 , β_1 , σ and τ . **WinBUGS** is executed using the **R** command `bugs()`. We set the option `debug=TRUE` if we want the **WinBUGS** GUI to stay open (useful for analyzing MCMC output and looking at the **WinBUGS** error log). Also, we set `working.dir=getwd()` so that **WinBUGS** output files and the log file are saved in the current **R** working directory. All of these activities look like this:

```
library("R2WinBUGS") # "attach" the R2WinBUGS library
data <- list ( "y","x")
inits <- function()
  list ( beta1=rnorm(1),beta0=rnorm(1),sigma=runif(1,0,2) )
parameters <- c("beta0","beta1","sigma","tau")
out<-bugs (data, inits, parameters, "normal.txt", n.thin=2, n.chains=2,
           n.burnin=2000, n.iter=6000, debug=TRUE,working.dir=getwd())
```

Remarks: A common question is “how should my data be formatted?” That depends on how you describe the model in the **BUGS** language, how your data are input into **R** and subsequently formatted. There is no unique way to describe any particular model and so you have some flexibility. We talk about data format further in the context of capture-recapture models and SCR models in chapter ?? and elsewhere. In general, starting values are optional but we recommend to always provide reasonable starting values for structural parameters, but are not always necessary for random effects. Note that the previously created objects defining data, initial values and parameters to monitor are passed to the function `bugs()`. In addition, various other things are declared: The number of Markov chains (`n.chains`), the thinning rate (`n.thin`), the number of burn-in iterations (`n.burnin`) and the total number of iterations (`n.iter`). To develop a detailed understanding of the various parameters and settings used for MCMC, consult a basic reference such as Kéry (2010).

You should execute all of the commands given above and then look at the resulting output. Kill the **WinBUGS** GUI and the data will be read back into **R** (or specify `debug=FALSE`). We don’t want to give instructions on how to navigate and use the GUI - see XYZ REF (XYZ) for that. The object `out` prints important summaries by default (this is slightly edited):

```
> print(out,digits=2)
Inference for Bugs model at "normal.txt", fit using WinBUGS,
2 chains, each with 6000 iterations (first 2000 discarded), n.thin = 2
n.sims = 4000 iterations saved
```

	mean	sd	2.5%	25%	50%	75%	97.5%	Rhat	n.eff
beta0	-2.43	1.84	-6.21	-3.50	-2.42	-1.34	1.27	1	4000
beta1	2.62	1.54	-0.42	1.68	2.62	3.57	5.67	1	4000
sigma	5.29	1.66	3.11	4.14	4.95	6.05	9.39	1	4000
tau	0.05	0.02	0.01	0.03	0.04	0.06	0.10	1	4000
deviance	59.85	3.24	56.18	57.47	59.00	61.37	68.32	1	840

873
 874 For each parameter, `n.eff` is a crude measure of effective sample size,
 875 and `Rhat` is the potential scale reduction factor (at convergence, `Rhat=1`).
 876
 877 DIC info (using the rule, `pD = Dbar-Dhat`)
 878 `pD = 2.6` and `DIC = 62.4`

879 **Remarks:** (1) convergence is assessed using the \hat{R} statistic – which we might
 880 sometimes write “*Rhat*”. A value of *Rhat* near 1 indicates convergence; (2) DIC
 881 is the “deviance information criterion” (Spiegelhalter et al., 2002) (see section 2.8)
 882 which some people use in a manner similar to AIC although it is recognized to
 883 have some problems in hierarchical models (Millar, 2009). We evaluate this in the
 884 context of SCR models in chapter XYZ XYZ.

885 2.7.2 Inference about functions of model parameters

886 Using the MCMC draws for a given model we can easily obtain the posterior distri-
 887 bution of any function of model parameters. We showed this in the above example
 888 by providing the posterior of τ when the model was parameterized in terms of stan-
 889 dard deviation σ . As another example, suppose that the normal regression model
 890 above had a quadratic response function of the form

$$E(y_i) = \beta_0 + \beta_1 x_i + \beta_2 x_i^2$$

891 Then the optimum value of x , i.e., that corresponding to the optimal expected
 892 response, can be found by setting the derivative of this function to 0 and solving
 893 for x . We find that

$$df/dx = \beta_1 + 2 * \beta_2 x = 0$$

894 yields that $x_{opt} = -\beta_1/(2 * \beta_2)$. We can just take our posterior draws for β_1
 895 and β_2 and obtain a posterior sample of x_{opt} by this simple calculation. As an
 896 exercise, take the normal model above and simulate a quadratic response and then
 897 describe the posterior distribution of x_{opt} .

2.8 MODEL CHECKING AND SELECTION

898 In general terms model checking - or assessing the adequacy of the model - and
 899 model selection are quite thorny issues and, despite contrary and, sometimes,
 900 strongly held belief among practitioners, there are not really definitive, general
 901 solutions to either problem. We're against dogma on these issues and think people
 902 need to be open-minded about such things and recognize that models can be useful
 903 whether or not they pass certain statistical tests. Some models are intrinsically
 904 better than others because they make more biological sense or foster understanding
 905 or achieve some objective that some bootstrap or other goodness-of-fit test can't

906 decide for you. That said, it gives you some confidence if your model seems ade-
 907 quate and we try to provide some fit assessment in most real applications of SCR
 908 models We provide a very brief overview of concepts here, but provide more detailed
 909 coverage in chapter 8. See also Kéry (2010, ch. xyz) and Link and Barker (2009,
 910 ch. xyz) for specific context related to Bayesian model checking and selection.

911 2.8.1 Goodness-of-fit

912 Goodness-of-fit testing is an important element of any analysis because our model
 913 represents a general set of hypotheses about the ecological and observation pro-
 914 cesses that generated our data. Thus, if our model “fits” in some statistical or
 915 scientific sense, then we believe it to be consistent with the hypotheses that went
 916 into the model. More formally, we would conclude that the data are *not inconsis-*
 917 *tent* with the hypotheses, or that the model appears adequate. If we have enough
 918 data, then of course we will reject any set of statistical hypotheses. Conversely,
 919 we can always come up with a model that fits by making the model extremely
 920 complex. Despite this paradox, it seems to us that simple models that you can
 921 understand should usually be preferred even if they don’t fit, for example if they
 922 embody essential mechanisms central to our understanding of things, or if we think
 923 that some contributing factors to lack-of-fit are minor or irrelevant to the scientific
 924 context and intended use of the model. In other words, models can be useful irre-
 925 spective of whether they fit according to some formal statistical test of fit. Yet the
 926 tension is there to obtain fitting models, and this comes naturally at the expense of
 927 models that can be easily interpreted and studied and effectively used. Moreover,
 928 conducting goodness-of-fit tests is not always so easy to do. Moreover, it is never
 929 really easy (or especially convenient) to decide if your goodness-of-fit test is worth
 930 anything. It might have 0 power! Despite this, we recommend attempting to assess
 931 model fit in real applications, as a general rule, and we provide some basic guidance
 932 here and some more specific to SCR models in chapter 8.

933 To evaluate goodness-of-fit in Bayesian analyses, we will most often use the
 934 Bayesian p-value (Gelman et al., 1996). The basic idea is to define a fit statistic or
 935 “discrepancy measure” and compare the posterior distribution of that statistic to
 936 the posterior predictive distribution of that statistic for hypothetical perfect data
 937 sets for which the model is known to be correct. For example, with count frequency
 938 data, a standard measure of fit is the sum of squares of the “Pearson residuals”,

$$D(y_i, \theta) = \frac{(y_i - E(y_i))^2}{\text{Var}(y_i)}$$

939 The fit statistic based on the squared residuals is

$$FIT = \sum_i D(y_i, \theta)^2$$

which can be computed at each iteration of a MCMC algorithm given the current values of parameters that determine the response distribution. At the same time (i.e., at each MCMC iteration), the equivalent statistic is computed for a “new” data set, simulated using the current parameter values. The Bayesian p-value is simply the posterior probability $\Pr(\text{Fit} > \text{Fit}_{\text{new}})$ ⁵ which should be close to 0.50 for a good model – one that “fits” in the sense that the observed data set is consistent with realizations simulated under the model being fitted to the observed data. In practice we judge “close to 0.50” as being “not too close to 0 or 1” and, as always, closeness is somewhat subjective. We’re happy with anything $> .1$ and $< .9$ but might settle for $> .05$ and < 0.95 . In summary, the Bayesian p-value seems like a bootstrap idea, is easy to compute, and widely used as a result.

Another useful fit statistic is the Freeman-Tukey statistic⁶, in which

$$D(\mathbf{y}, \theta) = \sum_i (\sqrt{y_i} - \sqrt{e_i})^2$$

(Brooks et al., 2000), where y_i is the observed value of observation i and e_i its expected value. In contrast to a chi-square discrepancy, the Freeman-Tukey statistic removes the need to pool cells with small expected values.

2.8.2 Model Selection

For model selection we typically use three different methods: First is, let’s say, common sense. If a parameter has posterior mass concentrated away from 0 then it seems like it should be regarded as important - that is, it is “significant.” This approach seems to have fallen out of favor with all of the interest over the last 10 or 15 years on model selection in ecology. It seems reasonable to us.

For regression problems we sometimes use the factor weighting idea which is to introduce a set of binary variables w_k for variable k , and express the model as, e.g., for a single covariate model:

$$E(y_i) = \alpha + w\beta x_i$$

where w is given a Bernoulli prior distribution with some prescribed probability. E.g., $w \sim \text{Bern}(0.50)$ to provide a prior probability of 0.50 that variable x should be an element of the linear predictor. The posterior probability of the event $w = 1$ is a gauge of the importance of the variable x . i.e., high values of $\Pr(w = 1)$ indicate stronger evidence to support that “ x is in the model” whereas values of $\Pr(w = 1)$ close to 0 suggest that x is less important.

This idea seems to be due to Kuo and Mallick (1998)⁷ and see Royle and Dorazio (2008, ch. XXXX) for an example in the context of logistic regression. This

⁵Check this definition!

⁶Ref for this?

⁷ Is this also what people call Zellner’s G-priors?

approach seems to even work sometimes with fairly complex hierarchical models of a certain form. E.g., Royle (2008) applied it to a random effects model to evaluate the importance of the random effect component of the model. The main problem with this approach is that its effectiveness and results will typically be highly sensitive to the prior distribution on the structural parameters (e.g., see Royle and Dorazio (2008, table xyz)). The reason for this is obvious: If $w = 0$ for the current iteration of the MCMC algorithm, so that β is sampled from the prior distribution, and the prior distribution is very diffuse, then extreme values of β are likely. Consequently, when the current value of β is far away from the mass of the posterior when $w = 1$, then the Markov chain may only jump from $w = 0$ to $w = 1$ infrequently. One seemingly reasonable solution to this problem (Aitken XYZ FIND THIS XXXXX⁸) is to fit the full model to obtain posterior distributions for all parameters, and then use those as prior distributions in a “model selection” run of the MCMC algorithm. This seems preferable to more-or-less arbitrary restriction of the prior support to improve the performance of the MCMC algorithm.

A third method that that we advocate is subject-matter context. It seems that there are some situations – some models – where one should not have to do model selection because it is necessitated by the specific context of the problem, thus rendering a formal hypothesis test pointless (Johnson, 1999). SCR models are such an example. In SCR models, we will see that “spatial location” of individuals is an element of the model. The simpler, reduced, model is an ordinary capture-recapture model which is not spatially explicit (i.e., chapter 7), but it seems silly and pointless to think about actually using the reduced model even if we could concoct some statistical test to refute the more complex model. The simpler model is manifestly wrong but, more importantly, not even a plausible data-generating model! Other examples are when effort, area or sample rate is used as a covariate. One might prefer to have such things in models regardless of whether or not they pass some statistical litmus test (although one can always find referees to argue for pedantic procedure over thinking).

Many problems can be approached using one of these methods but there are also broad classes of problems that can’t and, for those, you’re on your own. In later chapters we will address model selection in specific contexts and we hope those will prove useful for a majority of the situations you encounter.

2.9 POISSON GLMS

The Poisson GLM (also known as “Poisson regression”) is probably the most relevant and important class of models in all of ecology. The basic model assumes observations $y_i; i = 1, 2, \dots, n$ follow a Poisson distribution with mean λ which we write

$$y_i \sim \text{Poisson}(\lambda)$$

⁸see Royle 2008 paper for reference

Commonly y_i is a count of animals or plants at some point in space and λ_i might depend on i . For example, i might index point count locations in a forest, BBS route centers, or sample quadrats, or similar. If covariates are available it is typical to model them as linear effects on the log mean. If $x(i)$ is some measured covariate associated with observation i . Then,

$$\log(x(i)) = \alpha + \beta * x(i)$$

While we only specify the mean of the Poisson model directly, the Poisson model (and all GLMs) has a “built-in” variance which is directly related to the mean. In this case, $\text{Var}(y) = \text{E}(y) = \lambda$. Thus the model accommodates a linear increase in variance with the mean.

2.9.1 Important properties of the Poisson distribution

There are two properties of the Poisson distribution that make it extremely useful in ecology. First is the property of *compound additivity*. If y_1 and y_2 are Poisson random variables with means λ_1 and λ_2 , then their sum $N = y_1 + y_2$ is Poisson with mean $\lambda_1 + \lambda_2$. Thus, if the observations can be viewed as an aggregate of counts over some finer unit of measurement, then the mean aggregates in a corresponding manner. Secondly, the Poisson distribution has a direct relationship to the multinomial. If y_1 and y_2 are *iid* Poisson then, conditional on their sum $N = y_1 + y_2$, their joint distribution is multinomial with sample size N and cell probabilities $\lambda_1/(\lambda_1 + \lambda_2)$ and $\lambda_2/(\lambda_1 + \lambda_2)$. As a result of this, most multinomial models can be analyzed as a Poisson GLM and *vice versa*.

2.9.2 Example: Breeding Bird Survey Data

As an example we consider a classical situation in ecology where counts of an organism are made at a collection of spatial locations. In this particular example, we have mourning dove counts made along North American Breeding Bird Survey (BBS) routes in Pennsylvania, USA. A route consists of 50 stops separated by 0.5 mile. For the purposes here we are defining y_i = route total count and the sample location will be marked by the center point of the BBS route. The survey is run annually and the data set we have is 1966-1998. BBS data can be obtained online at <http://www.pwrc.usgs.gov/bbs/>. We will make use of the whole data set shortly but for now we’re going to focus on a specific year of counts – 1990 – for the sake of building a simple model. For 1990 there were 77 active routes. We have the data stored in a .csv file⁹ where rows index the unique route, column 1 is the route ID, columns 2-3 are the route coordinates (longitude/latitude), column 4 is a habitat covariate “forest cover” (standardized, see below) and the remaining columns are the yearly counts. Years for which a route was not run are coded as “NA” in the data matrix. We imagine that this will be a typical format for many ecological

⁹check this data format

1045 studies, perhaps with more columns representing covariates. To read in the data
1046 and display the first few elements of this matrix, do this:

```
1047 > a<-read.csv("pa-bbsdovedata-all.csv")
1048 > data[1:2,1:6]
1049      X      lon      lat      habitat X66 X67
1050 1 72002 -80.445 41.501 -0.3871372 NA 24
1051 2 72003 -80.347 41.214 -1.0171629 NA NA
```

1052 It is useful to display the spatial pattern in the observed counts. For that we
1053 use a spatial dot plot - where we plot the coordinates of the observations and mark
1054 the color of the plotting symbol based on the magnitude of the count. We have a
1055 special plotting function for that which is called `spatial.plot()` and it is available
1056 with the supplemental **R** package. Actually, what we want to do here is plot the
1057 log-count (+1 of course) which (Fig. 2.1) displays a notable pattern that could be
1058 related to something. The **R** commands for obtaining this figure are:

```
1059 data<-read.csv("pa-bbsdovedata-all.csv")
1060 y<-data[,29] # pick out 1990
1061 notna<-!is.na(y)
1062 y<-y[notna]
1063 spatial.plot(data[notna,2:3],y)
```

1064 We can ponder the potential effects that might lead to dove counts being
1065 high....corn fields, telephone wires, barn roofs along with misidentification of pi-
1066 geons, these could all correlated reasonably well with the observed count of mourn-
1067 ing doves. Unfortunately we don't have any of that information.

1068 We do have a measure of forest cover in the vicinity of each point which is
1069 contained in the data set (variable "habitat"). This was derived from a larger GIS
1070 coverage of the state (provided in the data file "pahabdata.csv") which can be
1071 plotted using the `spatial.plot` function using the following commands

```
1072 > map('state',regions="penn",lwd=2)
1073 > spatial.plot(pahabdata[,2:3],pahabdata[, "dfor"],cx=2)
1074 > map('state',regions="penn",lwd=2,add=TRUE)
```

1075 where the result appears in Fig. 2.2. We see a prominent pattern that indicates
1076 high forest coverage in the central part of the state and low forest cover in the SE.
1077 Inspecting the previous figure of log-counts suggests a relationship between counts
1078 and forest cover which is perhaps not surprising.

1079 2.9.3 Doing it in WinBUGS

1080 Here we demonstrate how to fit a Poisson GLM in **WinBUGS** using the covariate
1081 x_i = forest cover. It is advisable that x_i be standardized in most cases as this will
1082 improve mixing of the Markov chains. Recall that the data we have stored include
1083 a standardized covariate (forest cover) and so we don't have to worry about that
1084 here. To read the BBS data into **R** and get things set up for **WinBUGS** we issue
1085 the following commands:

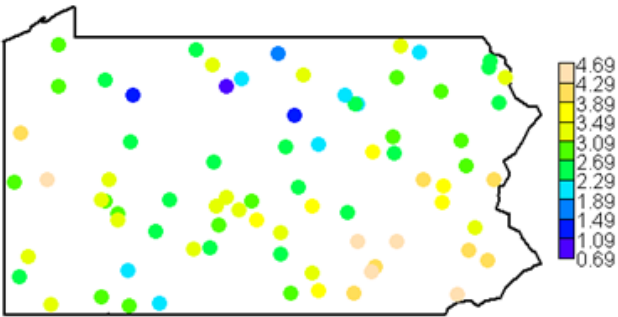


Figure 2.1. Needs a caption

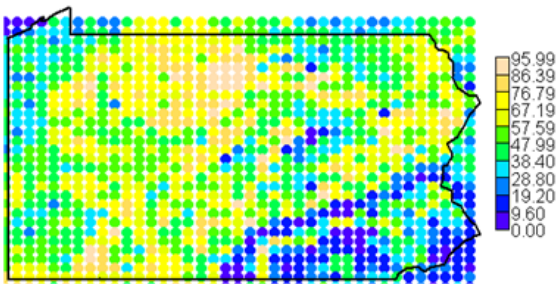


Figure 2.2. Needs a caption

```

1086 data<-read.csv("pa-bbsdovedata-all.csv")
1087 y<-data[,29] # pick out 1990
1088 notna<-!is.na(y)
1089 y<-y[notna] # discard missing
1090 habitat<-data[notna,4] # get habitat data
1091 library("R2WinBUGS") # load R2WinBUGS
1092 data <- list ( "y","M","habitat") # bundle data for WinBUGS

```

Now we write out the Poisson model specification in **WinBUGS** pseudo-code, provide initial values, identify parameters to be monitored and then execute **WinBUGS**:

```

1096 cat("
1097 model {
1098   for (i in 1:M){
1099     y[i]~dpois(lam[i])
1100     log(lam[i])<- beta0+beta1*habitat[i]
1101   }
1102   beta0~dunif(-5,5)
1103   beta1~dunif(-5,5)
1104 }
1105 ",file="PoissonGLM.txt")
1106
1107 inits <- function() list ( beta0=rnorm(1),beta1=rnorm(1))
1108 parameters <- c("beta0","beta1")
1109 out<-bugs (data, inits, parameters, "PoissonGLM.txt", n.thin=2,n.chains=2,
1110           n.burnin=2000,n.iter=6000,debug=TRUE,working.dir=getwd())

```

Remarks: (1) Note the close correspondence in how the model is specified here compared with the normal regression model previously. As an exercise you should discuss the specific differences between the **BUGS** model specifications for the normal and Poisson models.

```

1115 > print(out,digits=3)
1116 Inference for Bugs model at
1117 ‘‘PoissonGLM.txt’’, fit using WinBUGS,
1118 2 chains, each with 4000 iterations (first 1000 discarded), n.thin = 2
1119 n.sims = 3000 iterations saved

```

	mean	sd	2.5%	25%	50%	75%	97.5%	Rhat	n.eff
beta0	3.151	0.025	3.102	3.135	3.151	3.168	3.199	1.001	2300
beta1	-0.498	0.021	-0.539	-0.512	-0.498	-0.484	-0.457	1.001	3000
fit	869.930	19.856	835.500	855.700	868.600	881.900	913.602	1.002	1600
fitnew	76.709	12.519	54.098	68.107	76.215	84.510	102.602	1.001	3000
deviance	1116.605	2.014	1115.000	1115.000	1116.000	1117.000	1122.000	1.001	3000

We might wonder whether this model provides an adequate fit to our data. To evaluate that, we used a Bayesian p-value analysis with fit statistic based on the Freeman-Tukey residual by replacing the model specification above with this:

```

1129 cat("
1130 model {
1131     for (i in 1:M){
1132         y[i]~dpois(lam[i])
1133         log(lam[i])<- beta0+beta1*habitat[i]
1134         d[i]<- pow(pow(y[i],0.5)-pow(lam[i],0.5),2)    #
1135
1136         ynew[i]~dpois(lam[i])
1137         dnew[i]<-pow( pow(ynew[i],0.5)-pow(lam[i],0.5),2)
1138
1139     }
1140     fit<-sum(d[])
1141     fitnew<-sum(dnew[])
1142     beta0~dunif(-5,5)
1143     beta1~dunif(-5,5)
1144 }
1145 ",file="PoissonGLM.txt")

```

1146 The Bayesian p-value is the proportion of times $fitnew > fit$ which, for this
 1147 data set, is 0, which was 1.0 in this case (calculation omitted). This suggests that
 1148 the basic Poisson model does not fit well.

1149 2.9.4 Constructing your own MCMC algorithm

1150 It might be helpful to suffer through a couple examples building custom MCMC
 1151 algorithms. Here, we develop an MCMC algorithm for the Poisson regression model,
 1152 using a Metropolis-within-Gibbs sampling framework.

1153 We will assume that the two parameters have diffuse normal priors, say $[\alpha] =$
 1154 $\text{Norm}(0, 100)$ and $[\beta] = \text{Norm}(0, 100)$ where each has *standard deviation* 100 (recall
 1155 that **WinBUGS** parameterizes the normal in terms of $1/\sigma^2$). We need to assemble
 1156 the relevant elements of the model which are these two prior distributions and the
 1157 likelihood $[\mathbf{y}|\alpha, \beta] = \prod_i [y_i|\alpha, \beta]$ which is, mathematically, the product of the Poisson
 1158 pmf evaluated at each y_i , given particular values of α and β . Next, we need to
 1159 identify the full conditionals $[\alpha|\beta, \mathbf{y}]$ and $[\beta|\alpha, \mathbf{y}]$. We use the all-purpose rule for
 1160 constructing full conditionals (section 2.5.1) to discover that:

$$[\alpha|\beta, \mathbf{y}] \propto \left\{ \prod_i [y_i|\alpha, \beta] \right\} [\alpha]$$

1161 and

$$[\beta|\alpha, \mathbf{y}] \propto \left\{ \prod_i [y_i|\alpha, \beta] \right\} [\beta]$$

1162 Remember, we could replace the “ \propto ” with “ $=$ ” if we put $[y|\beta]$ or $[y|\alpha]$ in the de-
 1163 nominator. But, in general, $[y|\alpha]$ or $[y|\beta]$ will be quite a pain to compute and, more

importantly, it is a constant as far as the operative parameters (α or β , respectively) are concerned. Therefore, the MH acceptance probability will be the ratio of the full-conditional evaluated at a candidate draw to that evaluated at the current draw, and so the denominator required to change \propto to $=$ winds up canceling from the MH acceptance probability. Here we will use the random walk candidate generator so that, for example, $\alpha^* \sim \text{Normal}(\alpha^t, \delta)$ where δ is the standard-deviation of the proposal distribution, which is just a tuning parameter¹⁰. We remark also that calculations are often done on the log-scale to preserve numerical integrity of things when quantities evaluate to small or large numbers, so keep in mind, for example, $a*b = \exp(\log(a) + \log(b))$. The “Metropolis within Gibbs” algorithm for a Poisson regression turns out to be remarkably simple:

```

1175 set.seed(2013)
1176
1177 out<-matrix(NA,nrow=1000,ncol=2)  # matrix to store the output
1178 alpha<- -1                        # starting values
1179 beta <- -.8
1180
1181 # begin the MCMC loop ; do 1000 iterations
1182 for(i in 1:1000){
1183
1184   # update the alpha parameter
1185   lambda<- exp(alpha+beta*habitat)
1186   lik.curr<- sum(log(dpois(y,lambda)))
1187   prior.curr<- log(dnorm(alpha,0,100))
1188   alpha.cand<-rnorm(1,alpha,.25)      # generate candidate
1189   lambda.cand<- exp(alpha.cand + beta*habitat)
1190   lik.cand<- sum(log(dpois(y,lambda.cand)))
1191   prior.cand<- log(dnorm(alpha.cand,0,100))
1192   mhratio<- exp(lik.cand +prior.cand - lik.curr-prior.curr)
1193   if(runif(1)< mhratio)
1194     alpha<-alpha.cand
1195
1196   # update the beta parameter
1197   lik.curr<- sum(log(dpois(y,exp(alpha+beta*habitat))))
1198   prior.curr<- log(dnorm(beta,0,100))
1199   beta.cand<-rnorm(1,beta,.25)
1200   lambda.cand<- exp(alpha+beta.cand*habitat)
1201   lik.cand<- sum(log(dpois(y,lambda.cand)))
1202   prior.cand<- log(dnorm(beta.cand,0,100))
1203   mhratio<- exp(lik.cand + prior.cand - lik.curr - prior.curr)
1204   if(runif(1)< mhratio)
1205     beta<-beta.cand
1206

```

¹⁰ It would help lots of people out to see a non-symmetric proposal distribution, and the extra step needed to account for it.

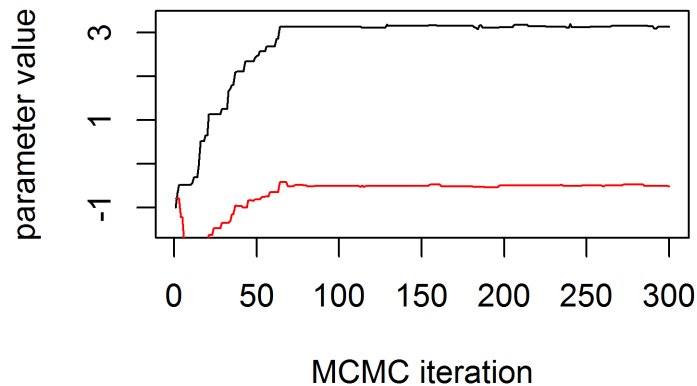


Figure 2.3. MCMC output for Poisson regression parameters (top trace: intercept α ; bottom trace: slope β). This is for $\delta = 0.25$.

```

1207 out[i,]<-c(alpha,beta)          # save the current values
1208 }
1209
1210
1211 plot(out[,1],ylim=c(-1.5,3.3),type="l",lwd=2,ylab="parameter value",
1212      xlab="MCMC iteration")
1213 lines(out[,2],lwd=2,col="red")

```

1214 The first 300 iterations of the MCMC history of each parameter is shown in
 1215 Fig. 2.3. The appearance of this is not very appealing but a couple of things are
 1216 evident: First, the Markov chains clearly stabilize - “burn-in” - after about 60 or
 1217 70 iterations. They also appear to mix very slowly once convergence is achieved,
 1218 although this is not so clear given the scale of the y -axis. We decreased the standard
 1219 deviation of the candidate generating distribution from $\delta = 0.25$ to $\delta = 0.05$ and
 1220 re-ran the MCMC algorithm producing the output shown in Fig. 2.4. We see
 1221 that the burn-in takes longer but it seems to mix better although it takes slightly
 1222 longer to burn-in. Using this value of δ we generated 10,000 posterior samples,
 1223 discarding the first 500 as burn-in, and the result is shown in Fig. 2.5, this time
 1224 separate panels for each parameter. The “grassy” look of the MCMC history is
 1225 diagnostic of Markov chains that are well-mixing and we would generally be very

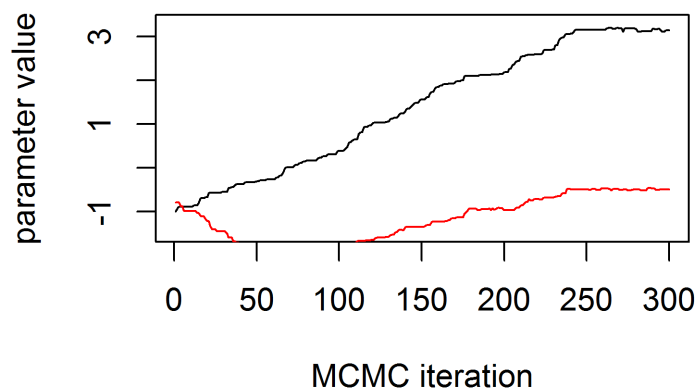


Figure 2.4. Same as previous fig but with $\delta = 0.05$.

1226 satisfied with results that look like this.

1227 **Remarks:** We used a specific set of starting values for these simulations. It
 1228 should be clear that starting values closer to the mass of the posterior distribution
 1229 might cause burn-in to occur faster. As an exercise, evaluate that. (2) Clearly
 1230 the influence of the proposal standard deviation term is important. Small values
 1231 lead to much better mixing but it should be noted that values that are too small
 1232 will slow down burn-in and also lead to high correlation. This suggests there is an
 1233 optimal value of the Metropolis-Hastings tuning parameter¹¹. As an exercise you
 1234 should contemplate finding that optimal value for this problem¹² (3) For the flat
 1235 normal prior distributions here we could leave the prior contribution out of the full
 1236 conditional evaluation since it is locally constant, i.e., constant in the vicinity of the
 1237 posterior mass, and thus has no practical effect. Removing the prior contribution
 1238 from the MH acceptance probability is equivalent to saying that the parameters
 1239 have an improper uniform prior, i.e., $\alpha \sim \text{const}$, which is commonly used for mean
 1240 parameters in practice. Note also that we have used a different prior than in our
 1241 **WinBUGS** model specification given previously. As an exercise, evaluate whether
 1242 this seems to affect the result.

¹¹Defined previously?????

¹²effective sample size definition?

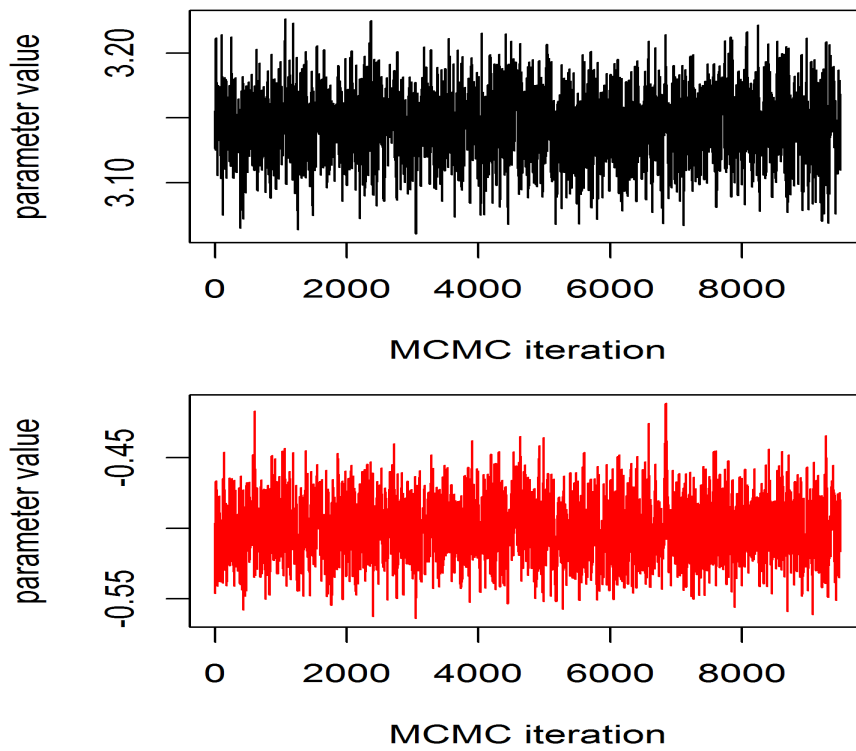


Figure 2.5. nice grassy mcmc output, longer run of previous with $\delta = 0.05$.

2.10 POISSON GLM WITH RANDOM EFFECTS

What we will be doing in most of this book is dealing with random effects in GLM-like models - similar to what are usually referred to as generalized linear mixed models (GLMMs). We provide a brief introduction by way of example, extending our Poisson regression model to include a random effect.

ANDY STOPPED HERE

The Log-Normal mixture: The classical situation involves a GLM with a normally distributed random effect that is additive on the linear predictor. For the Poisson case, we have:

$$\log(\lambda_i) = \alpha + \beta x_i + \eta_i$$

where $\eta_i \sim \text{Normal}(0, \sigma^2)$. A natural alternative is to have multiplicative gamma-distributed noise, $\exp(\eta_i) \sim \text{Gamma}(a, b)$ which would correspond to a negative binomial kind of over-dispersion, implying a different mean/variance relationship to the log-normal mixture (the interested reader should work that out). Choosing between such possibilities is not a topic we will get into here because it doesn't seem possible to provide general guidance on it. For this model we carried-out a goodness-of-fit evaluation using the Bayesian p-value based on a Pearson residual statistic. See also (Kéry, 2010, ch. 18) for an example involving a binomial mixed model¹³. Anyhow, it is really amazingly simple to express this model in **WinBUGS** and have **WinBUGS** draw samples from the posterior distribution using the following code for the BBS dove counts:

```
data<-read.csv("pa-bbsdovedata-all.csv")
locs<-data[,2:3]
habitat<-data[,4]
y<-data[,29]      # grab year 1990
M<-length(y)

set.seed(2013)

cat("
model {
  for (i in 1:M){
    y[i]~dpois(lam[i])
    log(lam[i])<- alpha+ beta*habitat[i] + eta[i]
    frog[i]<-beta*habitat[i] + eta[i]
    eta[i] ~ dnorm(0,tau)
    d[i]<- pow(pow(y[i],0.5)-pow(lam[i],0.5),2)

    ynew[i]~dpois(lam[i])
    dnew[i]<- pow(pow(ynew[i],0.5)-pow(lam[i],0.5),2)
  }
  fit<-sum(d[])
```

¹³Kéry has noticed that such tests probably have 0 power. Should use the marginal frequency of the data

```

1283   fitnew<-sum(dnew[])
1284
1285   alpha~dunif(-5,5)
1286   beta~dunif(-5,5)
1287   sigma~dunif(0,10)
1288   tau<-1/(sigma*sigma)
1289 }
1290
1291 ",file="model.txt")
1292 data <- list ( "y","M","habitat")
1293 inits <- function()
1294   list ( alpha=rnorm(1),beta=rnorm(1),sigma=runif(1,0,4))
1295 parameters <- c("alpha","beta","sigma","tau","fit","fitnew")
1296 library("R2WinBUGS")
1297
1298 out<-bugs (data, inits, parameters, "model.txt", n.thin=2,n.chains=2,
1299   n.burnin=1000,n.iter=5000,debug=TRUE)

```

1300 This produces the following posterior summary statistics:

```

1301 > print(out,digits=2)
1302 Inference for Bugs model at "model.txt", fit using WinBUGS,
1303 2 chains, each with 5000 iterations (first 1000 discarded), n.thin = 2
1304 n.sims = 4000 iterations saved
1305      mean    sd  2.5%   25%   50%   75%  97.5% Rhat n.eff
1306 alpha    2.98 0.08  2.82  2.93  2.98  3.03  3.12 1.00  1400
1307 beta   -0.53 0.07 -0.68 -0.58 -0.53 -0.49 -0.38 1.01   350
1308 sigma    0.60 0.06  0.49  0.56  0.59  0.64  0.73 1.00  2000
1309 tau     2.88 0.57  1.88  2.47  2.86  3.24  4.12 1.00  2000
1310 fit     26.58 3.72 19.87 23.96 26.37 29.01 34.46 1.00  4000
1311 fitnew   26.83 3.90 19.60 24.12 26.68 29.36 35.04 1.00  4000
1312 deviance 445.94 12.18 424.00 437.40 445.20 453.90 471.50 1.00  4000
1313
1314 [... some output deleted ...]

```

1315 The Bayesian p-value for this model is

```

1316 > mean(out$sims.list$fit>out$sims.list$fitnew)
1317 [1] 0.4815

```

1318 indicating a pretty good fit. Given the site-level random effect, it would be surpris-
 1319 ing for this model to not fit! One thing we notice is that the posterior standard
 1320 deviations of the regression parameters are much higher, a result of the excess vari-
 1321 ation. Wwe would also notice much less precise predictions of hypothetical new
 1322 observations.

1323 ANDY STOPPED HERE.

2.11 BINOMIAL GLMS

Another extremely important class of models in ecology are binomial models. We use binomial models for count data whenever the observations are counts or frequencies and it is natural to condition on a “sample size”, say K , the maximum frequency possible in a sample. The random variable, $y \leq K$, is then the frequency of occurrences out of K “trials”. The parameter of the binomial models is p , often called “success probability” which is related to the expected value of y by $E(y) = pK$. Usually we are interested in modeling covariates that affect the parameter p , and such models are called binomial GLMs, binomial regression models or logistic regression, although logistic regression really only applies when the logistic link is used to model the relationship between p and covariates (see below).

One of the most typical binomial GLMs occurs when the sample size equals 1 and the outcome, y , is “presence” ($y = 1$) or “absence” ($y = 0$) of a species. This is a classical “species distribution” modeling situation. A special situation occurs when presence/absence is observed with error (MacKenzie et al., 2002; Tyre et al., 2003). In that case, $K > 1$ samples are usually needed for effective estimation of model parameters.

In standard binomial regression problems the sample size is fixed by design but interesting models also arise when the sample size is itself a random variable. These are the N -mixture models (Royle, 2004b; Kéry et al., 2005; Royle and Dorazio, 2008; Kéry, 2010) and related models (in this case, N being the sample size, which we labeled K above)¹⁴. Another situation in which the binomial sample size is “fixed” is closed population capture-recapture models in which a population of individuals is sampled K times. The number of times each individual is encountered is a binomial outcome with parameter - encounter probability - p , based on a sample of size K . In addition, the total number of unique individuals observed, n , is also a binomial random variable based on population size N . We consider such models in the chapter 7.

2.11.1 Binomial regression

In binomial models, covariates are modeled on a suitable transformation (the link function) of the binomial success probability, p . Let x_i denote some measured covariate for sample unit i and let p_i be the success probability for unit i . The standard choice is the “logit” link function which is:

$$\log(p_i/(1 - p_i)) = \alpha + \beta * x_i.$$

¹⁴Some of the jargon is actually a little bit confusing here because the binomial index is customarily referred to as “sample size” but in the context of N -mixture models N is actually the “population size”

1356 The inverse-logit (or “expit”) is

$$p_i = \text{expit}(\alpha + \beta * x_i) = \frac{\exp(\alpha + \beta * x_i)}{1 + \exp(\alpha + \beta * x_i)}$$

1357 There are many other possible link functions. However, ecologists seem to adopt
 1358 the logit link function without question in most applications¹⁵. We sometimes use
 1359 the “complementary log-log” (= “cloglog”) link function in ecological applications
 1360 because it arises naturally in many situations (Royle and Dorazio, 2008, p. 150).
 1361 For example, consider the “probability of observing a count greater than 0” under
 1362 a Poisson model: $\Pr(y > 0) = 1 - \exp(-\lambda)$. In that case,

$$\text{cloglog}(p) = \log(-\log(1 - p)) = \log(\lambda)$$

1363 So that if you have covariates in your linear predictor for $E(y)$ under a Poisson
 1364 model then they are linear on the complementary log-log link of p . In models of
 1365 species occurrence it seems natural to view occupancy as being derived from local
 1366 abundance N (Royle and Nichols, 2003; Royle and Dorazio, 2006; Dorazio, 2007).
 1367 Therefore, models of local abundance in which $N \sim \text{Poisson}(A\lambda)$ for a habitat patch
 1368 of area A implies a model for occupancy ψ of the form

$$\text{cloglog}(\psi) = \log(A) + \log(\lambda).$$

1369 We will use the cloglog link in some analyses of SCR models in chapter ?? and
 1370 elsewhere.

1371 2.11.2 Example: Waterfowl Banding Data

1372 It would be easy to consider a standard “distribution modeling” application where
 1373 $K = 1$ and the outcome is occurrence ($y = 1$) or not ($y = 0$) of some species.
 1374 Such examples abound in books (e.g., Royle and Dorazio (2008, ch. 3); Kéry (2010,
 1375 ch. 21); Kéry and Schaub (2011, ch. 13)) and in the literature. Instead, we will
 1376 consider an example involving band returns of waterfowl which were analyzed by
 1377 Royle and Dubovsky (2001)¹⁶.

1378 For these data, y_i is the number of waterfowl bands recovered out of B_i birds
 1379 banded at some location \mathbf{s}_i . In this case B_i is fixed. Thinking about recovery rate
 1380 as being proportional to harvest rate, we use these data to explore geographic gra-
 1381 dients in recovery rate resulting from variability in harvest pressure experienced by
 1382 populations depending on their migration ecology. As such, we fit a basic binomial
 1383 GLM with a linear response to geographic coordinates (including an interaction
 1384 term). The data are provided with the **R** package **scrbook**. Here we provide the
 1385 part of the script for creating the model and fitting the model in **WinBUGS** using

¹⁵a notable exception is distance sampling, which is all about choosing among link functions

¹⁶I hate this example. Anyone got a better one thats not distribution modeling?

the `bugs` function. There are few structural differences between this model and the Poisson GLM fitted previously. The main things are due to the data structure (we have a matrix here instead of a vector) and otherwise we change the main distributional assumption to binomial (specified with `dbin`) and then use the `logit` function to relate the parameter p_{it} to the covariates. Here is the script:

```

1391 load("mallarddata") # not sure how this will look
1392
1393 sink("model.txt")
1394 cat("
1395 model {
1396   for(t in 1:5){
1397     for (i in 1:nobs){
1398       y[i,t] ~ dbin(p[i,t], B[i,t])
1399       logit(p[i,t]) <- alpha0[t] + alpha1*X[i,1] + alpha2*X[i,2] + alpha3*X[i,1]*X[i,2]
1400     }
1401   }
1402   alpha1~dnorm(0,.001)
1403   alpha2~dnorm(0,.001)
1404   alpha3~dnorm(0,.001)
1405   for(t in 1:5){
1406     alpha0[t] ~ dnorm(0,.001)
1407   }
1408 }
1409 ",fill=TRUE)
1410 sink()
1411
1412 data <- list(B=mallard.bandings, y=mallard.recoveries,
1413             nobs=nrow(banding.locs),X=banding.locs)
1414 inits <- function(){
1415   list(alpha0=rnorm(5),alpha1=0,alpha2=0,alpha3=0) }
1416 parms <- list('alpha0','alpha1','alpha2','alpha3')
1417 out <- bugs(data,inits, parms,"model.txt",n.chains=3,
1418            n.iter=2000,n.burnin=1000, n.thin=2,debug=TRUE)

```

Posterior summaries of model parameters are as follows:

```

1420 > print(out,digits=3)
1421 Inference for Bugs model at "model.txt", fit using WinBUGS,
1422 3 chains, each with 2000 iterations (first 1000 discarded), n.thin = 2
1423 n.sims = 1500 iterations saved

```

	mean	sd	2.5%	25%	50%	75%	97.5%	Rhat	n.eff
alpha0[1]	-2.346	0.036	-2.417	-2.370	-2.346	-2.323	-2.277	1.001	1500
alpha0[2]	-2.356	0.032	-2.420	-2.379	-2.356	-2.335	-2.292	1.001	1500
alpha0[3]	-2.220	0.035	-2.291	-2.244	-2.219	-2.197	-2.153	1.001	1500
alpha0[4]	-2.144	0.039	-2.225	-2.169	-2.143	-2.116	-2.068	1.000	1500
alpha0[5]	-1.925	0.034	-1.990	-1.949	-1.924	-1.901	-1.856	1.004	570

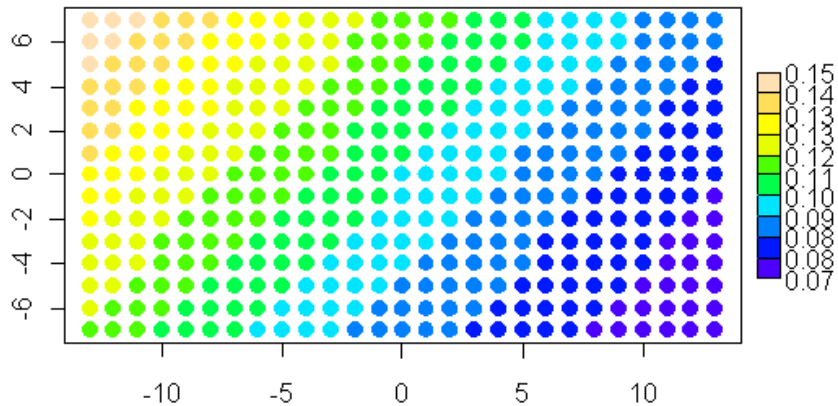


Figure 2.6. Predicted recovery rate of bands.

```
1430 alpha1      -0.023 0.003   -0.028  -0.025  -0.023  -0.022  -0.018  1.001  1500
1431 alpha2       0.020 0.006    0.009   0.016   0.020   0.024   0.031  1.001  1500
1432 alpha3       0.000 0.001   -0.002  -0.001   0.000   0.000   0.002  1.001  1500
1433 deviance  1716.001 4.091 1710.000 1713.000 1715.000 1718.000 1726.000 1.001  1500
1434
1435 [... some output deleted ...]
```

1436 The basic result suggests a negative east-west gradient and a positive south to
1437 north gradient but no interaction. A map of the response surface is shown in Fig.
1438 2.6. We did an additional MCMC run where we saved the binomial parameter
1439 p and computed the Bayesian p-value (double use of “p” here is confusing, but I
1440 guess that happens sometimes!) using a fit statistic based on the Freeman-Tukey
1441 statistic (see Section XXX above). The result indicates that the linear response
1442 surface model does not provide an adequate fit of the data. The reader should
1443 contemplate whether this invalidates the basic interpretation of the result.

2.12 SUMMARY AND OUTLOOK

1444 GLMs and GLMMs are the most useful statistical methods in all of ecology. The
1445 principles and procedures underlying these methods are relevant to nearly all mod-
1446 eling and analysis problems in every branch of ecology. Moreover, understanding
1447 how to analyze these models is crucial in a huge number of diverse problems. If you

1448 understand and can conduct classical likelihood and Bayesian analysis of Poisson
1449 and binomial GLM(M)s, then you will be successful analyzing and understanding
1450 more complex classes of models that arise. We will see shortly that spatial capture-
1451 recapture models are a type of GLMM and thus having a basic understanding of
1452 the conceptual origins and formulation of GLM(M)s and their analysis is extremely
1453 useful.

1454 We note that GLM(M)s are routinely analyzed by likelihood methods but we
1455 have focused on Bayesian analysis here in order to develop the tools that are less
1456 familiar to most ecologists. In particular, Bayesian analysis of models with ran-
1457 dom effects is relatively straightforward because the models are easy to analyze
1458 conditional on the random effect, using methods of MCMC. Thus, we will often
1459 analyze SCR models in later chapters by MCMC, explicitly adopting a Bayesian
1460 inference framework. In that regard, the various **BUGS** engines (**WinBUGS**,
1461 **OpenBUGS**, **JAGS**) are enormously useful because they provide an accessible
1462 platform for carrying out analyses by MCMC by just describing the model, and not
1463 having to worry about how to actually build MCMC algorithms. That said, the
1464 **BUGS** language is more important than just to the extent that it enables one to
1465 do MCMC - it is useful as a modeling tool because it fosters understanding, in the
1466 sense that it forces you to become intimate with your model. You have to write
1467 down all of the probability assumptions, the relationships between observations and
1468 latent variables and parameters. This is really a great learning paradigm that you
1469 can grow with.

1470 While we have emphasized Bayesian analysis in this chapter, and make primary
1471 use of it through the book, we will provide an introduction to likelihood analysis
1472 in chapter 6 and use those methods also from time to time. Before getting to that,
1473 however, it will be useful to talk about more basic, conventional closed population
1474 capture-recapture models and these are the topic of the next 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 accomplish 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

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

using standard methods that you are already familiar with (i.e., GLMs - see chapter 2).

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 (2008a, p. xyz)):

$$n_1, n_2, \dots, n_K \sim \text{Multin}(N, \pi(1), \pi(2), \dots, \pi(K)) \quad (3.1.1)$$

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 ??.

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).

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.

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 unconditional 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 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 individual 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.”

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 .

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 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

1672 to sampling. We assume that $z_i \sim \text{Bern}(\psi)$ where ψ is the probability that an
 1673 individual in the data set of size M is a member of the sampled population - in the
 1674 sense that $1 - \psi$ is the probability of realizing a “structural zero” in the augmented
 1675 data set. The zero-inflated binomial model which arises under data augmentation
 1676 can be formally expressed by the following set of assumptions:

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

1677 for $i = 1, \dots, M$, where $\delta(0)$ is a point mass at $y = 0$.

1678 We note that N is no longer an explicit parameter of this model. Instead, we
 1679 estimate ψ and functions of the latent variables. In particular, under the assump-
 1680 tions of the zero-inflated model, $z_i \stackrel{iid}{\sim} \text{Bern}(\psi)$; therefore, N is a function of these
 1681 latent variables:

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

1682 Further, we note that the latent z_i parameters can be removed from the model by
 1683 integration, in which case the joint probability of the data is

$$\Pr(y_1, \dots, y_M | p, \psi) = \prod_{i=1}^M \psi \text{Bin}(y_i | K, p) + I(y_i = 0)(1 - \psi) \quad (3.2.1)$$

1684 Which can be maximized directly to obtain the MLEs of the structural parameters
 1685 ψ and p or those of other more complex models (e.g., see Royle, 2006). We could
 1686 estimate these parameters and then use them to obtain an estimator of N using
 1687 the so-called “Best unbiased predictor” (see Royle and Dorazio, 2011).

1688 3.2.2 Model M_0 in BUGS

1689 For model M_0 in which we can aggregate the encounter data to individual-specific
 1690 encounter frequencies, the augmented data are given by the vector of frequencies
 1691 $(y_1, \dots, y_n, 0, 0, \dots, 0)$. The zero-inflated model of the augmented data combines
 1692 the model of the latent variables, $z_i \sim \text{Bern}(\psi)$ with the conditional-on- z binomial
 1693 model:

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

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

1694 It is convenient to express the conditional-on- z observation model concisely as:

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

1695 Thus, if $z_i = 0$ then the success probability of the binomial distribution is identically
 1696 0 whereas, if $z_i = 1$, then the success probability is p . This is useful in describing
 1697 the model in the **BUGS** language, as shown below. Note the last line of the
 1698 model specification here provides the expression for computing N from the data
 1699 augmentation variables z_i .

```

1700 p ~ dunif(0,1)
1701 psi~dunif(0,1)
1702
1703 # nind = number of individuals captured at least once
1704 # nz = number of uncaptured individuals added for PX-DA
1705 for(i in 1:(nind+nz)) {
1706     z[i]~dbern(psi)
1707     mu[i]<-z[i]*p
1708     y[i]~dbin(mu[i],K)
1709 }
1710
1711 N<-sum(z[1:(nind+nz)])
```

1712 Specification of a more general model in terms of the individual encounter obser-
 1713 vations y_{ik} is not much more difficult than for the individual encounter frequencies.
 1714 We define the observation model by a double loop and change the indexing of things
 1715 accordingly, i.e.,

```

1716 for(i in 1:(nind+nz)) {
1717     z[i]~dbern(psi)
1718     for(k in 1:K){
1719         mu[i,k]<-z[i]*p
1720         y[i,k]~dbin(mu[i,k],1)
1721     }
1722 }
```

1723 In this manner, it is straightforward to incorporate covariates on p (see discussion
 1724 of this below and also chapt. 8 (REF XYZ) and consider other extensions.

1725 3.2.3 Formal development of data augmentation

1726 Use of DA for solving inference problems with unknown N can be justified as
 1727 originating from the choice of uniform prior on N . The $\text{Unif}(0, M)$ prior for N is
 1728 innocuous in the sense that the posterior associated with this prior is equal to the
 1729 likelihood for sufficiently large M . One way of inducing the $\text{Unif}(0, M)$ prior on N

1730 is by assuming the following hierarchical prior:

$$\begin{aligned} N &\sim \text{Bin}(M, \psi) \\ \psi &\sim \text{Unif}(0, 1) \end{aligned} \tag{3.2.2}$$

1731 which includes a new model parameter ψ . This parameter denotes the probability
1732 that an individual in the super-population of size M is a member of the population
1733 of N individuals exposed to sampling. The model assumptions, specifically the
1734 multinomial model (eq. XYZ) and eq. 3.2.2, may be combined to yield a reparam-
1735 eterization of the conventional model that is appropriate for the augmented data
1736 set of known size M :

$$(n_1, n_2, \dots, n_K) \sim \text{Multin}(M, \psi\pi(1), \psi\pi(2), \dots, \psi\pi(K)) \tag{3.2.3}$$

1737 This arises by removing N from Eq. multinomial XYZ by integrating over the
1738 binomial prior distribution for N . Thus, the models we analyze under data aug-
1739 mentation arise formally by removing the parameter N from the ordinary model -
1740 the model conditional on N - by integrating over a binomial prior distribution for
1741 N .

1742 Note that the $M - n$ unobserved individuals in the augmented data set have
1743 probability $\psi\pi(0) + (1 - \psi)$, indicating that these unobserved individuals are a
1744 mixture of individuals that are sampling zeros ($\psi\pi_0$, and belong to the population
1745 of size N) and others that are “structural zeros” (occurring in the augmented
1746 data set with probability $1 - \psi$). In Eq. 3.2.3 N has been eliminated as a formal
1747 parameter of the model by marginalization (integration) and replaced with the new
1748 parameter ψ , which we will call the “data augmentation parameter.” However, the
1749 full likelihood containing both N and ψ can be analyzed (see Royle et al., 2007).

1750 3.2.4 Remarks on Data Augmentation

1751 Data augmentation may seem like a strange and mysterious black-box, and likely
1752 it is unfamiliar to most people even those with extensive experience with capture-
1753 recapture models. However, it really is a formal reparameterization of capture-
1754 recapture models in which N is removed from the ordinary (conditional-on- N)
1755 model by integration. In the case of Model M0, data augmentation produces the
1756 zero-inflated binomial which is distinct from the original observation model, but
1757 only in the sense that it embodies, explicitly, the $\text{Unif}(0, M)$ prior for N . Choice of
1758 M might be cause for some concern related to potential sensitivity to choice of M .
1759 The guiding principle is that it should be chosen large enough so that the posterior
1760 for N is not truncated, but no larger because large values entail more computational
1761 burden. It seems likely that the properties of the Markov chains should be affected
1762 by M and so some optimality might exist (Gopalaswamy, 2012), as in occupancy
1763 models (Mackenzie and Royle, 2005). Formal analysis of this is required.

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

There are other approaches to analyzing models with unknown N , using reversible jump MCMC (RJMCMC) or other so-called “trans-dimensional” (TD) 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; Royle et al., 2011a) 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.
## Good idea. This will be done in final draft
trapmat<-read.csv("FDtrapmat.csv")
bearArray<-source("FDbeararray.R")$value
nind<-dim(bearArray)[1]
```

²Look these citations up in Royle-Dorazio EURING paper

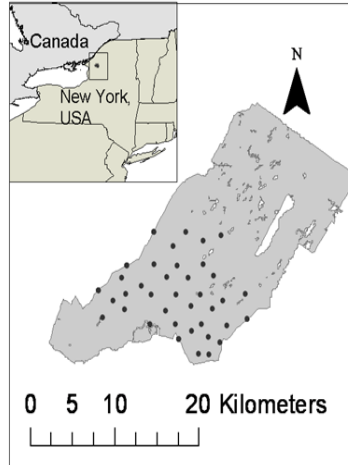


Figure 3.1. Fort Drum study area and hair snare locations.

```

1803 K<-dim(bearArray)[3]
1804 ntraps<-dim(bearArray)[2]
1805
1806 M=175
1807 nz<-M-nind
1808
1809 Xaug <- array(0, dim=c(M,ntraps,K))
1810 Xaug[1:nind,,]<-bearArray
1811 y<- apply(Xaug,c(1,3),sum)
1812 y[y>1]<-1
1813 ytot<-apply(y,1,sum) # total encounters out of K

```

1814 Note that the raw data, \mathbf{y} , is an $M \times K$ array of individual encounter events
 1815 (i.e., $y_{ik} = 1$ if individual i was encountered in any trap and 0 otherwise). For
 1816 $i = 48, \dots, 175$, $y_{ik}=0$ as these are augmented observations. For Model M0 it is
 1817 sufficient to reduce the data to individual encounter frequencies which we have
 1818 labeled \mathbf{y}_{tot} above. The BUGS model file along with commands to fit the model
 1819 are as follows:

```

1820 set.seed(2013) # to obtain the same results each time
1821 data0<-list(y=y,M=M,K=K)
1822 params0<-list('psi','p','N')
1823 zst=c(rep(1,nind),rbinom(M-nind, 1, .5))
1824 inits = function() {list(z=zst, psi=runif(1), p=runif(1)) }
1825
1826 cat("

```

```

1827 model {
1828
1829   psi~dunif(0, 1)
1830   p~dunif(0,1)
1831
1832   for (i in 1:M){
1833     z[i]~dbern(psi)
1834     for(k in 1:K){
1835       tmp[i,k]<-p*z[i]
1836       y[i,k]~dbin(tmp[i,k],1)
1837     }
1838   }
1839   N<-sum(z[1:M])
1840 }
1841 ",file="modelM0.txt")
1842
1843 fit0 = bugs(data0, inits, params0, model.file="modelM0.txt",
1844            n.chains=3, n.iter=2000, n.burnin=1000, n.thin=1,
1845            debug=TRUE,working.directory=getwd())

```

1846 The posterior summary statistics from this analysis are as follows:

```

1847 > print(fit0,digits=2)
1848 Inference for Bugs model at "modelM0.txt", fit using WinBUGS,
1849 3 chains, each with 2000 iterations (first 1000 discarded)
1850 n.sims = 3000 iterations saved
1851
1852      mean    sd  2.5%   25%   50%   75%  97.5% Rhat n.eff
1853 psi      0.29 0.04  0.22  0.26  0.29  0.31  0.36   1 3000
1854 p        0.30 0.03  0.25  0.28  0.30  0.32  0.35   1 3000
1855 N        49.94 1.99 47.00 48.00 50.00 51.00 54.00   1 3000
1856 deviance 489.05 11.28 471.00 480.45 488.80 495.40 513.70   1 3000
1857
1858 [.. some output deleted ...]

```

1858 **WinBUGS** did well in choosing an MCMC algorithm for this model – we have
1859 $\hat{R} = 1$ for each parameter, and an effective sample size of 3000, equal to the total
1860 number of posterior samples. We see that the posterior mean of N under this model
1861 is 49.94 and a 95% posterior interval is (48, 54). We revisit these data later in the
1862 context of more complex models.

1863 In order to obtain an estimate of density, D , we need an area to associate with
1864 the estimate of N , and commonly used procedures to conjure up such an area
1865 include buffering the trap array by the home range radius, often estimated by the
1866 mean maximum distance moved (MMDM)³, 1/2 MMDM (Dice, 1938) or directly
1867 from telemetry data (REF XXX NEED REF HERE XXXXX). Typically, the trap
1868 array is defined by the convex hull around the trap locations, and this is what we

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

1869 applied a buffer to. We computed the buffer by using an estimate of the mean female
 1870 home range radius (2.19 km) estimated from telemetry studies (Bales et al., 2005)
 1871 instead of using an estimate based on our relatively more sparse recapture data⁴.
 1872 For the Fort Drum study, the convex hull has area 157.135 km^2 , and the buffered
 1873 convex hull has area 277.011 km^2 . To create this we used functions contained in the
 1874 **R** package **rgeos** and created a utility function **bcharea** which is in our **R** package
 1875 **scrbook**. The commands are as follows:

```
1876 library("rgeos")
1877
1878 bcharea<-function(buff,traplocs){
1879   p1<-Polygon(rbind(traplocs,traplocs[1,]))
1880   p2<-Polygons(list(p1=p1),ID=1)
1881   p3<-SpatialPolygons(list(p2=p2))
1882   p1ch<-gConvexHull(p3)
1883   bp1<-gBuffer(p1ch, width=buff)
1884   plot(bp1, col='gray')
1885   plot(p1ch, border='black', lwd=2, add=TRUE)
1886   gArea(bp1)
1887 }
1888
1889 bcharea(2.19,traplocs=trapmat)
```

1890 The resulting buffered convex hull is shown in Fig. 3.2.

1891 To conjure up a density estimate under model M_0 , we compute the appropriate
 1892 posterior summary of N and the prescribed area (277.011 km^2):

```
1893 > summary(fit0$sims.list$N/277.011)
1894   Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
1895 0.1697 0.1733 0.1805 0.1803 0.1841 0.2130
1896
1897 > quantile(fit0$sims.list$N/277.011,c(0.025,0.975))
1898      2.5%      97.5%
1899 0.1696684 0.1949381
```

1900 which yields a density estimate of about 0.18 ind/ km^2 , and a 95% Bayesian confi-
 1901 dence interval of (0.170, 0.195).

1902 The obvious limitation of this estimate and, indeed, of the whole process, is that
 1903 our choice of “area” is completely subjective - which area should we use? MMDM?
 1904 One-half MMDM? Estimated from telemetry data? And, furthermore, how certain
 1905 are we of this area? Can we quantify our uncertainty about this quantity? More
 1906 important, what exactly is the meaning of this area and, in this context, how do
 1907 we gauge bias and/or variance of “estimators” of it? (i.e., what is it estimating?).

⁴BETH: Why?

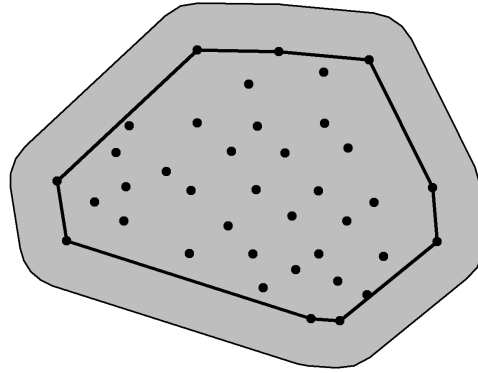


Figure 3.2. buffered convex hull of the bear hair snare array

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 (Royle et al., 2011c) - 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; Royle et al., 2011b). 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 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).

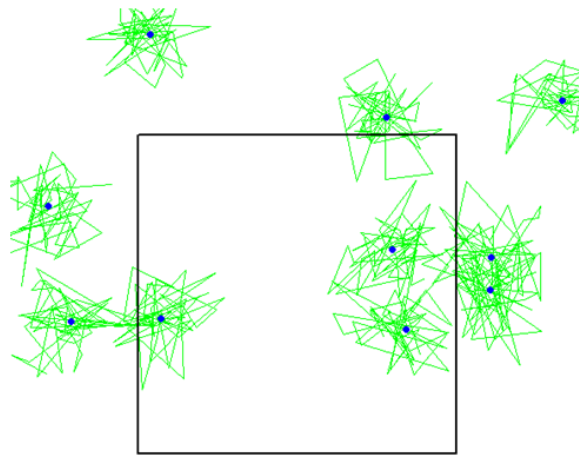


Figure 3.3. A quadrat searched for lizards and the locations of each lizard over some period of time.

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 $M = 500$ individuals. We ran the model using **JAGS** with the instructions given as follows⁵.

```

2042 [... get data as before ....]
2043
2044 set.seed(2013)
2045
2046 cat("
2047 model{
2048   p0 ~ dunif(0,1)          # prior distributions
2049   mup<- log(p0/(1-p0))
2050   sigmap ~ dunif(0,10)
2051   taup<- 1/(sigmap*sigmap)
2052   psi~dunif(0,1)
2053
2054   for(i in 1:(nind+nz)){
2055     z[i]~dbern(psi)        # zero inflation variables
2056     lp[i] ~ dnorm(mup,taup) # individual effect
2057     logit(p[i])<-lp[i]
2058     mu[i]<-z[i]*p[i]
2059     y[i]~dbin(mu[i],K)    # observation model
2060   }
2061
2062   N<-sum(z[1:(nind+nz)])
2063 }
2064 ",file="modelMh.txt")
2065
2066 data1<-list(y=ytot, nz=nz, nind=nind,K=K)
2067 params1= c('p0','sigmap','psi','N')
2068 inits = function() {list(z=as.numeric(ytot>=1), psi=.6, p0=runif(1),
2069   sigmap=runif(1,.7,1.2),lp=rnorm(M,-2)) }
2070
2071 library("rjags")
2072 jm<- jags.model("modelMh.txt", data=data1, inits=inits, n.chains=4,
2073   n.adapt=1000)
2074 jout<- coda.samples(jm, params1, n.iter=200000, thin=1)
2075
2076   This produces the posterior distribution for  $N$  shown in Fig. 3.4. Posterior
2077   summaries of parameters are given as follows:
2078
2079 > summary(jout)
2080
2081 Iterations = 2001:202000

```

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

```

2080 Thinning interval = 1
2081 Number of chains = 4
2082 Sample size per chain = 2e+05
2083
2084 1. Empirical mean and standard deviation for each variable,
2085    plus standard error of the mean:
2086
2087           Mean          SD Naive SE Time-series SE
2088 N      117.7740 56.31633 6.296e-02      1.960115
2089 p0      0.0728 0.05522 6.174e-05      0.001655
2090 psi     0.2366 0.11362 1.270e-04      0.003909
2091 sigmap  2.0795 0.53096 5.936e-04      0.016789
2092
2093 2. Quantiles for each variable:
2094
2095           2.5%      25%      50%      75%      97.5%
2096 N      62.000000 82.00000 102.00000 134.0000 277.0000
2097 p0      0.003143 0.02842 0.06077 0.1066 0.2036
2098 psi     0.117269 0.16377 0.20522 0.2712 0.5560
2099 sigmap  1.211900 1.69434 2.02113 2.4028 3.2694

```

2100 We used $M = 500$ for this analysis and we note that while the posterior mass
 2101 of N is concentrated away from this upper bound (Fig. 3.4), the posterior has an
 2102 extremely long right tail, with some posterior values at the upper bound $N = 500$.
 2103 Maybe or maybe not sufficient data augmentation.⁶ The model runs effectively in
 2104 **WinBUGS** but sometimes with apparently inefficient mixing for reasons that may
 2105 be related to bad starting values. In some cases this was resolved if we supplied
 2106 starting values for the $\text{logit}(p_i)$ parameters and τ .

2107 Because of the skewed posterior we see that the posterior mean ($N = 117$)
 2108 is considerably higher than the posterior mode ($N = 102$). Moreover, posterior
 2109 summaries are estimated with a relatively high error (“Time-series SE” of around
 2110 2.0)⁷. Further, it may be surprising that the posterior mode does not compare well
 2111 with the MLE. To compute the posterior mode we could easily find the posterior
 2112 value of N with the highest mass because N is discrete. But we want to smooth out
 2113 some of the Monte Carlo error a bit so we used a smoothing spline to the posterior
 2114 frequencies of N as follows:

```

2115 > tt<-table(jout[[1]][, "N"])[1:80]
2116 > xg<-as.numeric(names(tt))
2117 > plot(xg,tt)
2118 > sp<- smooth.spline(xg,tt,df=9)
2119 > sp$x[sp$y==max(sp$y)]
2120 [1] 80

```

⁶ to do: insert final results. longer run. more data augmentation. compare with winbugs.

⁷ need to define this somewhere

The `df` argument controls the degree of smoothing and we find in this case that the modal value (i.e., 80) is not too sensitive to the smoothing parameter but this should be checked in any specific instance⁸.

To compare with the MLE, we used 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 $\hat{N} = \exp(3.86) + 47 = 94.47$ which is not at all consistent with the apparent mode in Fig. 3.4.⁹

Comments: First of all the posterior for this model and data set is very sensitive to prior distributions. While MLEs are invariant to transformation of the parameters, the posterior distribution definitely is *not* invariant. In the present case, the use of a $\text{Unif}(0, 1)$ prior for $p_0 = \text{expit}(\mu)$ is somewhat informative – in particular, it is not at all “flat” on the scale of μ – and this affects the posterior. We generally always recommend use of a $\text{Unif}(0, 1)$ prior for $\text{expit}(\mu)$ in such models. That said, we were surprised at this result, and we experimented with other prior configurations including putting a flat prior on μ directly. This specific prior suggests the possibility that the posterior distribution may be improper for that prior specification. This kind of small sample instability has been widely noted in Model Mh (Fienberg et al., 1999; Dorazio and Royle, 2003) and is not unrelated to sensitivity to model which has also been identified as an important issue in model M_h (Dorazio and Royle, 2003; Link, 2003). Conclusion: The mode is well-defined but the data set is sparse and hence inferences are poor and sensitive to model choices. Get over it.

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 ?? we devise MCMC algorithms for spatial 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

⁸we need to give examples of using `density()` to obtain modes

⁹We note that the result is inconsistent with Gardner et al. (2009) who reported an MLE of 104.1 ($\text{density} = 0.437 \text{ inds/km}^2$) although we do not know the reason for this at the present time.

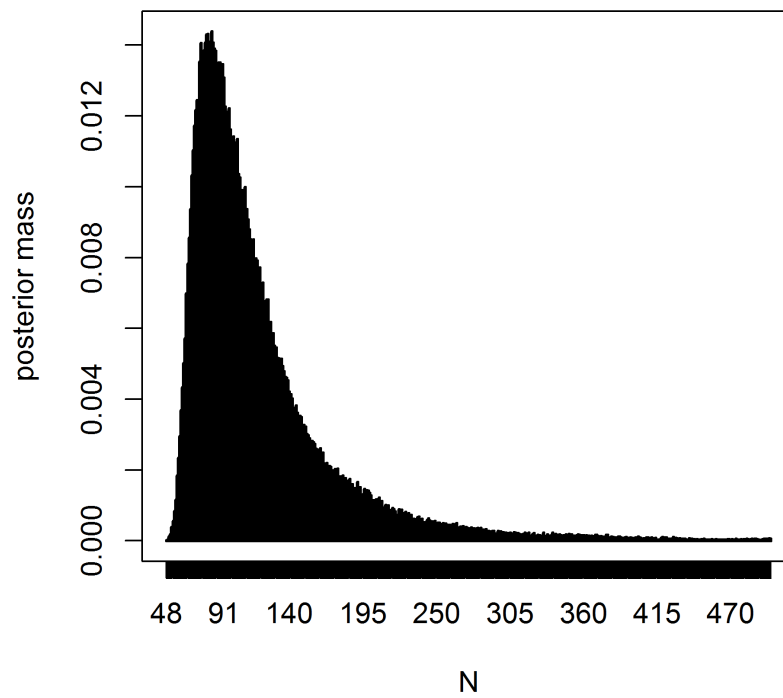


Figure 3.4. Posterior of N for Fort Drum bear study data under the logit-normal version of model M_h . From WinBUGS output. 200k samples.

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 :

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

We've identified each of the full conditional distributions in sufficient detail to apply the 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 data 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()
M<-temp$M
K<-temp$K
ytot<-temp$ytot
###
```

```

2185 ### MCMC algorithm for Model Mh
2186
2187 out<-matrix(NA,nrow=100000,ncol=4)
2188 dimnames(out)<-list(NULL,c("mu","sigma","psi","N"))
2189 lp<- rnorm(M,-1,1)
2190 p<-expit(lp)
2191 mu<- -1
2192 p0<-exp(mu)/(1+exp(mu))
2193 sigma<- 1
2194 psi<- .5
2195 z<-rbinom(M,1,psi)
2196 z[ytot>0]<-1
2197
2198 for(i in 1:100000){
2199
2200 ### update the logit(p) parameters
2201 lpc<- rnorm(M,lp,1) # 0.5 is a tuning parameter
2202 pc<-expit(lpc)
2203 lik.curr<-log(dbinom(ytot,K,z*p)*dnorm(lp,mu,sigma))
2204 lik.cand<-log(dbinom(ytot,K,z*pc)*dnorm(lpc,mu,sigma))
2205 kp<- runif(M) < exp(lik.cand-lik.curr)
2206 p[kp]<-pc[kp]
2207 lp[kp]<-lpc[kp]
2208
2209 p0c<- rnorm(1,p0,.05)
2210 if(p0c>0 & p0c<1){
2211 muc<-log(p0c/(1-p0c))
2212 lik.curr<-sum(dnorm(lp,mu,sigma,log=TRUE))
2213 lik.cand<-sum(dnorm(lp,muc,sigma,log=TRUE))
2214 if(runif(1)<exp(lik.cand-lik.curr)) {
2215   mu<-muc
2216   p0<-p0c
2217 }
2218 }
2219
2220 sigmac<-rnorm(1,sigma,.5)
2221 if(sigmac>0){
2222 lik.curr<-sum(dnorm(lp,mu,sigma,log=TRUE))
2223 lik.cand<-sum(dnorm(lp,mu,sigmac,log=TRUE))
2224 if(runif(1)<exp(lik.cand-lik.curr))
2225   sigma<-sigmac
2226 }
2227

```

```

2228 ### update the z[i] variables
2229 zc<- ifelse(z==1,0,1) # candidate is 0 if current = 1, etc..
2230 lik.curr<- dbinom(ytot,K,z*p)*dbinom(z,1,psi)
2231 lik.cand<- dbinom(ytot,K,zc*p)*dbinom(zc,1,psi)
2232 kp<- runif(M) < (lik.cand/lik.curr)
2233 z[kp]<- zc[kp]
2234
2235 psi<-rbeta(1, sum(z) + 1, M-sum(z) + 1)
2236
2237 out[i,]<- c(mu,sigma,psi,sum(z))
2238 }

```

2239 **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.

2246 3.4.4 Exercises related to model Mh

- 2247 (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.
- 2248
- 2249 (2) Execute the function and compare the results to those generated from WinBUGS in the previous section
- 2250
- 2251 (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.
- 2252
- 2253
- 2254 (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?
- 2255
- 2256 (5) Modify the MCMC algorithm so that the prior for μ_p is an improper flat prior. i.e., $[\mu_p] \propto 1$. Describe the posterior distribution of N .
- 2257

2258 3.5 INDIVIDUAL COVARIATE MODELS: TOWARD SPATIAL CAPTURE-RECAPTURE

2259 ANDY STOPPED EDITING HERE

2259 A standard situation in capture-recapture models is when an individual covariate is measured, and this covariate is thought to influence encounter probability. As
 2260 with other closed population models, we begin with the basic binomial observation
 2261 model:
 2262

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

2263 and we assume also a model for encounter probability according to:

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

2264 Classical examples of covariates influencing detection probability are type of animal
2265 (juvenile/adult or male/female), a continuous covariate such as body mass (Royle
2266 and Dorazio, 2008, chapt. 6), or a discrete covariate such as group or cluster
2267 size. For example, in models of aerial survey data, it is natural to model detection
2268 probabilities as a function of the observation-level individual covariate, “group size”
2269 (Royle, 2008, 2009; Langtimm, 2010).

2270 Such “individual covariate models” are similar in structure to Model M_h , except
2271 that the individual effects are *observed* for the n individuals that appear in the
2272 sample. These models are important here because spatial capture-recapture models
2273 are precisely a form of individual covariate model, an idea that we will develop
2274 here and elsewhere. Specifically, they are such models, but where the individual
2275 covariate is a partially observed latent variable similar.. That is, unlike Model M_h ,
2276 we do have some direct information about the latent variable, which comes from
2277 the spatial locations/distribution of individual recaptures. More on that later.

2278 Traditionally, estimation of N in individual covariate models is achieved using
2279 methods based on ideas of unequal probability sampling (i.e., Horwitz-Thompson
2280 estimation), see Huggins (1989) and Alho (1990). An estimator of N is

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

2281 where \tilde{p}_i is the probability that individual i appeared in the sample. That is,
2282 $\tilde{p}_i = \Pr(y_i > 0)$. In practice, \tilde{p}_i is estimated from the conditional-likelihood formed
2283 by the encounter histories. Namely,

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

2284 where we substitute

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

2285 with

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

2286 Here we take a formal model-based approach to Bayesian analysis of such models
2287 using data augmentation (Royle, 2009). Classical likelihood analysis of the so-
2288 called “full likelihood” is covered in some detail by Borchers et al. (2002). For
2289 Bayesian analysis of individual covariate models, because the individual covariate
2290 is unobserved for the $N - n$ uncaptured individuals, we require a model to describe
2291 variation among individuals, essentially allowing the sample to be extrapolated to
2292 the population. For our present purposes, we consider a continuous covariate and
2293 we assume that it has a normal distribution:

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

2294 Data augmentation can be applied directly to this class of models. In particular,
 2295 reformulation of the model under DA yields a basic zero-inflated binomial model of
 2296 the form:

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

2297 In addition, we assume that p_i is functionally related to a covariate x_i , e.g., by the
 2298 logit model given above, and we assume a distribution for x_i appropriate for the
 2299 context.

2300 Fully spatial capture-recapture models essentially use this formulation with a
 2301 latent covariate that is directly related to the individual detection probability (see
 2302 next Section). As with the previous models, implementation is trivial in the BUGS
 2303 language. The BUGS specification is very similar to that for model M_h , but we
 2304 require the distribution of the covariate to be specified, along with priors for the
 2305 parameters of that distribution.

2306 3.5.1 Example: Location of capture as a covariate.

2307 If we had a regular grid of traps over some closed geographic system then we imagine
 2308 that the average location of capture would be a decent estimate (heuristically) of
 2309 an individual's home range center. Intuitively some measure of typical distance
 2310 from home range center to traps for an individual should be a decent covariate to
 2311 explain heterogeneity in encounter probability, i.e., individuals with more exposure
 2312 to traps should have higher encounter probabilities and vice versa. A version of
 2313 this idea was put forth by Boulanger and McLellan (2001) (see also Ivan (2012)),
 2314 but using the Huggins-Alho estimator and with covariate "distance to edge" of the
 2315 trapping array. A limitation of this basic approach is that it does not provide a
 2316 solution to the problem that the trap area is fundamentally ill-defined, nor does
 2317 it readily accommodate the inherent and heterogeneous variation in this measured
 2318 covariate. Here, we provide an example of this type of heuristically motivated
 2319 approach using the fully model-based individual covariate model described above
 2320 analyzed by data augmentation. We take a slightly different approach than that
 2321 adopted by Boulanger and McLellan (2001). By analyzing the full likelihood and
 2322 placing a prior distribution on the individual covariate, we resolve the problem of
 2323 having an ill-defined area over which the population size is distributed. After you
 2324 read later chapters of this book, it will be apparent that SCR models represent a
 2325 formalization of this heuristic procedure.

2326 For our purposes here, we define $x_i = ||s_i - x_0||$ where s_i is the average encounter
 2327 location of individual i and x_0 is the centroid of the trap array. Conceptually,
 2328 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:

```

2367 minx<- min(trapmat[,1]-Cx)
2368 maxx<-max(trapmat[,1]-Cx)
2369 miny<- min(trapmat[,2]-Cy)
2370 maxy<- max(trapmat[,2]-Cy)
2371 # most extreme point determines maxD
2372 ul<- c(minx,maxy)
2373 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 centroid¹⁰. The BUGS model specification and R commands to package the data and fit the model are as follows:

```

2378 cat("
2379 model{
2380   p0 ~ dunif(0,1)          # prior distributions
2381   mup<- log(p0/(1-p0))
2382   psi~dunif(0,1)
2383   beta~dnorm(0,.01)
2384
2385   for(i in 1:(nind+nz)){
2386     xcent[i]~dunif(0,maxD)
2387     z[i]~dbern(psi)        # DA variables
2388     lp[i] <- mup + beta*xcent[i] # individual effect
2389     logit(p[i])<-lp[i]
2390     mu[i]<-z[i]*p[i]
2391     y[i]~dbin(mu[i],K)    # observation model
2392   }
2393   N<-sum(z[1:(nind+nz)])
2394 }
2395 ",file="modelMcov.txt")
2396 data2<-list(y=ytot,nz=nz,nind=nind,K=T,xcent=xcent,maxD=11.5)
2397 params2<-list('p0','psi','N','beta')
2398 inits = function() {list(z=z, psi=psi, p0=runif(1),beta=rnorm(1) ) }
2399 fit2 = bugs(data2, inits, params2, model.file="modelMcov.txt",working.directory=getwd(),
2400             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

¹⁰To be convincing this might need a little bit of hand-holding

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”¹¹ 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}
\begin{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 whether we can choose a better

¹¹This is a bad use of this term. We have never defined ETA or ESA. What is it, exactly?

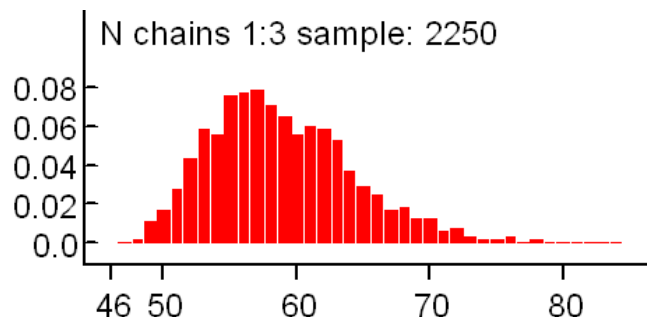


Figure 3.5. Needs a caption

2444 distribution for $\max D$ - one that doesn't imply a decreasing density as distance
 2445 from the centroid increases. Conceptually, what we want to do is impose a prior on
 2446 distance from the centroid, x , such that density is proportional to the amount of
 2447 area in each successive distance band as you move farther away from the centroid.
 2448 In fact, there is theory that exists which tells us what the correct distribution
 2449 of x is $2x/\max D^2$. This can be derived by noting that $F(x) = \Pr(X < x) =$
 2450 $\pi * x * x / \pi * \max D * \max D$. Then, $f(x) = dF/dx = 2 * x / (\max D * \max D)$. This
 2451 might be called a triangular distribution, I think, which makes sense because the
 2452 incremental area in each additional distance band increases linearly with radius (i.e.,
 2453 distance from centroid). It is sometimes comforting to verify things empirically:

```

2454 > u<-runif(10000,-1,1)
2455 > v<-runif(10000,-1,1)
2456 > d<- sqrt(u*u+v*v)
2457 > hist(d[d<1])
2458 > hist(d[d<1],100)
2459 > hist(d[d<1],100,probability=TRUE)
2460 > abline(0,2)
  
```

2461 It would be useful if we could describe this distribution in *BUGS but there is
 2462 not a built-in way to do this. One possibility is to use a discrete version of the pdf.
 2463 We might also be able to use what is referred to in WinBUGS jargon as the “zeros
 2464 trick” (see Advanced BUGS tricks) although we haven't pursued this approach.
 2465 Instead, we consider using a discrete version and break D_{\max} into L distance classes
 2466 of width δ , with probabilities proportional to $2 * x$. In particular, if the cut-points
 2467 are $xg[1] = 0, xg[2], \dots, xg[L + 1] = D_{\max}$ and the interval midpoints are $xm[i] =$
 2468 $xg[i + 1] - \delta$. Then, the interval probabilities are $p[i] = 2 * xm[i] * \delta / (D_{\max} * D_{\max})$, 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 .

```

2475 delta<-.2
2476 xround<-xcent/%delta + 1
2477 Dgrid<- seq(delta,maxD,delta)
2478 xprobs<- delta*(2*Dgrid/(maxD*maxD))
2479 xprobs<-xprobs/sum(xprobs)
2480
2481 cat("
2482 model{
2483   p0 ~ dunif(0,1)          # prior distributions
2484   mup<- log(p0/(1-p0))
2485   psi~dunif(0,1)
2486   beta~dnorm(0,.01)
2487
2488   for(i in 1:(nind+nz)){
2489     xround[i]~dcat(xprobs[])
2490     z[i]~dbern(psi)          # zero inflation variables
2491     lp[i] <- mup + beta*xround[i]*delta # individual effect
2492     logit(p[i])<-lp[i]
2493     mu[i]<-z[i]*p[i]
2494     y[i]~dbin(mu[i],K)      # observation model
2495   }
2496
2497   N<-sum(z[1:(nind+nz)])
2498 }
2499 ",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:

```

2502 data2<-list(y=ytot,nz=nz,nind=nind,K=T,xround=xround,xprobs=xprobs,delta=delta)
2503 params2<-list('p0','psi','N','beta')
2504 inits = function() {list(z=z, psi=psi, p0=runif(1),beta=rnorm(1) ) }
2505 fit = bugs(data2, inits, params2, model.file="modelMcov.txt",working.directory=getwd(),
2506           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 `maxD`. We can apply the model for different values of `maxD` and

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	0.043	[6,]	20	0.250	0.044
----------	----	----	------	----	-------	-------	------	----	-------	-------	------	----	-------	-------	------	----	-------	-------	------	----	-------	-------	------	----	-------	-------

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 array) 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 population¹² 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 $Area(\max D) = \pi *$

¹²We 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.

2542 $\max D * \max D$ and $E[N(\max D)] = \lambda * A(\max D)$ and thus $E[\text{Density}(\max D)] = \lambda$
 2543 which is constant. This should be interpreted as the *prior* density. Absent data,
 2544 then realizations under the model will have density λ regardless of what $\max D$ is
 2545 prescribed to be. As we verified empirically above, the posterior density is also
 2546 invariant if $\max D$ as long as the implied area (implied by $\max D$) is large enough so
 2547 that the data no longer provide information about density (i.e., “far away”), then
 2548 our estimator of density should become insensitive.

2549 3.5.4 Toward Fully Spatial Capture-recapture Models

2550 We developed this model for the average observed location and equated it to home
 2551 range center s_i . Intuitively, taking the average encounter location as an estimate
 2552 of home range center makes sense but more so when the trapping grid is dense and
 2553 expansive relative to typical home range sizes. However, our approach also ignored
 2554 the variable precision with which each $s[i]$ is estimated and also, as noted previously,
 2555 estimates of $s[i]$ around the “edge” (however we define that) are biased because the
 2556 observations are truncated (we can only observe locations within the trap array). In
 2557 the next Chapter we provide a further extension of this individual covariate model
 2558 that definitively resolves the ad hoc nature of the individual covariate approach we
 2559 took here. In that model we build a model in which $s[i]$ are regarded as latent
 2560 variables and the observation locations (i.e., trap specific encounters) are linked
 2561 to those latent variables with an explicit model. We note that the model fitted
 2562 previously could be adapted easily to deal with s_i as a latent variable, simply by
 2563 adding a prior distribution for s_i . The reader should contemplate how to do this
 2564 in WinBUGS.

2565 3.6 DISTANCE SAMPLING: A PRIMITIVE SPATIAL 2566 CAPTURE-RECAPTURE MODEL

2565 Distance sampling is one of the most popular methods for estimating animal abun-
 2566 dance. One of the great benefits of distance sampling is that it provides explicit
 2567 estimates of *density*. The distance sampling model is a special case of a closed
 2568 population model with a covariate. The covariate in this case, x_i , is the distance
 2569 between an individual’s location “ u ” and the observation location or transect. In
 2570 fact, the model underlying distance sampling is precisely the same model as that
 2571 which applies to the individual-covariate models, except that observations are made
 2572 at only $K = 1$ sampling occasion. In a sense, distance sampling is a spatial capture-
 2573 recapture model, but without the “recapture.” This first and most basic spatial
 2574 capture-recapture model has been used routinely for decades and, formally, it is a
 2575 spatially-explicit model in the sense that it describes, explicitly, the spatial organi-
 2576 zation of individual locations (although this is not always stated explicitly) and, as
 2577 a result, somewhat general models of how individuals are distributed in space can
 2578 be specified (Royle et al., 2004; Johnson, 2010; Sillett, 2011). As before, the dis-

2579 tance sampling model, under data augmentation, includes a set of M zero-inflation
 2580 variables z_i and the binomial model expressed conditional on z (binomial for $z = 1$,
 2581 and fixed zeros for $z = 0$). In distance sampling we pay for having only a single
 2582 sample (i.e., $K = 1$) by requiring constraints on the model of detection probability.
 2583 A standard model is

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

2584 for $b < 0$, where x_i denotes the distance at which the i th individual is detected
 2585 relative to some reference location where perfect detectability ($p = 1$) is assumed.
 2586 This function corresponds to the “half-normal” detection function (i.e., with $b =$
 2587 $1/\sigma^2$). If $K > 1$ then the intercept alpha is identifiable and such models are
 2588 usually called “capture-recapture distance sampling” (Borchers, missing) and others
 2589 XYZ????).

2590 As with previous examples, we require a distribution for the individual covariate
 2591 x_i . The customary choice is

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

2592 wherein $B > 0$ is a known constant, being the upper limit of data recording by the
 2593 observer (i.e., the point count radius, or transect half-width). In practice, this is
 2594 sometimes asserted to be infinity, but in such cases the distance data are usually
 2595 truncated. Specification of this distance sampling model in the BUGS language is
 2596 shown in Panel 3.1. Royle and Dorazio (2008), p. xyz) provide a distance sampling
 2597 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.

2598 As with the individual covariate model in the previous section, the distance
 2599 sampling model can be equivalently specified by putting a prior distribution on
 2600 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 data¹³. 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.

¹³Formally we could also say that $[u] = \int [y|s][s]ds$

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.

```

2641 library("R2WinBUGS")
2642 data<- read.csv("Muntjac.csv")
2643 nind<-nrow(data)
2644 y<-rep(1,nind)
2645 nz<-400
2646 y<-c(y,rep(0,nz))
2647 x<-data[,3]
2648 x<-c(x,rep(NA,nz))
2649 z<-y
2650 data<-list(y=y,x=x,nz=nz,nind=nind,B=150,striparea=708*.15*2)
2651
2652 cat("
2653 model{
2654   b~dunif(0,10)
2655   psi~dunif(0,1)
2656
2657   for(i in 1:(nind+nz)){
2658     z[i]~dbern(psi)    # DA Variables
2659     x[i]~dunif(0,B)    # B=strip width
2660     p[i]<-exp(logp[i]) # DETECTION MODEL
2661     logp[i]<- -((x[i]*x[i])*b)
2662     #logp[i]<- -b*log(x[i]+1)
2663     mu[i]<-z[i]*p[i]
2664     y[i]~dbern(mu[i]) # OBSERVATION MODEL
2665   }
2666   N<-sum(z[1:(nind+nz)])
2667   D<- N/striparea # area of transects
2668 }
2669 ",file="dsamp.txt")

```

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


```

2672 params<-list('b','N','D','psi')
2673 inits = function() {list(z=z, psi=runif(1), b=runif(1,0,.02) )}
2674 fit = bugs(data, inits, params, model.file="dsamp.txt",
2675 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.¹⁴

	node	mean	sd	MC error	2.5% median	97.5% start	sample
2678	D	1.096	0.1694	0.009122	0.8098	1.078	1.474 501 4500
2679	N	232.8	35.99	1.938	172.0	229.0	313.0 501 4500
2680	b	5.678E-4	1.05E-4	4.129E-6	3.867E-4	5.616E-4	7.949E-4 501 4500
2681	deviance	681.2	16.72	0.7536	650.8	680.6	716.6 501 4500
2682	psi	0.5099	0.08238	0.004442	0.3681	0.5033	0.6918 501 4500
2683							

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 to the size of a hypothetical “complete” data set) is unknown. This requires special consideration in the analysis of capture-recapture models. The classical approach to inference recognizes that the observations don’t have a standard binomial distribution but, rather, a truncated binomial (from which the so-called “conditional likelihood” derives) since we only have encounter frequency data on observed individuals. If instead we analyze the models using data augmentation, the observations can be modeled using a zero-inflated binomial distribution. In short, when we deal with the unknown- N problem using data augmentation then we are left with zero-inflated GLM and GLMMs instead of ordinary GLM or GLMMs. The analysis of such zero-inflated models is practically convenient, especially using the various Bayesian analysis packages that use the BUGS language.

Spatial capture-recapture models that we will consider in the rest of the chapters of this book are closely related to what have been called individual covariate models. Heuristically, spatial capture-recapture models arise by defining individual covariates based on observed locations of individuals – we can think of using some function of mean encounter location as an individual covariate. We did this in a novel way, by using distance to the centroid of the trapping array as a covariate. We analyzed the “full likelihood” using data augmentation, and placed a prior distribution on the individual covariate which was derived from an assumption that individual locations are, a priori, uniformly distributed in space. This assumption provides for invariance of the density estimator to the choice of population size area

¹⁴ much 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.

(induced by maximum distance from the centroid of the). The model addressed some important problems in the use of closed population models: it allows for heterogeneity in encounter probability due to the spatial context of the problem and it also provides a direct estimate of density because area is a feature of the model (via the prior on the individual covariate). The model is still not completely general because the model does not make use of the fully spatial encounter histories, which provide direct information about the locations and density of individuals. A specific individual covariate model that is in widespread use is classical “distance sampling.” The model underlying distance sampling is precisely a special kind of SCR model - but one without replicate samples. Understanding distance sampling and individual covariate models more broadly provides a solid basis for understanding and analyzing spatial capture-recapture models.

4

FULLY SPATIAL CAPTURE-RECAPTURE MODELS

In previous sections we discussed some classes of models that could be viewed as primitive spatial capture-recapture models. We looked at a basic distance sampling model and we also considered a classical individual covariate modeling approach in which we defined a covariate to be the distance from (estimated) home range center to the center of the trap array. These were spatial in the sense that they included some characterization of where individuals live but, on the other hand, only a primitive or no characterization of trap location. That said, very little distinguishes these two models from spatial capture-recapture models that we consider in this chapter which fully recognize the spatial attribution of both individual animals *and* the locations of encounter devices.

Fully spatial capture-recapture models must accommodate the spatial organization of individuals and the encounter devices because the encounter process occurs at the level of individual traps. Failure to consider the trap-specific collection of data is the key deficiency with classical ad-hoc approaches which aggregate encounter information to the resolution of the entire trap array. We have seen previously some problems that this induces - imbalance in trap-level effort over time is problematic, and not being able to deal with trap-specific behavioral responses. Here, we resolve that by developing what is basically an individual covariate model but operating at the level of traps. That is, we develop our first fully spatial capture-recapture model which turns out to be precisely the model considered in section 3.XXX but instead of defining the individual covariate to be distance to centroid of the array we define J individual covariates - the distance to *each* trap. And, instead of using estimates of individual locations \mathbf{s} , we consider a fully hierarchical model in which we regard \mathbf{s} as a latent variable and impose a prior distribution on

it. We can think of having J independent capture-recapture studies generating one data set for each trap, and applying the individual covariate model with random activity centers, and that is all the basic SCR model is.

In the following sections of this chapter we investigate the basic spatial capture-recapture model and address some important considerations related to its analysis in **WinBUGS**. We also demonstrate how to summarize posterior output for the purposes of producing density maps or spatial predictions of density.

4.1 SAMPLING DESIGN AND DATA STRUCTURE

In our development here, we will assume a standard sampling design in which an array of J traps is operated for K time periods (say, nights) producing encounters of n individuals. Because sampling occurs by traps and also over time, the most general data structure yields encounter histories for *each individual* that are temporally *and* spatially indexed. Thus a typical data set will include an encounter history *matrix* for each individual. For the most basic model, there are no time-varying covariates that influence encounter, there are no explicit individual-specific covariates, and there are no covariates that influence density we will develop models in this chapter for encounter data that are aggregated over the temporal replicates. For example, suppose we observe 6 individuals in sampling at 4 traps over 3 nights of sampling then a plausible data set is the 6×4 matrix of encounters, out of 3, of the form:

	trap1	trap2	trap3	trap4
[1,]	1	0	0	0
[2,]	0	2	0	0
[3,]	0	0	0	1
[4,]	0	1	0	0
[5,]	0	0	1	1
[6,]	1	0	1	0

We develop models in this chapter for devices such as “hair snares” or other DNA sampling methods (Kéry et al., 2010; Gardner et al., 2010) and related types of sampling problems so that we can suppose that “traps” may capture any number of individuals and an individual may be captured in any number of traps during each occasion but individuals can be encountered at most 1 time in a trap during any occasion. Thus, this is a “multi-catch” type of sampling (?, p. xyz). The statistical assumptions are that individual encounters within and among traps are independent. These basic (but admittedly at this point somewhat imprecise) assumptions define the basic spatial capture-recapture model, which we will refer to as “SCR0” henceforth¹ so that we may use that model as a point of reference

¹RC: It would be nice to have a running series of figures to display the various types of models. Each figure could have the same set of traps, use the same symbols, etc... It’s probably worth showing example data (and latent variables) in a table too

without having to provide a long-winded enumeration of assumptions and sampling design each time we do. We will make things more precise as we develop a formal statistical definition of the model shortly.

While the model is mostly directly relevant for hair snares and other DNA sampling methods for which multiple detections of an individual are not distinguishable, we will also make use of the model for data that arise from camera-trapping studies. In practice, with camera trapping, individuals might be photographed several times in a night but we will typically distill such data into a single binary encounter event for reasons discussed later in chapter 6.

4.2 THE BINOMIAL OBSERVATION MODEL

We assume that the individual and trap-specific encounters, y_{ij} , are mutually independent outcomes of a binomial random variable:

$$y_{ij} \sim \text{Bin}(K, p_{ij}) \quad (4.2.1)$$

This is the basic model underlying “logistic regression” (chapter 2) as well as standard closed population models (chapter 3). The key element of the model is that the encounter probability p_{ij} is indexed by (i.e., depends on) both individual and trap. In a sense, then, we can think of each *trap* as producing individual level encounter history data of the classical variety - an $n_{\text{ind}} \times n_{\text{rep}}$ matrix of 0's and 1's (this is the “encountered at most 1 time” assumption).

As we did in section XXX.YYY, we will make explicit the notion that p_{ij} is defined conditional on “where” individual i lives. Naturally, we think about defining an individual home range and then relating p_{ij} explicitly to the centroid of the individual's home range, or its center of activity (Efford, 2004; Borchers and Efford, 2008; Royle and Young, 2008). Therefore, define \mathbf{s}_i , a two-dimensional spatial coordinate, to be the activity center for individual i . Then, the basic SCR model postulates that encounter probability, p_{ij} , is related by a decreasing function to distance between trap j , having location \mathbf{x}_j , and \mathbf{s}_i . Naturally, if we think of modeling binomial counts using logistic regression, we might specify the model according to:

$$\text{logit}(p_{ij}) = \alpha_0 + \theta * ||\mathbf{s}_i - \mathbf{x}_j|| \quad (4.2.2)$$

where, here, $||\mathbf{s}_i - \mathbf{x}_j||$ is the distance between \mathbf{s}_i and \mathbf{x}_j . We sometimes write $||\mathbf{s}_i - \mathbf{x}_j|| = \text{dist}(\mathbf{s}_i, \mathbf{x}_j) = d_{ij}$. Alternatively, if we think about distance sampling then we might use the “half-normal” model of the form:

$$p_{ij} = p_0 * \exp(-\theta * ||\mathbf{s}_i - \mathbf{x}_j||^2)$$

Or any of a large number of standard detection models that are commonly used (we consider more in chapter XYZ). The half-normal model implies

$$\log(p_{ij}) = \log(p_0) - \theta * ||\mathbf{s}_i - \mathbf{x}_j||^2 \quad (4.2.3)$$

Whatever model encounter probability we choose, we should always keep in mind that the model is described conditional on \mathbf{s}_i , which is an unobserved random variable. Thus, to be precise about this, we should write the observation model as

$$y_{ij}|\mathbf{s}_i \sim \text{Bin}(K, p(\mathbf{s}_{ij}; \theta))$$

Note that we probably expect that the parameter θ in Eq. 4.2.2 or 4.2.3 should be negative, so that the probability of encounter decreases with distance between the trap and individual home range center. The joint likelihood for the data, conditional on the collection of individual activity centers, can therefore be expressed as

$$\mathcal{L}(\theta|\{\mathbf{y}_i, \mathbf{s}_i\}_{i=1}^N) = \prod_i \prod_j \text{Bin}(y_{ij}|p_{ij}(\theta))$$

Which, if we switch the indices on the product operators, this shows the SCR likelihood (conditional on \mathbf{s}) to be the product of J *independent* capture-recapture likelihoods - one for each trap. However, the data have a “repeated measures” type of structure, with each of the j likelihood contributions for each individual being grouped by individual. Thus, we cannot analyze the model meaningfully by J trap-specific models. In classical repeated measures types of models, we accommodate the group structure of the data using random effects (random individual or group level variables). For SCR models we take the same basic approach, which we develop subsequently.

4.2.1 Distance as a latent variable

If we knew precisely every \mathbf{s}_i in the population (and how many, N), then the model specified by eqs. 4.2.1 and 4.2.2 or 4.2.3 is just an ordinary logistic regression type of a model which we learned how to fit using **WinBUGS** previously (chapt. 2), with a covariate d_{ij} . However, the activity centers are unobservable even in the best possible circumstances. In that case, d_{ij} is an unobserved variable, analogous to classical “random effects” models. We need to therefore extend the model to accommodate these random variables with an additional model component. A standard, and perhaps not unreasonable, assumption is the so-called “uniformity assumption” which is to say that the \mathbf{s}_i are uniformly distributed over space (the obvious next question “which space?” is addressed below). This uniformity assumption amounts to a uniform prior distribution on \mathbf{s}_i , i.e., the pdf of \mathbf{s}_i is constant, which we may express

$$\Pr(\mathbf{s}_i) \text{propto} \text{const} \quad (4.2.4)$$

To summarize the preceeding model developing, a basic SCR model is defined by 3 essential components:

- (1) Observation model: $y_{ij}|\mathbf{s}_i \sim \text{Bin}(K, p_{ij})$
- (2) Encounter probability: $\text{logit}(p_{ij}) = \alpha_0 + \theta * \|\mathbf{s}_i - \mathbf{x}_j\|$

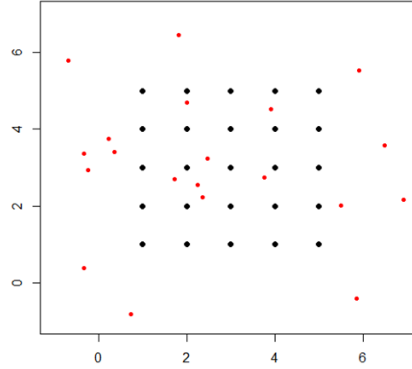


Figure 4.1. Realization of a binomial point process

2849 (3) Point process model: $\Pr[\mathbf{s}_i] \propto \text{const}$

2850 Therefore, the SCR model is little more than an ordinary capture-recapture model
 2851 for closed populations. It is such a model, but augmented with a set of “individual
 2852 effects”, \mathbf{s}_i , which relate some sense of individual location to encounter probability.
 2853 As it turns out, assumption (3) is usually not precise enough to fit a model in
 2854 practice for reasons we discuss in the following section. We will give another way to
 2855 represent this prior distribution that is more concrete, but it depends on specifying
 2856 the “state-space” of the random variable \mathbf{s}_i . The term “state-space” is a technical
 2857 way of saying “possible outcomes”.

4.3 THE BINOMIAL POINT-PROCESS MODEL

2858 The collection of individual activity centers $\mathbf{s}_1, \dots, \mathbf{s}_N$ represent a realization of a
 2859 *binomial point process* (Illian, 2008a, p. xyz). The binomial point process (BPP)
 2860 is analogous to a Poisson point process in the sense that it represents a “random
 2861 scatter” of points in space - except that the total number of points is *fixed*, whereas,
 2862 in a Poisson point process it is random (having a Poisson distribution). As an
 2863 example, we show in Fig. 4.1 locations of 20 individual activity centers (black
 2864 dots) in relation to a grid of 25 traps. For a Poisson point process the number of
 2865 such points in the prescribed state-space would be random whereas often we will
 2866 simulate fixed numbers of points, e.g., for evaluating the performance of procedures
 2867 such as how well does our estimator perform of $N = 50$?

It is natural to consider a binomial point process in the context of capture-recapture models because it preserves N in the model and thus preserves the linkage directly with closed population models. In fact, under the binomial point process model then Model M0 and other closed models are simple limiting cases of SCR models. In addition, use of the BPP model allows us to use data augmentation for Bayesian analysis of the models as in chapter 3, thus yielding a methodologically coherent approach to analyzing the different classes of models. Despite this, making explicit assumptions about N , such as Poisson, is convenient in some cases (see chapt. XYZ).

One consequence of having fixed N , in the BPP model, is that the model is not strictly a model of “complete spatial randomness”. This is because if one forms counts $n(A_1), \dots, n(A_k)$ in any set of disjoint regions say A_1, \dots, A_k , then these counts are *not* independent. In fact, they have a multinomial distribution (see Illian, 2008a, p. XYZ). Thus, the BPP model introduces a slight bit of dependence in the distribution of points. However, in most situations this will have no practical effect on any inference or analysis and, as a practical matter, we will usually regard the BPP model as one of spatial independence among individual activity centers because each activity center is distributed independently of each other activity center. Despite this implicit independence we see in Fig. 4.1 that realizations of randomly distributed points will typically exhibit distinct non-uniformity. Thus, independent, uniformly distributed points will almost never appear regularly, uniformly or systematically distributed. For this reason, the basic binomial (or Poisson) point process models are enormously useful in practical settings. More relevant for SCR models is that we actually have a little bit of data for some individuals and thus the resulting posterior point pattern can deviate strongly from uniformity (we should note this elsewhere too). The uniformity hypothesis is only a *prior* distribution which is directly affected by the quantity and quality of observations.

4.3.1 Definition of home range center

Some will be offended by our use of the concept of “home range center” and thus will have difficulty in believing that the resulting model is really useful for anything. Indeed, the idea of a home range or activity center is a vague concept anyway, a purely phenomenological construct. Despite this, it doesn’t really matter whether or not a home range makes sense for a particular species - individuals of any species inhabit *some* region of space and we can define the “home range center” to be the center of the space that individual was occupying (or using) during the period in which traps were active. Thinking about it in that way, it could even be observable (almost) as the centroid of a very large number of radio fixes over the course of a survey period or a season. Thus, this practical version of a home range center is a well-defined construct regardless of whether one thinks the home range concept is meaningful, even if individuals are not particularly territorial. This is why we usually use the term “activity center” or maybe even “centroid of space usage”

and we recognize that this construct is a transient thing which applies only to a well-defined period of study.

4.3.2 The state-space of the point process

Shortly we will focus on Bayesian analysis of this model with N known so that we can directly apply what we learned in chapter 2 to this situation. To do this, we note that the individual effects $\mathbf{s}_1, \dots, \mathbf{s}_N$ are unknown quantities and we will need to be able to simulate each \mathbf{s}_i in the population from the posterior distribution. It should be self-evident that we cannot simulate the \mathbf{s}_i unless we describe precisely the region over which those \mathbf{s}_i 's are uniformly distributed. This is the quantity referred to above as the state-space, denoted henceforth by \mathcal{S} , which is a region or a set of points comprising the potential values of \mathbf{s}_i . Thus, an equivalent explicit statement of the “uniformity assumption” is

$$\mathbf{s}_i \sim \text{Unif}(\mathcal{S})$$

Prescribing the state-space

Evidently, we need to define the state-space, \mathcal{S} . How can we possibly do this objectively? Prescribing any particular \mathcal{S} seems like the equivalent of specifying a “buffer” which we criticized previously as being ad hoc. How is it that choosing a state-space is *not* ad hoc? As a practical matter, it turns out that estimates of density are insensitive to choice of the state-space. As we observed in chapter 7, it is true that N increases with \mathcal{S} , but only at the same rate as \mathcal{S} under the prior assumption of constant density. As a result, we say that density is invariant to \mathcal{S} as long as \mathcal{S} is sufficiently large. Thus, while choice of \mathcal{S} is (or can be) essentially arbitrary, once \mathcal{S} is chosen, it defines the population being exposed to sampling, which scales appropriately with the size of the state-space.

For our simulated system developed previously in this chapter, we defined the state space to be a square within which our traps were centered perfectly. For many practical situations this might be an acceptable approach to defining the state-space. We provide an example of this in section 4.7 below in which the trap array is irregular and also situated within a realistic landscape that is distinctly irregular. In general, it is most practical to define the state-space as a regular polygon (e.g., rectangle) containing the trap array without differentiating unsuitable habitat. Although defining the state-space to be a regular polygon has computational advantages (e.g., we can implement this more efficiently in **WinBUGS** and cannot for irregular polygons), a regular polygon induces an apparent problem of admitting into the state-space regions that are distinctly non-habitat (e.g., oceans, large lakes, ice fields, etc.). It is difficult to describe complex sets in mathematical terms that can be admitted to this spatial model. As an alternative, we can provide a representation of the state-space as a discrete set of points (section 4.9) that will allow specific points to be deleted or not depending on whether they represent habitat, or we can define the state-space as an intersection of polygons, and analysis of

models with state-space defined in that way can be analyzed easily using MCMC (see section XYZ in chapt. 6). In what follows below we provide an analysis of the camera data defining the state-space to be a regular continuous polygon (a rectangle).

4.3.3 Invariance and the State-space as a model assumption

We will assert for all models we consider in this book that density is invariant to the size and extent of \mathcal{S} , if \mathcal{S} is sufficiently large. In fact, this only holds as long as our model relating p_{ij} to \mathbf{s}_i is a decreasing function of distance. We can prove this thinking about a 1-d case where $E[y]$ for the “last cell” (i.e., for $d > B$ for B large enough) is 0. So it always contributes nothing to the likelihood, i.e., $E[n(\text{lastcell})] = 0$. [sketch out a proof of this], in regular situations in which the detection function decays monotonically with distance and prior density is constant. Sometimes our estimate of density can be influenced if we make \mathcal{S} too small but this might be sensible if \mathcal{S} is naturally well-defined. As we discussed in chapter 1, **choice of \mathcal{S} is part of the model and thus it makes sense that estimates of density might be sensitive to its definition in problems where it is natural to restrict \mathcal{S} .** One could imagine however that in specific cases where you’re studying a small population with well-defined habitat preferences that a problem could arise because changing the state-space around based on differing opinions and GIS layers really changes the estimate of total population size. But this is a real biological problem and a natural consequence of the spatial formalization of capture-recapture models - a feature, not a bug or some statistical artifact - and it should be resolved with better information and research, and not some arbitrary statistical artifact. For situations where there is not a natural choice of \mathcal{S} , we should default to choosing \mathcal{S} to be very large in order to achieve invariance or otherwise evaluate sensitivity of density estimates by trying a couple of different values of \mathcal{S} . This is a standard “sensitivity to prior” argument that Bayesians always have to be conscious of. We demonstrate this in our analysis of section 4.7 below. Note that $area(\mathcal{S})$ affects data augmentation. If you increase $area(\mathcal{S})$ then there are more individuals to account for and therefore the size of the augmented data set M must increase.

We have been told that one can carry-out non-Bayesian analyses of SCR models without having to specify the state-space of the point process or perhaps while only specifying it imprecisely. This assertion is incorrect. We assume people are thinking this because *they* don’t have to specify it explicitly because someone else has done it for them in a package that does integrated likelihood. Even to do integrated likelihood (see chapter 6) we have to integrate the conditional-on- \mathbf{s} likelihood over some 2-dimensional space. It might work that the integration can be done from $-\infty$ to $+\infty$ but that is a mathematical artifact of specific detection functions, and an implicit definition of a state-space that doesn’t make biological sense, even though it may in fact be innocuous;

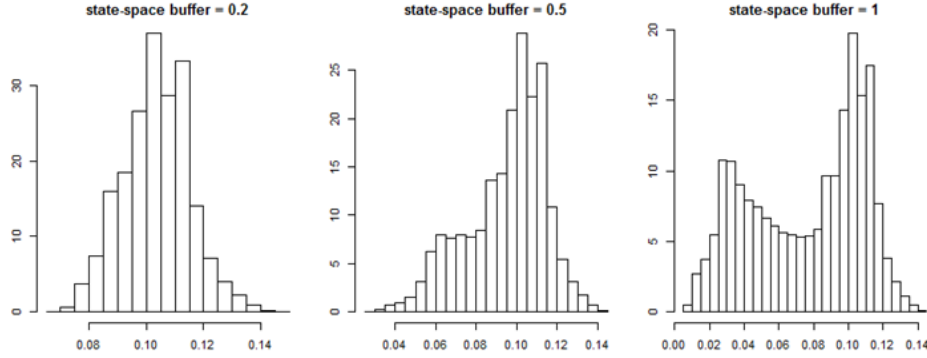


Figure 4.2. Needs a caption

4.3.4 Connection to Model Mh

SCR models are closely related to heterogeneity models. In SCR models, heterogeneity in encounter probability is induced by both the effect of distance in the model for detection probability and also from specification of the state-space. Clearly then the state-space is explicitly part of the model. To understand this, we have a random effect with some prior distribution:

$$\mathbf{s} \sim \text{uniform}(\mathcal{S})$$

And $p(\mathbf{s}) = p(y = 1|\mathbf{s})$ is some function of \mathbf{s} . Therefore, for any specific $g(p)$ and \mathcal{S} we can work out what the implied heterogeneity model is for example, the mean, variance or other moments of the population distribution of p can be evaluated by integrating $p(\mathbf{s})$ over the state-space of \mathbf{s} . Obviously the choice of $p(\mathbf{s})$ and the choice of \mathcal{S} interact to determine the effective heterogeneity in p . We show an illustration in Fig. 4.2 below which shows a histogram of p for a hypothetical population of 100000 individuals on a state-space enclosing our 5×5 trap array above, under the logistic model for distance. **R** code is provided in the **R** package **scrbook** to produce this analysis for the logistic and half-normal models. The histogram shows the encounter probability under buffers of 0.2, 0.5 and 1.0. We see the mass shifts to the left as the buffer increases, implying more individuals in the population but with lower encounter probability as their home range centers increase in distance from the trap array.

Another way to understand this is by representing \mathcal{S} as a set of discrete points on a grid. In the coarsest possible case where \mathcal{S} is a single arbitrary point, then every individual has exactly the same p . As we increase the number of points in \mathcal{S} then more distinct values of p are possible. As such, when \mathcal{S} is characterized by discrete points then SCR models are precisely a type of finite-mixture model (Norris III and

Pollock, 1996; Pledger, 2000), except where we have some information about which group an individual belong (i.e., where their activity center is), as a result of their captures in traps.

This context suggests the problem raised by Link (2003). He showed that in most practical situations N may not be identifiable across classes of mixture distributions which in the context of SCR models is the pair (g, \mathcal{S}) . The difference, however, is that we do obtain some direct information about \mathbf{s} in SCR models and therefore N is identifiable across models characterized by (g, \mathcal{S}) .

4.3.5 Connection to Distance Sampling

It is worth emphasizing that the basic SCR model is a binomial encounter model in which distance is a covariate. As such, it is striking similarity to a classical distance sampling model. Both have distance as a covariate but in classical distance sampling problems the focus is on the distance between the observer and the animal at an instant in time, not the distance between a trap and an animal's home range center. Thus in distance sampling, "distance" is *observed* for those individuals that appear in the sample. Conversely, in SCR problems, it is only imperfectly observed (we have partial information in the form of trap observations). Clearly, it is preferable to observe distance if possible, but as we will discuss in chapter XYZ, distance sampling requires field methods that are often not practical in many situations, e.g. when surveying tigers. Furthermore, SCR models allow us to relax many of the assumption made in classical distance sampling, and SCR models allow for estimates of quantities other than density, such as home range size.

4.4 SIMULATING SCR DATA

It is always useful to simulate data because it allows you to understand the system that you're modeling and also calibrate your understanding with the parameter values of the model. That is, you can simulate data using different parameter values until you obtain data that "looks right" based on your knowledge of the specific situation that you're interested in. Here we provide a simple script to illustrate how to simulate spatial encounter history data. In this exercise we simulate data for 100 individuals and a 25 trap array laid out in a 5×5 grid of unit spacing. The specific encounter model is the half-normal model given above and we used this code to simulate data used in subsequent analyses. The 100 activity centers were simulated on a state-space defined by a 8×8 square within which the trap array was centered (thus the trap array is buffered by 2 units). Therefore, the density of individuals in this system is fixed at $100/64$.

```
set.seed(2013)
# create 5 x 5 grid of trap locations with unit spacing
traplocs<- cbind(sort(rep(1:5,5)),rep(1:5,5))
```

```

3050 Dmat<-e2dist(traplocs,traplocs) # in cases where speed doesn't matter, it might be
3051                                # clearer to just show the slow for-loop.
3052                                # Plus, people will want to copy/paste this stuff
3053 ntraps<-nrow(traplocs)
3054
3055 # define state-space of point process. (i.e., where animals live).
3056 # "delta" just adds a fixed buffer to the outer extent of the traps.
3057 delta<-2
3058 Xl<-min(traplocs[,1] - delta)
3059 Xu<-max(traplocs[,1] + delta)
3060 Yl<-min(traplocs[,2] - delta)
3061 Yu<-max(traplocs[,2] + delta)
3062
3063 N<-100    # population size
3064 K<- 20    # number nights of effort
3065
3066 sx<-runif(N,Xl,Xu)    # simulate activity centers
3067 sy<-runif(N,Yl,Yu)
3068 S<-cbind(sx,sy)
3069 D<- e2dist(S,traplocs) # distance of each individual from each trap
3070
3071 alpha0<- -2.5        # define parameters of encounter probability
3072 sigma<- 0.5          #
3073 theta<- 1/(2*sigma*sigma)
3074 probcap<- expit(-2.5)*exp( - theta*D*D)    # probability of encounter
3075 # now generate the encounters of every individual in every trap
3076 Y<-matrix(NA,nrow=N,ncol=ntraps)
3077 for(i in 1:nrow(Y)){
3078     Y[i,<-rbinom(ntraps,K,probcap[i,])
3079 }

```

Subsequently we will generate data using this code packaged in an R function called `simSCR0.fn` which takes a number of arguments including `discard0` which, if `TRUE`, will return only the encounter histories for captured individuals. A second argument is `array3d` which, if `TRUE`, returns the 3-d encounter history array instead of the aggregated `nind × ntraps` encounter frequencies (see below). Finally we provide a random number seed, `sd` which we always set to 2013 in our analyses. Thus we obtain a data set as above using the following command

```

3087 data<-simSCR0.fn(discard0=TRUE,array3d=FALSE,sd=2013)

```

The **R** object `data` is a list, so let's take a look at what's in the list and then harvest some of its elements for further analysis below.

```

3090 > names(data)
3091 [1] "Y"          "traplocs" "xlim"      "ylim"      "N"          "alpha0"    "beta"
3092 [8] "sigma"      "K"

```

```

3093 > Y<-data$Y
3094 > traplocs<-data$traplocs

```

3095 4.4.1 Formatting and manipulating real data sets

3096 Conventional capture-recapture data are easily stored and manipulated as a 2-
 3097 dimensional array, an $nind \times nperiod$ matrix, which is maximally informative for
 3098 any conventional capture-recapture model, but not for spatial capture-recapture
 3099 models. For SCR models we must preserve the spatial information in the encounter
 3100 history information. We will routinely analyze data from 3 standard formats:

- 3101 (1) The basic 2-dimensional data format, which is an $nind \times ntraps$ encounter
 3102 frequency matrix such as that simulated previously;
- 3103 (2) The maximally informative 3-dimensional array which we establish here the
 3104 convention that it has dimensions $nind \times nperiods \times ntraps$ and
- 3105 (3) We use a compact format - the “SCR flat format” - which we describe below
 3106 in section 4.7.

3107 To simulate data in the most informative format - the “3-d array” - we can use the
 3108 **R** commands given previously but replace the last 4 lines with the following:

```

3109 Y<-array(NA,dim=c(N,K,ntraps))
3110 for(i in 1:nrow(Y)){
3111   for(j in 1:ntraps){
3112     Y[i,1:K,j]<-rbinom(K,1,probcap[i,j])
3113   }
3114 }

```

3115 We see that a collection of K binary encounter events are generated for *each*
 3116 individual and for *each* trap. The probabilities have those Bernoulli trials are
 3117 computed based on the distance from each individuals home range center and the
 3118 trap (see calculation above), and those are housed in the matrix probcap. Our
 3119 data simulator function `simSRC0.fn` will return the full 3-d array if `array3d=TRUE`
 3120 is specified in the function call. To recover the 2-d matrix from the 3-d array, and
 3121 subset the 3-d array to individuals that were captured, we do this:

```

3122 Y2d<- apply(Y,c(1,3),sum) # sum over the ‘‘replicates’’ dimension (2nd margin of the array)
3123 ncaps<-apply(Y2d,1,sum)   # compute how many times each individual was captured
3124 Y<-Y[ncaps>0,,]          # keep those individuals that were captured

```

4.5 FITTING AN SCR MODEL IN BUGS

3125 Clearly if we somehow knew the value of N then we could fit this model directly
 3126 because, in that case, it is a special kind of logistic regression model - one with a
 3127 random effect, but that enters into the model in a peculiar fashion - and also with
 3128 a distribution (uniform) which we don’t usually think of as standard for random

3129 effects models. So our aim here is to analyze the known- N problem, using our
 3130 simulated data, as an incremental step in our progress toward fitting more generally
 3131 useful models.

3132 To begin, we use our simulator to grab a data set and then harvest the elements
 3133 of the resulting object for further analysis.

```
3134 data<-simSCR0.fn(discard0=FALSE,sd=2013)
3135 y<-data$Y
3136 traplocs<-data$traplocs
3137 nind<-nrow(y)
3138 X<-data$traplocs
3139 J<-nrow(X)
3140 y<-rbind(y,matrix(0,nrow=(100-nrow(y)),ncol=J ) )
3141 Xl<-data$xlim[1]
3142 Yl<-data$ylim[1]
3143 Xu<-data$xlim[2]
3144 Yu<-data$ylim[2]
```

3145 Note that we specify `discard0 = FALSE` so that we have a "complete" data set,
 3146 i.e., one with the all-zero encounter histories corresponding to uncaptured individ-
 3147 uals. Now, within an **R** session, we can create the **BUGS** model file and fit the
 3148 model using the following commands. This model describes the half-normal detec-
 3149 tion model but it would be trivial to modify that to various others including the
 3150 logistic described above. One consequence of using the half-normal is that we have
 3151 to constrain the encounter probability to be in $[0, 1]$ which we do here by defining
 3152 `alpha0` to be the logit of the intercept parameter `p0`. Note that the distance co-
 3153 variate is computed within the **BUGS** model specification given the matrix of trap
 3154 locations, `X`, which is provided to **WinBUGS** as data.

```
3155 cat("
3156 model {
3157   alpha0~dnorm(0,.1)
3158   logit(p0)<- alpha0
3159   theta~dnorm(0,.1)
3160   for(i in 1:N){
3161     s[i,1]~dunif(Xl,Xu)
3162     s[i,2]~dunif(Yl,Yu)
3163     for(j in 1:J){
3164       d[i,j]<- pow(pow(s[i,1]-X[j,1],2) + pow(s[i,2]-X[j,2],2),0.5)
3165       y[i,j] ~ dbin(p[i,j],K)
3166       p[i,j]<- p0*exp(- theta*d[i,j]*d[i,j])
3167     }
3168   }
3169 }
3170 ",file = "SCR0a.txt")
3171
```

Next we do a number of organizational activities including bundling the data for **WinBUGS**, defining some initial values, the parameters to monitor and some basic MCMC settings. We choose initial values for the activity centers **s** by generating uniform random numbers in the state-space but, for the observed individuals, we replace those values by each individual's mean trap coordinate for all encounters

```

3177 sst<-cbind(runif(nind,Xl,Xu),runif(nind,Yl,Yu)) # starting values for s
3178 for(i in 1:nind){
3179   if(sum(y[i,])==0) next
3180   sst[i,1]<- mean( X[y[i,]>0,1] )
3181   sst[i,2]<- mean( X[y[i,]>0,2] )
3182 }
3183
3184 data <- list (y=y,X=X,K=K,N=nind,J=J,Xl=Xl,Yl=Yl,Xu=Xu,Yu=Yu)
3185 inits <- function(){
3186   list (alpha0=rnorm(1,-4,.4),theta=runif(1,1,2),s=sst)
3187 }
3188
3189 library("R2WinBUGS")
3190 parameters <- c("alpha0","theta")
3191 nthin<-1
3192 nc<-3
3193 nb<-1000
3194 ni<-2000
3195 out <- bugs (data, inits, parameters, "SCROa.txt", n.thin=nthin,
3196   n.chains=nc, n.burnin=nb,n.iter=ni,debug=TRUE,working.dir=getwd())

```

There is little to say about the preceding basic operations other than to suggest that the interested reader explore the output and additional analyses by running the script provided in the **R** package **scrbook**. We ran 1000 burn-in and 1000 after burn-in, 3 chains, to obtain 3000 posterior samples. Because we know N for this particular data set we only have 2 parameters of the detection model to summarize (**alpha0** and **theta**). When the object **out** is produced we print a summary of the results as follows:

```

3204 > print(out,digits=3)
3205 Inference for Bugs model at "SCROa.txt", fit using WinBUGS,
3206 3 chains, each with 2000 iterations (first 1000 discarded)
3207 n.sims = 3000 iterations saved
3208
3209      mean      sd    2.5%    25%    50%    75%   97.5%  Rhat n.eff
3210 alpha0  -2.496  0.224  -2.954  -2.648  -2.48  -2.340  -2.091  1.013   190
3211 theta    2.442  0.419   1.638   2.145   2.44   2.721   3.303  1.005   530
3212 deviance 292.803 21.155 255.597 277.500 291.90 306.000 339.302 1.006   380
3213
3214 For each parameter, n.eff is a crude measure of effective sample size,
3215 and Rhat is the potential scale reduction factor (at convergence, Rhat=1).
3216
3217 DIC info (using the rule, pD = Dbar-Dhat)

```


3217 `pD = -138.8 and DIC = 154.0`
 3218 `DIC is an estimate of expected predictive error (lower deviance is better).`

3219 We know the data were generated with `alpha0 = -2.5` and `theta = -2`. The
 3220 estimates look reasonably close to those data-generating values and we probably feel
 3221 pretty good about the performance of the Bayesian analysis and MCMC algorithm
 3222 that WinBUGS cooked-up based on our sample size of 1 data set. It is worth noting
 3223 that the Rhat statistics indicate reasonable convergence but, as a practical matter,
 3224 we might choose to run the MCMC algorithm for additional time to bring these
 3225 closer to 1.0 and to increase the effective posterior sample size (`n.eff`). Other
 3226 summary output includes “deviance” and related things including the deviance
 3227 information criterion (DIC). We discuss these things in chapter XXXX.

4.6 UNKNOWN N

3228 In all real applications N is unknown and that fact is kind of an important feature
 3229 of the capture-recapture problem! We handled this important issue in chapter 3
 3230 using the method of data augmentation which we apply here to achieve a realistic
 3231 analysis of Model SCR0. As with the basic closed population models considered
 3232 previously, we formulate the problem here by augmenting our observed data set
 3233 with a number of “all zero” encounter histories - what we referred to in Chapter
 3234 3 as potential individuals. If n is the number of observed individuals, then let
 3235 $M - n$ be the number of potential individuals in the data set. For the basic y_{ij}
 3236 data structure (individuals x traps encounter frequencies) we simply add additional
 3237 rows of “all 0” observations to that data set. This is because such “individuals” are
 3238 unobserved, and therefore necessarily have $y_{ij} = 0$ for all j . A data set, say with 4
 3239 traps and 6 individuals, augmented with 4 pseudo-individuals therefore might look
 3240 like this:

	trap1	trap2	trap3	trap4
[1,]	1	0	0	0
[2,]	0	2	0	0
[3,]	0	0	0	1
[4,]	0	1	0	0
[5,]	0	0	1	1
[6,]	1	0	1	0
[7,]	0	0	0	0
[8,]	0	0	0	0
[9,]	0	0	0	0
[10,]	0	0	0	0

3252 We typically have more than 4 traps and, if we’re fortunate, many more indi-
 3253 viduals in our data set.

3254 For the augmented data, we introduce a set of binary latent variables (the data
 3255 augmentation variables), z_i , and the model is extended to describe $\Pr(z_i = 1)$
 3256 which is, in the context of this problem, the probability that an individual in the

augmented data set is a member of the population that was sampled. In other words, if $z_i = 1$ for one of the “all zero” encounter histories, this is implied to be a sampling zero whereas observations for which $z_i = 0$ are “structural zeros” under the model.

How big does the augmented data set have to be? We discussed this issue in chapt. 3 where we noted that the size of the data set is equivalent to the upper limit of a uniform prior distribution on N . Practically speaking, it should be sufficiently large so that the posterior distribution for N is not truncated. On the other hand, if it is too large then unnecessary calculations are being done. An approach to choosing M by trial-and-error is indicated. You can take a ballpark estimate of the probability that an individual is captured (at all during the study), obtain N as $n/pcap$, and then set $M = 2 * N$, as a first guess. Do a short MCMC run and then consider whether you need to do something different. See chapt. ?? for an example of this. Kery and Schaub (2011, ch. 6) provide an assessment of choosing M in closed population models.

Analysis by data augmentation removes N as an explicit parameter of the model. Instead, N is a derived parameter, computed by $N = \sum_{i=1}^M z_i$. Similarly, *density*, D , is also a derived parameter computed as $D = N/area(\mathcal{S})$. For our simulator, we’re using an 8×8 state-space and thus we will compute D as $D = N/64$.

4.6.1 Analysis using data augmentation in WinBUGS

As before we begin by obtaining a data set using our `simSCR0.fn` routine and then harvesting the required data objects from the resulting data list. Note that we use the `discard0=TRUE` option this time so that we get a “real” data set with no all-zero encounter histories. After harvesting the data we produce the **WinBUGS** model specification which now includes M encounter histories including the augmented potential individuals, the data augmentation parameters z_i , and the data augmentation parameter ψ .

```

data<-simSCR0.fn(discard0=TRUE,sd=2013)
y<-data$Y
traplocs<-data$traplocs
nind<-nrow(y)
X<-data$traplocs
J<-nrow(X)
Xl<-data$xlim[1]
Yl<-data$ylim[1]
Xu<-data$xlim[2]
Yu<-data$ylim[2]

cat("
model {
  alpha0~dnorm(0,.1)
  logit(p0)<- alpha0

```

```

3299 theta~dnorm(0,.1)
3300 psi~dunif(0,1)
3301
3302 for(i in 1:M){
3303   z[i] ~ dbern(psi)
3304   s[i,1]~dunif(Xl,Xu)
3305   s[i,2]~dunif(Yl,Yu)
3306   for(j in 1:J){
3307     d[i,j]<- pow(pow(s[i,1]-X[j,1],2) + pow(s[i,2]-X[j,2],2),0.5)
3308     y[i,j] ~ dbin(p[i,j],K)
3309     p[i,j]<- z[i]*p0*exp(- theta*d[i,j]*d[i,j])
3310   }
3311 }
3312 N<-sum(z[])
3313 D<-N/64
3314 }
3315 ",file = "SCR0a.txt")

```

3316 To prepare our data we have to augment the data matrix y with $M - n$ all-
 3317 zero encounter histories, we have to create starting values for the variables z_i and
 3318 also the activity centers s_i of which, for each, we require M values. Otherwise the
 3319 remainder of the code for bundling the data, creating initial values and executing
 3320 **WinBUGS** looks much the same as before except with more or differently named
 3321 arguments.

```

3322 ## Data augmentation stuff
3323 M<-200
3324 y<-rbind(y,matrix(0,nrow=M-nind,ncol=ncol(y)))
3325 z<-c(rep(1,nind),rep(0,M-nind))
3326
3327 sst<-cbind(runif(M,Xl,Xu),runif(M,Yl,Yu)) # starting values for s
3328 for(i in 1:nind){
3329   if(sum(y[i,])==0) next
3330   sst[i,1]<- mean( X[y[i,]>0,1] )
3331   sst[i,2]<- mean( X[y[i,]>0,2] )
3332 }
3333 data <- list (y=y,X=X,K=K,M=M,J=J,Xl=Xl,Yl=Yl,Xu=Xu,Yu=Yu)
3334 inits <- function(){
3335   list (alpha0=rnorm(1,-4,.4),theta=runif(1,1,2),s=sst,z=z)
3336 }
3337
3338 library("R2WinBUGS")
3339 parameters <- c("alpha0","theta","N")
3340 nthin<-1
3341 nc<-3
3342 nb<-1000
3343 ni<-2000

```

```

3344 out <- bugs (data, inits, parameters, "SCR0a.txt", n.thin=nthin,n.chains=nc,
3345   n.burnin=nb,n.iter=ni,debug=TRUE,working.dir=getwd())

```

3346 **Remarks:** (1) Note the differences in this new **WinBUGS** model with that
 3347 appearing in the known- N version. (2) Also the input data has changed - the
 3348 augmented data set has more rows of all-zeros. Previously we knew that $N = 100$
 3349 but in this analysis we pretend not to know N , but think that $N = 200$ is a good
 3350 upper-bound; (3) Population size $N(S)$ is a derived parameter, being computed by
 3351 summing up all of the data augmentation variables z_i (as we've done previously);
 3352 (4) Density, $D \equiv D(S)$, is also a derived parameter. Summarizing the output from
 3353 **WinBUGS** produces:

```

3354 > print(out1,digits=2)
3355 Inference for Bugs model at "SCR0a.txt", fit using WinBUGS,
3356   3 chains, each with 2000 iterations (first 1000 discarded)
3357   n.sims = 3000 iterations saved
3358
3358      mean    sd   2.5%   25%   50%   75%  97.5% Rhat n.eff
3359 alpha0  -2.57  0.23  -3.04  -2.72  -2.56  -2.41  -2.15  1.01   320
3360 theta    2.46  0.42   1.63   2.16   2.46   2.73   3.33  1.02   120
3361 N       113.62 15.73  86.00 102.00 113.00 124.00 147.00 1.01   260
3362 D        1.78  0.25   1.34   1.59   1.77   1.94   2.30  1.01   260
3363 deviance 302.60 23.67 261.19 285.47 301.50 317.90 354.91 1.00  1400
3364
3365 For each parameter, n.eff is a crude measure of effective sample size,
3366 and Rhat is the potential scale reduction factor (at convergence, Rhat=1).
3367
3368 DIC info (using the rule, pD = var(deviance)/2)
3369 pD = 279.9 and DIC = 582.5
3370 DIC is an estimate of expected predictive error (lower deviance is better).

```

3371 The column labeled “MC error” is the Monte Carlo error - the error inherent in
 3372 the attempt to compute these posterior summaries by MCMC. It is desirable to run
 3373 the Markov chain algorithm long enough so as to reduce the MC error to a tolerable
 3374 level. What constitutes tolerable is up to the investigator. Certainly less than 1% is
 3375 called for. As a general rule, Rhat gets closer to 1 and MC error decreases toward 0
 3376 as the number of iterations increases. We see that the estimated parameters (α_0 and
 3377 θ) are comparable to the previous results obtained for the known- N case, and also
 3378 not too different from the data-generating values. The posterior of N overlaps the
 3379 data-generating value substantially with a mean of 113.62. To obtain these results
 3380 we fitted the true data-generating model, that based on the half-normal detection
 3381 model, to a single simulated data set. For fun and excitement we fit the *wrong*
 3382 model - that with the logistic-linear detection model - to the same data set. This is
 3383 easily achieved by modifying the **WinBUGS** model specification above, although
 3384 we provide the **R** script in the **R** package **scrbook**. Those results are given below.
 3385 We see that the estimate of N , the main parameter of interest, is very similar to
 3386 that obtained under the correct model, convergence is worse (as measured by Rhat)
 3387 which probably doesn't have anything to do with the model being wrong, and the

posterior deviance and DIC favor the correct model. We consider the use of DIC for carrying-out model selection in chapter 8.

```

> print(out2,digits=2)
Inference for Bugs model at "SCR0a.txt", fit using WinBUGS,
  3 chains, each with 2000 iterations (first 1000 discarded)
  n.sims = 3000 iterations saved
      mean      sd    2.5%    25%    50%    75%   97.5%  Rhat  n.eff
alpha0  -1.59  0.27   -2.16  -1.77  -1.58  -1.42  -1.07  1.05    60
beta     3.77  0.43    2.92   3.48   3.79   4.05   4.66  1.04    70
N       122.57 18.67   90.00 109.00 122.00 135.00 163.00 1.00 3000
D        1.92  0.29    1.41   1.70   1.91   2.11   2.55  1.00 3000
deviance 312.67 22.43 271.00 297.20 311.50 327.00 359.60 1.02  130

For each parameter, n.eff is a crude measure of effective sample size,
and Rhat is the potential scale reduction factor (at convergence, Rhat=1).

DIC info (using the rule, pD = var(deviance)/2)
pD = 247.5 and DIC = 560.1
DIC is an estimate of expected predictive error (lower deviance is better).

```

4.6.2 Use of other BUGS engines: JAGS

There are two other popular **BUGS** engines in widespread use: **OpenBUGS** (Thomas et al., 2006) and **JAGS** (Plummer, 2003). Both of these are easily called from **R**. **OpenBUGS** can be used instead of **WinBUGS** by changing the package option in the bugs call to `package=OpenBUGS`. **JAGS** can be called using the function `jags()` in package **R2JAGS** which has nearly the same arguments as `bugs()`. We prefer to use the **R** library `rjags` (Plummer, 2009) which has a slightly different implementation that we demonstrate here as we reanalyze the simulated data set in the previous section (note: the same **R** commands are used to generate the data and package the data, inits and parameters to monitor). The function `jags.model` is used to initialize the model and run the MCMC algorithm for a period in which adaptive rejection (XXXX not sure XXXX???) sampling is used. Then the Markov chains are updated using `coda.samples()` to obtain posterior samples for analysis, as follows:

```

jm<- jags.model("SCR0a.txt", data=data, inits=inits, n.chains=nc,
               n.adapt=nb))
jm<- coda.samples(jm, parameters, n.iter=ni-nb, thin=nthin)

```

We find that JAGS seems to be 20-30% faster for the basic SCR model which the reader can evaluate using the script `jags.winbugs.R` in the **R** package `scrbook`.

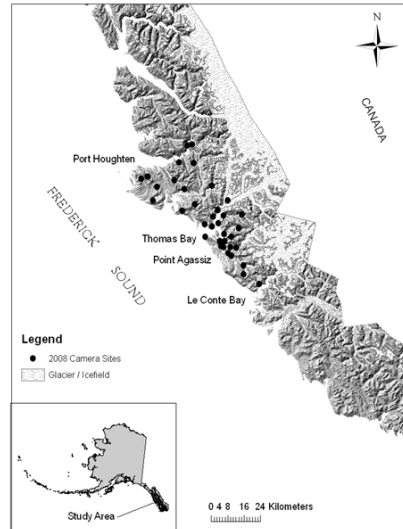


Figure 4.3. Wolverine camera trap locations from Magoun et al. (2011).

4.7 CASE STUDY: WOLVERINE CAMERA TRAPPING STUDY

We provide an analysis here of A. Magoun’s wolverine data (Magoun et al., 2011; Royle et al., 2011c). The study took place in SE Alaska (Fig. 4.3) where 37 cameras were operational for variable periods of time (min = 5 days, max = 108 days, median = 45 days). A consequence of this is that the binomial sample size K (see Eq. 4.2.1) is variable for each camera. Thus, we must provide a matrix of sample sizes as data to BUGS and modify the model specification in sec. 4.6 accordingly. Our treatment of the data here is based on the analysis of Royle et al. (2011c).

To carry-out an analysis of these data, we require the matrix of trap coordinates and the encounter history data. We store data in an the “scr flat format” (see sec. 4.4.1 above), an efficient file format which is easily manipulated and also used as the input file format in our custom **R** script (ch. xxx) and **SPACECAP** (Gopalaswamy, 2012). To illustrate this format, the wolverine data are available as an encounter data **R** object named “**wcaps**” which has 3 columns and 115 rows, each representing a unique encounter event including the trap identity, the individual identity and the sample occasion index (**sample**). The first 10 rows of this matrix are as follows:

```
> wcaps
      trapid individual sample
```

3445	[1,]	1	2	127
3446	[2,]	1	2	128
3447	[3,]	1	2	129
3448	[4,]	1	18	130
3449	[5,]	2	3	106
3450	[6,]	2	18	104
3451	[7,]	5	5	73
3452	[8,]	5	5	89
3453	[9,]	6	18	117
3454	[10,]	6	18	118

3455 This “encounter data file” contains 1 row for each unique individual/trap en-
 3456 counter, and 3 variables (columns): `trapid` is an integer that runs from `1:ntraps`,
 3457 individual runs from `1:nind` and sample runs from `1:nperiods`. Often (as the case
 3458 here) “sample” will correspond to daily sample intervals. The variable `trapid` will
 3459 have to correspond to the row of a matrix containing the trap coordinates - a file
 3460 named `traplocs.csv` available in the **R** package `scrbook`.

3461 Note that these data do not represent a completely informative summary of the
 3462 data. For example, if no individuals were captured in a certain trap or during a
 3463 certain period, then this compact data format will have no record. Thus we will
 3464 need to know `ntraps` and `nperiods` when reformatting this SCR data format into a
 3465 2-d encounter frequency matrix or 3-d array. In addition, the encounter data file
 3466 does not provide information about which periods each trap was operated. This
 3467 additional information is also necessary as the trap-specific sample sizes must be
 3468 passed to **BUGS** as data. We provide this information in a 2nd data file - which
 3469 we call the “trap deployment” file (described below).

3470 The “encounter data file” `wcaps.csv` exists in the **R** package `scrbook` as a .csv
 3471 file that people can read into **R** and do some basic summary statistics on. For our
 3472 purposes we need to convert these data into the “individual x trap” array of binary
 3473 encounter frequencies, although more general models might require an encounter-
 3474 history formulation of the model which requires a full 3-d array. To obtain our `nind`
 3475 x `ntrap` encounter frequency matrix, we do this the hard way by first converting the
 3476 encounter data file into a 3-d array and then summarize to trap totals. We have a
 3477 handy function `SCR23darray.fn` which takes the compact encounter data file with
 3478 optional arguments `ntraps` and `nperiods`, and converts it to a 3-d array, and then
 3479 we use the **R** function `apply` to summarize over the “sample” period dimension (by
 3480 convention here, this is the 2nd dimension):

```

3481 SCR23darray.fn <- function(caps,ntraps=NULL,nperiods=NULL){
3482   nind<-max(caps[,2])
3483   if(is.null(ntraps)) ntraps<-max(caps[,1])
3484   if(is.null(nperiods)) nperiods<- max(caps[,3])
3485
3486   y<-array(0,c(nind,nperiods,ntraps))
3487   tmp<-cbind(caps[,2],caps[,3],caps[,1])
3488   y[tmp]<-1

```

```

3489 y
3490 }
3491
3492 # for the wolverine data do this:
3493
3494 Y3d <-SCR23darray.fn(wcaps,ntraps=37,nperiods=165)
3495 y <- apply(y3d,c(1,3),sum)

```

If `ntraps` and `nperiods` are not specified then they are assumed to be equal to the maximum value provided in the encounter data file. The 3-d array is necessary to fit certain types of models (e.g., behavioral response) and this is why we sometimes will require this maximally informative 3-d data format.

The other data file that we must have is the “trap deployment” file (henceforth “traps file”) which provides the additional information not contained in the encounter data file. The traps file has `nperiods + 3` columns. The first column is assumed to be a trap identifier, columns 2 and 3 are the easting and northing coordinates (assumed to be in a Euclidean coordinate system), and columns 4 to (`nperiods + 3`) are binary indicators of whether each trap was operational in each time period. The first 5 rows (out of 37) and 10 columns (out of 168) of the traps file for the wolverine data (“`wtraps.csv`” in the **R** package `scrbook` are:

	Trap	Easting	Northing	1	2	3	4	5	6	7	<- column names
3508	1	39040	19216	0	0	0	0	0	0	0	
3509	2	41324	19772	1	1	1	1	1	1	1	
3510	3	44957	12985	0	0	0	0	0	0	0	
3511	4	41151	23220	0	0	0	0	0	0	0	
3512	5	44240	17198	0	0	0	0	0	0	0	

This tells us that trap 2 was operated in periods 1-7 but the other traps were not operational during those periods. To extract the relevant information to fit the model in **WinBUGS** we do this:

```

3517 traps<- read.csv("wtraps.csv")
3518 traplocs<- traps[,2:3]
3519 K<- apply(traps[,4:ncol(traps)],1,sum)

```

This results in a matrix `traplocs` which contains the coordinates of each trap and a vector `K` containing the number of days that each trap was operational. We now have all the information required to fit a basic SCR model in **WinBUGS**.

Summarizing these data files for the wolverine study, we see that 21 unique individuals were captured a total of 115 times. Most individuals were captured 1-6 times, with 4, 1, 4, 3, 1, and 2 individuals captured 1-6 times, respectively. In addition, 1 individual was captured each 8 and 14 times and 2 individuals each were captured 10 and 13 times. The number of unique traps that captured a particular individual ranged from 1-6, with 5, 10, 3, 1, 1, and 1 individual captured in each of 1-6 traps, respectively, for a total of 50 unique wolverine-trap encounters. These

numbers might be hard to get your mind around whereas some tabular summary is often more convenient. For that it seems natural to tabulate individuals by trap and total encounter frequencies. The spatial information in SCR data is based on multi-trap captures, and so, it is informative to understand how many unique traps each individual is captured in. At the same, it is useful to understand how many total captures we have of each individual because this is, in an intuitive sense, the effective sample size. So, we reproduce Table 1 from Royle et al. (2011c) which shows the trap and total encounter frequencies:

Table 4.1. Individual frequencies of capture for wolverines captured in camera traps in South-east Alaska in 2008. Rows index unique trap frequencies and columns represent total number of captures (e.g., we captured 4 individuals 1 time, necessarily in only 1 trap; we captured 3 individuals 3 times but in 2 different traps)

No. of traps	No. of captures									
	1	2	3	4	5	6	8	10	13	14
1	4	1	0	0	0	0	0	0	0	0
2	0	0	3	3	0	2	1	2	0	0
3	0	0	1	1	0	0	0	0	0	1
4	0	0	0	0	0	0	0	0	1	0
5	0	0	0	0	1	0	0	0	0	0
6	0	0	0	0	0	0	0	0	1	0

4.7.1 Fitting the model in WinBUGS

For illustrative purposes here we fit the simplest SCR model with the half-normal distance function although we revisit these data with more complex models in later chapters. The model is summarized by the following 3 components:

- (1) $y_{ij} | \mathbf{s}_i \sim \text{Bin}(K, z_i p_{ij})$
- (2) $p_{ij} = p_0 \exp(-\theta \|\mathbf{s}_i - x_j\|^2)$
- (3) $\mathbf{s}_i \sim \text{Unif}(\mathcal{S})$
- (4) $z_i \sim \text{Bern}(\psi)$

We assume customary flat priors on the structural (hyper-) parameters of the model, $\alpha_0 = \text{logit}(p_0)$, θ and ψ . It remains to define the state-space \mathcal{S} . For this, we nested the trap array (Fig. 4.3) in a rectangular state-space extending 20 km beyond the traps in each cardinal direction. We also considered larger state-spaces up to 50 km to evaluate that choice. The buffer of the state space should be larger enough so that individuals beyond the state-space boundary are not likely to be encountered. Thus some knowledge of typical space usage patterns of the species is useful. The coordinate system was scaled so that a unit distance was equal to 10km, producing a rectangular state-space of dimension 9.88x10.5 units ($\text{area} = 10374 \text{km}^2$) within which the trap array was nested. As a general rule, we recommend scaling the state-space so that it is defined near the origin $(x, y) = (0, 0)$. While the scaling of the

coordinate system is theoretically irrelevant, a poorly scaled coordinate system can produce Markov chains that mix poorly. We fitted this model in **WinBUGS** using data augmentation with $M = 300$ potential individuals, using 3 Markov chains each of 12000 total iterations, discarding the first 2000 as burn-in. [R commands for reading in the data and executing the analysis are as follows:

provide those commands here

The output follows (note, we have a parameter “sigma” which we discuss shortly):

```

3564 Buffer = 10 km
3565 > print(out1$out,digits=2)
3566 Inference for Bugs model at "modelfile.txt", fit using WinBUGS,
3567 3 chains, each with 12000 iterations (first 2000 discarded)
3568 n.sims = 30000 iterations saved
3569      mean    sd  2.5%   25%   50%   75%  97.5% Rhat n.eff
3570 psi      0.11 0.02  0.07  0.10  0.11  0.13  0.17   1  2400
3571 sigma    1.79 0.29  1.31  1.58  1.75  1.97  2.46   1   600
3572 p0       0.03 0.00  0.02  0.03  0.03  0.03  0.04   1 13000
3573 N       33.02 4.99 25.00 29.00 32.00 36.00 44.00   1  1600
3574 D       4.93 0.75  3.73  4.33  4.78  5.38  6.57   1  1600
3575 beta     0.17 0.05  0.08  0.13  0.16  0.20  0.29   1   600
3576 deviance 441.97 11.49 421.50 434.00 441.20 449.20 466.30   1  6600
3577
3578
3579 Buffer = 20 km
3580 > print(out2$out,digits=2)
3581 Inference for Bugs model at "modelfile.txt", fit using WinBUGS,
3582 3 chains, each with 12000 iterations (first 2000 discarded)
3583 n.sims = 30000 iterations saved
3584      mean    sd  2.5%   25%   50%   75%  97.5% Rhat n.eff
3585 psi      0.16 0.04  0.10  0.13  0.16  0.18  0.24   1  4200
3586 sigma    1.78 0.32  1.29  1.55  1.73  1.94  2.56   1 20000
3587 p0       0.03 0.00  0.02  0.03  0.03  0.03  0.04   1  3000
3588 N       47.40 9.19 32.00 41.00 46.00 53.00 68.00   1  5900
3589 D       4.57 0.89  3.08  3.95  4.43  5.11  6.55   1  5900
3590 beta     0.17 0.06  0.08  0.13  0.17  0.21  0.30   1 20000
3591 deviance 444.36 11.84 423.60 436.00 443.60 451.80 469.70   1  1800
3592
3593 Buffer = 25 km
3594 > print(out3$out,digits=2)
3595 Inference for Bugs model at "modelfile.txt", fit using WinBUGS,
3596 3 chains, each with 12000 iterations (first 2000 discarded)
3597 n.sims = 30000 iterations saved
3598      mean    sd  2.5%   25%   50%   75%  97.5% Rhat n.eff
3599 psi      0.19 0.04  0.11  0.16  0.19  0.22  0.29 1.00   790
3600 sigma    1.80 0.34  1.30  1.56  1.75  1.98  2.59 1.01   400

```

```

3601 p0      0.03 0.00 0.02 0.03 0.03 0.03 0.04 1.00 2800
3602 N      56.66 11.47 37.00 48.00 56.00 64.00 82.00 1.00 570
3603 D      4.53 0.92 2.96 3.84 4.48 5.11 6.55 1.00 570
3604 beta   0.17 0.06 0.07 0.13 0.16 0.20 0.30 1.01 400
3605 deviance 444.75 11.87 423.60 436.40 444.00 452.30 469.80 1.00 24000
3606
3607 Buffer = 30 km
3608 > print(out4$out,digits=2)
3609 Inference for Bugs model at "modelfile.txt", fit using WinBUGS,
3610 3 chains, each with 12000 iterations (first 2000 discarded)
3611 n.sims = 30000 iterations saved
3612      mean      sd  2.5%   25%   50%   75%  97.5% Rhat n.eff
3613 psi      0.23 0.05  0.14  0.19  0.22  0.26  0.34 1.00 1500
3614 sigma    1.79 0.34  1.29  1.55  1.73  1.97  2.58 1.01 560
3615 p0      0.03 0.00  0.02  0.03  0.03  0.03  0.04 1.00 30000
3616 N      67.39 14.12 43.00 57.00 66.00 76.00 98.00 1.00 1200
3617 D      4.54 0.95  2.90  3.84  4.44  5.12  6.60 1.00 1200
3618 beta    0.17 0.06  0.07  0.13  0.17  0.21  0.30 1.01 560
3619 deviance 444.58 11.83 423.60 436.40 443.80 452.20 469.90 1.00 4700
3620
3621 Buffer = 40 km (need to add this)
3622
3623
3624
3625 Buffer = 45 km
3626 > print(out7$out,digits=2)
3627 Inference for Bugs model at "modelfile.txt", fit using WinBUGS,
3628 3 chains, each with 12000 iterations (first 2000 discarded)
3629 n.sims = 30000 iterations saved
3630      mean      sd  2.5%   25%   50%   75%  97.5% Rhat n.eff
3631 psi      0.36 0.08  0.21  0.30  0.35  0.41  0.53 1 5000
3632 sigma    1.78 0.34  1.29  1.55  1.72  1.95  2.60 1 850
3633 p0      0.03 0.00  0.02  0.03  0.03  0.03  0.04 1 3600
3634 N      106.57 23.34 67.00 90.00 104.00 121.00 157.00 1 3400
3635 D      4.62 1.01  2.90  3.90  4.51  5.25  6.81 1 3400
3636 beta    0.17 0.06  0.07  0.13  0.17  0.21  0.30 1 850
3637 deviance 444.80 11.84 423.60 436.40 444.10 452.30 470.00 1 30000
3638
3639 Buffer = 50 km
3640 > print(out8$out,digits=2)
3641 Inference for Bugs model at "modelfile.txt", fit using WinBUGS,
3642 3 chains, each with 12000 iterations (first 2000 discarded)
3643 n.sims = 30000 iterations saved
3644      mean      sd  2.5%   25%   50%   75%  97.5% Rhat n.eff
3645 psi      0.40 0.09  0.23  0.33  0.39  0.45  0.60 1.01 1300
3646 sigma    1.82 0.48  1.30  1.56  1.74  1.97  2.68 1.05 200

```

3647	p0	0.03	0.00	0.02	0.03	0.03	0.03	0.04	1.00	5800
3648	N	118.47	26.81	71.00	100.00	117.00	135.00	176.00	1.01	1200
3649	D	4.52	1.02	2.71	3.82	4.46	5.15	6.72	1.01	1200
3650	beta	0.17	0.06	0.07	0.13	0.17	0.21	0.30	1.05	200
3651	deviance	444.84	11.90	423.90	436.50	444.10	452.20	470.30	1.00	500

3652 We see that the estimated density is roughly consistent as we increase the state-
3653 space buffer from 20 to 50 *km*. We do note that the data augmentation parameter
3654 ψ (and, correspondingly, N) increase with the size of the state space in accordance
3655 with the deterministic relationship $N = D * A$. However, density is constant more
3656 or less as we increase the size of the state-space beyond a certain point. For the 10
3657 *km* state-space buffer, we see a noticeable effect on the posterior distribution of D .
3658 This is not a bug but rather a feature. As we noted above, the state-space is part
3659 of the model.

3660 One thing we haven't talked about yet is that we can calibrate the desired size
3661 of the state-space by looking at the estimated home range radius of the species. For
3662 some models it is possible to convert the parameter θ directly into the home range
3663 radius (section XXX XYZ). For the half-normal model we interpret the half-normal
3664 scale parameter σ which is related to θ by $\theta = 1/(2\sigma^2)$ as the radius of a bivariate
3665 normal movement model.

3666 4.7.2 Conclusion of Analysis

3667 Our point estimate of wolverine density from this study of approximately 4.5 indi-
3668 viduals/1000 *km*² and a 95% posterior interval is around [2.7, 6.3]. Density is esti-
3669 mated imprecisely which might not be surprising given the low sample size ($n = 21$
3670 individuals!). This seems to be a basic feature of carnivore studies although it
3671 should not (in our view) preclude the study of their populations nor attempts to
3672 estimate density or vital rates.

3673 It is worth thinking about this model, and these estimates, computed under a
3674 rectangular state space roughly centered over the trapping array (Fig. 4.3). Does it
3675 make sense to define the state-space to include, for example, ocean? What are the
3676 possible consequences of this? What can we do about it? There's no reason at all
3677 that the state space has to be a regular polygon – we defined it as such here strictly
3678 for convenience and for ease of implementation in **WinBUGS** where it enables us
3679 to specify the prior for the activity centers as uniform priors for each coordinate.
3680 While it would be possible to define a more realistic state-space using some general
3681 polygon, it might take some effort to implement that in the **BUGS** language (see
3682 chapter XYZXYZ² for example of a simple case). Alternatively, we recommend
3683 using a discrete representation of the state-space – i.e., approximate \mathcal{S} by a grid of
3684 G points. We discuss this in the following section.

²raccoon example or something?

4.8 CONSTRUCTING DENSITY MAPS

One of the most useful aspects of SCR models is that they are parameterized in terms of individual locations - i.e., *where* each individual lives – and, thus, we can compute many useful or interesting summaries of the activity centers. For example, we can make a spatial density plot by tallying up the number of activity centers \mathbf{s}_i in boxes of arbitrary size and then producing a nice multi-color spatial plot of those which, we find, increases the acceptance probability of your manuscripts by a substantial amount. We discussed in chapter 2 the idea of estimating derived parameters from MCMC output. In SCR models, there are many derived parameters that are functions of the latent point locations $(\mathbf{s}_1, \dots, \mathbf{s}_N)$. In the present context, the number of individuals living in any well-defined polygon is a derived parameter. Specifically, let $B(x)$ indicate a box centered at x then

$$N(x) = \sum_i I(\mathbf{s}_i \in B(x))$$

is the population size of box $B(x)$, and $D(x) = N(x)/|B(x)|$ is the local density. These are just “derived parameters” (see chapter 2) which are estimated from MCMC output using the appropriate Monte Carlo average. One thing to be careful about, in the context of models in which N is unknown, is that, for each MCMC iteration m , we only tabulate those activity centers which correspond to individuals in the sampled population. i.e., for which the data augmentation variable $z_i = 1$. In this case, we take all of the output for MCMC iterations $m = 1, 2, \dots, \text{niter}$ and compute this summary:

$$N(x, m) = \sum_{z_{i,m}=1} I(s_{i,m} \in B(x))$$

Thus, $N(x, 1), N(x, 2), \dots$, is the Markov chain for parameter $N(x)$. In what follows we will provide a set of **R** commands for doing this calculations and making a basic image plot from the MCMC output.

Step 1: Define the center points of each box, $B(x)$, or point at which local density will be estimated:

```
xg<-seq(Xl,Xu,,50)
yg<-seq(Yl,Yu,,50)
```

Step 2: Extract the MCMC histories for the activity centers and the data augmentation variables. Note that these are each $N \times \text{niter}$ matrices:

```
Sxout<-out$sims.list$s[,1]
Syout<-out$sims.list$s[,2]
z<-out$sims.list$z
```

3716 **Step 3:** We associate each coordinate with the proper box using the **R** command
 3717 `cut()`. Note that we keep only the activity centers for which $z = 1$ (i.e., individuals
 3718 that belong to the population of size N):

```
3719 Sxout<-cut(Sxout[z==1],breaks=xg,include.lowest=TRUE)
3720 Syout<-cut(Syout[z==1],breaks=yg,include.lowest=TRUE)
```

3721 **Step 4:** Use the `table()` command to tally up how many activity centers are in
 3722 each $B(x)$:

```
3723 Dn<-table(Sxout,Syout)
```

3724 **Step 5:** Use the `image()` command to display the resulting matrix.

```
3725 image(xg,yg,Dn/nrow(z),col=terrain.colors(10))
```

3726 Praise the Lord! This map is somewhat useful or at least it looks pretty and will
 3727 facilitate the publication of your papers.

3728 It is worth emphasizing here that density maps will not usually appear uniform
 3729 despite that we have assumed that activity centers are uniformly distributed. This is
 3730 because the observed encounters of individuals provide direct information about the
 3731 location of the $i = 1, 2, \dots, n$ activity centers and thus their “estimated” locations
 3732 will be affected by the observations. In a limiting sense, were we to sample space
 3733 intensely enough, every individual would be captured a number of times and we
 3734 would have considerable information about all N point locations. Consequently,
 3735 the uniform prior would have almost no influence at all on the estimated density
 3736 surface in this limiting situation. Thus, in practice, the influence of the uniformity
 3737 assumption increases as the fraction of the population encountered decreases.

3738 **On the non-intuitiveness of `image()`** – the **R** function `image()` might not
 3739 be very intuitive to some – it plots $M[1, 1]$ in the lower left corner. If you want $M[]$
 3740 to be plotted “as you look at it” then $M[1, 1]$ should be in the upper left corner.
 3741 We have a function `rot()` which does that. If you do `image(rot(M))` then it puts
 3742 it on the monitor as if it was a map you were looking at. You can always specify
 3743 the x and y – labels explicitly as we did above.

3744 **Spatial dot plots** – Now here is a cruder version based on the “spatial
 3745 dot map” function `spatial.plot`. The useful functions in **R** are `image()` and
 3746 `image.scale()` which is a function we grabbed off the web somewhere. Use of
 3747 this function requires arguments of point locations and the resulting value to be
 3748 displayed. The function is defined and applied as follows:

```
3749 spatial.plot<- function(x,y){
3750   nc<-as.numeric(cut(y,20))
3751   plot(x,pch=" ")
3752   points(x,pch=20,col=topo.colors(20)[nc],cex=2)
3753   image.scale(y,col=topo.colors(20))
```

```

3754 }
3755 # To execute the function do this:
3756 spatial.plot(cbind(xg,yg), Dn/nrow(z))

```

3757 4.8.1 Example: Wolverine density map.

3758 We used the posterior output from the wolverine model fitted previous to compute
 3759 a relatively coarse version of a density map, using a 10×10 grid (Fig. 4.4) and
 3760 using a 30×30 grid (Fig. 4.5)³. In these figures density is expressed in units of
 3761 individuals per 1000 km^2 , while the area of the pixels is about 1037 km^2 and 115
 3762 km^2 , respectively. That calculation is based on⁴:

```

3763 > total.area<- (Yu-Yl)*(Xu-Xl)*1000
3764 > total.area/(10*10)
3765 [1] 1037.427
3766 > total.area/(30*30)
3767 [1] 115.2697

```

3768 A couple of things are worth noting: First is that as we move away from “where
 3769 the data live” - away from the trap array - we see that the density approaches
 3770 the mean density. This is a property of the estimator as long as the “detection
 3771 function” decreases sufficiently rapidly as a function of distance. Relatedly, it is
 3772 also a property of statistical smoothers such as splines, kernel smoothers, and re-
 3773 gression smoothers - predictions tend toward the global mean as the influence of
 3774 data diminishes. Another way to think of it is that it is a consequence of the prior
 3775 - which imposes uniformity, and as you get far away from the data, the predictions
 3776 tend to the prior. The other thing to note about this map is that density is not
 3777 0 over water (although the coastline is not shown). This might be perplexing to
 3778 some who are fairly certain that wolverines do not like water. However, there is
 3779 nothing about the model that recognizes water from non-water and so the model
 3780 predicts over water *as if* it were habitat similar to that within which the array is
 3781 nested. But, all of this is ok as far as estimating density goes and, furthermore, we
 3782 can compute valid estimates of N over any well-defined region which presumably
 3783 wouldn’t include water if we so choose.

4.9 DISCRETE STATE-SPACE

3784 The SCR model developed previously in this chapter assumes that individual activ-
 3785 ity centers are distributed uniformly over the prescribed state-space. Clearly this
 3786 will not always be a reasonable assumption. In chapter 11 we talk about developing

³Note: Not sure if we should use quantiles for color to make equal area slices. ??? Also should we use the same scale?

⁴This is wrong and needs fixed. Move decimal one place over. i.e., 100 instead of 1000.

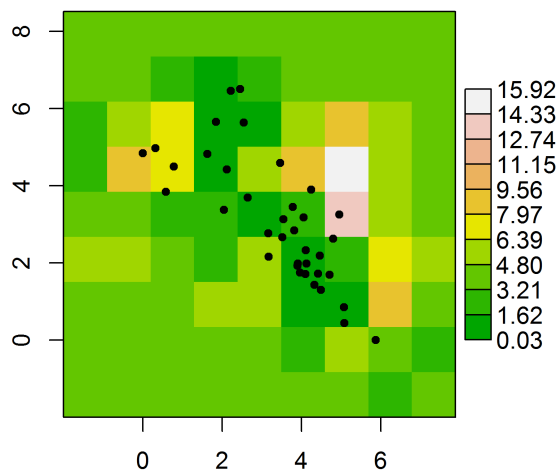


Figure 4.4. Needs a caption

models that allow explicitly for non-uniformity of the activity centers by modeling covariate effects on density. A simpler method of affecting the distribution of activity centers, which we address here, is to modify the shape of the state-space explicitly. For example, we might be able to classify the state-space into distinct blocks of habitat and non-habitat. In that case we can remove the non-habitat from the state-space and assume uniformity of the activity centers over the remaining portions judged to be suitable habitat. There are two ways to approach this: We can use a regular grid of points to represent the state-space, i.e., by the set of coordinates s_1, \dots, s_G , and assign a equal probabilities to each possible value, or we can retain the continuous formulation of the state-space but use basic polygon operations to induce constraints on the state-space We focus here on the formulation of our basic SCR model in terms of a discrete state-space but later on (chapter ?? and also Appendix XYZ) we demonstrate the latter approach based on using polygon operations to define an irregular state-space.

Use of a discrete state-space can be computationally expensive in **WinBUGS**. That said, it isn't too difficult to do the MCMC calculations in **R** which we discuss briefly in chapter ?. The **R** package **SPACECAP** (Gopalaswamy et al., 2011) arose from the **R** implementation developed for the application in Royle et al. (2009). As we will see in chapter 6, we must prescribe the state-space by a discrete mesh of points in order to do integrated likelihood and so if we are using a discrete

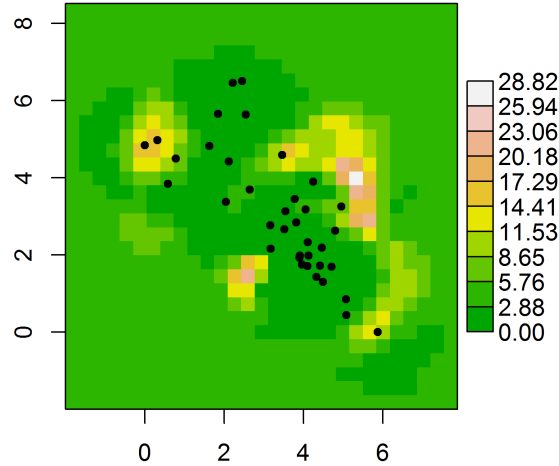


Figure 4.5. Needs a caption

state-space this can be accommodated directly in our code for obtaining MLEs.

While clipping out non-habitat seems like a good idea, its not obvious that we accomplish any biologically reasonable objective by doing so. We might prefer to do it when non-habitat represents a clear-cut restriction on the state-space such as a reserve boundary or a lake, ocean or river. It makes sense in those situations. Unfortunately, having the capability to do this also causes people to start defining “habitat” vs. “non-habitat” based on their understanding of the system whereas it can’t be known whether the animal being studied has the same understanding. Moreover, differentiating of the landscape by habitat or habitat quality probably affects the geometry and morphology of home ranges much more than the plausible locations of activity centers. That is, a home range centroid could, in actual fact, occur in a walmart parking lot if there is pretty good habitat around walmart, so there is probably no sense to cut out the walmart lot and preclude it as the location for an activity center. It would generally be better to include some definition of habitat quality in the model for the detection probability (see chapter XYZ).

4.9.1 Evaluation of Coarseness of Discrete Approximation

The coarseness of the state-space should not really have much of an effect on estimates if the grain is sufficiently fine relative to typical animal home range sizes.

Why is this? We have two analogies that can help us understand this. First is the relationship to Model M_h . As noted in section 4.3.4 above, we can think about SCR models as a type of finite mixture (Norris III and Pollock, 1996; Pledger, 2000) where we are fortunate to be able to obtain direct information about which “group” individuals belong to (group being location of activity center). In the standard finite mixture models we typically find that only 1 or a very small number of groups (e.g., 2 or 3 at the most) can explain really high levels of heterogeneity and are adequate for most data sets of small to moderate sample sizes. We therefore expect a similar effect in SCR models when we discretize the state-space. We can also think about discretizing the state-space as being related to numerical integration where we find (see chapter 6) that we don’t need a very fine grid of support points to evaluate the integral to a reasonable level of accuracy. We demonstrate this here by reanalyzing simulated data using a state-space defined by a different numbers of support points. We provide an R script called `simSCR0discrete.fn` in the R package `scrbook`. We note that for this comparison we generated the actual activity centers as a continuous random variable and thus the discrete state-space is, strictly speaking, an approximation to truth. That said, we regard all state-space specifications as approximations to truth because they are all, strictly speaking, models of some unknown truth. Thus the use of any specific discrete state-space is not intrinsically more “wrong” than any specific continuous representation.

We used **JAGS** from the `rjags` function to obtain the results for 6×6 , 9×9 , 12×12 , 15×15 , 20×20 , 25×25 and 30×30 state-space grids. We used 2000 burn, 12000 total iters with 3 chains, therefore a total of 30000 posterior samples. For **WinBUGS** we used 3 chains of 5k total with 1k burnin means 12k total posterior samples. Summary results for these analyses are shown in Table XYZ⁵.

Table XYZ.

		Mean	SD	NaiveSE	Time-seriesSE	runtime
6	N	109.7717	15.98959	0.0923160	0.377737	1239
9	N	114.4621	16.72025	0.0965344	0.468659	1267
12	N	115.4309	17.12403	0.098866	0.464830	1576
15	N	114.7699	17.0242	0.0982894	0.425238	1638
20	N	116.0370	17.10686	0.0987665	0.486867	1647
25	N	116.3228	16.98323	0.0980527	0.465527	1661
30	N	116.4252	17.4078	0.100504	0.533735	1806
WinBUGS						
		Mean	SD	NaiveSE	Time-seriesSE	runtime
6	N	111.67	16.61			2274
9	N	114.23	17.99			4300
12	N	115.98	17.38			7100
15	N	115.38	17.94			13010

⁵Andy to finish later

3866 Note: WinBUGS based on fewer samples too!

3867

3868 To get SE and time-series SE do this:

3869 You can use `as.mcmc.list()` to convert to a coda object. Then use `summary`.

3870 The results in terms of the posterior summaries are, as we expect, very similar
 3871 using **WinBUGS**. However, it was interesting to note that **WinBUGS** runtime is
 3872 much worse (note the number of iterations is lower for **WinBUGS** yet the runtime
 3873 is much longer) and, furthermore, it seems to scale with the size of the discrete
 3874 state-space grid. While that was expected, it was unexpected that the runtime of
 3875 **JAGS** would seem relatively consistent as we increase the grid size. We suspect
 3876 that **WinBUGS** is evaluating the full-conditional for each activity center at all
 3877 G possible values whereas it may be that **JAGS** is evaluating the full-conditional
 3878 only at a subset of values or perhaps using previous calculations more effectively.

3879 While this might suggest that one should always use **JAGS** for this analysis, we
 3880 found in our analysis of the wolverine (next section) that **JAGS** could be extremely
 3881 sensitive to starting values, producing MCMC algorithms that sometimes simply
 3882 did not work.

3883 4.9.2 Analysis of the wolverine camera trapping data

3884 We reanalyzed the wolverine data using discrete state-space grids with points spaced
 3885 by 2, 4 and 8 km (depicted in Fig. ??). These were constructed from the 40 km
 3886 buffered state-space, and deleting the points over water (see Royle et al., 2011c).
 3887 Our interest in doing this was to evaluate the relative influence of grid resolution
 3888 on estimated density because the coarser grids will be more efficient from a compu-
 3889 tational stand-point and so we would prefer to use them, but perhaps not if there
 3890 is a strong influence on estimated density.

3891 **Note:** Results from WinBUGS are given below based on short runs that took
 3892 a long long time. I am rerunning those. I will also show a density map for each
 3893 analysis.

3894 based on 2k burn 3k total and 3 chains = 3k total posterior samples.
 3895 lots of MC error here.

3896

3897 2km

3898 For each parameter, `n.eff` is a crude measure of effective sample size,
 3899 and `Rhat` is the potential scale reduction factor (at convergence, `Rhat=1`).

	mean	sd	2.5%	25%	50%	75%	97.5%	Rhat	n.eff
psi	0.28	0.06	0.17	0.24	0.27	0.32	0.41	1.01	230
sigma	0.64	0.05	0.55	0.60	0.64	0.67	0.73	1.02	88
lam0	-3.00	0.16	-3.33	-3.11	-3.00	-2.90	-2.69	1.04	52
p0	0.05	0.01	0.03	0.04	0.05	0.05	0.06	1.04	52
N	82.95	16.26	55.00	72.00	82.00	93.00	119.02	1.01	240

```

3906
3907 4 km
3908 For each parameter, n.eff is a crude measure of effective sample size,
3909 and Rhat is the potential scale reduction factor (at convergence, Rhat=1).
3910      mean      sd 2.5% 25% 50% 75% 97.5% Rhat n.eff
3911 psi    0.30 0.06 0.19 0.26 0.29 0.34 0.43 1.01 580
3912 sigma 0.62 0.05 0.54 0.59 0.62 0.65 0.72 1.00 2000
3913 lam0 -3.00 0.16 -3.33 -3.10 -2.99 -2.90 -2.67 1.01 390
3914 p0     0.05 0.01 0.03 0.04 0.05 0.05 0.06 1.01 390
3915 N      88.78 16.76 60.00 77.00 87.00 99.00 125.00 1.01 690
3916
3917 8km
3918 For each parameter, n.eff is a crude measure of effective sample size,
3919 and Rhat is the potential scale reduction factor (at convergence, Rhat=1).
3920      mean      sd 2.5% 25% 50% 75% 97.5% Rhat n.eff
3921 psi    0.27 0.06 0.17 0.23 0.27 0.31 0.40 1.00 1500
3922 sigma 0.69 0.05 0.60 0.65 0.68 0.72 0.80 1.00 3000
3923 lam0 -3.07 0.17 -3.41 -3.20 -3.07 -2.95 -2.74 1.01 210
3924 p0     0.04 0.01 0.03 0.04 0.04 0.05 0.06 1.01 200
3925 N      82.01 15.98 55.00 71.00 80.00 92.00 118.00 1.00 1300

```

3926 We did the analysis in JAGS also. The results are shown below. **Note:** I am
3927 going to run these again but for longer to finalize the results.

```

3928 2km
3929 Iterations = 7001:13000
3930 Thinning interval = 1
3931 Number of chains = 3
3932 Sample size per chain = 6000
3933
3934      Mean      SD Naive SE Time-series SE
3935 N      86.28522 16.950626 1.263e-01 0.4878973
3936 lam0    0.04807 0.007512 5.599e-05 0.0002199
3937 p0      0.04581 0.006820 5.083e-05 0.0001996
3938 psi     0.28904 0.062117 4.630e-04 0.0017481
3939 sigma   0.62769 0.043596 3.249e-04 0.0018724
3940
3941 4km
3942      Mean      SD Naive SE Time-series SE
3943 N      85.53139 16.998966 1.267e-01 0.5181297
3944 lam0    0.04636 0.007542 5.621e-05 0.0002382
3945 p0      0.04425 0.006867 5.118e-05 0.0002172
3946 psi     0.28650 0.061922 4.615e-04 0.0018276
3947 sigma   0.64281 0.048321 3.602e-04 0.0022911
3948
3949 8km
3950      Mean      SD Naive SE Time-series SE

```

3951	N	83.97039	16.508146	1.230e-01	0.4548782
3952	lam0	0.04519	0.006919	5.157e-05	0.0001738
3953	p0	0.04319	0.006319	4.710e-05	0.0001589
3954	psi	0.28146	0.060653	4.521e-04	0.0016555
3955	sigma	0.66956	0.040989	3.055e-04	0.0015070

3956 4.9.3 SCR models as multi-state models

3957 While we invoke a discrete state-space artificially, by gridding the underlying con-
 3958 tinuous state-space, sometimes the state-space is more naturally discrete. Consider
 3959 a situation in which discrete patches of habitat are searched using some method
 3960 and it might be convenient (or occur inadvertently) to associate samples to the
 3961 patch level instead of recording observation locations. In this case we might use a
 3962 model $\mathbf{s}_i \sim \text{dcat}(\text{probs}[])$ where $\text{probs}[]$ are the probabilities that an individual in-
 3963 habits a particular patch. We consider such a case study in chapter XXPoissonXXX
 3964 from Mollet et al. (2012) who obtained a population size estimate of a large grouse
 3965 species known as the capracaille. Forest patches were searched for scat which was
 3966 identified to individual by DNA analysis. Even when space is *not* naturally discrete,
 3967 measurements are often made at a fairly coarse grain (e.g., meters or tens of meters
 3968 along a stream), or associated with spatial quadrats for scat searches and therefore
 3969 the state-space may be effectively discrete in many situations.

3970 This discrete formulation of SCR models suggests that SCR models are related
 3971 to ordinary multi-state models (Kery and Schaub, 2011, ch. 9) which are also
 3972 parameterized in terms of a discrete state variable which is often defined as a
 3973 spatially-indexed state related either to location of capture or breeding location.
 3974 While many multi-state models exist in which the state variable is not related to
 3975 space, multi-state models have been extremely useful in development models of
 3976 movements among geographic states and indeed this type of problem motivated
 3977 their early developments by Arnason (1973, 1974) and Hestbeck (1991). We pursue
 3978 this connection a little bit more in chapter XXX XYZ.

4.10 SUMMARY AND OUTLOOK

3979 A point we tried to emphasize in this chapter is that the basic SCR model is not
 3980 much more than an ordinary capture-recapture model for closed populations – it
 3981 is simply that model but augmented with a set of “individual effects”, \mathbf{s}_i , which
 3982 relate encounter probability to some sense of individual location. SCR models are
 3983 therefore a type of individual covariate model (as introduced in chapter 7 – but
 3984 with imperfect information about the individual covariate. In other words, they
 3985 are GLMM type models when N is known or, when N is unknown, they are zero-
 3986 inflated GLMMs (see Royle (2006)). Another class of capture-recapture models
 3987 that SCR models are closely related to is so-called “Model M_h .” The effect of
 3988 introducing a spatial location for individuals is that it induces heterogeneity in

detection probability, as in Model M_h . However, unlike Model M_h , we obtain some information about the individual effect which is completely latent in Model M_h . If the state-space of the random effect \mathbf{s} is discrete then the SCR model resembles more closely the finite-mixture class of heterogeneity models (Norris III and Pollock, 1996) which parameterizes heterogeneity by assuming that individuals belong to discrete classes or groups (e.g., high, medium, low). In the context of SCR models we obtain some information about the “group membership” in the locations where individuals are captured. Given the direct relationship of SCR models with so many standard classes of models, we find that they are really quite easy to analyze using standard MCMC methods encased in black boxes such as **WinBUGS** or **JAGS** and possibly other packages. They are also easy to analyze using classical likelihood methods, which we address in chapter 6.

Formal consideration of the collection of individual locations $(\mathbf{s}_1, \dots, \mathbf{s}_N)$ in the model is fundamental to all of the models considered in this book. In statistical terminology, we think of the collection of points $\{\mathbf{s}_i\}$ as a realization of a point process and part of the promise, and ongoing challenge, of SCR models is to develop models that reflect interesting biological processes, for example interactions among points or temporal dynamics in point locations. Here we considered the simplest possible point process model - the points are independent and uniformly (“randomly”) distributed over space. Despite the simplicity of this assumption, it should suffice in many applications of SCR models although we do address generalizations of this model in later chapters. Moreover, even though the *prior* distribution on the point locations is uniform, the realized pattern may deviate markedly from uniformity as the observed encounter data provide information to impart deviations from uniformity. Thus, the estimated density map will typically appear distinctly non-uniform. As a general rule, information in the data will govern estimates of individual point locations so even fairly complex patterns of non-independence or non-uniformity will appear in the data. That is, we find in applications of the basic SCR model that this simple *a priori* model can effectively reflect or adapt to complex realizations of the underlying point process. For example, if individuals are highly territorial then the data should indicate this in the form of individuals not being encountered in the same trap - the resulting posterior distribution of point locations should therefore reflect non-independence. Obviously the complexity of posterior estimates of the point pattern will depend on the quantity of data, both number of individuals and captures per individual. Because the point process is such an integral component of SCR models, the state-space of the point process plays an important role in developing SCR models. As we tried to emphasize in this chapter, the choice of the state-space is part of the model. It can have an influence on parameter estimates and other inferences such as model selection (see chapter 8). We emphasize however that this is not an arbitrary decision like “buffering” because the model induces an explicit interpretation of parameters and statistical effect on estimators.

We showed how to conduct inference about the underlying point process includ-

ing calculation of density maps from posterior output. We can do other things we normally do with spatial point processes such as compute “K-functions” and test for “complete spatial randomness” (CSR) which we develop in chapter 8. Modifying and applying point process methods to SCR problems seems to us to be a fruitful area of research.

An obvious question that might be floating around in your mind is why should we ever go through all of this trouble when we could just use **MARK** or **CAPTURE** to get an estimate of N and apply 1/2 MMDM methods? The main reason is that these conventional methods are predicated on models that represent explicit misspecifications of both the observation and ecological process - they are wrong! Not just wrong, because of course all models are wrong, but they’re not even *plausible* models! Thus while we might be able to show adequate fit or whatever, we think as a conceptual and philosophical model one should not be using models that are not even plausible data-generating models – even if the plausible ones don’t fit! Perhaps more charitably, these ordinary non-spatial models are models of the wrong system. They do not account for trap identity. They don’t account for spatial organization or “clustering” of individual encounters in space. And, “density” is not a parameter of those models because density has no meaning absent an explicit representation of space. If we do define space explicitly, e.g., as a buffered minimum convex hull, then the normal models (M_0 , M_h , etc..) assume that individual capture-probability is not related to space, no matter how we define the buffer. Conversely, the SCR model is a model for trap-specific encounter data - how individuals are organized in space and interact with traps. SCR models provide a coherent framework for inference about density or population size and also, because of the formality of their derivation, can be extended and generalized to a large variety of different situations, as we demonstrate in subsequent chapters.

In the next few chapters we continue to work with this basic SCR design and model but consider some important extensions of the basic model. For example, we consider extensions to include covariates that vary by individual, trap, or over time (chapter 9), spatial covariates on density (chapter 11), open populations (chapter 12), model assessment and selection (chapter 8) and other topics. We also consider technical details of Bayesian (chapter ??) and maximum likelihood (chapter 6) estimation so that the interested reader can develop or extend their own methods to suit their needs.

5

4066

4067

4068

OTHER OBSERVATION MODELS

6

LIKELIHOOD ANALYSIS OF SPATIAL CAPTURE-RECAPTURE MODELS

In this book we mainly focus on Bayesian analysis of spatial capture-recapture models. And, in the previous chapters we learned how to fit some basic spatial capture-recapture models using a Bayesian formulation of the models analyzed in BUGS engines including **WinBUGS** and **JAGS**. Despite our focus on Bayesian analysis, it is instructive to develop the basic conceptual and methodological ideas behind classical analysis based on likelihood methods and frequentist inference. In fact, simple SCR models can be analyzed fairly easily using such methods. This has been the approach taken by Borchers and Efford (2008); Dawson and Efford (2009) and related papers.

This chapter provides some conceptual and technical footing for likelihood-based analysis of spatial capture-recapture models. We recognized earlier (chapt. 4) that SCR models are versions of binomial (or other) GLMs, but with random effects i.e., GLMMs. These models are routinely analyzed by likelihood methods. In particular, likelihood analysis is based on the integrated likelihood in which the random effects are removed by integration from the likelihood. In SCR models, the random effect, \mathbf{s} , i.e., the 2-dimensional coordinate, is a bivariate random effect.

In this chapter, we show that it is straightforward to compute the maximum likelihood estimates (MLE) for SCR models by integrated likelihood. We develop the MLE framework using **R**, and we also provide a basic introduction to an **R** package **secr** (Efford, 2011) which is based on the stand-alone package **DENSITY** (Efford et al., 2004). To set the context we analyze the SCR model here when N is known because, in that case, it is precisely a GLMM and does not pose any difficulty at all. We generalize the model to allow for unknown N using both conventional ideas based on the “joint likelihood” (e.g., Borchers et al., 2002) and also using

4097 a formulation based on data augmentation. We obtain the MLEs for the SCR
 4098 model from the wolverine camera trapping study (Magoun et al., 2011) analyzed
 4099 in previous chapters to compare/contrast the results.

6.1 LIKELIHOOD ANALYSIS

4100 We noted in chapter 4 that, with N known, the basic SCR model is a type of
 4101 binomial regression with a random effect. For such models we can easily obtain
 4102 maximum likelihood estimators of model parameters based on integrated likelihood.
 4103 The integrated likelihood is based on the marginal distribution of the data y in
 4104 which the random effects are removed by integration. Conceptually, our model is a
 4105 specification of the conditional-on- \mathbf{s} model $[y|\mathbf{s}, \theta]$ and we have a “prior distribution”
 4106 for \mathbf{s} , say $[\mathbf{s}]$, and the marginal distribution of the data y is

$$[y|\theta] = \int_{\mathbf{s}} [y|\mathbf{s}, \theta][\mathbf{s}]d\mathbf{s}.$$

4107 When viewed as a function of θ for purposes of estimation, the marginal distribu-
 4108 tion $[y|\theta]$ is often referred to as the *integrated likelihood*.

4109 It is worth analyzing the simplest SCR model with known- N in order to un-
 4110 derstand the underlying mechanics and basic concepts. These are directly relevant
 4111 to the manner in which many capture-recapture models are classically analyzed,
 4112 such as model Mh, and individual covariate models (see chapt. 7 and Royle and
 4113 Dorazio (2008, chapt. 6)). To develop integrated likelihood for SCR models, we
 4114 first identify the conditional likelihood.

4115 The observation model for each encounter observation y_{ij} , specified conditional
 4116 on \mathbf{s}_i , is

$$y_{ij}|\mathbf{s}_i \sim \text{Bin}(K, p_{\theta}(\mathbf{x}_j, \mathbf{s}_i)) \quad (6.1.1)$$

4117 where we have indicated the dependence of p_{ij} on \mathbf{s} and parameters θ explicitly.
 4118 For the random effect we have $\mathbf{s}_i \sim \text{Unif}(S)$. The joint distribution of the data
 4119 for individual i is the product of J such terms (i.e., contributions from each of J
 4120 traps).

$$[\mathbf{y}_i|\mathbf{s}_i, \theta] = \prod_{j=1}^J \text{Bin}(K, p_{\theta}(\mathbf{x}_j, \mathbf{s}_i))$$

4121 We note that this assumes that encounter of individual i in each trap is independent
 4122 of encounter in every other trap, conditional on \mathbf{s}_i , this is the fundamental property
 4123 of SCR0 or “multi-catch” traps.

4124 The so-called marginal likelihood is computed by removing \mathbf{s}_i , by integration
 4125 (hence also *integrated likelihood*), from the conditional-on- \mathbf{s} likelihood and regarding
 4126 the *marginal* distribution of the data as the likelihood. That is, we compute:

$$[y|\theta] = \int_S [\theta|\mathbf{y}_i|\mathbf{s}_i]g(\mathbf{s}_i)d\mathbf{s}_i$$

4127 In most SCR models, $g(\mathbf{s}) = 1/||\mathcal{S}||$ (but see chapt. 11).

4128 The joint likelihood for all N individuals, assuming independence of encounters
4129 among individuals, is the product of N such terms:

$$\mathcal{L}(\theta|\mathbf{y}_1, \mathbf{y}_2, \dots, \mathbf{y}_N) = \prod_{i=1}^N [\mathbf{y}_i|\theta]$$

4130 We emphasize that two independence assumptions are explicit in this development:
4131 independence of trap-specific encounters within individuals and also independence
4132 among individuals. In particular, this would only be valid when individuals are not
4133 physically restrained or removed upon capture, and when traps do not “fill up”.

4134 The key operation for computing the likelihood is solving a 2-dimensional inte-
4135 gration problem. There are some general purpose **R** packages that implement
4136 a number of multi-dimensional integration routines including **adapt** (Genz et al.,
4137 2007) and **R2cuba** (Hahn et al., 2011). In practice, we won’t rely on these extrane-
4138 ous **R** packages (except see chapt. 11 for an application of **Rcuba**) but instead will
4139 use perhaps less efficient methods in which we replace the integral with a summa-
4140 tion over an equal area mesh of points on the state-space \mathcal{S} and explicitly evaluate
4141 the integrand at each point. We invoke the rectangular rule for integration here¹
4142 in which we evaluate the integrand on a regular grid of points of equal area and
4143 compute the average of the integrand over that grid of points. Let $u = 1, 2, \dots, nG$
4144 index a grid of nG points, \mathbf{s}_u , where the area of grid cell u is constant, say A . In
4145 this case, the integrand, i.e., the marginal pmf of \mathbf{y}_i , is approximated by

$$[\mathbf{y}_i|\theta] = \frac{1}{nG} \sum_{u=1}^{nG} [\mathbf{y}_i|\mathbf{s}_u, \theta] \quad (6.1.2)$$

4146 This is a specific case of the general expression that could be used for approxi-
4147 mating the integral for any arbitrary (bivariate or otherwise) distribution $g(\mathbf{s})$. The
4148 general case is

$$[y] = \frac{A}{nG} \sum_u [y|\mathbf{s}_u][\mathbf{s}_u]$$

4149 In the present context it happens that $[\mathbf{s}] = (1/A)$ and thus the grid-cell area
4150 cancels in the above expression to yield eq. 6.1.2, but we commonly apply this in
4151 the context of normal prior distributions, as we did for likelihood analysis of Model
4152 M_h in sec. 3.4). The rectangular rule for integration can be seen as an application
4153 of the Law of Total Probability for a discrete random variable \mathbf{s} , having nG unique
4154 values with equal probabilities $1/nG$.

¹e.g., http://en.wikipedia.org/wiki/Rectangle_method

6.1.1 Implementation (simulated data)

Here we will illustrate how to carryout this integration and optimization based on the integrated likelihood using simulated data (i.e., following that from Chapter 4). Using `simSCRO.fn` we simulate data for 100 individuals and a 25 trap array layed out in a 5×5 grid of unit spacing. The specific encounter model is the half-normal model. The 100 activity centers were simulated on a state-space defined by a 8×8 square within which the trap array was centered (thus the trap array is buffered by 2 units). Therefore, the density of individuals in this system is fixed at $100/64$.

In the following set of R commands we generate the data and then harvest the required data objects:

```

4165 data<-simSCRO.fn(discard0=FALSE,sd=2013)
4166 y<-data$Y
4167 traplocs<-data$traplocs
4168 nind<-nrow(y)
4169 X<-data$traplocs
4170 J<-nrow(X)
4171 K<-data$K
4172 Xl<-data$xlim[1]
4173 Yl<-data$ylim[1]
4174 Xu<-data$xlim[2]
4175 Yu<-data$ylim[2]

```

Now we need to define the integration grid, say **G**, which we do with the following set of **R** commands (here, `delta` is the grid spacing):

```

4178 delta<- .2
4179 xg<-seq(Xl+delta/2,Xu-delta/2,by=delta)
4180 yg<-seq(Yl+delta/2,Yu-delta/2,by=delta)
4181 npix<-length(xg)      # assumes xg and yg same dimension here
4182 area<- (Xu-Xl)*(Yu-Yl)/((npix)*(npix)) # dont need area for anything
4183 G<-cbind(rep(xg,npix),sort(rep(yg,npix)))
4184 nG<-nrow(G)

```

In this case, the integration grid is set up as a grid with spacing $\delta = 0.2$ which produces a 40×40 grid of points for evaluating the integrand if the state-space buffer is set at 2.

We next create an **R** function that defines the likelihood as a function of the data objects *y* and *X* which were created above but, in general, you would read these files into **R**, e.g., from a .csv file. In addition to these data objects, we need to have defined the quantities *G* and *nG* associated with the integration grid. However, instead of worrying about making all of these objects and keeping track of them we just put that code above into the likelihood function and pass δ as an additional (optional) argument and a few other things that we need such as the

boundary of the state-space over which the integration (summation) is being done. Here is one reasonably useful variation of a function for estimation based on the integrated likelihood:

```

4198 intlik1<-function(parm,y=y,delta=.2,X=traplocs,ssbuffer=2){
4199
4200   Xl<-min(X[,1]) - ssbuffer
4201   Xu<-max(X[,1]) + ssbuffer
4202   Yu<-max(X[,2]) + ssbuffer
4203   Yl<-min(X[,2]) - ssbuffer
4204
4205   xg<-seq(Xl+delta/2,Xu-delta/2,,length=npix)
4206   yg<-seq(Yl+delta/2,Yu-delta/2,,length=npix)
4207   npix<-length(xg)
4208
4209   G<-cbind(rep(xg,npix),sort(rep(yg,npix)))
4210   nG<-nrow(G)
4211   D<- e2dist(X,G)
4212
4213   alpha<-parm[1]
4214   theta<-parm[2]
4215   probcap<- plogis(alpha)*exp(-theta*D*D)
4216   Pm<-matrix(NA,nrow=nrow(probcap),ncol=ncol(probcap))
4217   # all zero encounter histories
4218   n0<-sum(apply(y,1,sum)==0)
4219   # encounter histories with at least 1 detection
4220   ymat<-y[apply(y,1,sum)>0,]
4221   ymat<-rbind(ymat,rep(0,ncol(ymat)))
4222   lik.marg<-rep(NA,nrow(ymat))
4223   for(i in 1:nrow(ymat)){
4224     Pm[1:length(Pm)]<- (dbinom(rep(ymat[i,],nG),K,probcap[1:length(Pm)],log=TRUE))
4225     lik.cond<- exp(colSums(Pm))
4226     lik.marg[i]<- sum( lik.cond*(1/nG))
4227   }
4228   nv<-c(rep(1,length(lik.marg)-1),n0)
4229   -1*( sum(nv*log(lik.marg)) )
4230 }

```

The function accepts as input the encounter history matrix, y , the trap locations, X , and the state-space buffer. This allows us to vary the state-space buffer and easily evaluate the sensitivity of the MLE to the size of the state-space. Note that we have a peculiar handling of the encounter history matrix y . In particular, we remove the all-zero encounter histories from the matrix and tack-on a single all-zero encounter history as the last row which then gets weighted by the number of such encounter histories ($n0$). This is a bit long-winded and strictly unnecessary when N is known, but we did it this way because the extension to the unknown- N case

is now transparent (as we demonstrate in the following section). The matrix Pm holds the log-likelihood contributions of each encounter frequency for each possible state-space location of the individual. The log contributions are summed up and the result exponentiated on the next line, producing `lik.cond`, the conditional-on-s likelihood (Eq. 6.1.1 above). The marginal likelihood (`lik.marg`) sums up the conditional elements weighted by $\Pr(\mathbf{s})$ (Eq. 6.1.2 above). This is a fairly primitive function which doesn't allow much flexibility in the data structure. For example, it assumes that K , the number of replicates, is constant for each trap. Further, it assumes that the state-space is a square. We generalize this to some extent later in this chapter.

Here is the **R** command for maximizing the likelihood and saving the results into an object called `frog`. The output is a list of the following structure and these specific estimates are produced using the simulated data set:

```
# should take 15-30 seconds
> starting.values <- c(-2, 2)
> frog<-nlm(intlik1,starting.values,y=y,delta=.1,X=traplocs,ssbuffer=2,hessian=TRUE)
> frog

$minimum
[1] 297.1896

$estimate
[1] -2.504824  2.373343

$gradient
[1] -2.069654e-05  1.968754e-05

$hessian
      [,1]      [,2]
[1,] 48.67898 -19.25750
[2,] -19.25750 13.34114

$code
[1] 1

$iterations
[1] 11
```

Details about this output can be found on the help page for `nlm`. We note briefly that `frog$minimum` is the negative log-likelihood value at the MLEs, which are stored in the `frog$estimate` component of the list. The hessian is the observed Fisher information matrix, which can be inverted to obtain the variance-covariance matrix using the commands:


```
4282 > solve(frog$hessian)
```

4283 It is worth drawing attention to the fact that the estimates are different than
 4284 the Bayesian estimates reported previously in chapt. ???. How can that be?! There
 4285 are several reasons for this. First Bayesian inference is based on the posterior
 4286 distribution and it is not generally the case that the MLE should correspond to any
 4287 particular value of the posterior distribution. If the prior distributions in a Bayesian
 4288 analysis are uniform, then the (multivariate) mode of the posterior is the MLE,
 4289 but note that Bayesians almost always report posterior *means* and so there will
 4290 typically be a discrepancy there. Secondly, we have implemented an approximation
 4291 to the integral here and there might be a slight bit of error induced by that. We
 4292 will evaluate that shortly. Third, the Bayesian analysis by MCMC is subject to
 4293 some amount of Monte Carlo error which the analyst should always be aware of
 4294 in practical situations. All of these different explanations are likely responsible for
 4295 some of the discrepancy. Accounting for these, we see general consistency between
 4296 the two estimates.

4297 To compute the integrated likelihood we used a discrete representation of the
 4298 state-space so that the integral could be approximated as a summation over possible
 4299 values of \mathbf{s} with each value being weighted by its probability of occurring, which
 4300 is $1/nG$ under the assumption that \mathbf{s} is uniform on the state-space \mathcal{S} . Recall in
 4301 chapt. ??? we used a discrete state-space in developing a Bayesian analysis of the
 4302 model in order to be able to modify the state-space in a flexible manner. In that
 4303 case, we could use the discretized state-space as the integration grid and just feed
 4304 it into our integrated likelihood routine.

4305 In summary, we note that, for the basic SCR model, integrated likelihood is
 4306 a really easy calculation when N is known. Even for N unknown it is not too
 4307 difficult, and we will do that shortly. However, if you can solve the known- N
 4308 problem then you should be able to do a real analysis, for example by considering
 4309 different values of N and computing the results for each value and then making a
 4310 plot of the log-likelihood or AIC and choosing the value of N that produces the
 4311 best log likelihood or AIC. As a homework problem we suggest that the reader take
 4312 the code given above and try to estimate N without modifying the code by just
 4313 repeatedly calling that code for different values of N and trying to deduce the best
 4314 value. Nevertheless, we will formalize the unknown- N problem shortly.

4315 The software package **DENSITY** (Efford et al., 2004) implements certain types
 4316 of SCR models using integrated likelihood methods. **DENSITY** has been made
 4317 into an **R** package called **secr** (Efford, 2011) and we provide an analysis of some
 4318 data using **secr** shortly along with a discussion of its capabilities.

6.2 MLE WHEN N IS UNKNOWN

4319 Here we build on the previous introduction to integrated likelihood but we consider
 4320 now the case in which N is unknown. We will see that adapting the analysis based

on the N -known model is really straightforward for the more general problem. The main distinction is that we don't observe the all-zero encounter history so we have to make sure we compute the probability for that encounter history which we do by tacking a row of zeros onto the encounter history matrix. In addition, we include the number of such all-zero encounter histories as an unknown parameter of the model. Call that unknown quantity n_0 . In addition, we have to be sure to include a combinatorial term to account for the fact that of the n observed individuals there are $\binom{N}{n}$ ways to realize a sample of size n . The combinatorial term involves the unknown n_0 and thus it must be included in the likelihood.

Operationally then, things proceed much as before: We compute the marginal probability of each observed \mathbf{y}_i , i.e., by removing the latent \mathbf{s}_i by integration. In addition, we compute the marginal probability of the “all-zero” encounter history \mathbf{y}_{n+1} , and make sure to weight it n_0 times. We accomplish this by “padding” the data set with a single encounter history having $y_{n+1,j} = 0$ for all traps $j = 1, 2, \dots, J$. Then we be sure to include the combinatorial term in the likelihood or log-likelihood computation. We demonstrate this shortly.

To analyze a specific case, we'll read in our fake data set (simulated using the parameters given above). To set some things up in our workspace we do this:

```
data<-simSCR0.fn(discard0=TRUE,sd=2013)
y<-data$Y
nind<-nrow(y)
X<-data$traplocs
J<-nrow(X)
K<-data$K
Xl<-data$xlim[1]
Yl<-data$ylim[1]
Xu<-data$xlim[2]
Yu<-data$ylim[2]
```

Recall that these data were generated with $N = 100$, on an 8×8 unit state-space representing the trap locations (\mathbf{X}) buffered by 2 units. As before, the likelihood is defined in the **R** workspace as an **R** function which takes an argument being the unknown parameters of the model and additional arguments as prescribed. In particular, we provide the encounter history matrix \mathbf{y} , the trap locations `traplocs`, the spacing of the integration grid (δ) and the state-space buffer. Here is the new likelihood function:

```
intlik2<-function(parm,y=y,delta=.3,X=traplocs,ssbuffer=2){
  Xl<-min(X[,1]) -ssbuffer
  Xu<-max(X[,1])+ ssbuffer
  Yu<-max(X[,2])+ ssbuffer
  Yl<-min(X[,2])- ssbuffer
```

```

4362
4363 #delta<- (Xu-Xl)/npix
4364 xg<-seq(Xl+delta/2,Xu-delta/2,delta)
4365 yg<-seq(Yl+delta/2,Yu-delta/2,delta)
4366 npix.x<-length(xg)
4367 npix.y<-length(yg)
4368 area<- (Xu-Xl)*(Yu-Yl)/((npix.x)*(npix.y))
4369 G<-cbind(rep(xg,npix.y),sort(rep(yg,npix.x)))
4370 nG<-nrow(G)
4371 D<- e2dist(X,G)
4372
4373 alpha<-parm[1]
4374 theta<-parm[2]
4375 n0<-exp(parm[3])
4376 probcap<- plogis(alpha)*exp(-theta*D*D)
4377 Pm<-matrix(NA,nrow=nrow(probcap),ncol=ncol(probcap))
4378 ymat<-rbind(y,rep(0,ncol(y)))
4379
4380 lik.marg<-rep(NA,nrow(ymat))
4381 for(i in 1:nrow(ymat)){
4382   Pm[1:length(Pm)]<- (dbinom(rep(ymat[i,],nG),K,probcap[1:length(Pm)],log=TRUE))
4383   lik.cond<- exp(colSums(Pm))
4384   lik.marg[i]<- sum( lik.cond*(1/nG) )
4385 }
4386 nv<-c(rep(1,length(lik.marg)-1),n0)
4387 part1<- lgamma(nrow(y)+n0+1) - lgamma(n0+1)
4388 part2<- sum(nv*log(lik.marg))
4389 -1*(part1+ part2)
4390 }

```

4391 To execute this function for the data that we created with `simSCRO.fn`, we
 4392 execute the following command (saving the result in our friend `frog`). This re-
 4393 sults in the usual output, including the parameter estimates, the gradient, and the
 4394 numerical Hessian which is useful for obtaining asymptotic standard errors (see
 4395 below):

```

4396 > frog<-nlm(intlik2,c(-2.5,2,log(4)),hessian=TRUE,y=y,X=X,delta=.2,ssbuffer=2)
4397 There were 50 or more warnings (use warnings() to see the first 50)
4398 >
4399 >
4400 > frog
4401 $minimum
4402 [1] 113.5004
4403

```

```

4404 $estimate
4405 [1] -2.538334  2.466515  4.232810
4406
4407 [. Additional output deleted .]

```

While this produces some **R** warnings, these happen to be harmless in this case, and we will see from the **nlm** output that the algorithm performed satisfactory in minimizing the objective function. The estimate of population size for the state-space (using the default state-space buffer) is

```

4412 > nrow(y)+exp(4.2328)
4413 [1] 110.9099

```

Which differs from the data-generating value ($N = 100$) as we might expect. We usually will present an estimate of uncertainty associated with this MLE which we can obtain by inverting the Hessian. Note that $Var(\hat{N}) = n + Var(\hat{n}_0)$. Since we have parameterized the model in terms of $\log(n_0)$ we use a delta approximation to obtain the variance on the scale of n_0 as follows:

```

4419 > (exp(4.2328)^2)*solve(frog$hessian)[3,3]
4420 [1] 260.2033
4421 > sqrt(260)
4422 [1] 16.12452

```

Therefore, the asymptotic “Wald-type” confidence interval for N is $110.91 + / - 1.96 \times 16.125 = (79.305, 142.515)$. To report this in terms of density, we scale appropriately by the area of the prescribed state-space which is 64 units of area (i.e., an 8×8 square).

6.2.1 Exercises

1. Run the analysis with different state-space buffers and comment on the result.
2. Conduct a brief simulation study using this code by simulating 100 data sets and obtain the MLEs for each data set. Do things seem to be working as you expect?
3. Further extensions: It should be straightforward to generalize the integrated likelihood function to accommodate many different situations. For examples, if we want to include more covariates in the model we can just add stuff to the object **probcap**, and add the relevant parameters to the argument that gets passed to the main function. For the simulated data, make up a covariate by generating a Bernoulli covariate (“trap type” perhaps baited or not baited) randomly and try to modify the likelihood to accommodate that.
4. We would probably be interested in devising the integrated likelihood for the full 3-d encounter history array so that we could include temporally varying covariates. This is not difficult but naturally will slow down the execution substantially. The interested reader should try to expand the capabilities of this basic **R** function.

4442 6.2.2 Integrated Likelihood using the model under data augmentation

4443 Note that this likelihood analysis is based on the standard likelihood in which N
 4444 (or n_0) is an explicit parameter. This is usually called the “joint likelihood” or
 4445 “unconditional likelihood”. We could also express the joint likelihood using data
 4446 augmentation, replacing the parameter N with ψ (e.g., see sec. 7.1.6 Royle and
 4447 Dorazio, 2008, for an example). We don’t go into detail here, but we note that the
 4448 likelihood under data augmentation is a zero-inflated binomial mixture precisely
 4449 an occupancy type model (Royle, 2006). Thus, while it is possible to carryout
 4450 likelihood analysis of models under data augmentation, we primarily advocate data
 4451 augmentation for Bayesian analysis.

4452 6.2.3 Extensions

4453 We have only considered basic SCR models with no additional covariates. However,
 4454 in practice, we are interested in other types of covariate effects including “behavioral
 4455 response”, sex-specificity of parameters, and potentially other effects. Some of these
 4456 can be added directly to the likelihood if the covariate is fixed and known for all
 4457 individuals captured or not. An example is a behavioral response, which amounts
 4458 to having a covariate $x_{ik} = 1$ if individual i was captured prior to occasion k and
 4459 $x_{ik} = 0$ otherwise. For uncaptured individuals, $x_{ik} = 0$ for all k . Royle et al.
 4460 (2011c) called this a global behavioral response because the covariate is defined
 4461 for all traps, no matter the trap in which an individual was captured. We could
 4462 also define a *local* behavioral response which occurs at the level of the trap, i.e.,
 4463 $x_{ijk} = 1$ if individual i was captured in trap j prior to occasion k , etc.. Trap-
 4464 specific covariates such as trap type or status, or time-specific covariates such as
 4465 date, are easily accommodated as well. As an example, Kéry et al. (2010) develop
 4466 a model for the European wildcat in which traps are either baited or not (a trap-
 4467 specific covariate with only 2 values), and also encounter probability varies over time
 4468 in the form of a quadratic seasonal response. We consider models with behavioral
 4469 response or fixed covariates in chapter XXXX, although the integrated likelihood
 4470 routines we provided above can be modified directly for such cases, which we leave
 4471 to the interested reader.

4472 Sex-specificity is more difficult to deal with since sex is not known for uncaptured
 4473 individuals (and sometimes not even for all captured individuals). To analyze
 4474 such models, we do Bayesian analysis of the joint likelihood facilitated by the use of
 4475 data augmentation (Gardner et al., 2010; R.E. et al., 2012). For covariates that are
 4476 not fixed and known for all individuals, it is somewhat more challenging to do MLE
 4477 for these based on the joint likelihood as we have developed above. Instead it is
 4478 more conventional to use what is colloquially referred to as the “Huggins-Alho” type
 4479 model which is one of the approaches taken in the software package `secr` (Efford,
 4480 2011, see sec. 6.5). This idea is motivated by thinking about unequal probability
 4481 sampling methods known as Horvitz-Thompson sampling (e.g., see Overton and

4482 Stehman, 1995). We don't use that method anywhere in this book because it rep-
 4483 represents a paradigm shift in the inference framework which is done historically only
 4484 for convenience (i.e., ease of constructing an estimator) and not for philosophical
 4485 or theoretical reasons.

6.3 CLASSICAL MODEL SELECTION AND ASSESSMENT

4486 In most analyses, one is interested in choosing from among various potential mod-
 4487 els. A good thing about classical analysis based on likelihood is we can apply AIC
 4488 methods without difficulty (Burnham and Anderson, 2002). There are two distinct
 4489 contexts for model-selection that we think are relevant to SCR models. First is se-
 4490 lecting among models that represent distinct biological hypotheses (e.g., covariates
 4491 affecting encounter probability or density), and AIC is convenient for assessing the
 4492 relative merits of these different models although if there are only a few models
 4493 it is not objectionable to use hypothesis tests or confidence intervals to determine
 4494 importance of effects. The second context is selecting among various detection func-
 4495 tions. Indeed, when distance is used as a covariate (e.g., distance sampling), AIC
 4496 is usually applied to some large and arbitrary selection of distance functions with
 4497 no biological motivation. As a general rule, we don't recommend this given there
 4498 is hardly ever (if at all) a rational subject-matter based reason motivating specific
 4499 distance functions. As a result, we believe that doing too much model selection
 4500 will invariably lead to over-fitting and thus over-statement of precision. This is the
 4501 main reason that we haven't loaded you down with a basket of models for detection
 4502 probability so far, although we discuss many possibilities in chapter XYZ.

4503 Goodness-of-fit: For many standard capture-recapture models, it is possible to
 4504 identify goodness-of-fit statistics based on the multinomial likelihood and evaluate
 4505 model adequacy using formal statistical tests. Similar strategies can be applied
 4506 to SCR models using expected cell-frequencies based on the marginal distribution
 4507 of the observations. Also, because computing MLEs is somewhat more efficient in
 4508 many cases compared to Bayesian analysis, it is also sometimes easy to use boot-
 4509 strap methods². Bayesian goodness-of-fit is almost always addressed with Bayesian
 4510 p-values or some other posterior predictive check (chapter 2 REF XXX and see
 4511 chapter 8). Royle et al. (2011b) suggested checking model fit by decomposing
 4512 fit into two components: an evaluation of the encounter process model based on
 4513 expected encounter frequencies computed *conditional* on **s**, and then independent
 4514 evaluation of the "spatial randomness" hypothesis. We discuss this in chapter 8.

6.4 LIKELIHOOD ANALYSIS OF THE WOLVERINE CAMERA TRAPPING DATA

4515 ANDY STOPPED HERE

²I could use some references in the context of SCR models for this stuff

Here we compute the MLEs for the wolverine data using an expanded version of the function we developed in the previous section. To accommodate that each trap might be operational a variable number of nights, we provided an additional argument to the likelihood function (allowing for a vector K), which requires also a modification to the construction of the likelihood. In addition, we had to accommodate that the state-space is a general rectangle, and we included a line in the code to compute the state-space area which we apply below for computing density. The more general function (`intlik3`) is given in the **R** package. It has a general purpose wrapper named `scr` which has other capabilities too.

The data were read into our R session and manipulated using the following commands. Note that we use the utility **R** function `SCR23darray.fn` which we defined in chapt. 4.

```

4528 > wcaps<-source("wcaps.R")$value
4529 > wtraps<-source("wtraps.R")$value
4530 > K.wolv<-apply(wtraps[,4:ncol(wtraps)],1,sum)
4531 >
4532 > xx<-SCR23darray.fn(wcaps,ntraps=37,nperiods=165)
4533 > y.wolv<- apply(xx,c(1,3),sum)
4534 > traplocs.wolv<-wtraps[,2:3]
4535 > traplocs.wolv<-traplocs.wolv/10000
4536 >
4537 > frog<-nlm(intlik3,c(-1.5,1.2,log(4)),hessian=TRUE,y=y.wolv,K=K.wolv,X=traplocs.wolv,delt
4538 There were 23 warnings (use warnings() to see them)
4539 > frog
4540
4541 $minimum
4542 [1] 220.4355
4543
4544 $estimate
4545 [1] -2.817570  1.255112  3.599040
4546
4547 $gradient
4548 [1] -6.274309e-06  2.146722e-05 -1.045566e-05
4549
4550 $hessian
4551      [,1]      [,2]      [,3]
4552 [1,] 37.687931 -11.852236  4.688911
4553 [2,] -11.852236 30.846144 -9.199113
4554 [3,]  4.688911 -9.199113 13.050428
4555
4556 $code
4557 [1] 1
    
```

```
4558
4559 $iterations
4560 [1] 12
4561
4562 > exp(3.599)*sqrt(solve(frog$hessian)[3,3])
4563 [1] 11.41059
4564 >
4565
```

4566 We obtained the MLEs for a state-space buffer of 2 (standardized units) and
4567 for integration grid with spacing $\delta = .3, .2, .1, .05$. The MLEs for these 4 cases
4568 including the relative runtime are given in Table 6.1.

Table 6.1. Run time and MLEs for different integration grid resolutions.

δ	runtime	Estimates		
		α_0	θ	$\log(n_0)$
0.30	8.4	-2.819786	1.258468	3.569731
0.20	22.6	-2.817610	1.254757	3.583690
0.10	99.0	-2.817570	1.255112	3.599040
0.05	403.0	-2.817559	1.255281	3.607158

4569 We see the results change only slightly as the fineness of the integration grid
4570 increases. Conversely, the runtime on the platform of the day for the 4 cases
4571 increases rapidly which, as we have suggested before, could probably be regarded
4572 in relative terms, across platforms, for gaging the decrease in speed as the fineness
4573 of the integration grid increases. The effect of this is that we anticipate some
4574 numerical error in approximating the integral on a mesh of points, and that error
4575 increases as the coarseness of the mesh increases.

4576 In section 4.9 back in chapt. 4 we used a discrete representation of the state-
4577 space in order to have control over its extent and shape, for example so that we
4578 could clip out “non-habitat”. Clearly that formulation of the model is relevant
4579 to the use of integrated likelihood in the sense that such a representation of the
4580 state-space underlies the computation of the integral. Thus, for example, we could
4581 easily compute the MLE of parameters under some model with a restricted state-
4582 space merely by creating the required state-space at whatever grid resolution is
4583 desired, and then feed that state-space into the likelihood evaluation above. The
4584 **R** function `scr` which comes with the **R** package for this book accommodates an
4585 arbitrary state-space fashioned in this manner, as well as state-spaces created by
4586 polygons or GIS shapefiles³.

4587 Next we studied the effect of the state-space buffer on the MLEs, using a fixed
4588 $\delta = .2$ for all analyses. We used state-space buffers of 1 to 4 units stepped by .5.
4589 This produced the following results, given here are the state-space buffer, area of

³to be completed!

the state-space, the MLE of N for the prescribed state-space and the corresponding MLE of density:

	ssbuff	Ass	Nhat	Dhat
[1,]	1.0	66.98212	37.73338	0.5633352
[2,]	1.5	84.36242	46.21008	0.5477567
[3,]	2.0	103.74272	57.00617	0.5494956
[4,]	2.5	125.12302	69.03616	0.5517463
[5,]	3.0	148.50332	82.17550	0.5533580
[6,]	3.5	173.88362	96.44018	0.5546249
[7,]	4.0	201.26392	111.83524	0.5556646

The estimates of D stabilize rapidly and the incremental difference is within the numerical error associated with approximating the integral. The results suggest that wolverine density is around 0.56 individuals per 100 km^2 (recall that a state-space unit is $10 \times 10 km$). This is about 5.6 individuals per thousand km^2 which compares with XYZ-lookup-XYZ reported in Royle et al. (2011c) based on a clipped state-space as described in section XYZ (XYZ chapter 4 XYZ).

6.4.1 Exercises

1. Compute the 95% confidence interval for wolverine density, somehow.
2. Compute the AIC of this model and modify `intlik3` to consider alternative link functions (at least one additional) and compare the AIC of the different models and the estimates. Comment.

6.5 PROGRAM DENSITY AND THE R PACKAGE SECR

DENSITY is a software program developed by Efford (2004) for fitting spatial capture-recapture models based mostly on classical maximum likelihood estimation and related inference methods. Efford (2011) has also released an **R** package named **secr**, that contains many of the functions within **DENSITY** but also incorporates new models and features. Here, we will focus on **secr** as it will continue to be developed, contains more functionality and is based in **R**. To install and run models in **secr**, you must download the package and load it in **R**.

```
> install.packages(secr)
> library(secr)
```

secr allows the user to simulate data and fit a suite of models with various detection functions and covariate responses. **secr** uses the standard **R** model specification framework using tildes. E.g., the model command is `secr.fit` and is generally written as

```
4624 > secr.fit(capturedata, model = list(D~1, g0~1, sigma~1), buffer = 20000)
```

4625 where we have `g0~1` indicating the intercept model. To include covariates, this
 4626 would be written as `g0~b` where *b* is a behavioral response covariate. Possible
 4627 predictors for detection probability include both pre-defined variables (e.g., `t` and
 4628 `b` corresponding to “time” and “behavior”), and user-defined covariates of several
 4629 kinds. The discussion of covariates is developed in chapter XX(8)⁴

4630 Before we can fit the models, the data must first be entered into `secr`. Two
 4631 input files are required: trap layout (location and identification information for
 4632 each trap) and capture data (e.g., sampling session, animal identification, trap
 4633 day, and trap location). SECR requires that you specify the trap type, the two
 4634 most common for camera trapping/hair snares are proximity detectors and count
 4635 detectors. The ‘proximity’ detector type allows, at most, one detection of each
 4636 individual at a particular detector on any occasion. The count detector designation
 4637 allows repeat encounters of each individual at a particular detector on any occasion.
 4638 There are other detector types that one can select such as: ‘polygon’ detector type
 4639 which allows for a trap to be a sampled polygon, e.g., scat surveys, and ‘signal’
 4640 detector which allows for traps that have a strength indicator, e.g., acoustic arrays.
 4641 The detector types single and multi can be confusing as multi seems like it would
 4642 appropriate for something like a camera trap, but instead these two designations
 4643 refer to traps that retain individuals, thus precluding the ability for animals to be
 4644 captured in other traps during the sampling occasion. The single type indicates
 4645 trap that can only catch one animal at a time, while multi indicates traps that may
 4646 catch more than one animal at a time. For a full review of the detector types, one
 4647 should look at the help manual, which can be accessed in R after installing the
 4648 SECR package by using the command:

```
4649 > RShowDoc("secr-manual", package = "secr")
```

4650 As with all of the `scr` models, `secr` fits a detection function relating the proba-
 4651 bility of detection to the distance of a detector from an individual activity center.
 4652 `secr` allows the user to specify one of a variety of detection functions including the
 4653 commonly used half-normal, hazard rate, and exponential. There are 12 different
 4654 functions, but some are only available for simulating data, and one should take
 4655 caution when using different detection functions as the interpretation of the pa-
 4656 rameters, such as sigma, may not be consistent across formulations. The different
 4657 detection functions are defined in the `secr` manual and can be found by calling the
 4658 `help` function for the detection function:

```
4659 > ?detectfn
```

4660 It is useful to note that `secr` requires the buffer distance to be defined in meters
 4661 and density will be returned as number of animals per hectare. Thus to make

⁴Beth: does `secr` fit a local trap-specific response or just a global behavioral response?

comparisons between `secr` and other models, we will often have to convert the density to the same units. Also, note that sigma is returned in units of meters.

5

6.5.1 Analysis using the `secr` package

To demonstrate the use of the `secr` package, we will show how to do the same analysis on the wolverine study as shown in section 4.6. To use the `secr` package, the data need to be formatted in a similar but slightly different manner than we use in WinBUGS. After installing the `secr` package, we first have to read in the trap locations and other related information, such as if the trap is operational during a sampling occasion. The `secr` package reads in the trap data through a command called `read.traps`, which requires the detector type as input. The detector type is important because it will determine the likelihood that `secr` will use to fit the model. Here, we have selected proximity since individuals are captured at most once in each trap during each sampling occasion.

```
> traps= read.csv(wtraps.csv)
> colnames(traps)[1:3]<- c("trapID","x", "y") #name the first 3 columns
# to match the secr nomenclature
> trapfile <- read.traps(data = traps, detector = "proximity")
```

After reading in the data, we now need to create the encounter matrix or array. The `secr` package does this through the use of the `make.capthist` command, where we provide the capture histories in raw data format (each line contains the session, identification number, occasion, and trap id for only 1 individual). This is the format that was shown in the data input file `wcaps`, and we only need a line or two to organize the data into the order that the `make.capthist` command wants. In creating the capture history, we provide also the trapfile with the trap information, and the format (e.g., here `fmt= trapID`) so that `secr` knows how to match the encounters to the trap, and finally, we provide the number of occasions.

```
> wolv.dat <- wcaps[,c(2, 3, 1)]
#NEED TO UPDATE THIS WHEN I GET THE FILES,
### I JUST GUESSED AT THE CODE, BUT WOULD LIKE TO TRY IT.
> wolv.dat <- cbind(rep(1, dim(wolv.dat)[1], wolv.dat)
> colnames(wolv.dat) <- c("Session", "ID", "Occasion", "trapID")
> wolvcapt=make.capthist(wolv.dat, trapfile, fmt = "trapID", noccasions = 165)
```

⁵One question: SECR only ever reports sigma. What exactly is sigma? It is a scale parameter of a detection function and all detection functions have a scale parameter. But in what sense is this sigma parameter related to home range diameter? Efford doesn't explain this, does he? In some sections in chapter 4 or possibly 6 we get into this issue.

```

4697     Calling the secr.fit command, will run the model. We are using the basic model
4698 (SCR0), so we do not need to make any specifications in the command line except
4699 for the providing the buffer size (in m). To specify different models, you can change
4700 the default  $D \sim 1$ ,  $g0 \sim 1$ ,  $\sigma \sim 1$ , which the interested reader can do with very little
4701 difficulty.

4702 > wolv.secr=secr.fit(wolvcapt, model = list( $D \sim 1$ ,  $g0 \sim 1$ ,  $\sigma \sim 1$ ), buffer = 20000)
4703
4704 > wolv.secr
4705
4706 secr.fit( capthist = wolvcapt, buffer = 20000, binomN = 1 )
4707 secr 2.0.0, 18:26:39 05 Jul 2011
4708
4709 Detector type      proximity
4710 Detector number    37
4711 Average spacing    4415.693 m
4712 x-range            593498 652294 m
4713 y-range            6296796 6361803 m
4714 N animals          : 21
4715 N detections       : 115
4716 N occasions        : 165
4717 Mask area          : 1037069 ha
4718
4719 Model              :  $D \sim 1$   $g0 \sim 1$   $\sigma \sim 1$ 
4720 Fixed (real)       : none
4721 Detection fn       : halfnormal
4722 Distribution        : poisson
4723 N parameters       : 3
4724 Log likelihood     : -746.754
4725 AIC                 : 1499.508
4726 AICc               : 1500.920
4727
4728 Beta parameters (coefficients)
4729          beta      SE.beta      lcl      ucl
4730 D      -9.749576 0.23027860 -10.200913 -9.298238
4731 g0      -4.275736 0.15846104  -4.586313 -3.965158
4732 sigma   8.699202 0.07868944   8.544973  8.853430
4733
4734 Variance-covariance matrix of beta parameters
4735          D          g0          sigma
4736 D      0.053028233 0.000546922 -0.005226926
4737 g0      0.000546922 0.025109900 -0.005885213
4738 sigma -0.005226926 -0.005885213  0.006192027

```

```

4739
4740 Fitted (real) parameters evaluated at base levels of covariates
4741      link      estimate SE.estimate      lcl      ucl
4742 D      log 5.831941e-05 1.360973e-05 3.713638e-05 9.158548e-05
4743 g0     logit 1.371121e-02 2.142902e-03 1.008756e-02 1.861207e-02
4744 sigma  log 5.998124e+03 4.727205e+02 5.140849e+03 6.998355e+03

```

4745 Under the fitted (real) parameters, we find D , the density, given in units of in-
4746 dividuals/hectare (1 hectare = 100 m²). To convert this into individuals/1000km²,
4747 we multiply by 100000, thus our density estimate is 5.83 individuals/1000 km².
4748 Sigma is given in units of meters, to convert to kilometers, we divide by 1000,
4749 which puts sigma at 5.99 km. Both of these estimates are very similar to those
4750 provided in section 4.6 for the buffer size equal to 20 km. As an exercise, run this
4751 analysis for 30 and 40 km buffers and compare those found in section 4.6 under
4752 **WinBUGS**. NOTE: The function `secr.fit` will return a warning when the buffer
4753 size appears to be too small. This is useful particularly with the different units
4754 being used between programs and packages.

6.6 SUMMARY AND OUTLOOK

4755 In this chapter, we showed that classical analysis of SCR models based on likeli-
4756 hood methods is a relatively simple proposition. Analysis is based on the so-called
4757 integrated likelihood in which the individual activity centers (random effects) are
4758 removed from the conditional-on-s likelihood by integration. We showed how to
4759 construct the integrated likelihood and fit some simple models in the R program-
4760 ming language. In addition, likelihood analysis for some broad classes of SCR
4761 models can be accomplished in the software package DENSITY or in the equivalent
4762 **R** library `secr` which we provided an illustration of here. In later chapters we
4763 provide more detailed analyses of SCR data using the `secr` package.

4764 To compute the integrated likelihood we have to precisely describe the state-
4765 space of the underlying point process. In practice, this leads to a buffer around
4766 the trap array. We note that this is not really a buffer strip in the sense of Wilson
4767 et al. (XYZ) which is a feature of the analysis but it is somewhat more general
4768 here. In particular, it establishes the support of the integrand which we generally
4769 require to compute any integral. It might be that the integrand itself is finite even
4770 if the support is infinity but that may or may not be the case depending on the
4771 choice of detection function. As a practical matter then, it will typically be the case
4772 that, while estimates of N increase with the size of the buffer, estimates of density
4773 stabilize. This is not a feature of the classical methods based on using model M0
4774 or model Mh and buffering the trap array.

4775 Why or why not use likelihood inference exclusively? For certain specific models,
4776 it is probably more computationally efficient to produce MLEs. However, **Win-**
4777 **BUGS** is extremely flexible in terms of describing models, although it sometimes

can be quite slow. We can devise models in **WinBUGS** easily that we cannot fit in secr. E.g., random individual effects of various types (see next chapter), we can handle missing covariates in complete generality and seamlessly, and impose arbitrary distributions on random variables. Moreover, models can easily be adapted to include auxiliary data types. For example, we might have camera trapping and genetic data and we can describe the models directly in WinBUGS and fit a joint model. For the MLE we have to write a custom new piece of code for each model or hope someone has done it for us. Later we consider open population models which are straightforward to develop in WinBUGS but, so far, there is no available platform for doing MLE although we imagine one could develop this. Another thing that is more conceptual here is non-CSR point processes (see chapter XYZ) and generating predictions of how many individuals have home range centers in any particular polygon. Basic benefits of Bayesian analysis have been discussed elsewhere (Chapter 2? BPA book? Link and Barker?) and we believe these are compelling. On the other hand, likelihood analysis makes it easy to do model-selection by AIC. Goodness-of-fit is probably no more difficult or easy under either paradigm (see next chapter?).

In summary, basic SCR models are easy to implement by either likelihood or Bayesian methods but we feel that the typical user will realize much more flexibility in model development using existing platforms for Bayesian analysis. While these tend to be slow (sometimes excruciatingly slow), this will probably not be an impediment in most problems, especially at some near point in the future. Since we spent a lot of time here talking about specific technical details on how to implement likelihood analysis of SCR models, we provided a corresponding treatment in the next chapter on how to devise MCMC algorithms for SCR models. This is a bit more tedious and requires more coding, but is not technically challenging (except perhaps to develop highly efficient algorithms which we don't excel at).

MCMC DETAILS

7.1 INTRODUCTION

In this chapter we will dive a little deeper into Markov chain Monte Carlo (MCMC) sampling. We will construct custom MCMC samplers in R, starting with easy-to-code GLMs and GLMMs and moving on to simple SCR models. We will also demonstrate some tricks and simple extensions to the 'spatial null model'. Finally, we will illustrate some alternative ready-to-use software packages for MCMC sampling. We will NOT provide exhaustive background information on the theory and justification of MCMC sampling there are entire books dedicated to that subject and we refer you to Robert and Casella (2004) and Robert and Casella (2010). Rather we aim to provide you with enough background and technical know-how to start building your own MCMC samplers for SCR models in R.

7.1.1 Why build your own MCMC algorithm?

The standard program we have used so far to run MCMC analyses is WinBUGS (Gilks et al., 1994). The wonderful thing about WinBUGS is that it will automatically use the most appropriate and efficient form of MCMC sampling for the model specified by the user.

The fact that we have such a Swiss Army knife type of MCMC machine begs the question: Why would anyone want to build their own MCMC algorithm? For one, there are a limited number of distributions and functions implemented in WinBUGS. While OpenBUGS provides more options, some more complex models may be impossible to build within these programs. A very simple example from spatial capture-recapture that can give you a headache in WinBUGS is when your state-space is an irregular-shaped polygon, rather than an ideal rectangle that can be characterized by four pairs of coordinates. It is easy to restrict activity centers

to any arbitrary polygon in R using an ESRI shapefile (and we will show you an example in a little bit), but you cannot use a shape file in a BUGS model.

Sometimes implementing an MCMC algorithm in R may be faster than in WinBUGS - especially if you want to run simulation studies where you have hundreds or more simulated data sets, several years' worth of data or other large models, this can be a big advantage.

Finally, building your own MCMC algorithm is a great exercise to understand how MCMC sampling works. So while using the BUGS language requires you to understand the structure of your model, building an MCMC algorithm requires you to think about the relationship between your data, priors and posteriors, and how these can be efficiently analyzed and characterized. Not to mention that, if you are an R junkie, it can actually be fun. However, if you don't think you will ever sit down and write your own MCMC sampler, consider skipping this chapter - apart from coding it will not cover anything SCR-related that is not covered by other, more model-oriented chapters as well.

7.2 MCMC AND POSTERIOR DISTRIBUTIONS

As mentioned in Chapter 2, MCMC is a class of simulation methods for drawing (correlated) random numbers from a target distribution, which in Bayesian inference is the posterior distribution. As a reminder, the posterior distribution is a probability distribution for an unknown parameter, say θ , given a set of observed data and its prior probability distribution (the probability distribution we assign to a parameter before we observe data). The great benefit of computing the posterior distribution of θ is that it can be used to make probability statements about θ , such as the probability that θ is equal to some value, or the probability that θ falls within some range of values. As an example, suppose we conducted a Bayesian analysis to estimate detection probability of some species at a study site (p), and we obtained a posterior distribution of $\text{beta}(20,10)$ for the parameter p . The following R commands demonstrate how we make inferences based upon summaries of the posterior distribution. Fig 1 shows the posterior along with the summary statistics.

```
> (post.median <- qbeta(0.5, 20, 10))
[1] 0.6704151
> (post.95ci <- qbeta(c(0.025, 0.975), 20, 10))
[1] 0.4916766 0.8206164
```

Thus, we can state that there is a 95% probability that θ lies between 0.49 and 0.82.

The posterior distribution summarizes all we know about a parameter and thus, is the central object of interest in Bayesian analysis. Unfortunately, in many if not most practical applications, it is nearly impossible to directly compute the posterior.

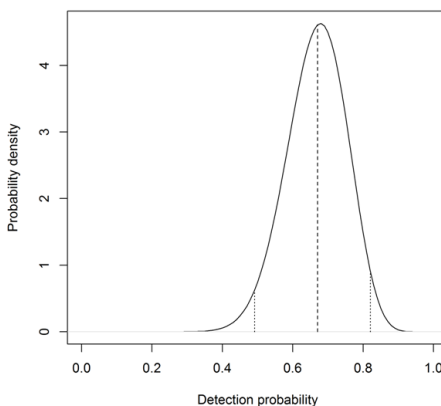


Figure 7.1. Probability density plot of a hypothetical posterior distribution of $\text{beta}(20,10)$; dashed lines indicate mean and upper and lower 95% interval

4869 Recall Bayes theorem:

$$p(\theta|y) = p(y|\theta) * p(\theta) / p(y), \quad (7.2.1)$$

4870 where θ is the parameter of interest, y is the observed data, $p(\theta|y)$ is the posterior,
 4871 $p(y|\theta)$ the likelihood of the data conditional on θ , $p(\theta)$ the prior probability of θ ,
 4872 and, finally, $p(y)$ is the marginal probability of the data, which can also be written
 4873 as

$$p(y) = \int p(y|\theta) * p(\theta) d\theta$$

4874 This marginal probability is a normalizing constant that ensures that the pos-
 4875 terior integrates to 1. You read in Chapter 2 that this integral is often hard or
 4876 impossible to evaluate, unless you are dealing with a really simple model. For ex-
 4877 ample, consider that you have a Normal model, with a set of n observations, y that
 4878 come from a Normal distribution:

$$y \sim \text{Normal}(\mu, \sigma),$$

4879 where σ is known and our objective is to obtain an estimate of μ using Bayesian
 4880 statistics. To fully specify the model in a Bayesian framework, we first have to
 4881 define a prior distribution for μ . Recall from Chapter 2 that for certain data
 4882 models, certain priors lead to conjugacy i.e. if you choose the right prior for your

parameter, your posterior distribution will be of a known parametric form. The conjugate prior for the mean of a normal model is also a Normal distribution:

$$\mu \sim \text{Normal}(\mu_0, \sigma_0^2)$$

If μ_0 and σ_0^2 are fixed, the posterior for μ has the following form (for the algebraic proof, see XXX):

$$\mu|y \sim \text{Normal}(\mu_n, \sigma_n^2) \quad (7.2.2)$$

where

$$\mu_n = (\text{sig}^2 / \text{sig}^2 + n * \text{sig}0^2) * \text{mu}0 + (n * \text{sig}0^2 / \text{sig}^2 + n * \text{sig}0^2) * y - \text{bar}$$

And

$$\text{sign}^2 = \text{sig}^2 * \text{sig}0^2 / (\text{sig}^2 + n * \text{sig}0^2)$$

We can directly obtain estimates of interest from this Normal posterior distribution, such as the mean μ -hat and its variance; we do not need to apply MCMC, since we can recognize the posterior as a parametric distribution, including the normalizing constant $p(y)$. But generally we will be interested in more complex models with several, say n , parameters. In this case, computing $p(y)$ from Eq. 7.2.1 requires n -dimensional integration, which is can be difficult or impossible. Thus, the posterior distribution is generally only known up to a constant of proportionality:

$$p(\theta|y) \propto p(y|\theta) * p(\theta)$$

The power of MCMC is that it allows us to approximate the posterior using simulation without evaluating the high dimensional integrals and to directly sample from the posterior, even when the posterior distribution is unknown! The price is that MCMC is computationally expensive. Although MCMC first appeared in the scientific literature in 1949 (Metropolis and Ulam, 1949), widespread use did not occur until the 1980s when computational power and speed increased (Gelfand and Smith, 1990). It is safe to say that the advent of practical MCMC methods is the primary reason why Bayesian inference has become so popular during the past three decades. In a nutshell, MCMC lets us generate sequential draws of θ (the parameter(s) of interest) from distributions approximating the unknown posterior over T iterations. The distribution of the draw at t depends on the value drawn at $t-1$; hence, the draws form a Markov chain.¹ As T goes to infinity, the Markov chain converges to the desired distribution. In our case the posterior distribution for θ — y . Thus, once the Markov chain has reached its stationary distribution, the generated samples can be used to characterize the posterior distribution, $p(\theta|y)$, and point estimates of θ , its standard error and confidence bounds, can be obtained directly from this approximation of the posterior. In practice, although we know that

¹In case you are not familiar with Markov chains, for t random samples $\theta(1), \dots, \theta(t)$ from a Markov chain the distribution of $\theta(t)$ depends only on the most recent value, $\theta(t-1)$.

a Markov chain will eventually converge, we can only generate a limited number of samples a process that depending on the model can be quite time consuming. Assessing whether our Markov chain has indeed converged is an important part of MCMC sampling and we will speak about some common diagnostics in Section XX.

7.3 TYPES OF MCMC SAMPLING

There are several MCMC algorithms, the most popular being Gibbs sampling and Metropolis-Hastings sampling. We will be dealing with these two classes in more detail and use them to construct the MCMC algorithms for SCR models. Also, we will briefly review alternative techniques that are applicable in some situations.

7.3.1 Gibbs sampling

Gibbs sampling was named after the physicist J.W. Gibbs by Geman and Geman (1984), who applied the algorithm to a Gibbs distribution². The roots of Gibbs sampling can be traced back to work of Metropolis et al. (1953), and it is actually closely related to Metropolis sampling (see Chapter 11.5 in Gelman et al. (2004), for the link between the two samplers). We will focus on the technical aspects of this algorithm, but if you find yourself hungry for more background, Casella and George (1992) provide a more in-depth introduction to the Gibbs sampler.

In Chapter 2 you already heard about the basic principles of Gibbs sampling³. But as a refresher, let's go back to our simple example from above to understand the motivation and functioning of Gibbs sampling. Recall that for a Normal model with known variance and a Normal prior for μ , the posterior distribution of $\mu|y$ is also Normal. Conversely, with a fixed (known) μ , but unknown variance, the conjugate prior for σ^2 is an Inverse-Gamma distribution with shape and scale parameters a and b :

$$\sigma^2 \sim \text{Inv-Gamma}(a, b),$$

With fixed a and b , the posterior $p(\text{sig}|\mu, y)$ is also an Inverse Gamma distribution, namely:

$$\text{sig}|\mu, y \sim \text{InvGamma}(an, bn), \quad (7.3.1)$$

where $an = n/2 + a$ and $bn = 1/2\sigma(y_i - \mu)^2 + b$. However, what if we know neither μ nor sig , which is probably the more common case? The joint posterior distribution of μ and sig now has the general structure

$$p(\mu, \text{sig}|y) = \frac{p(y|\mu) * p(\mu) * p(\text{sig})}{\int p(y|\mu) * p(\mu) * p(\text{sig}) d\mu d\text{sig}}$$

²a distribution from physics we are not going to worry about, since it has no immediate connection with Gibbs sampling other than giving its name

³maybe we should think out chapter 2 and concentrate that material here?

Or

$$p(\mu, \sigma|y) \propto p(y|\mu) * p(\mu) * p(\sigma)$$

This cannot easily be reduced to a distribution we recognize. However, we can condition μ on σ (i.e., we treat σ as fixed) and remove all terms from the joint posterior distribution that do not involve μ to construct the full conditional distribution,

$$p(\mu|\sigma, y) \propto p(y|\mu) * p(\mu)$$

The full conditional of μ again takes the form of the Normal distribution shown in Eq. ??; similarly, $p(\sigma|\mu, y)$ takes the form of the Inverse Gamma distribution shown in Eq. Eq. 7.3.1 both distribution we can easily sample from. And this is precisely what we do when using Gibbs sampling we break down high-dimensional problems into convenient one-dimensional problems by constructing the full conditional distributions for each model parameter separately; and we sample from these full conditionals, which, if we choose conjugate priors, are known parametric distributions. Let's put the concept of Gibbs sampling into the MCMC framework of generating successive samples, using our simple Normal model with unknown μ and σ and conjugate priors as an example. These are the steps you need to build a Gibbs sampler:

Step 0: Begin with some initial values for θ , $\theta(0)$. In our example, we have to specify initial values for μ and σ , for example by drawing a random number from some uniform distribution, or by setting them close to what we think they might be. (Note: This step is required in any MCMC sampling chains have to start from somewhere. We will get back to these technical details a little later.)

Step 1: Draw $\theta_1(1)$ from the conditional distribution $p(\theta_1(1) | \theta_2(0), \dots, \theta_d(0))$. Here, θ_1 is μ , which we draw from the Normal distribution in Eq. ?? using $\sigma(0)$ as value for σ .

Step 2: Draw $\theta_2(1)$ from the conditional distribution $p(\theta_2(1) | \theta_1(1), \theta_3(0), \dots, \theta_d(0))$. Here, θ_2 is σ , which we draw from the Inverse Gamma distribution of Eq. 7.3.1, using $\mu(1)$ as value for μ ...

Step d: Draw $\theta_d(1)$ from the conditional distribution $p(\theta_d(1) | \theta_1(1), \dots, \theta_{d-1}(1))$

In our example we have no additional parameters, so we only need step 0 through to 2. Repeat Steps 1 to d for $K =$ a large number of samples. In terms of R coding, this means we have to write Gibbs updaters for μ and σ and embed them into a loop over K iterations. The final code in the form of an R function is shown in Panel 1.

Andy will build the panel environment here soon.

Panel 1: R-code for a Gibbs sampler for a Normal model with unknown μ

4978 and sig and conjugate (Normal and Inverse Gamma, respectively) priors
4979 for both parameters.

```
4980
4981 Normal.Gibbs<-function(y=y,mu0=mu0, sig0=sig0, a=a,b=b,niter=niter) {
4982
4983   ybar<-mean(y)
4984   n<-length(y)
4985   mu<-runif(1) #mean initial value
4986   sig<-runif(1) #sd initial value
4987   an<-n/2 + a
4988
4989   out<-matrix(nrow=niter, ncol=2)
4990   colnames(out)<-c('mu', 'sig')
4991
4992   for (i in 1:niter) {
4993
4994     #update mu
4995     mun<- (sig/(sig+n*sig0))*mu0 + (n*sig0/(sig+n* sig0))*ybar
4996     sign <- (sig*sig0)/ (sig+n*sig0)
4997     mu<-rnorm(1,mun, sqrt(sign))
4998
4999     #update sig
5000     bn<- 0.5 * (sum((y-mu)^2)) +b
5001     sig<-1/rgamma(1,shape=an, rate=bn)
5002     out[i,<-c(mu,sqrt(sig))
5003
5004   }
5005   return(out)
5006 }
```

5007 This is it! You can use the code `NormalGibbs.R` in the **R** package `scrbook` to
5008 simulate some data, $y \sim \text{Normal}(5, 0.5)$ and run your first Gibbs sampler. Your
5009 output will be a table with two columns, one per parameter, and K rows, one per
5010 iteration. For this 2-parameter example you can visualize the joint posterior by
5011 plotting samples of μ against samples of σ (Fig. 2 XXX):

```
5012 plot(out[,1], out[,2])
```

5013 The marginal distribution of each parameter is approximated by just examining the
5014 samples of this particular parameter you can visualize it by plotting a histogram
5015 of the samples (Fig. 3 a, b XXX):

```
5016 par(mfrow=c(1,2))
5017 hist(out[,1]); hist (out[,2])
```

Finally, recall an important characteristic of Markov chains, namely, that the chain has to have converged (reached its stationary distribution) for samples to come from the posterior distribution. In practice, that means you have to throw out some of the initial samples called the burn-in. We will talk about this in more when we talk about convergence diagnostics. For now, you can use the `plot(out[,1])` or `plot(out[,2])` command to make a time series plot of the samples of each parameter and visually assess how many of the initial samples you should discard. Figure 3 c and d shows plots for the estimates of mu and sigma from our simulated data set; you see that in this simple example the Markov chain apparently reaches its stationary distribution very quickly the chains look 'grassy' seemingly from the start. It is hard to discern a burn-in phase visually (but we will see examples further on where the burn-in is clearer) and you may just discard the first 500 draws to be sure you only use samples from the posterior distribution. The mean of the remaining samples are your estimates of mu and sig:

```
> summary(mod[501:10000,])
      mu          sig
Min.   : 4.936    Min.   : 0.4569
1st Qu.: 4.984    1st Qu.: 0.4889
Median : 4.994    Median : 0.4961
Mean   : 4.994    Mean   : 0.4964
3rd Qu.: 5.005    3rd Qu.: 0.5037
Max.   : 5.062    Max.   : 0.5356
```

7.3.2 Metropolis-Hastings sampling

Although it is applicable to a wide range of problems, the limitations of Gibbs sampling are immediately obvious what if we do not want to use conjugate priors (or what if we cannot recognize the full conditional distribution as a parametric distribution, or simply do not want to worry about these issues)? The most general solution is to use the Metropolis-Hastings (MH) algorithm, which also goes back to the work by Metropolis et al. (1953). You saw the basics of this algorithm in Chapter 2. In a nutshell, because we do not recognize the posterior $p(\theta|y)$ as a parametric distribution, the MH algorithm generates samples from a known proposal distribution, say $h(\theta)$, that depends on θ at $t-1$. The t^{th} sample is accepted or rejected based on its joint posterior probability density compared to the density of the sample at $t-1$. The original Metropolis algorithm requires $h(\theta)$ to be symmetric so that $h(\theta^t|\theta^{t-1}) = h(\theta^{t-1}|\theta^t)$; but a later development of the algorithm by Hastings (1970) lifted this condition. Using a symmetric proposal distribution makes life a little easier and we are going to limit our coverage of the Metropolis-Hastings sampler to this specific case. Specifically, we are going to use a Normal proposal distribution, which is also referred to as 'random walk Metropolis-Hastings

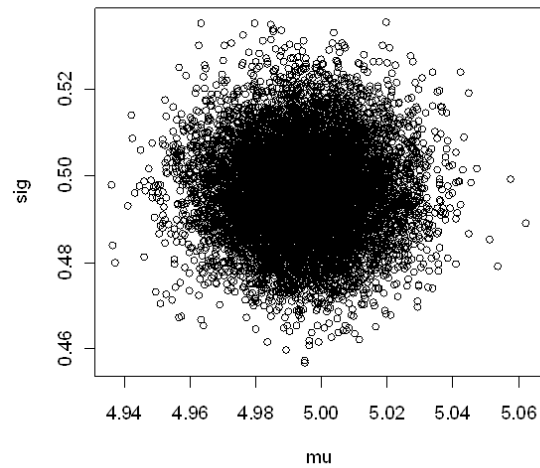


Figure 7.2. Joint posterior distribution of μ and σ from a Normal Model

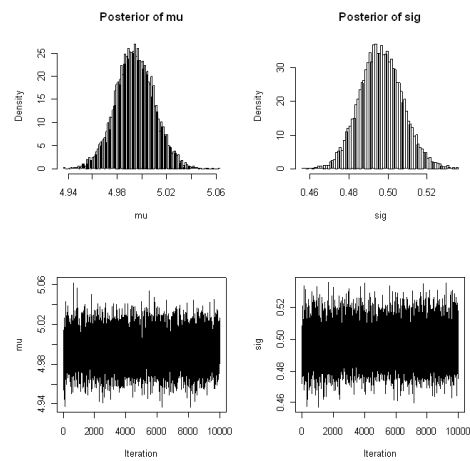


Figure 7.3. Plots of the posterior distributions of μ (a) and σ (b) from a Normal model and time series plots of μ (c) and σ (d).

sampling'. It is worth knowing that there are alternative formulations of the algorithm. For example, in the independent M-H, θ^t does not depend on θ^{t-1} , while the Langevin algorithm (Roberts and Rosenthal, 1998) aims at avoiding the random walk by favoring moves towards regions of higher posterior probability density. The interested reader should look up these algorithms in Robert and Casella (2004) or Robert and Casella (2010).

Building a MH sampler can be broken down into several steps. We are going to demonstrate these steps using a different but still simple and common model the logit-normal or logistic regression model. For simplicity, assume that

$$y \sim \text{Bern}(\exp(\theta)/(1 + \exp(\theta)))$$

and

$$\theta \sim \text{Normal}(\mu_0, \sigma)$$

The following steps are required to set up a random walk MH algorithm:

Step 0: Choose initial values, $\theta(0)$.

Step 1: Generate a proposed value of θ at t from $h(\theta^t - \theta^{t-1})$. We often use a Normal proposal distribution, so we draw θ_1 from $\text{Normal}(\theta^t, \text{sig}^2)$, where sig^2 is the variance of the Normal proposal distribution, a tuning parameter that we have to set.

Step 2: Calculate the ratio of posterior densities for the proposed and the original value for θ :

$$r = p(\theta^t|y)/p(\theta^{t-1}|y)$$

In our example,

$$r = \text{Bern}(y|\theta^t) * \text{Normal}(\theta^t|\mu_0, \sigma_0) / \text{Bernoulli}(y|\theta^{t-1}) * \text{Normal}(\theta^{t-1}|\mu_0, \text{sig}^2)$$

Step 3: Set

```
\begin{eqnarray*}
\theta(t) &= & \theta(t) \text{ with probability } \min(r,1) //
&= & \theta(t-1) \text{ otherwise }
\end{eqnarray*}
```

We can do that by drawing a random number u from a $\text{Unif}(0, 1)$ and accept θ^t if $u < r$. Repeat for $t = 1, 2, \dots$ a large number of samples. The **R** code for this MH sampler is provided in Panel 2 XXXX.

Panel 2: R code to run a Metropolis sampler on a simple Logit-Normal model.

```
Logreg.MH<-function(y=y, mu0=mu0, sig0=sig0, niter=niter) {
```

```

5088 out<-c()
5089
5090 theta<-runif(1, -3,3) #initial value
5091
5092 for (iter in 1:niter){
5093   theta.cand<-rnorm(1, theta, 0.2)
5094
5095   loglike<-sum(dbinom(y, 1, exp(theta)/(1+exp(theta)), log=TRUE))
5096   logprior <- dnorm(theta,mu0 ,sig0, log=TRUE)
5097   loglike.cand<-sum(dbinom(y, 1, exp(theta.cand)/(1+exp(theta.cand)), log=TRUE))
5098   logprior.cand <- dnorm(theta.cand, mu0, sig0, log=TRUE)
5099
5100   if (runif(1)<exp((loglike.cand+logprior.cand)-(loglike+logprior))){
5101     theta<-theta.cand
5102   }
5103   out[iter]<-theta
5104 }
5105
5106 return(out)
5107 }

```

5108 The reason we sum the logs of the likelihood and the prior, rather than multiply-
5109 ing the original values, is simply computational. The product of small probabilities
5110 can be numbers very close to 0, which computers do not handle well. Thus we add
5111 the logarithms, sum, and exponentiate to achieve the desired result. Similarly, in
5112 case you have forgotten some elementary math, $x/y = \exp(\log(x) - \log(y))$, with
5113 the latter being favored for computational reasons.

5114 Comparing MH sampling to Gibbs sampling, where all draws from the con-
5115 ditional distribution are used, in the MH algorithm we discard a portion of the
5116 candidate values, which inherently makes in less efficient than Gibbs sampling the
5117 price you pay for its increased generality. In Step 1 of the MH sampler we had to
5118 choose a variance for the Normal proposal distribution. Choice of the parameters
5119 that define our candidate distribution is also referred to as 'tuning', and it is im-
5120 portant since adequate tuning will make your algorithm more efficient, i.e. your
5121 Markov chain will converge faster. The variance should be chosen so that (a) each
5122 step of drawing a new proposal value for θ can cover a reasonable distance in the
5123 parameter space, as otherwise, the random walk moves too slowly; and (b) proposal
5124 values are not rejected too often, as otherwise the random walk will 'get stuck' at
5125 specific values for too long. As a rule of thumb, your candidate value should be ac-
5126 cepted in about 40% of all cases. Acceptance rates of 20-80% are probably ok, but
5127 anything below or above may well render your algorithm inefficient (this does not
5128 mean that it will give you wrong results only that you will need more iterations to
5129 converge to the posterior distribution). In practice, tuning will require some 'trial-
5130 and-error' and some common sense. Or, one can use an adaptive phase, where the
5131 tuning parameter is automatically adjusted until it reaches a user-defined accep-

5132 tance rate, at which point the adaptive phase ends and the actual Markov chain
 5133 begins. This is computationally a little more advanced. Link and Barker (2009)
 5134 discuss this in more detail. It is important the samples drawn during the adaptive
 5135 phase are discarded. You can easily check acceptance rates for the parameters you
 5136 monitor (that are part of your output) using the `rejectionRate()` function of the
 5137 package `coda` (we will talk more about this package a little later on). Do not let
 5138 the term 'rejection rate' confuse you; it is simply $1 - \text{acceptance rate}$. There may
 5139 be parameters for example, individual values of a random effect or latent variables
 5140 that you do not want to save, though, and in our next example we will show you a
 5141 way to monitor their acceptance rates with a few extra lines of code.

5142 7.3.3 Metropolis-within-Gibbs

5143 One weakness of the MH sampler is that formulating the joint posterior when
 5144 evaluating whether to accept or reject the candidate values for θ becomes increas-
 5145 ingly complex or inefficient as the number of parameters in a model increases. It
 5146 is probably going to sound like MCMC sampling is too good to be true but in
 5147 these cases you can simply combine MH sampling and Gibbs sampling. You can
 5148 use Gibbs sampling to break down your high-dimensional parameter space into
 5149 easy-to-handle one-dimensional conditional distributions and use MH sampling for
 5150 these conditional distributions. Better yet if you have some conjugacy in your
 5151 model, you can use the more efficient Gibbs sampling for these parameters and
 5152 one-dimensional MH for all the others. You have already seen the basics of how to
 5153 build both types of algorithms, so we can jump straight into an example here and
 5154 build a Metropolis-within-Gibbs algorithm.

7.4 GLMMS POISSON REGRESSION WITH A RANDOM EFFECT

5155 Let's assume a model that gets us closer to the problem we ultimately want to
 5156 deal with a GLMM. Here, we assume we have Poisson counts, y , from i plots
 5157 in j different study sites, and we believe that the counts are influenced by some
 5158 plot-specific covariate, x , but that there is also a random site effect. So our model
 5159 is:

$$y_{ij} \sim \text{Poisson}(l_{amij})$$

5160

$$l_{amij} = \exp(a_j + b * x_i)$$

5161 Let's use Normal priors on a and b ,

$$a_j \sim \text{Normal}(\mu_{a_j}, \sigma_{a_j})$$

5162 and

$$b \sim \text{Normal}(\mu_b, \sigma_b)$$

.⁴ Since we want to estimate the random effect in this model, we do not specify μ_a and σ_a , but instead, estimate them as well, so we have to specify hyperpriors for these parameters:

$$\begin{aligned}\mu_a &\sim \text{Normal}(\mu_0, \text{sig}_0) \\ \sigma_a &\sim \text{InvGamma}(a_0, b_0)\end{aligned}$$

With the model fully specified, we can compile the full conditionals, breaking the multi-dimensional parameter space into one-dimensional components:

```
\begin{eqnarray*}
p(a_1|a_2,a_3,a_j,b,y) &\propto p(y_{i1}|a_1,b) * p(a_1|mua, \text{sig}_a) \\
&\propto \text{Poisson}(y_{i1} | \exp(a_1 + b*x[j=1])) * \text{Normal}(a_1|mua, \text{sig}_a)
\end{eqnarray*}
\begin{eqnarray*}
p(a_2|a_1,a_3,a_j,b,y) &\propto p(y_{i2}|a_2,b) * p(a_2|mua, \text{sig}_a) \\
&\propto \text{Poisson}(y_{i2} | \exp(a_2 + b*x[j=1])) * \text{Normal}(a_2|mua, \text{sig}_a)
\end{eqnarray*}
and so on for all elements of a.
\begin{eqnarray*}
p(b|a,y) &\propto p(y|a,b) * p(b) \\
&\propto \text{Poisson}(y | \exp(a + b*x)) * \text{Normal}(b|mub, \text{sig}_b)
\end{eqnarray*}
```

Finally, we need to update the hyperparameters for a:

$$\begin{aligned}p(mua|a) &\propto p(a|mua, \text{sig}_a) * p(mua) \\ p(\text{sig}_a|a) &\propto p(a|mua, \text{sig}_a) * p(\text{sig}_a)\end{aligned}$$

Since we assumed a to come from a Normal distribution, the choice of priors for mua Normal and sig_a Inverse Gamma leads to the same conjugacy we observed in our initial Normal model, so that both hyperparameters can be updated using Gibbs sampling.

Now let's build the updating steps for these full conditionals. Again, for the MH steps that update a and b we use Normal proposal distributions with standard deviations sig_a and sig_b.

First, we set the initial values a(0) and b(0). Then, starting with a1, we draw a1(1) from Normal(a1(0), sig_a), calculate the conditional posterior density of a1(0) and a1(1) and compare their ratios,

$$r = \text{Poisson}(y(j=1) | \exp(a1(1) + b*x)) * \text{Normal}(a1(1) | mua, \text{sig}_a) / \text{Poisson}(y(j=1) | \exp(a1(0) + b*x)) * \text{Normal}(a1(0) | mua, \text{sig}_a)$$

and accept a1(1) with probability min(r,1). We repeat this for all a's.

⁴Why is b a hyperparameter?

5194 For b, we draw $b(1)$ from $\text{Normal}(b(0), \text{sigbh})$, compare the posterior densities
5195 of $b(0)$ and $b(1)$,

$$r = \text{Poisson}(y|\exp(a+b(1)*x)) * \text{Normal}(b(1)|\text{mub}, \text{sigb}) / \text{Poisson}(y|\exp(a+b(0)*x)) * \text{Normal}(b(0)|\text{mub}, \text{sigb}),$$

5196 and accept $b(1)$ with probability $\min(r, 1)$.

5197 For mua and sig , we sample directly from the full conditional distributions (Eq
5198 XX and Eq XX):

$$\text{mua}(1) \sim \text{Normal}(\text{mun}, \text{sign})$$

5199 where $\text{mun} = (\text{sig}a(0)/\text{sig}a(0) + n_a * \text{sig}0) * \text{mu}0 + (n_a * \text{sig}0/\text{sig}a(0) + n_a * \text{sig}0) * \text{abar}(1)$ and $\text{sign} = \text{sig}a(0) * \text{sig}0 / (\text{sig}a(0) + n * \text{sig}0)$. Here, abar is the
5200 current mean of the vector a , which we updated before, and n_a is the length of
5201 a . For sig we use $\text{sig}a(1) \sim \text{InvGamma}(an, bn)$, where $an = n_a/2 + a0$, and
5202 $bn = 1/2 \sum (\text{a}(1) - \text{mua}(1))^2 + b0$.
5203

5204 We repeat these steps over K iterations of the MCMC algorithm. In this example
5205 we may not want to save each value for a , but are only interested in their mean and
5206 standard deviation. Since these two parameters will change as soon as the value for
5207 one element in a changes, their acceptance rates will always be close to 1 and are
5208 not representative of how well your algorithm performs. To monitor the acceptance
5209 rates of parameters you do not want to save, you simply need to add a few lines
5210 of code into your updater to see how often the individual parameters are accepted.
5211 The full code for the MCMC algorithm of our Poisson GLMM in Panel 3 shows
5212 one way how to monitor acceptance of individual a 's.

5213 Panel 3: R code for the Metropolis-within-Gibbs sampler for
5214 a Poisson regression with random intercepts.

```
5215
5216 Pois.reg<-function(y=y,site=site,mu0=mu0,sig0=sig0,a0=a0,b0=b0,
5217                   mub=mub, sigb=sigb, niter=niter){
5218
5219   lev<-length(unique(site))      #number of sites
5220   a<-runif(lev,-5,5) #initial values a
5221   b<-runif(1,0,5) #initial value b
5222   mua<-mean(a)
5223   siga<-sd(a)
5224
5225   out<-matrix(nrow=niter, ncol=3)
5226   colnames(out)<-c('mua','sig','b')
5227
5228   for (iter in 1:niter) {
5229
5230     #update a
5231     aUps<-0 #initiate counter for acceptance rate of a
5232     for (j in 1:lev) { #loop over sites
5233       a.cand<-rnorm(1, a[j], 0.1) #update intercepts a one at a time
```

```

5234 loglike<- sum(dpois (y[site==j], exp(a[j] + b*x[site==j]), log=TRUE))
5235 logprior<- dnorm(a[j], mua,siga, log=TRUE)
5236 loglike.cand<- sum(dpois (y[site==j], exp(a.cand + b *x[site==j]), log=TRUE))
5237 logprior.cand<- dnorm(a.cand, mua,siga, log=TRUE)
5238 if (runif(1)< exp((loglike.cand+logprior.cand) (loglike+logprior))) {
5239   a[j]<-a.cand
5240   aUps<-aUps+1
5241 }
5242 }
5243
5244 if(iter %% 100 == 0) { #this lets you check the acceptance rate of a at every 100th iteration
5245   cat("   Acceptance rates\n")
5246   cat("     a =", aUps/lev, "\n")
5247 }
5248
5249 #update b
5250 b.cand<-rnorm(1, b, 0.1)
5251 avec<-rep(a, times=c(rep(10,10)))
5252 loglike<- sum(dpois (y, exp(avec + b*x), log=TRUE))
5253 logprior<- dnorm(b, mub,sigb, log=TRUE)
5254 loglike.cand<- sum(dpois (y, exp(avec + b.cand *x), log=TRUE))
5255 logprior.cand<- dunif(b.cand, mub,sigb, log=TRUE)
5256 if (runif(1)< exp((loglike.cand+logprior.cand) (loglike+logprior) )) {
5257   b<-b.cand
5258 }
5259
5260 #update mua using Gibbs sampling
5261 abar<-mean(a)
5262 mun<- (siga/(siga+lev*sig0))*mu0 + (lev*sig0/(siga+lev* sig0))*abar
5263 sign <- (siga*sig0)/ (siga+lev*sig0)
5264 mua<-rnorm(1,mun, sqrt(sign))
5265
5266 #update siga using Gibbs sampling
5267 a0n<-lev/2 + a0
5268 b0n<- 0.5 * (sum((a-mua)^2)) +b0
5269 siga<-1/rgamma(1,shape=a0n, rate=b0n)
5270
5271 out[iter,]<-c(mua, sqrt(siga), b)
5272
5273 }
5274
5275 return(out)
5276 }

```

7.4.1 Rejection sampling and slice sampling

While MH and Gibbs sampling are probably the most widely applied algorithms for posterior approximation, there are other options that work under certain circumstances and may be more efficient when applicable. WinBUGS applies these algorithms and we want you to be aware that there is more out there to approximate posterior distributions than Gibbs and MH. One alternative algorithm is rejection sampling. Rejection sampling is not an MCMC method, since each draw is independent of the others. The method can be used when the posterior $p(\theta|y)$ is not a known parametric distribution but can be expressed in closed form. Then, we can use a so-called envelope function, say, $g(\theta)$, that we can easily sample from, with the restriction that $p(\theta|y) < M * g(\theta)$. We then sample a candidate value for θ from $g(\theta)$, calculate $r = p(\theta|y) / M * g(\theta)$ and keep the sample with the probability r . M is a constant that has to be picked so that $r \in [0,1]$, for example by evaluating both $p(\theta|y)$ and $g(\theta)$ at n points and looking at their ratios. Rejection sampling only works well if $g(\theta)$ is similar to $p(\theta|y)$, and packages like WinBUGS use adaptive rejection sampling (Gilks and Wild, 1992), where a complex algorithm is used to fit an adequate and efficient $g(\theta)$ based on the first few draws. Though efficient in some situations, rejection sampling does not work well with high-dimensional problems, since it becomes increasingly hard to define a reasonable envelope function. For an example of rejection sampling in the context of SCR models, see Chapter 9. Another alternative is slice sampling (Neal, 2003). In slice sampling, we sample uniformly from the area under the plot of $p(\theta|y)$. Considering a single univariate θ . Let's define an auxiliary variable, $U \sim \text{Uniform}(0, p(\theta|y))$. Then, θ can be sampled from the vertical slice of $p(\theta|y)$ at U (Figure 4):

$$\theta|U \sim \text{Unif}(B),$$

where $B = \{\theta : U < p(\theta|y)\}$

5

Slice sampling can be applied in many situations; however, implementing an efficient slice sampling procedure can be complicated. We refer the interested reader to chapter 7 of Robert and Casella (2010) for a simple example. Both rejection sampling and slice sampling can be applied on one-dimensional conditional distributions within a Gibbs sampling setup.

7.5 MCMC FOR CLOSED CAPTURE-RECAPTURE MODEL MH

6

⁵there are supposed to be equations in the caption of figure 4 but it kept causing errors

⁶Andy could move material from chapter 3 to here.

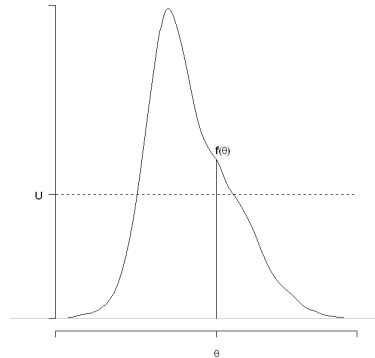


Figure 7.4. Slice sampling. For...

7.6 MCMC ALGORITHM FOR THE BASIC SPATIAL CAPTURE-RECAPTURE MODEL

By now you have seen how to build MCMC algorithms for some basic generalized linear models. Now, we'll walk you through the steps of building your own MCMC sampler for the basic SCR model (i.e. without any individual, site or time specific covariates) with both a Poisson and a binomial encounter process. As usual, we will have to go through two general steps before we write the MCMC algorithm:

- (1) Identify your model with all its components (including priors)
- (2) Recognize and express the full conditional distributions for all parameters

It is worthwhile to go through all of step 1 for an SCR model, but you have probably seen enough of step 2 in our previous examples to get the essence of how to express a full conditional distribution. Therefore, we will exemplify step 2 for some parameters and tie these examples directly to the respective R code.

Step 1 Identify your model

Recall the components of the basic SCR model with a Poisson encounter process from Chapter 3: We assume that individuals i , or rather, their activity centers s_i , are uniformly distributed across our state space S ,

$$s_i \sim U(S)$$

and that the number of times individual i encounters trap j , y_{ij} , is a random Poisson variable with mean λ_{mij} ,

$$y_{ij} \sim \text{Poisson}(\lambda_{mij})$$

The tie between individual location, movement and trap encounter rates is made by the assumption that λ_{mij} , is a decreasing function of the distance between s_i

5329 and j , D_{ij} , of the half-normal form

$$Lam_{ij} = lam0 * \exp(-D_{ij}^2/2 * sig^2),$$

5330 where $lam0$ is the baseline trap encounter rate at $D_{ij} = 0$ and sig controls the
5331 shape of the half-normal function.

5332 In order to estimate the number of s_i in S , N , we use data augmentation (sect.
5333 3.XYZ) and create M - n all-0 encounter histories, where n is the number of individ-
5334 uals we observed and M is an arbitrary number that is larger than N . We estimate
5335 N by summing over the auxiliary data augmentation variables, z_i , which is 1 if the
5336 individual is part of the population and 0 if not, and assume that z_i is a random
5337 Bernoulli variable,

$$z_i \sim \text{Bern}(\psi)$$

5338 To link the two model components, we modify our trap encounter model to

$$Lam_{ij} = lam0 * \exp(-D_{ij}^2/2 * sig^2) * z_i.$$

5339 The model has the following structural parameters, for which we need to specify
5340 priors ψ the Uniform (0,1) is required as part of the data augmentation procedure
5341 and in general is a natural choice of an uninformative prior for a probability; note
5342 that this is equivalent to a Beta(1,1) prior, which will come in handy later. s_i since
5343 s_i is a pair of coordinates it is two-dimensional and we use a uniform prior limited
5344 by the extent of our state-space over both dimensions. σ we can conceive several
5345 priors for sigma but let's assume an improper prior one that is Uniform over (-Inf,
5346 Inf). We will see why this is convenient when we construct the full conditionals for
5347 sigma. λ_0 analogous, we will use a Uniform (-Inf, Inf) improper prior for sigma.
5348 The parameter that is the objective of our modeling, N , is a derived parameter that
5349 we can simply obtain by summing all z 's:

$$N = \text{sum}(z)$$

5350 **Step 2 - Construct the full conditionals** Having completed step 1, let's
5351 look at the full conditional distributions for some of these parameters. We find
5352 that with improper priors, full conditionals are proportional only to the likelihood
5353 of the observations; for example, take the movement parameter sigma:

$$Sig|s, lam0, z, ypropto[y|s, lam0, z, sig] * [sig]$$

5354 Since the improper prior implies that $[sig]$ propto 1, we can reduce this further to

$$Sig|s, lam0, z, ypropto[y|s, lam0, z, sig]$$

5355 The R code to update sigma is shown in Panel 4. ⁷

⁷ Somewhere in chapter 2 i added a comment about rejecting parameters outside of the parameter space as being an ok thing to do. Richard said he read something in Robert and Casellas book on that. Hopefully he can remember where and we can cite it back in Ch 2 and again here. It could be mentioned in a sentence or two up in the MCMC section.

5356 Panel 4: R code to update sigma within an MCMC algorithm for
 5357 an SCR model when using an improper prior

```
5358
5359
5360 sig.cand <- rnorm(1, sigma, 0.1) #draw candidate value
5361 if(sig.cand>0){ #automatically reject sig.cand that are <0
5362   lam.cand <- lam0*exp(-(D*D)/(2*sig.cand*sig.cand))
5363   ll<- sum(dpois(y, lam*z, log=TRUE))
5364   llcand <- sum(dpois(y, lam.cand*z, log=TRUE))
5365   if(runif(1) < exp( llcand - ll) ){
5366     ll<-llcand
5367     lam<-lam.cand
5368     sigma<-sig.cand
5369   }
5370 }
5371
```

5372 These steps are analogous for lam0 and si and we will use MH steps for all
 5373 of these parameters. Similar to the random intercepts in our Poisson GLMM, we
 5374 update each si individually. Note that to be fully correct, the full conditional for
 5375 si contains both the likelihood and prior component, since we did not specify an
 5376 improper, but a Uniform prior on si. However, with a Uniform distribution the
 5377 probability density of any value is 1/(upper limit - lower limit) = constant. Thus,
 5378 the prior components are identical for both the current and the candidate value
 5379 and can be ignored (formally, when you calculate the ratio of posterior densities, r,
 5380 the identical prior component appears both in the numerator and denominator, so
 5381 that they cancel each other out).

5382 We still have to update zi. The full conditional for zi is

$$z_i|y, \sigma, \lambda_0, \text{sprpto}[y|z, \sigma, \lambda_0, s] * [z_i]$$

5383 and since $z_i \sim \text{Bernoulli}(\psi_i)$, the term has to be taken into account when updating
 5384 zi. The R code for updating zi is shown in Panel 5.

5385 Panel 5: R code to update z

```
5386
5387 zUps <- 0 #set counter to monitor acceptance rate
5388 for(i in 1:M) {
5389   if(seen[i]) #no need to update seen individuals, since their z =1
5390     next
5391   zcand <- ifelse(z[i]==0, 1, 0)
5392   llz <- sum(dpois(y[i,], lam[i,]*z[i], log=TRUE))
5393   llcand <- sum(dpois(y[i,], lam[i,]*zcand, log=TRUE))
5394
5395   prior <- dbinom(z[i], 1, psi, log=TRUE)
5396   prior.cand <- dbinom(zcand, 1, psi, log=TRUE)

```

```

5397         if(runif(1) < exp( (llcand+prior.cand) - (llz+prior) )) {
5398             z[i] <- zcand
5399             zUps <- zUps+1
5400         }
5401     }

```

5402 ψ itself is a hyperparameter of the model, with an uninformative prior distribu-
5403 tion of Unif(0,1) or Beta(1,1), so that

$$Psi|z \propto [z|psi] * Beta(1, 1)$$

5404 The Beta distribution is the conjugate prior to the Binomial and Bernoulli distribu-
5405 tions (remember that $z \sim Bernoulli(psi)$). The general form of a full conditional
5406 of a Beta-Binomial model with $y_i \sim Bernoulli(p)$ and $p \sim Beta(a, b)$ is

$$p(p|y) \propto Beta(a + sum(yi), b + n - sum(yi))$$

5407 In our case, this means we update psi as follows:

```

5408 si<-rbeta(1, 1+sum(z), 1 + M-sum(z))

```

5409 These are all the building blocks you need to write the MCMC algorithm for
5410 the spatial null model with a Poisson encounter process. You can find the full R
5411 code (SCR0pois.R) in the online supplementary material.

5412 7.6.1 SCR model with binomial encounter process

5413 The equivalent SCR model with a binomial encounter process is very similar. Here,
5414 each individual i can only be detected once at any given trap j during a sampling
5415 occasion k . Thus

$$y_{ij} \sim Binomial(p_{ij}, K)$$

5416 Where p_{ij} is some function of distance between s_i and trap location x_j . Here we
5417 use:

$$p_{ij} = 1 - \exp(-lam_{ij})$$

5418 Recall from Chapter 2 that this is the complementary log-log (cloglog) link func-
5419 tion, which constrains p_{ij} to fall between 0 and 1. For our MCMC algorithm that
5420 means that, instead of using a Poisson likelihood, $Poisson(y|sigma, lam0, s, z)$, we
5421 use a Binomial likelihood, $Binomial(y, K|sigma, lam0, s, z)$, in all the conditional
5422 distributions. As an example, Panel 6 shows the updating step for $lam0$ under
5423 a binomial encounter model. The full MCMC code for the binomial SCR can be
5424 found in the online supplements.

5425 Panel 6: MCMC updater for $lam0$ in a SCR model with Binomial encounter
5426 process and cloglog link function on detection. Here, `pmat =`

```

5427 1-exp(-lam).
5428
5429     lam0.cand <- rnorm(1, lam0, 0.1)
5430     if(lam0.cand > 0){ #automatically reject lam0.cand that are <0
5431         lam.cand <- lam0.cand*exp(-(D*D)/(2*sigma*sigma))
5432         p.cand <- 1-exp(-lam.cand)
5433         ll<- sum(dbinom(y, K, pmat *z, log=TRUE))
5434         llcand <- sum(dbinom(y, K, p.cand *z, log=TRUE))
5435         if(runif(1) < exp( llcand - ll) ){
5436             ll<-llcand
5437             pmat<-p.cand
5438             lam0<- lam0.cand
5439         }
5440     }

```

Another possibility is to model variation in the individual and site specific detection probability, p_{ij} , directly, without any transformation, such that

```

5443 pij<-p0 * exp(-Dij2/(2*sig^2))

```

and $p_0 = \{0,1\}$. This formulation is analogous to how detection probability is modeled in distance sampling under a half-normal detection function; however, in distance sampling p_0 - detection of an individual on the transect line - is assumed to be 1 (Buckland, 2001). Under this formulation the updater for lam_0 (equivalent to p_0 in Eq XX) becomes:

```

5449     lam0.cand <- rnorm(1, lam0, 0.1)
5450     if(lam0.cand > 0 & lam0.cand < 1 ){ #automatically reject lam0.cand that are not
5451         lam.cand <- lam0.cand*exp(-(D*D)/(2*sigma*sigma))
5452         ll<- sum(dbinom(y, K, lam *z, log=TRUE)) #no transformation needed
5453         llcand <- sum(dbinom(y, K, lam.cand *z, log=TRUE))
5454         if(runif(1) < exp( llcand - ll) ){
5455             ll<-llcand
5456             lam<-lam.cand
5457             lam0<- lam0.cand
5458         }
5459     }

```

5460 7.6.2 Looking at model output

Now that you have an MCMC algorithm to analyze spatial capture-recapture data with, let's run an actual analysis so we can look at the output. As an example, we will use the bear data ...⁸ You can use the same script provided back in

⁸Does this data set come up before Ch6? If not, introduce data here. Or, Andy, would you rather use simulated data?

Chapter XX to read in the data and build the augmented encounter history array; then source the MCMC code for the binomial encounter model algorithm with the cloglog link and run 5000 iterations. This should take approximately 25 minutes.

```
> source('SCR0binom.txt')
> mod0<-SCR.0(y=bigTrap, X=trapmat, M=M, xl=xl, xu=xu, yl=yl, yu=yu, K=8, niter=5000)
```

Before, we used simple R commands to look at model results. However, there is a specific R package to summarize MCMC simulation output and perform some convergence diagnostics package coda (Plummer et al., 2006). Download and install coda, then convert your model output to an mcmc object

```
> chain<-mcmc(mod0)
```

Markov chain time series plots

Start by looking at time series plots of your Markov chains using `plot(chain)`. This command produces a time series plot and marginal posterior density plots for each monitored parameter, similar to what we did before using the `hist()` and `plot()` commands (Fig. 5). Time series plots will tell you several things: First, the way the chains move through the parameter space gives you an idea of whether your MH steps are well tuned. If chains were constant over many iterations you would probably need to decrease the tuning parameter of the (Normal) proposal distribution. If a chain moves along some gradient to a stationary state very slowly, you may want to increase the tuning parameter so that the parameter space is explored more efficiently.

Second, you will be able to see if your chains converged and how many initial simulations you have to discard as burn-in. In the case of the chains shown in Figure 5, we would probably consider the first 750 - 1000 iterations as burn-in, as afterwards the chains seem to be fairly stationary.

A word of caution about chain convergence

Since we do not know what the stationary posterior distribution of our Markov chain should look like (this is the whole point of doing an MCMC approximation), we effectively have no means to assess whether it has converged to this desired distribution or not. As mentioned before, the only certainty is that a Markov chain will *eventually* converge to its stationary distribution, but no-one can tell us how long this will take. Also, you only now the part of your posterior distribution that the Markov chain has explored so far for all you know the chain could be stuck in a local maximum, while other maxima remain completely undiscovered. Acknowledging that there is truly nothing we can do to ever proof convergence of our MCMC chains, there are several things we can do to increase the degree of confidence we have about the convergence of our chains. One option, and that advocated by what we will loosely call the WinBUGS community, is to run several Markov chains and to start them off at different initial values that are overdispersed relative to the posterior distribution. Such initial values help to explore different

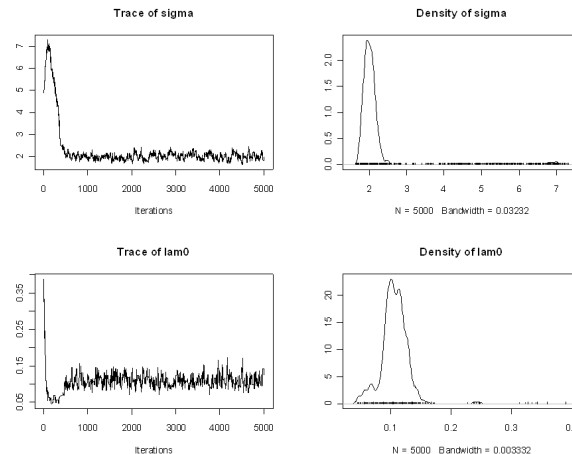


Figure 7.5. Time series and posterior density plots for sigma and lam0.

5504 areas of the parameter space simultaneously; if after a while all chains oscillate
 5505 around the same average value, chances are good that they indeed converged to
 5506 the posterior distribution. Gelman and Rubin came up with a diagnostic statistic
 5507 that essentially compares within-chain and between-chain variance to check for
 5508 convergence of multiple chains (Gelman et al., 2004). Of course, running several
 5509 parallel chains is computationally expensive. Extra computational demands are not
 5510 the only and by no means the major concern some people voice when it comes to
 5511 running several parallel MCMC chains to assess convergence. Again, consider the
 5512 fact that we do not know anything about the true form of the posterior distribution
 5513 we are trying to approximate. How do we, then, know how to pick overdispersed
 5514 initial values? We don't all we can do is pick overdispersed values relative to our
 5515 expectations of what the posterior should look like. To use a quote from the home
 5516 page of Charlie Geyer, a Bayesian statistician from the University of Minnesota,
 5517 "If you don't know any good starting points [...], then restarting the sampler at
 5518 many bad starting points is [...] part of the problem, not part of the solution."
 5519 (<http://users.stat.umn.edu/~charlie/mcmc/diag.html>). His suggestion is that your
 5520 only chance to discover a potential problem with your MCMC sampler is to run it
 5521 for a very long time. But again, there is no way of knowing how long is long enough.
 5522 It is up to you to decide, which school of thoughts appeals more to you one long
 5523 versus several parallel Markov chains. Irrespectively, part of developing an MCMC
 5524 sampler should be to make sure (within reasonable limits) that you are not missing
 5525 regions of high posterior density because of the way you specify your starting values.
 5526 Once you have explored the behavior of your chain under a reasonable range of

starting values, you may feel comfortable enough to run only one long chain. The fact that convergence cannot be proven does not mean that you should not look for potential problems in your MCMC sampler. Some problems are easily detected using simple plots, such as the time series plots we discussed above. If the overall trajectory of your chain at the end of your simulations is still upward or downward, your chain clearly has not converged and you need to run your model much longer. If you run several parallel chains and their stationary distributions look different, you may be looking at a multi-modal posterior or a problem with your sampler. With these words of caution, let's get back to looking at our model output.

7.6.3 Posterior density plots

The `plot()` command also produces posterior density plots and it is worthwhile to look at those carefully. For parameters with priors that have bounds (e.g. Uniform over some interval), you will be able to see if your choice of the prior is truncating the posterior distribution. In the context of SCR models, this will mostly involve our choice of M , the size of the augmented data set. If the posterior of N has a lot of mass concentrated close to M (or equivalently the posterior of ψ has a lot of mass concentrated close to 1), as in the example in Figure 6, we have to re-run the analysis with a larger M . A flat posterior plot shows you that the parameter essentially cannot be identified there may not be enough information in your data to estimate model parameters and you may have to consider a simpler model. Finally, posterior density plots will show you if the posterior distribution is symmetrical or skewed if the distribution has a heavy tail, using the mean as a point estimate of your parameter of interest may be biased and you may want to opt for the median or mode instead.

7.6.4 Serial autocorrelation and effective sample size

Even when we can be relatively confident that our chains have converged, the subsequent samples generated from a Markov chain are not iid samples from the posterior distribution, due to the correlation amongst samples introduced by the Markov process. As a consequence, the variance of the mean cannot simply be derived with the standard variance estimator, which takes into account the sample size (here, number of iterations). Rather, the sample size has to be adjusted to account for the autocorrelation in subsequent samples (see Chapter 8 in Robert and Casella (2010) for more details). This adjusted sample size is referred to as the effective sample size. Checking the degree of autocorrelation in your Markov chains and estimating the effective sample size your chain has generated should be part of evaluating your model output. If you use WinBUGS through the R2WinBUGS package, the `print()` command will automatically return the effective sample size for all monitored parameters. In the coda package there are several functions you

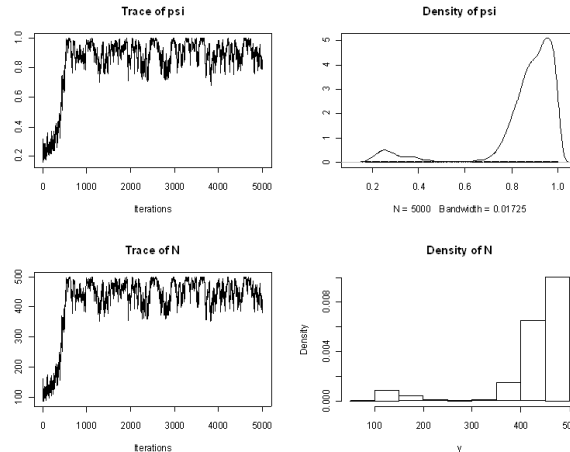


Figure 7.6. Time series and posterior density plots of ψ and N for the bear data set truncated by the upper limit of M (500).

5565 can use to do so. `effectiveSize()` will directly give you an estimate of the effective
5566 sample size for your parameters:

```
5567 > effectiveSize(chain)
5568     sigma     lam0     psi      N
5569 3.930303 78.259159 30.436348 32.047392
```

5570 Alternatively, you can use the `autocorr.diag()` function, which will show you the
5571 degree of autocorrelation for different lag values (which you can specify within the
5572 function call, we use the defaults below):

```
5573 > autocorr.diag(mcmc(mod))
5574     sigma     lam0     psi      N
5575 Lag 0  1.0000000 1.0000000 1.0000000 1.0000000
5576 Lag 1  0.9979948 0.9494134 0.9847503 0.9774201
5577 Lag 5  0.9915567 0.8038168 0.9111951 0.9113525
5578 Lag 10 0.9836016 0.6714021 0.8462108 0.8509803
5579 Lag 50 0.8985337 0.1983780 0.6138516 0.6233994
```

5580 Whichever function you use, if you find that your supposedly long Markov chain
5581 has not generated enough pseudo-iid samples, you should consider a longer run. In
5582 the present case we see that autocorrelation is especially high for the parameter
5583 `sigma` and our effective sample size for this parameter is 4!⁹ This means we would

⁹Anyone have any idea how the autocorrelation in `sigma` could be reduced?

have to run the model for much longer to obtain a reasonable effective sample size. Unfortunately, with many SCR models we observe high degrees of serial autocorrelation, which means we have to run long chains to obtain enough samples that can be considered iid, in order to obtain reasonable estimates of our parameters and their variances. What exactly constitutes a reasonable effective sample size is hard to say, but as a rule of thumb you should probably aim at several hundreds of these pseudo-iid samples. A more meaningful measure of whether you've run your chain for enough iterations is the time-series or Monte Carlo error the 'noise' introduced into your samples by the stochastic MCMC process which we introduced in Chapter 2. The MC error decreases with increasing sample size and its magnitude can thus be controlled by adjusting the length of the Markov chain. As a rule of thumb, the MC error should be 1% or less of the parameter estimate. Once you have reached this level, the estimates of the mean, standard error and 95% quantiles should no longer change significantly with additional iterations. For highly correlated samples, it will take more iterations to reduce the MC error. In coda, the MC error is given as part of the summary results (see below). Another option to deal with the serial autocorrelation of samples is to 'thin' Markov chains by some rate r and save only every r -th iteration. But as discussed in Chapter 2, this is not efficient and should only be applied if needed for practical reasons (e.g. a large number of parameters and iterations may force you to thin your samples so you object storing the model output does not become unmanageably large). For now, let's continue using this small set of samples to continue looking at the output.

7.6.5 Summary results

Now that we checked that our chains apparently have converged and pretending that we have generated enough samples from the posterior distribution, we can look at the actual parameter estimates. The `summary()` function will return two sets of results: the mean parameter estimates, with their standard deviation, the naive standard error - i.e. your regular standard error calculated for K (= number of iterations) samples without accounting for serial autocorrelation - and the corrected MC error (Time-series SE), which accounts for autocorrelation. In WinBUGS, this latter value is referred to as MC error and is only given in the log output within BUGS itself. You should adjust the `summary()` call by removing the burn-in from calculating parameter summary statistics. To do so, use the `window()` command, which lets you specify at which iteration to start 'counting'. In contrast to WinBUGS, which requires you to set the burn-in length before you run the model, this command gives us full flexibility to make decisions about the burn-in after we have seen the trajectories of our Markov chains. For our example, `summary(window(chain, start=1001))` returns the following output:

```
Iterations = 1001:5000
Thinning interval = 1
```



```

5624 Number of chains = 1
5625 Sample size per chain = 4000
5626
5627 1. Empirical mean and standard deviation for each variable,
5628    plus standard error of the mean:

```

```

5629
5630      Mean      SD Naive SE Time-series SE
5631 sigma  1.9986  0.13805 0.0021827      0.016091
5632 lam0   0.1096  0.01523 0.0002407      0.001401
5633 psi    0.6113  0.09148 0.0014465      0.010734
5634 N      489.8535 71.79695 1.1352094      8.431119

```

```

5635
5636 2. Quantiles for each variable:

```

```

5637
5638      2.5%      25%      50%      75%      97.5%
5639 sigma  1.75780  1.89847  1.9900  2.0944  2.2772
5640 lam0   0.08357  0.09824  0.1087  0.1192  0.1427
5641 psi    0.45110  0.54838  0.6052  0.6639  0.8192
5642 N      366.00000 440.00000 485.0000 530.0000 654.0000

```

5643 Looking at the MC errors, we see that in spite of the high autocorrelation, the
 5644 MC error for sigma is below the 1Our algorithm gives us a posterior distribution of
 5645 N, but we are usually interested in the density, D. Density itself is not a parameter
 5646 of our model, but we can derive a posterior distribution for D by dividing each
 5647 value of N (N at each iteration) by the area of the state-space (here 3032.719 km²)
 5648 and we can use summary statistics of this distribution to characterize D:

```

5649 > summary(window(chain[,4]/ 3032.719, start=1001))
5650 Iterations = 1001:5000
5651 Thinning interval = 1
5652 Number of chains = 1
5653 Sample size per chain = 4000
5654
5655 1. Empirical mean and standard deviation for each variable,
5656    plus standard error of the mean:
5657
5658      Mean      SD      Naive SE Time-series SE
5659 0.1615229 0.0236741 0.0003743      0.0027801
5660
5661 2. Quantiles for each variable:
5662
5663      2.5%      25%      50%      75%      97.5%
5664 0.1207 0.1451 0.1599 0.1748 0.2156

```

If we compare our mean density of 0.16/km² (and other parameters) with results from the same model run in secr and WinBUGS in Chapter XX, we see that estimates are almost identical (Table 1).

7.6.6 Other useful commands

While inspecting the time series plot gives you a first idea of how well you tuned your MH algorithm, use `rejectionRate()` to obtain the rejection rates (1 - acceptance rates) of the parameters that are written to your output:

```
> rejectionRate(chain)
      sigma      lam0      psi      N
0.44108822 0.77675535 0.00000000 0.01940388
```

Recall that rejection rates should lie between 0.2 and 0.8, so our tuning seems to have been appropriate here. Psi is never rejected since we update it with Gibbs sampling, where all candidate values are kept. And since N is the sum of all z, all it takes for N to change from one iteration to the next are small changes in the z-vector, so the rejection rate of N is always low. If you have run several parallel chains, you can combine them into a single mcmc object using the `mcmc.list()` command on the individual chains (note that each chain has to be converted to an mcmc object before combining them with `mcmc.list()`). You can then easily obtain the Gelman-Rubin diagnostic (Gelman et al., 2004), in WinBUGS called R-hat, using `gelman.diag()`, which will indicate if all chains have converged to the same stationary distribution. For details on these and other functions, see the coda manual, which can be found together with the package on the CRAN mirror.

7.7 MANIPULATING THE STATE-SPACE

So far, we have constrained the location of the activity centers to fall within the outermost coordinates of our rectangular state space by posing upper and lower bounds for x and y. But what if S has an irregular shape maybe there is a large water body we would like to remove from S, because we know our terrestrial study species does not occur there. Or the study takes place in a clearly defined area such as an island. As mentioned before, this situation is difficult to handle in WinBUGS. In some simple cases we can adjust the state space by setting `SXi` to be some function of `SYi` or vice versa. In this manner, we can cut off corners of the rectangle to approximate the actual state space. In R, we are much more flexible, as we can use the actual state-space polygon to constrain out si.¹⁰ To illustrate that, let's look at a camera trapping study of Florida panthers (*Puma concolor coryi*) conducted in the Picayune Strand Restoration Project (PSRP) area, southwest Florida (Fig. 7), by XXX, and financed by XXX. In the 1960ies the PSRP area was slated for

¹⁰ Have to check if we can use panther stuff for the book; otherwise, use raccoon example.

housing development, but then bought back by the State of Florida and is currently being restored to its original hydrology and vegetation. In an effort to estimate the density of the local Florida panther population, 98 camera traps were operated in the area for 21 months between 2005 and 2007. Florida panthers are wide-ranging animals and in order to account for their wide movements, the state-space was defined as the trapping grid buffered by 15 km around its outermost coordinates. However, the resulting rectangle contained some ocean in its southwestern corner (Fig. 7). In order to precisely describe the state-space, the ocean has to be removed. You can create a precise state-space polygon in ArcGIS and read it into R, or create the polygon directly within R. In the present case we intersected two shape files one of the state of Florida and one of the rectangle defined by a strip of 15 km around the camera-trapping grid. While you will most likely have to obtain the shapefile describing the landscape of and around your trapping grid (coastlines, water bodies etc.) from some external source, a polygon shapefile buffering your outermost trapping grid coordinates can easily be written in R.

If `xmin`, `xmax`, `ymin` and `ymax`, mark the outermost `x` and `y` coordinates of your trapping grid and `b` is the distance you want to buffer with, load the package `shapefiles` (Stabler, 2006) and use:

```

5718 x1= xmin-b
5719 xu= xmax+b
5720 y1= ymin-b
5721 yu= ymax+b
5722
5723 dd <- data.frame(Id=c(1,1,1,1,1),X=c(x1,xu,xu,x1,x1),Y=c(y1,y1,yu,yu,y1)) #create data fra
5724 ddTable <- data.frame(Id=c(1),Name=c("Item1"))
5725 ddShapefile <- convert.to.shapefile(dd, ddTable, "Id", 5) #convert #to shapefile, type pol
5726 write.shapefile(ddShapefile, 'c:/, arcgis=T) # save to location of #choice

```

You can read shapefiles into R loading the package `maptools` (Lewin-Koh et al., 2011) and using the function `readShapeSpatial()`. Make sure you read in shapefiles in UTM format, so that units of the trap array, the movement parameter `sigma` and the state-space are all identical. Intersection of polygons can be done in R also, using the package `rgeos` (Bivand and Rundel, 2011) and the function `gIntersect()`. The area of your single - polygon can be extracted directly from the state-space object `SSp`:

```

5734 > area <- SSp@polygons[[1]]@Polygons[[1]]@area /1000000

```

Note that dividing by 1000000 will return the area in km² if your coordinates describing the polygon are in UTM. If your state-space consists of several disjunct polygons, you will have to sum the areas of all polygons to obtain the size of the state-space. To include this polygon into our MCMC sampler we need one last spatial R package `sp` (Pebesma and Bivand, 2011), which has a function, `over()`,

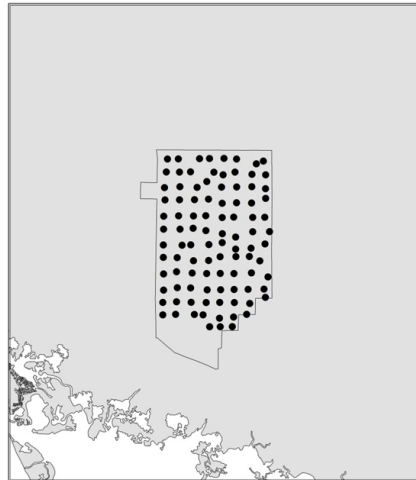


Figure 7.7. Rectangular state-space for a Florida panther camera trapping study in the PSRP area (grey outline, red block inset map of Florida) contain some ocean (white) that needs to be removed from the state-space.

```

5740 which allows us to check if a pair of coordinates falls within a polygon or not. All
5741 we have to do is embed this new check into the updating steps for s:

5742         Scand <- as.matrix(cbind(rnorm(M, S[,1], 2),
5743                                 rnorm(M, S[,2], 2)))          #draw candidate value
5744
5745 Scoord<-SpatialPoints(Scand*1000)      #convert to spatial points on UTM (m) scale
5746 SinPoly<-over(Scoord,SSp) # check if scand is within the polygon
5747
5748         for(i in 1:M) {
5749 if(is.na(SinPoly[i])==FALSE) { #if scand falls within polygon, continue update
5750   [rest of the updating step remains the same]

```

```

5751 Note that it is much more time-efficient to draw all M candidate values for s and
5752 check once if they fall within the state-space, rather than running the over() com-
5753 mand for every individual pair of coordinates. To make sure that our initial values
5754 for s also fall within the polygon of S, we use the function runifpoint() from the
5755 package spatstat (Baddeley and Turner, 2005), which generates random uniform
5756 points within a specified polygon. You'll find this modified MCMC algorithm in
5757 the online supplementary material (SCR0poisSSp). Finally, observe that we are
5758 converting candidate coordinates of S back to meters to match the UTM polygon.
5759 In all previous examples, for both the trap locations and the activity centers we

```

5760 have used UTM coordinates divided by 1000 to estimate sigma on a km scale. This
5761 is adequate for wide ranging individuals like bears. In other cases you may center
5762 all coordinates on 0. No matter what kind of transformation you use on your co-
5763 ordinates , make sure to always convert candidate values for S back to the original
5764 scale (UTM) before running the over() command.

7.8 MCMC SOFTWARE PACKAGES

5765 Throughout most of this book we will use WinBUGS and, occasionally, JAGS to
5766 run MCMC analyses. Here, we will briefly discuss the main pros and cons of these
5767 two programs as well as WinBUGS successor OpenBUGS. You can find scripts to
5768 simulate data and run the basic SCR model in all three programs in the online
5769 supplementary material (simSCR0poisBUGS).

7.8.1 WinBUGS

5770 In a nutshell, WinBUGS (and the other programs) do everything that we just went
5771 through in this chapter (and quite a bit more). Looking through your model, Win-
5772 BUGS determines which parameters it can use standard Gibbs sampling for (i.e.
5773 for conjugate full conditional distributions). Then, it determines, in the following
5774 hierarchy, whether to use adaptive rejection sampling, slice sampling or in the
5775 'worst' case Metropolis-Hastings sampling for the other full conditionals (Spiegel-
5776 halter et al., 2003). If it uses MH sampling, it will automatically tune the updater
5777 so that it works efficiently. While WinBUGS is a convenient piece of software that
5778 is still widely used, its major drawback is that it is no longer being developed, i.e.
5779 no new functions or distributions are added and no bugs are fixed.
5780

7.8.2 OpenBUGS

5781 OpenBUGS is essentially the successor of WinBUGS. While the latter is no longer
5782 worked on, OpenBUGS is constantly developed further. The name 'OpenBUGS'
5783 refers to the software being open source, so users do not need to download a license
5784 key, like they have to for WinBUGS (although the license key for WinBUGS is free
5785 and valid for life).
5786

5787 Compared to WinBUGS, OpenBUGS has a lot more built-in functions. The
5788 method of how to determine the right updater for each model parameter has
5789 changed and the user can manually control the MCMC algorithm used to update
5790 model parameters. Several other changes have been implemented in OpenBUGS
5791 and a detailed list of differences between the two BUGS versions, can be found at
5792 <http://www.openbugs.info/w/OpenVsWin>

5793 While OpenBUGS is a useful program for a lot of MCMC sampling applications,
5794 for reasons we do not understand, simple SCR models do not converge in Open-
5795 BUGS. It is therefore advisable that you check any OpenBUGS SCR model results

against result from WinBUGS. Also, currently, the R package BRugs (Thomas et al., 2006) necessary for running OpenBUGS through R has problems with 64-bit machines, so you may have to use the 32-bit version of R and OpenBUGS in order to make it work. The BUGS project site at <http://www.openbugs.info> provides a lot of information on and download links for OpenBUGS.

There is an extensive help archive for both WinBUGS and OpenBUGS and you can subscribe to a mailing list, where people pose and answer questions of how to use these programs at <http://www.mrc-bsu.cam.ac.uk/bugs/overview/list.shtml>

7.8.3 JAGS Just Another Gibbs Sampler

JAGS, currently at Version 3.1.0, is another free program for analysis of Bayesian hierarchical models using MCMC simulation. Originally, JAGS was the only program using the BUGS language that would run on operating systems other than the 32 bit Windows platforms. By now, there are OpenBUGS versions for Linux or Macintosh machines. JAGS 'only' generates samples from the posterior distribution; analysis of the output is done in R either by running JAGS through R using either the packages `rjags` (Plummer, 2011) or `R2jags` (Su and Yajima, 2011), or by using `coda` on your JAGS output. The program, manuals and `rjags` can be downloaded at <http://sourceforge.net/projects/mcmc-jags/files/> When run from within R using the package `rjags` or `R2jags`, writing a JAGS model is virtually identical to writing a WinBUGS model. However, some functions may have slightly different names and you can look up available functions and their use in the JAGS manual. One potential downside is that JAGS can be very particular when it comes to initial values. These may have to be set as close to truth as possible for the model to start. Although JAGS lets you run several parallel Markov chains, this characteristic interferes with the idea of using overdispersed initial values for the different chains. Also, we have occasionally experienced JAGS to crash and take the R GUI with it. Only re-installing both JAGS and `rjags` seemed to solve this problem. On the plus side, JAGS usually runs a little faster than WinBUGS, sometimes considerably faster (see section 4.XYZ), is constantly being developed and improved and it has a variety of functions that are not available in WinBUGS. For example, JAGS allows you to supply observed data for some deterministic functions of unobserved variables. In BUGS we cannot supply data to logical nodes. Another useful feature is that the adaptive phase of the model (the burn-in) is run separately from the sampling from the stationary Markov chains. This allows you to easily add more iterations to the adaptive phase if necessary without the need to start from 0. There are other, more subtle differences and there is an entire manual section on differences between JAGS and OpenBUGS. For questions and problems there is a JAGS forum online at <http://sourceforge.net/projects/mcmc-jags/forums/forum/610037>.

¹¹

¹¹As we make progress on the book, let's be sure to add linkages to places where we use JAGS in examples.

7.9 SUMMARY AND OUTLOOK

While there are a number of flexible and extremely useful software packages to perform MCMC simulations, it sometimes is more efficient to develop your own MCMC algorithm. Building an MCMC code follows three basic steps: Identify your model including priors and express full conditional distributions for each model parameter. If full conditionals are parametric distributions, use Gibbs sampling to draw candidate parameter values from this distributions; otherwise use Metropolis-Hastings sampling to draw candidate values from a proposal distribution and accept or reject them based on their posterior probability densities. These custom-made MCMC algorithms give you more modeling flexibility than existing software packages, especially when it comes to handling the state-space: In BUGS (and JAGS for that matter) we define a continuous rectangular state-space using the corner coordinates to constrain the Uniform priors on the activity centers s . But what if a continuous rectangle isn't an adequate description of the state-space? In this chapter we saw that in R it only takes a few lines of code to use any arbitrary polygon shapefile as the state-space, which is especially useful when you are dealing with coastlines or large bodies of water that need removing from the state-space. Another example is the SCR R package SPACECAP (Gopalaswamy et al., 2011) that was developed because implementation of an SCR model with a discrete state-space was inefficient in WinBUGS. Another situations in which using BUGS/JAGS becomes increasingly complicated or inefficient is when using point processes other than the Uniform Poisson point process which underlies the basic SCR model (see Chapter X). In the Chapters 9 and XX you will see examples of different point processes, implemented using custom-made MCMC algorithms.¹² Finally, the Chapters XX and XX deal with unmarked or partially marked populations using hand-made MCMC algorithms to handle the (partially) latent individual encounter histories. While some of these models can be written in BUGS/JAGS,¹³ they are painstakingly slow; others cannot be implemented in BUGS/JAGS at all. In conclusion, while you can certainly get by using BUGS/JAGS for standard SCR models, knowing how to write your own MCMC sampler allows you to tailor these models to your specific needs.

¹²Richard, Beth expand on that?

¹³the Poisson one for partially marked we wrote in BUGS and it should work with a known number of marked; the Bernoulli in JAGS with the `dsum()` function should work for the fully unknown; maybe some others? I don't remember. We may have to try writing the others before saying that they don't work in BUGS/JAGS; they are certainly much faster in R, though.

8

5865

5866

5867

GOODNESS OF FIT AND STUFF

9

5868
5869
5870

COVARIATE MODELS

STATE-SPACE COVARIATES

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

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

In this chapter we will present a method for fitting inhomogeneous binomial point process models using covariates in much the same way as is done with GLMs. The covariates we consider differ from those covered in previous chapters, which were typically attributes of the animal (*e.g.* sex, age) and were used to model movement or encounter rate. In contrast, here we wish to model covariates that

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

are defined for all points in \mathcal{S} , which we will refer to as state-space, or density, covariates. These may include continuous covariates such as elevation, or discrete covariates such as habitat type.

Borchers and Efford (2008) were the first to propose an inhomogeneous point process model for SCR models, and our approach is similar to theirs with the exception that we will use a binomial rather than a Poisson model because the binomial model is easily integrated into our data augmentation scheme and is consistent with the objective of determining how a *fixed* number of activity centers are distributed with respect to covariates.

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

10.1 HOMOGENEOUS POINT PROCESS REVISITED

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

```

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

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

```

5938 Note that in both models, the N points are independent of one another and
 5939 distributed uniformly throughout \mathcal{S} . Thus, the intensity at any point $x \in \mathcal{S}$ is
 5940 $\mu = 1/A(\mathcal{S})$ where $A(\mathcal{S})$ denotes the area of the state-space. In the **R** code above,
 5941 the area of the state-space is 1 unit, and thus the intensity is $\mu = 1/1$.

5942 Although the Poisson model is typically described in terms of μ , the binomial
 5943 model is not; rather, it is more common to consider a discrete state space, such
 5944 as a grid with with K pixels. Under the binomial model, the number of points
 5945 in each region is $n(B_k) \sim \text{Bin}(N, p_k)$ where $p_k = A(B_k)/A(\mathcal{S})$, ie p_k is simply the
 5946 fraction of the state-space area in B_k . This discrete space representation of the
 5947 binomial point process is shown in Fig. 10.1. The state-space in this case is the
 5948 unit square, and thus the probability of a point falling in each of the 25 disjunct
 5949 regions is $p_k = 1/25$ and thus the expected counts are simply $\mathbb{E}(n(B_k)) = Np_k$. In
 5950 the figure $N = 50$ and thus we would expect 2 points per pixel, which happens to be
 5951 the empirical mean of the data in Fig. 10.1. Note also that these counts are not in-
 5952 dependent realizations from a binomial distribution since $\sum_k n(B_k) = N$. Instead,
 5953 the model for the entire vector is $\mathbf{n}(\mathbf{B}) \sim \text{Multinomial}(N, \pi = (p_1, p_2, \dots, p_K))$
 5954 (Illian, 2008b). The dependence among counts has virtually no practical conse-
 5955 quence when the number of pixels is large. For example, if we have 100 pixels,
 5956 the number of counts in one pixels tells you very little about the expected count
 5957 in another pixel. However, if there are only 2 pixels, then clearly the number of
 5958 points in one pixel tells you exactly how many will occur in the remaining pixel. To
 5959 gain familiarity with the multinomial distribution and the discrete representation of
 5960 space, use the `rmultinom` function in **R** to simulate counts similar to those shown
 5961 in Fig. 10.1, for example using a command such as:

```
5962 n.B_k <- rmultinom(1, size=50, prob=rep(1/25, 25))
5963 matrix(n.B_k, 5, 5)
```

5964 The discrete space representation of the binomial point process is of practical
 5965 importance when fitting SCR models because spatial covariates are almost always
 5966 represented in a discrete format, often called “rasters” in GIS-speak. In such cases,
 5967 we often need to change our definition of the prior for an activity center from
 5968 $s_i \sim \text{Uniform}(\mathcal{S})$ to $s_i \sim \text{Multinomial}(1, \pi)$. In the latter case, the activity
 5969 center is simply defined as an integer representing pixel “id”. Note also that the
 5970 multinomial distribution with an index of 1 (*i.e.* `size=1` in `rmultinom`) is referred
 5971 to as the categorical distribution, which we will frequently use in the BUGS language.

10.2 INHOMOGENEOUS BINOMIAL POINT PROCESS

5972 As with the homogeneous model, the inhomogeneous binomial point process model
 5973 is developed conditional on N . The primary distinction is that the uniform distri-
 5974 bution is replaced with another distribution allowing for the intensity parameter to
 5975 vary spatially. To arrive at this new distribution, define $\mu(x, \beta)$ to be a function of

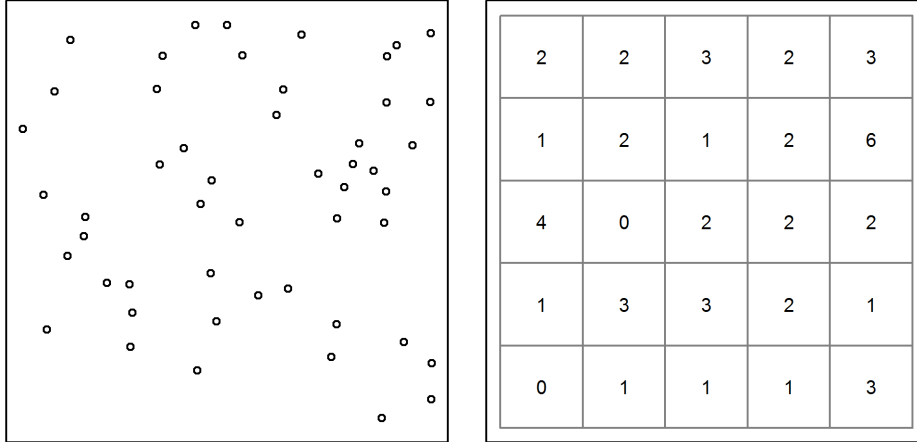


Figure 10.1. Homogeneous binomial point process with $N=50$ points represented in continuous and discrete space.

spatially-referenced covariates (β) available at all points of the state space. To be
concise we will subsequently drop the vector of coefficients from our notation, and
simply use $\mu(x)$. Since an intensity must be strictly positive, it is natural to model
 $\mu(x)$ using the log-link.

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

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

Now that we have a model of the intensity parameter $\mu(x)$, we need to develop
the associated probability density function to use in place of the uniform prior.
Remembering that the integral of a pdf must be unity, we can create a pdf by
dividing $\mu(x)$ by a normalizing constant, which in this case is the integral of $\mu(x)$
evaluated over the entire state-space. **ANDY, is there a better justification for this?**

5994 The probability density function is therefore

$$f(x) = \frac{\mu(x)}{\int_{x \in S} \mu(x) dx} \quad (10.2.1)$$

5995 Substituting this distribution for the uniform prior allows us to fit inhomogeneous
 5996 binomial point process models to spatial capture-recapture data. We can also use
 5997 this distribution to obtain the expected number of individuals in any given region.
 5998 Specifically, the proportion of N expected to occur in any region B when hetero-
 5999 geneity in density is present is $p(B) = \int_B f(x) dx$. These are also the multinomial
 6000 cell probabilities if the regions are disjoint and compose the entire state-space.

6001 As a practical matter, note that the integral in the denominator of $f(x)$ is
 6002 evaluated over space, and since we almost always regard space as two-dimensional,
 6003 this is a two-dimensional integral that can be approximated using the methods
 6004 discussed in refChXXX. These methods include Monte Carlo integration, Gaussian
 6005 quadrature, etc... Alternatively, if our state-space covariates are in raster format,
 6006 *i.e* they are in discrete space, the integral can be replaced with a sum over all pixels,
 6007 which is much more efficient computationally.

6008 We now have all the tools needed to fit inhomogeneous point process (IPP)
 6009 models. Before doing so, we note that the IPP for the activity centers results in
 6010 another IPP for the observation process, $\lambda(x)$. As a reminder, $\lambda(x)$ is the expected
 6011 number of captures for a trap at point x . As was true for the homogeneous model,
 6012 this intensity function is a product of the point process intensity and the encounter
 6013 rate function, $\lambda(x) = \mu(x)g(x)$.

6014 In the next section we walk through a few examples, building up from the
 6015 simplest case where we actually observe the activity centers as though they were
 6016 data. In the second example, we fit our new model to simulated data in which
 6017 density is a function of a single continuous covariate. Example three shows an
 6018 analysis in discrete space using both **secr** (Efford, 2011) and **JAGS** (Plummer,
 6019 2003). In the last example, we model the intensity of activity centers for a real
 6020 dataset collected on jaguars (*Panthera onca*) in Argentina.

10.3 EXAMPLES

6021 10.3.1 Simulation and analysis of inhomogeneous point processes

6022 In SCR models, the point process is not directly observed, but in other contexts
 6023 it is. Examples include the locations of disease outbreaks or the locations of trees
 6024 in a forest. Fitting inhomogeneous point process models to such data is straight-
 6025 forward and illustrates the fundamental process that we will later embed in our
 6026 MCMC algorithm used to fit SCR models.

6027 Suppose we knew the locations of 100 animals' activity centers. To estimate
 6028 the intensity surface $\mu(x)$ underlying these points, we need to derive the likelihood
 6029 for our data under this model. Given the pdf $f(x)$ (Eq. 10.2.1) and assuming that

the points are mutually independent of one another, we may write the likelihood as the product of R such terms, where $R = 100$ is the sample size in this case, *ie* the observed number of activity centers.

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

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

First, let's simulate some data. Simulating data under an inhomogeneous point process model is often accomplished using indirect methods such as rejection sampling. Rejection sampling proceeds by simulating data from a standard distribution and then accepting or rejecting each sample using probabilities defined by the distribution of interest. For more information, readers should consult an accessible text such as Robert and Casella (2004). In our example, we simulate from a uniform distribution and then accept or reject using the (scaled) probability density function $f(x)$. Note that we first define a spatial covariate (elevation) that is a simple function of the spatial coordinates increasing from the southwest to the northeast of our state-space.²

The following **R** commands demonstrate the use of rejection sampling to simulate an inhomogeneous point process for the covariate depicted in Fig. 10.3.1. The code uses the **cuhre** function in the **R2Cuba** package to integrate the intensity function over space (Hahn et al., 2011).

```
# spatial covariate (with mean 0)
elev.fn <- function(x) x[1]+x[2]-1
# intensity function
mu <- function(x, beta) exp(beta*elev.fn(x=x))

# Simulate PP using rejection sampling
set.seed(300225)
N <- 100
count <- 1
s <- matrix(NA, N, 2)
beta <- 2 # parameter of interest
int.mu <- R2Cuba::cuhre(2, 1, mu, beta=beta)$value
elev.min <- elev.fn(c(0,0)) #elev.fn(cbind(0,0))
elev.max <- elev.fn(c(1,1)) #elev.fn(cbind(1,1))
Q <- max(c(exp(beta*elev.min) / int.mu, #2d(beta),
           exp(beta*elev.max) / int.mu)) #2d(beta))
while(count <= 100) {
```

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

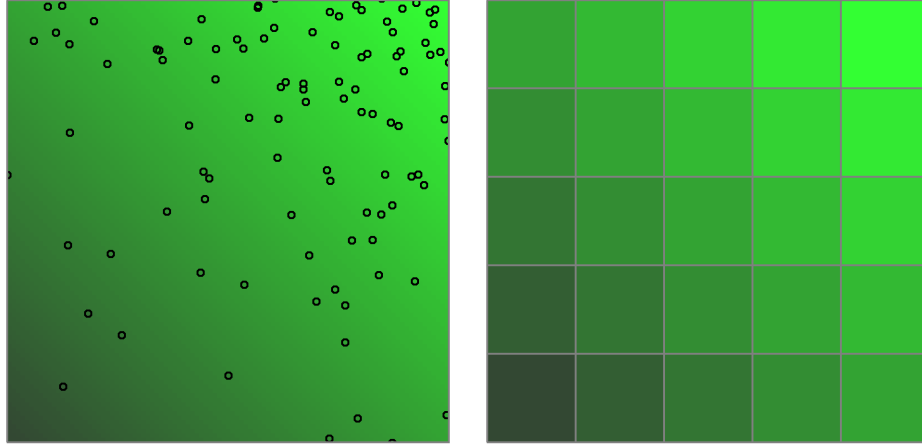


Figure 10.2. An example of a spatial covariate, say elevation, and a realization of an inhomogeneous binomial point process with $N=100$ and $\mu(x) = \exp(\beta \text{Elev})$ where $\beta = 2$.

```

6067 x.c <- runif(1, 0, 1); y.c <- runif(1, 0, 1)
6068 s.cand <- c(x.c,y.c)
6069 pr <- exp(beta*elev.fn(s.cand)) / int.mu #2d(beta)
6070 if(runif(1) < pr/Q) {
6071   s[count,] <- s.cand
6072   count <- count+1
6073 }
6074 }

```

6075 The simulated data are shown in Fig 10.3.1. High elevations are represented by
 6076 light green and low elevations by dark green. The activity centers of one hundred
 6077 animals are shown as points, and it is clear that these simulated animals prefer the
 6078 high elevations. Perhaps they are mountain goats. The underlying model describing
 6079 this preference is $\log(\mu(x)) = \exp(\beta \times \text{Elevation}(x))$ where $\beta = 2$ is the parameter
 6080 to be estimated and $\text{Elevation}(x)$ is a function of the coordinates at x , as displayed
 6081 on the map.

6082 Given these points, we will now estimate β by minimizing the negative-log-
 6083 likelihood using R's `optim` function.

```

6084 # Negative log-likelihood
6085 nll <- function(beta) {
6086   int.mu <- cuhre(2, 1, mu, beta=beta)$value
6087   -sum(beta*elev.fn(s) - log(int.mu))

```

```

6088 }
6089 starting.value <- 0
6090 fm <- optim(starting.value, nll, method="Brent",
6091             lower=-5, upper=5, hessian=TRUE)
6092 c(Est=fm$par, SE=sqrt(1/fm$hessian)) # estimates and SEs

```

6093 Maximizing the likelihood took a small fraction of a second, and we obtained
 6094 an estimate of $\hat{\beta} = 1.99$. We could plug in this estimate to our linear model at each
 6095 point in the state-space to obtain the MLE for the intensity surface.

6096 This example demonstrates that if we had the data we wish we had, *i.e.* if we
 6097 knew the coordinates of the activity centers, we could easily estimate the parameters
 6098 governing the underlying point process. Unfortunately, in SCR models, the activity
 6099 centers cannot be directly observed, but spatial re-captures, that is captures of
 6100 individuals at multiple locations in space, provide us with the information needed
 6101 to estimate these latent parameters.

6102 10.3.2 Fitting inhomogeneous point process SCR models

6103 Continuous space

6104 One of the nice things about hierarchical models is that they allow us to break a
 6105 problem up into a series of simple conditional relationships. Thus, we can simply
 6106 add the methods described above into our existing MCMC algorithm to simulate
 6107 the posteriors of β conditional on the simulated values of \mathbf{s}_i . To demonstrate, we
 6108 will continue with the previous example. Specifically, we will overlay a grid of
 6109 traps upon the map shown in Fig. 10.3.1. We will then simulate capture histories
 6110 conditional upon the activity centers shown on the map. Then, we will attempt to
 6111 estimate the activity center locations as though we did not know where they were,
 6112 as is the case in real applications.

6113 Here is some **R** code to simulate the encounter histories under a Poisson ob-
 6114 servation model, which would be appropriate if animals could be detected multiple
 6115 times at a trap during a single occasion.

```

6116 # Create trap locations
6117 xsp <- seq(-0.8, 0.8, by=0.2)
6118 len <- length(xsp)
6119 X <- cbind(rep(xsp, each=len), rep(xsp, times=len))
6120
6121 # Simulate capture histories, and augment the data
6122 ntraps <- nrow(X)
6123 T <- 5
6124 y <- array(NA, c(N, ntraps, T))
6125
6126 nz <- 50 # augmentation
6127 M <- nz+nrow(y)
6128 yz <- array(0, c(M, ntraps, T))

```

```

6129
6130 sigma <- 0.1 # half-normal scale parameter
6131 lam0 <- 0.5 # basal encounter rate
6132 lam <- matrix(NA, N, ntraps)
6133
6134 set.seed(5588)
6135 for(i in 1:N) {
6136   for(j in 1:ntraps) {
6137     distSq <- (s[i,1]-X[j,1])^2 + (s[i,2] - X[j,2])^2
6138     lam[i,j] <- exp(-distSq/(2*sigma^2)) * lam0
6139     y[i,j,] <- rpois(T, lam[i,j])
6140   }
6141 }
6142 yz[1:nrow(y),,] <- y # Fill

```

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

```

6150 D1 <- cuhre(2, 1, mu, lower=c(xlims[1], ylims[1]),
6151             upper=c(xlims[2], ylims[2]), beta=beta1)$value
6152 beta1.cand <- rnorm(1, beta1, tune[3])
6153 D1.cand <- cuhre(2, 1, mu, lower=c(xlims[1], ylims[1]),
6154                 upper=c(xlims[2], ylims[2]), beta=beta1.cand)$value
6155 ll.beta1 <- sum( beta1*elev.fn.v(S) - log(D1) )
6156 ll.beta1.cand <- sum( beta1.cand*elev.fn.v(S) - log(D1.cand) )
6157 if(runif(1) < exp(ll.beta1.cand - ll.beta1) ) {
6158   beta1 <- beta1.cand
6159 }

```

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

```

6161 #ln(prior), denominator is constant
6162 prior.S <- beta1*cov(S[i,1], S[i,2]) # - log(D1)
6163 prior.S.cand <- beta1*(Scand[1] + Scand[2]) # - log(D1)
6164 if(runif(1) < exp((ll.S.cand+prior.S.cand) - (ll.S+prior.S))) {
6165   S[i,] <- Scand
6166   lam <- lam.cand
6167   D[i,] <- dtmp
6168 }

```

We can apply this modified sampler to our data using the code shown in the help file for **scrIPP**. We obtain posterior distributions summarized in Table 10.2.

Mixing is good, and as usual, life is very nice when we are working with simulated data.

Fitting continuous space IPP models is somewhat difficult in **BUGS** because our prior $f(x)$ is not one of the available distributions that come with the software³ **secr** allows users to fit continuous space using polynomials of the x- and y- coordinates, but not for truly continuous covariates. However, these are not really important limitations because discrete space versions are straight-forward, and virtually all spatial covariates are defined as such.

Discrete space

To fit discrete space models, we follow the same steps as outlined in Chapter XXX—we define s_i as pixel ID, and we use the categorical distribution as a prior. A good example of this is in +citeKery capricaille. Here we present an analysis of the simulated data shown in the right panel of Fig. 10.3.1. The spatial covariate, let's call it elevation again, was simulated from a kriging type of model as shown on the help page `ch9simData` in `scrbook`. The points are the number of activity centers in each pixel, generated from a single realization of the IPP $mu(x) = 2elev$.

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

```

model{
  sigma ~ dunif(0, 1)
  lam0 ~ dunif(0, 5)
  beta ~ dnorm(0,0.1)
  psi ~ dbeta(1,1)

  for(j in 1:nPix) {
    theta[j] <- exp(beta*elevation[j])
    probs[j] <- theta[j]/sum(theta[])
  }

  for(i in 1:M) {
    w[i] ~ dbern(psi)
    s[i] ~ dcat(probs[])
    x0g[i] <- Sgrid[s[i],1]
  }
}
```

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

Table 10.1. Posterior summaries from inhomogeneous point proces model

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

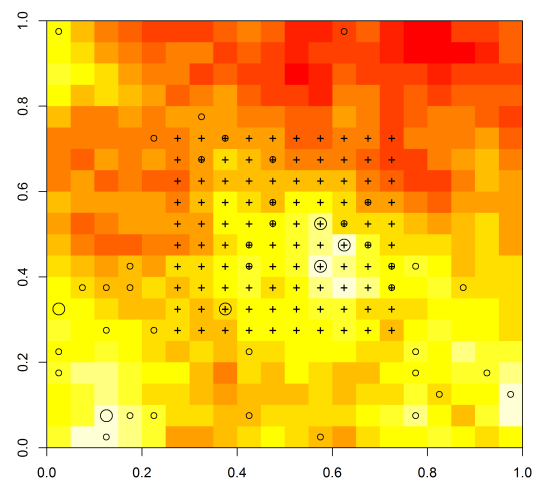


Figure 10.3. Simulated activity centers in discrete space. The spatial covariate, elevation, is highest in the higher areas. Density of activity centers (circles) increases with elevation. Trap locations are shown as crosses.

```

6204   y0g[i] <- Sgrid[s[i],2]
6205   for(j in 1:ntraps) {
6206     dist[i,j] <- sqrt(pow(x0g[i]-grid[j,1],2) + pow(y0g[i]-grid[j,2],2))
6207     lambda[i,j] <- lam0*exp(-dist[i,j]*dist[i,j]/(2*sigma*sigma)) * w[i]
6208     y[i,j] ~ dpois(lambda[i,j])
6209   }
6210 }
6211
6212 N <- sum(w[])
6213 Density <- N/1 # unit square
6214 }

```

6215 This model can also be fit in **secr**, which refers to the pixel locations as a
 6216 “mask”. **R** code to fit the models using **secr** and **JAGS** is available in **scrbook** ,
 6217 see **help(ch9secrYjags)**. Results of the comparison are shown in Table ?? and
 6218 are very similar as expected.

6219 Density surface maps can be created for fun, and of course to inform manage-
 6220 ment decisions. [describe how to do this]

6221 10.3.3 The jaguar data

6222 Estimating density of large felines has been a priority for many conservation orga-
 6223 nizations, but no robust methodologies existed before the advent of SCR. Distance
 6224 sampling is not feasible for such rare and cryptic species, and traditional capture-
 6225 recapture methods yield estimates that are highly sensitive to the subjective choice
 6226 of the effective survey area. In this example, we demonstrate how readily density
 6227 can be estimated for a globally imperilled species using SCR. Furthermore, we show
 6228 how inhomogeneous point process models can be used to test important hypotheses
 6229 regarding the factors affecting density.

6230 [describe study]

6231 A few aspects of this design are noteworthy. First, the dimensions and config-
 6232 uration of the trap array differed among the regions of the trap array. This fact
 6233 alone could explain variation in the number of animals exposed to sampling, which

Table 10.2. Comparison of **secr** and **JAGS** results

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

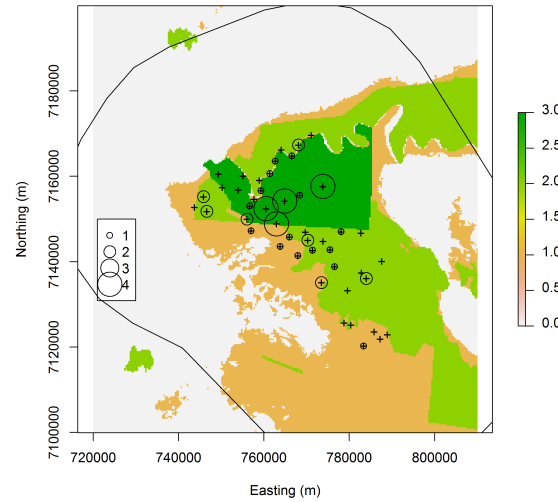


Figure 10.4. Jaguar detections

would have no biological meaning. Furthermore, the area of inference is an irregular polygon that was not sampled uniformly. Only by estimating density can we hope to extrapolate our estimates from the sampled region to get what we are after. In this case, this is readily accomplished since the entire state-space can be classified as one of the 3 levels of protection from poaching. Of course, it general it is always preferable to sample more uniformly throughout the area of interest in case some unmeasured covariate biases the extrapolation.

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

10.4 SUMMARY

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

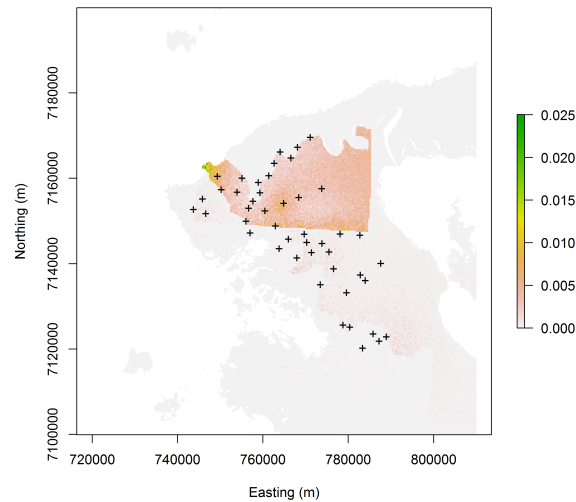


Figure 10.5. Estimated density surface for the jaguar dataset

6252 and found in the package `scrbook`.

6253 All the examples in this section included a single state-space covariate, but this
 6254 was for simplicity only. Including multiple covariates poses no additional challenges.
 6255 Likewise, additional model structure such sex-specific encounter rate parameters or
 6256 behavioral responses can be accommodated.

10.5 OTHER IDEAS

6257 Should have some discussion on some ideas for building flexible models. Might be
 6258 cool to use the Ickstadt/Wolpert as a model for the inhomogeneous point process.
 6259 Dont have to do it, just mention it. Also some kind of a spline model or similar.

11

6260

6261

6262

INHOMOGENEOUS POINT PROCESS

12

OPEN MODELS

6263
6264
6265

SPATIAL CAPTURE-RECAPTURE FOR UNMARKED POPULATIONS

Traditional capture-recapture models share the fundamental assumption that each individual in a population can be uniquely identified when captured. This can often be accomplished by marking individuals with color bands, ear tags, or some other artificial mark that can be read in the field. For other species, such as tigers or marbled salamanders, individuals can be easily identified using only their natural markings. In a great number of cases, however, species do not possess sufficient natural markings and are too difficult to capture to make it practical to apply artificial marks. So we must throw up our hands and not study these species. End of chapter.

When capture-recapture methods are not a viable option, researchers often collect simple count data or even detection/non-detection data to estimate population parameters. These data are often analyzed using Poisson regression or logistic regression, perhaps with random effects; but when detection is imperfect, as it almost always is, these methods cannot be used to obtain unbiased estimates of population size or occurrence probability. Even when these data are used as an index of abundance or occurrence, standard models may yield unreliable results when covariates affect both the state variable and detection probability. A classic example is the finding by Bibby and Buckland (1987) who reported that the probability of detecting songbirds in restocked conifer plantations decreased with vegetation height; whereas population density was positively related to vegetation height. This intuitive and common phenomenon has led to the development of a vast number of methods to model population size or density while controlling for factors affecting detection probability. A review of these models is beyond the scope of this chapter, but we mention a few deficiencies of existing methods that warrant the exploration of alternatives.

Distance sampling, which we briefly introduced in chapter XXXX, is perhaps the most widely used method for estimating population density when individuals are unmarked and detection probability is less than one. This class of methods is known to work impeccably when estimating the number of stakes in a field or the number of duck nests in a wetland. It can also work very well in more interesting situations; however, common issues such as animal movement and measurement error may result in substantial bias. In addition, traditional distance sampling methods assume that individuals are randomly located with respect to the observer and are available for detection (but see Johnson (2010); Chandler et al. (2011)). Most other methods, such as double-observer sampling and repeated counts, can be used to estimate population size, but as with traditional CR methods, it may be difficult to convert abundance estimates to density estimates because the effective area sampled is unknown. We mention these issues not to suggest that existing models do not have value—indeed we believe that they can be used to obtain reliable density estimates in many situations—rather our aim to highlight the need for alternative methods when the assumptions of existing methods cannot be met. Additionally, the model we develop in this chapter serves as the foundation for a broad class of SCR models in which all or some of the individuals cannot be uniquely identified.

In this chapter we highlight the work of Chandler and Royle (2012) who demonstrated that the individual recognition assumption of CR models is not a requirement of spatial capture-recapture models. The ability to fit SCR models to data from unmarked populations has important consequences in several respects. For one, it means that SCR models can be applied to data collected using methods like points counts in which observers record simple counts of animals at an array of survey points. This development also has important implications for traditional SCR studies because many resulting datasets include some individuals that cannot be identified due to poor photo quality or the indistinguishable natural markings.

In order to apply SCR models to data collected unmarked animals, one requirement is critical—counts must be spatially correlated. Of course, this condition holds true in virtually all SCR models since animals are often detected at more than one trap. In fact, efficient SCR designs should try to ensure correlation in counts among neighboring traps because this is the primary source of information about the encounter rate parameter, σ .

13.1 DATA REQUIREMENTS AND SURVEY DESIGNS

13.2 ENCOUNTER HISTORIES AS LATENT VARIABLES

Just when you thought we ran out of things to treat as latent variables, we are now going to regard even the data itself as latent.

State model is the same as other SCR models.

It is natural to regard the encounter rate of an individual as a function of the

Euclidean distance between the individual's activity center and the trap location, $d_{ir} = \|\mathbf{x}_i - \mathbf{s}_r\|$. To be precise about this, we let z_{irt} be the encounter frequency of individual i in trap r during occasion t . While we will adopt the view that the variables z_{irt} are latent variables (see below), it will be convenient to formulate the model in terms of these variables.

Therefore, we assume that the expected encounter frequency of an individual in some trap is related to d_{ir} as follows:

$$E[z_{irt}] = \lambda_{ir} = \lambda_0 k_{ir}$$

where λ_0 is the expected encounter rate at $d = 0$ and k_{ir} is some positive-valued function of distance d_{ir} . We assume

$$k_{ir} = \exp(-d_{ir}^2/2\sigma^2)$$

where σ is a scale parameter related to home range size. σ also determines the degree of correlation among counts since animals with large home ranges are more likely to be detected at multiple traps relative animals with small home ranges. The phenomenon is analogous to correlation induced by averaging spatial noise, in which case there is a unique correlation between the smoothing kernel and the induced covariance function (Higdon, 2002).

We emphasize that our focus is on situations in which individuals are *not* uniquely identifiable, and therefore the encounter frequencies for each individual cannot be observed, and so they are latent variables. We assume that these latent variables are realizations from a Poisson distribution with mean λ_{ir} :

$$z_{irt} \sim \text{Poisson}(\lambda_{ir}). \quad (13.2.1)$$

In traditional SCR models, z_{irt} are the observed data, *i.e.*, the frequency of encounters of individual i at trap r on replicate survey t . However, when individual identity is not known, the observed data are the sample- and trap-specific totals, aggregated over all individuals:

$$n_{rt} = \sum_{i=1}^N z_{irt}.$$

Thus the data required by our model are a reduced-information summary of the latent encounter histories.

Under the Poisson encounter model we have that

$$n_{rt} \sim \text{Poisson}(\Lambda_r) \quad (13.2.2)$$

where

$$\Lambda_r = \lambda_0 \sum_i k_{ir}.$$

Further, because Λ_r does not depend on t , we can aggregate the replicated counts, defining $n_r. = \sum_t n_{rt}$ and then

$$n_r. \sim \text{Poisson}(T\Lambda_r)$$

As such, T and λ_0 serve equivalent roles as affecting baseline encounter rate. This formulation of the model in terms of the aggregate count simplifies computations as the latent variables z_{irt} do not need to be updated in the MCMC estimation scheme (see below). However, retaining z_{irt} in the formulation of the model is important if some individuals are uniquely marked, in which case modifying the MCMC algorithm (see below) to include both types of data is trivial. This is because uniquely identifiable individuals produce observations of some of the z_{irt} variables.

We imagine that other observation models might be possible (see Discussion) although we focus here on the Poisson encounter model because it has considerable relevance to animal surveys, and has additional methodological context related to point process models which we address in the Discussion.

13.3 ESTIMATION BY MCMC

We adopt a Bayesian framework for inference allowing estimation of N while retaining the formulation of the model that is conditional on the latent activity centers \mathbf{s}_i . Specifically, we employ Markov chain Monte Carlo (MCMC) to simulate posterior distributions of the parameters. However, the fact that N is unknown presents a technical challenge because the size of the parameter space can change with each MC iteration. To resolve this, we adopt the formulation of data augmentation in Royle et al. (2007) who used a specific prior construction for N in terms of individual level Bernoulli trials. In particular, we assume $N \sim \text{Unif}(0, M)$ for some large integer M . We construct this prior by assuming $N|M, \phi \sim \text{Bin}(M, \phi)$ and $\phi \sim \text{DUnif}(0, 1)$ which implies, marginally, that N has the requisite $\text{DUnif}(0, M)$ distribution. However the hierarchical formulation of the prior suggests an implementation in which we introduce a set of latent indicator variables $w_i \sim \text{Bern}(\phi)$ and, furthermore, the model implies that z_{irt} are obtained from the specified distribution (Eq. 13.2.1) if $w_i = 1$, or if $w_i = 0$, $z_{irt} = 0$ with probability 1. In effect, extending the model in this way induces a reparameterization for the latent counts that is a zero-inflated version of the original conditional-on- N model. Specifically, the model under data augmentation becomes

$$\begin{aligned} z_{irt}|w_i &\sim \text{Poisson}(\lambda_{ir}w_i) \\ w_i &\sim \text{Bern}(\phi) \end{aligned}$$

Under this formulation $N = \sum_{i=1}^M w_i$, and population density is simply $D = N/A(\mathcal{S})$ where $A(\mathcal{S})$ is the area of the point process state-space \mathcal{S} .

We developed two distinct MCMC implementations for this model (??). In the first, we devised an algorithm for the model conditional on the latent variables z_{irt} . This formulation is useful for problems in which one or more individual identities are available, in which case the z_{irt} are observable for those individuals. The unobserved z_{irt} are easily updated using their full-conditional distribution which is multinomial with sample size n_{rt} . The remaining parameters are updated using Metropolis-Hastings steps (see ??). In the second formulation of the algorithm we applied the Metropolis-Hastings algorithm to the model *unconditional* on the z_{irt} variables. In that case, the marginal distribution for n_{rt} is precisely Eq. 13.2.2. This algorithm is slightly more convenient because it avoids having to update the z_{irt} variables of which there are many.

13.4 NORTHERN PARULA EXAMPLE

To apply our model to data collected in the field, we designed a point count study of the northern parula (*Parula americana*), a Neotropical-Nearctic migratory passerine. This species defends well-defined territories during the breeding season (?), and thus our modeling effort was focused on estimating the number and location of territory centers. Points were located on a 50-m grid to ensure spatial correlation. This small grid spacing contrasts with the conventional practice of spacing points by > 200 m to obtain *i.i.d.* counts. Figure 13.1 depicts the spatially-correlated counts (n_r) from the 105 point count locations surveyed three times each during June 2006 at the Patuxent Wildlife Research Center in Laurel Maryland, USA. A total of 226 detections were made with a maximum count of 4 during a single survey. At 38 points, no warblers were detected. All but one of the detections were of singing males, and this one observation was not included in the analysis.

In our analysis of the parula data, we defined the point process state-space by buffering the grid of point count locations by 250 m and used $M = 300$. We simulated posterior distributions using three Markov chains, each consisting of 300000 iterations after discarding the initial 10000 draws. Convergence was satisfactory, as indicated by an \hat{R} statistic of < 1.02 (Gelman and Rubin, 1992).

One benefit of a Bayesian analysis is that it can accommodate prior information on the home range size and encounter rate parameters, which are readily available for many species. To illustrate, we analyzed the parula data using two sets of priors. In the first set, all priors were improper, customary non-informative priors (see Table 13.1). Uniform priors were also used in the second set, with the exception of an informative prior for the scale parameter $\sigma \sim \text{Gamma}(13, 10)$. We arrived at this prior using the methods described by Royle et al. (2011b) and published information on the warbler's home range size and detection probability (Simons et al., 2009). More details on this derivation are found in ?. We briefly note here that this prior includes the biologically-plausible range of values from σ suggested by the published literature.

The posterior distribution for N was highly skewed with a long right tail re-

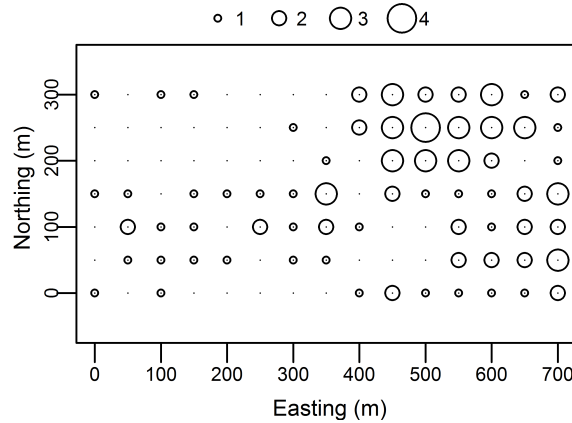


Figure 13.1. Spatially-correlated counts of northern parula on a 50-m grid. The size of the circle represents the total number of detections at each point.

6433 sulting in a wide 95% credible interval (Table 13.1). Nonetheless, the interval for
 6434 density, D , includes estimates reported from more intensive field studies (?). This
 6435 was true when considering both sets of priors, although posterior precision was
 6436 higher under the informative set of priors. Specifically, the use of prior information
 6437 reduced posterior density at high, biologically implausible, values of σ , and hence
 6438 decreased the posterior mass for low values of N (Fig. 13.2).

6439 In addition to estimating density, our model can be used to produce density
 6440 surface maps, which are often used in applied ecological research to direct manage-
 6441 ment efforts and develop hypotheses regarding the factors influencing abundance.
 6442 Density surface maps can be produced by discretized the state-space and tallying
 6443 the number of activity centers occurring in each pixel during each MCMC iteration.
 6444 Parula density was highest near the northeastern corner of the study plot, which
 6445 may correspond to important habitat features such as suitable nest site locations
 6446 (Fig. 13.3). We anticipate future model extensions to directly model the point
 6447 process intensity using habitat covariates.

Table 13.1. Posterior summary statistics for spatial Poisson-count model applied to the northern parula data. Two sets of priors were considered. $M = 300$ was used in both cases. Parulas/ha, D , is a derived parameter.

Par	Prior	Mean	SD	Mode	q0.025	q0.50	q0.975
σ	$U(0, \infty)$	2.154	1.222	1.230	0.896	1.665	5.170
λ_0	$U(0, \infty)$	0.284	0.149	0.212	0.084	0.256	0.665
N	$U(0, M)$	40.953	38.072	4.000	3.000	31.000	143.000
D	—	0.427	0.397	0.0417	0.0313	0.323	1.490
σ	$G(13, 10)$	1.301	0.258	1.230	0.889	1.266	1.908
λ_0	$U(0, \infty)$	0.298	0.132	0.240	0.098	0.279	0.603
N	$U(0, M)$	59.321	36.489	36.000	18.000	50.000	157.000
D	—	0.618	0.380	0.375	0.188	0.521	1.635

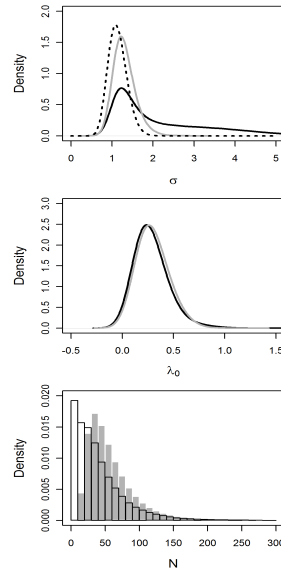


Figure 13.2. Effects of $\sigma \sim \text{Gamma}(13, 10)$ prior on the posterior distributions from the northern parula model. Posteriors from model with uniform priors are shown in black, and posteriors from the informative prior model are shown in gray. The prior itself is shown as dotted line in the upper panel.

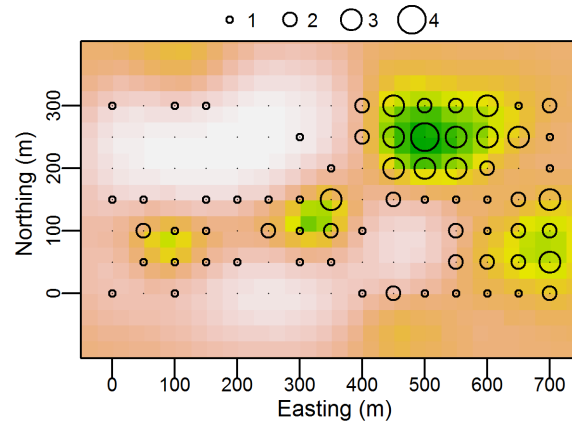


Figure 13.3. Estimated density surface of northern parula activity centers. The grid of point count locations with count totals is superimposed. See Fig. 1 for additional details.

13.5 ON (IM)PRECISION

13.6 HOW MUCH CORRELATION IS ENOUGH?

13.7 MUTANTS

6448 13.7.1 Other observation models

6449 13.7.2 Linear designs

13.8 SUMMARY

6450 In this paper, we confronted one of the most difficult challenges faced in wildlife
 6451 sampling — estimation of density in the absence of data to distinguish among in-
 6452 dividuals. To do so, we developed a novel class of spatially-explicit models that
 6453 applies to spatially organized counts, where the count locations or devices are lo-
 6454 cated sufficiently close together so that individuals are exposed to encounter at
 6455 multiple devices. This design yields correlation in the observed counts, and this
 6456 correlation proves to be informative about encounter probability parameters and
 6457 hence density. We note that sample locations in count-based studies are typically
 6458 *not* organized close together in space because conventional wisdom and standard
 6459 practice dictate that independence of sample units is necessary (Hurlbert, 1984).
 6460 Our model suggests that in some cases it might be advantageous to deviate from
 6461 the conventional wisdom if one is interested in direct inference about density. Of
 6462 course, this is also known in the application of standard spatial capture-recapture
 6463 models (Borchers and Efford, 2008) where individual identity is preserved across
 6464 trap encounters, but it is seldom, if ever, considered in the design of more traditional

count surveys.

Our model has broad relevance to an incredible number of animal sampling problems. Our motivating problem involved bird point counts where individual identity is typically not available. The model also applies to other standard methods used to sample unmarked populations, such as camera traps or even methods that yield sign (*e.g.* scat, track) counts indexed by space. However, results of our simulation study reveal some important limitations of the basic estimator applied to situations in which none of the individuals can be uniquely identified. In particular, posterior distributions are highly skewed in typical small to moderate sample size situations and posterior precision is low.

Several modifications of the model can lead to improved performance of the estimator. Our simulation results demonstrate that marking a subset of individuals can yield substantial increases in posterior precision. Marking a subset of individuals is commonplace in animal studies such as when a small number of individuals are radio-collared in conjunction with a count-based survey (Bartmann et al., 1987). In many other situations a subset of individuals can be identified by natural marks alone, and thus our model could be applied to data from camera-trapping studies of species such as mountain lions, deer, coyotes for which traditional SCR methods are not effective (Kelly et al., 2008). Thus, the ability to study partially-marked populations adds flexibility to existing SCR methods, and also creates new opportunities for designing efficient SCR studies since the costs of marking all individuals in a population can be prohibitive.

We note the existence of traditional approaches to combining data on marked and unmarked animals based on either the Lincoln-Peterson estimator or so-called “mark-resight” methods. (Bartmann et al., 1987; ?; ?). In their simplest form, mark-resight methods involve fitting standard closed-population mark-recapture models to the data on marked individuals, and the resultant estimate of detection probability (\hat{p}) is used to estimate population size as $\hat{N} = m + u/\hat{p}$ where m and u are the number of marked and unmarked individual, respectively. In this case, the unmarked individuals provide no information about the encounter rate parameters, and thus mark-resight methods cannot be used unless a large sample of marked individuals is available. This contrasts with our approach which can be used even when all individuals are unmarked.

In some cases, such as in point counts of birds, it may not be practical to mark individuals. An alternative to increasing posterior precision is to utilize prior information on home range size. Indeed, extensive information on home range size has been compiled for many species in diverse habitats (*e.g.*, DeGraaf and Yamasaki, 2001). It is easy to embody this information in a prior distribution as we demonstrated for the parula data.

An additional design extension that could increase precision is to use multiple sampling methods, in which one method generates encounter frequencies and the other method generates individuality. For example, camera traps are now commonly used with surveys for sign (scat or tracks), or hair snares for sampling bear

populations. These distinct methods would have different basal detection rates but share an underlying spatial model describing the organization of individuals in space. Our models show promise for using these disparate data types efficiently for estimating density.

13.8.1 N -mixture models

Parallel developments which appear ostensibly orthogonal to SCR models have addressed the problem of estimating population size when individuals are unmarked. So-called N -mixture models (Royle, 2004a; ?; ?) can be applied to a repeated-measures type of data structure wherein data are collected at R sites, with J replicate surveys are conducted at each. N -mixture models regard abundance at each site (N_r) as an *i.i.d.* realization of a discrete distribution such as the Poisson or negative binomial with expectation θ . In the standard binomial N -mixture model, the observed counts are treated as binomial outcomes with N_r “trials” and detection probability p .

Although these models have proven useful for studies of factors that affect variation in abundance, interpretation of model parameters is strongly dependent on the assumption that populations are closed with respect to demographic processes and movement. The closure assumption can be an important practical limitation (but see Dail and Madsen, 1999; Chandler et al., 2011). Furthermore the *i.i.d.* assumption is violated if spatial correlation exists among sites, such as if animals move among plots. Although we formulated the model developed in our paper as an extension of spatially explicit capture-recapture models, it clearly can also be viewed as a spatially explicit extension of N -mixture models where the local population sizes N_r are dependent owing to the nature of the sampling design.

Thus, two recently developed methodological frameworks, spatial capture-recapture and N -mixture models, address different problems that arise in sampling animal populations. SCR models address non-closure by accommodating information on the spatial organization of individuals and juxtaposition of individuals with traps, and N -mixture models address inability to uniquely identify individuals. Our model unifies these two modeling frameworks by addressing both issues simultaneously.

13.8.2 Alternative Observation Models

Several aspects of our “spatial N -mixture model” can be modified to accommodate alternative sampling designs or parametric distributions. We considered situations where an individual can be detected more than once at a trap during a single occasion, but under some designs this is not possible. When collecting DNA samples, for instance, an individual can often be detected at most once during an occasion, because multiple samples of biological material cannot be attributed to distinct episodes. Therefore, rather than $z_{irt} \sim \text{Poisson}(\lambda_{ir})$ we have $z_{irt} \sim \text{Bernoulli}(p_{ir})$ where, for example, $p_{ir} = p_0 \exp(-d_{ir}^2/(2\sigma^2))$, and p_0 is the probability of detecting

an individual whose home range is centered on trap r . This Bernoulli model is a focus of ongoing investigations.

Both the Poisson and the Bernoulli models produce count observations when aggregated over individuals to form trap-specific totals; however, ecologists often collect so-called “detection/non-detection” data because it can be easier to determine if “at least one” individual was present rather than enumerating all individuals in a location. In this case, the underlying z_{irt} array is the same as the above cases, but we observe $y_{rt} = I(\sum_{i=1}^N z_{irt} > 0)$ where I is the indicator function. This “Poisson-binary model” is a spatially explicit extension of the model of Royle and Nichols (2003) in which the underlying abundance state is inferred from binary data. We have investigated this model to a limited extent but do not report on those results here.

13.8.3 Spatial point process models

Our model has some direct linkages to existing point process models. We note that the observation intensity function (i.e., corresponding to the observation locations) is a compound Gaussian kernel similar to that of the Thomas process (??, pp. 61-62). Also, the Poisson-Gamma Convolution models (Wolpert and Ickstadt, 1998) are structurally similar (see also Higdon (1998) and Best et al. (2000)). In particular, our model is such a model but with a *constant* basal encounter rate λ_0 and *unknown* number and location of “support points”, which in our case are the animal activity centers, \mathbf{s}_i . We can thus regard our model as a model for *estimating* the location and local density of support points in such models, which we believe could be useful in the application of convolution models. Best et al. (2000) devise an MCMC algorithm for the Poisson-Gamma model based on data augmentation, which is similar to the component of our algorithm for updating the z variables in the conditional-on- z formulation of the model. We emphasize that our model is distinct from these Poisson-Gamma models in that the number *and* location of such support points are estimated.

If individuals were perfectly observable then the resulting point process of locations is clearly a standard Poisson or Binomial (fixed N) cluster process or Neyman-Scott process. If detection is uniform over space but imperfect, then the basic process is unaffected by this random thinning. Our model can therefore be viewed formally as a Poisson (or Binomial) cluster process model but one in which the thinning is non-uniform, governed by the encounter model which dictates that thinning rate increases with distance from the observation points. In addition, our inference objective is, essentially, to estimate the number of parents in the underlying Poisson cluster process, where the observations are biased by an incomplete sampling apparatus (points in space).

As a model of a thinned point process, our model has much in common with classical distance sampling models (Buckland, 2001). The main distinction is that our data structure does *not* include observed distances, although the underlying

6588 observation model is fundamentally the same as in distance sampling if there is
6589 only a single replicate sample and \mathbf{s}_i is defined as an individual's location at an
6590 instant in time. For replicate samples, our model preserves (latent) individuality
6591 across samples and traps which is not a feature of distance sampling. We note
6592 that error in measurement of distance is not a relevant consideration in our model,
6593 and we explicitly do not require the standard distance sampling assumption that
6594 the probability of detection is 1 if an individual occurs at the survey point. More
6595 importantly, distance sampling models cannot be applied to data from many of
6596 the sampling designs for which our model is relevant. For example, many rare
6597 and endangered species can only be effectively surveyed using methods such as hair
6598 snares and camera traps that do not produce distance data (O'Connell et al., 2010).

13.9 CONCLUSION

6599 Concerns about “statistical independence” have prompted ecologists to design count-
6600 based studies such that observed random variables can be regarded as *i.i.d.* out-
6601 comes (Hurlbert, 1984). Interestingly, this often proves impossible in practice, and
6602 elaborate methods have been devised to model spatial dependence as a nuisance
6603 parameter. Our paper presents a modeling framework that directly confronts this
6604 view by demonstrating that spatial correlation carries information about the loca-
6605 tions of individuals, which can be used to estimate density even when individuals
6606 are unmarked and distance-related heterogeneity exists in encounter probability.

BIBLIOGRAPHY

- Alho, J. (1990), “Logistic regression in capture-recapture models,” *Biometrics*, 623–635.
- Arnason (1973), “Missing,” *Missing*, Missing, Missing.
- (1974), “Missing,” *Missing*, Missing, Missing.
- Baddeley, A. and Turner, R. (2005), “Spatstat: an R package for analyzing spatial point patterns,” *Journal of Statistical Software*, 12, 1–42, ISSN 1548-7660.
- Bales, S. L., Hellgren, E. C., Leslie Jr., D. M., and Hemphill Jr., J. (2005), “Dynamics of recolonizing populations of black bears in the Ouachita Mountains of Oklahoma,” *Wildlife Society Bulletin*, 1342–1351.
- Bartmann, R. M., White, G. C., Carpenter, L. H., and Garrott, R. A. (1987), “Aerial Mark-Recapture Estimates of Confined Mule Deer in Pinyon-Juniper Woodland,” *The Journal of Wildlife Management*, 51, 41–46.
- Berger, J. O., Liseo, B., and Wolpert, R. L. (1999), “Integrated likelihood methods for eliminating nuisance parameters,” *Statistical Science*, 1–22.
- Best, N. G., Ickstadt, K., and Wolpert, R. L. (2000), “Spatial Poisson Regression for Health and Exposure Data Measured at Disparate Resolutions,” *Journal of the American Statistical Association*, 95, 1076.
- Bibby, C. and Buckland, S. (1987), “Bias of bird census results due to detectability varying with habitat,” *Acta Ecologica*, 8, 103–112.
- Bivand, R. and Rundel, C. (2011), *rgeos: Interface to Geometry Engine - Open Source (GEOS)*, r package version 0.1-8.
- Borchers, D. and Efford, M. (2008), “Spatially explicit maximum likelihood methods for capture-recapture studies,” *Biometrics*, 64, 377–385.
- Borchers, D. L. (missing), “missing,” *Missing*, missing.
- Borchers, D. L., Buckland, S. T., and Zucchini, W. (2002), *Estimating animal abundance: closed populations*, vol. 13, Springer Verlag.
- Boulanger, J. and McLellan, B. (2001), “Closure violation in DNA-based mark-recapture estimation of grizzly bear populations,” *Canadian Journal of Zoology*, 79, 642–651.
- Brooks, S. P., Catchpole, E. A., and Morgan, B. J. T. (2000), “Bayesian Animal Survival Estimation,” *Statistical Science*, 15, 357–376.
- Buckland, S. T. (2001), *Introduction to distance sampling: estimating abundance of biological populations*, Oxford, UK: Oxford University Press.

- 6642 Burnham, K. P. and Anderson, D. R. (2002), *Model selection and multimodel in-*
6643 *ference: a practical information-theoretic approach*, Springer Verlag.
- 6644 Burnham, K. P. and Overton, W. S. (1978), “Estimation of the size of a closed
6645 population when capture probabilities vary among animals,” *Biometrika*, 65,
6646 625.
- 6647 Casella, G. and George, E. I. (1992), “Explaining the Gibbs sampler,” *American*
6648 *Statistician*, 46, 167–174.
- 6649 Chandler, R. and Royle, J. (2012), “Spatially-explicit models for inference about
6650 density in unmarked populations,” *Biometrics (in review)*.
- 6651 Chandler, R., Royle, J., and King, D. (2011), “Inference about density and tempo-
6652 rary emigration in unmarked populations,” *Ecology*, 92, 1429–1435.
- 6653 Converse, S. J. and Royle, J. A. (2010), “Missing,” *Missing*, Missing.
- 6654 Coull, B. A. and Agresti, A. (1999), “The Use of Mixed Logit Models to Reflect
6655 Heterogeneity in Capture-Recapture Studies,” *Biometrics*, 55, 294–301.
- 6656 Dail, D. and Madsen, L. (????), “Web Supplementary Materials Models for Esti-
6657 mating Population Size from Repeated Counts of an Open Population,” 1, 1–7.
- 6658 Dawson, D. and Efford, M. (2009), “Bird population density estimated from acous-
6659 tic signals,” *Journal of Applied Ecology*, 46, 1201–1209.
- 6660 DeGraaf, R. M. and Yamasaki, M. (2001), *New England wildlife: habitat, natural*
6661 *history, and distribution*, University Press of New England.
- 6662 Dice, L. R. (1938), “Some census methods for mammals,” *Journal of Wildlife Man-*
6663 *agement*, 2, 119–130.
- 6664 Dorazio, R. and Royle, J. (2003), “Mixture models for estimating the size of a closed
6665 population when capture rates vary among individuals,” *Biometrics*, 351–364.
- 6666 Dorazio, R. M. (2007), “On the choice of statistical models for estimating occurrence
6667 and extinction from animal surveys,” *Ecology*, 88, 2773–2782.
- 6668 Durbin and Elston (2012), “Missing,” *Missing*, Missing.
- 6669 Efford, M. (2004), “Density estimation in live-trapping studies,” *Oikos*, 106, 598–
6670 610.
- 6671 — (2011), “secre-spatially explicit capture-recapture in R,” .
- 6672 Efford, M., Dawson, D., and Robbins, C. (2004), “DENSITY: software for analysing
6673 capture-recapture data from passive detector arrays,” *Animal Biodiversity and*
6674 *Conservation*, 217–228.
- 6675 Fienberg, S. E., Johnson, M. S., and Junker, B. W. (1999), “Classical multilevel and
6676 Bayesian approaches to population size estimation using multiple lists,” *Journal*
6677 *of the Royal Statistical Society of London A*, 163, 383–405.
- 6678 Gardner, B. (2009), “missing,” *Missing*, missing.
- 6679 Gardner, B., Royle, J., Wegan, M., Rainbolt, R., and Curtis, P. (2010), “Estimating
6680 black bear density using DNA data from hair snares,” *The Journal of Wildlife*
6681 *Management*, 74, 318–325.
- 6682 Gelfand, A. and Smith, A. (1990), “Sampling-based approaches to calculating
6683 marginal densities,” *Journal of the American statistical association*, 85, 398–409.
- 6684 Gelman, A., Carlin, J. B., Stern, H. S., and Rubin, D. B. (2004), *Bayesian data*

- analysis, second edition., Boca Raton, Florida, USA: CRC/Chapman & Hall.
- Gelman, A., Meng, X. L., and Stern, H. (1996), "Posterior predictive assessment of model fitness via realized discrepancies," *Statistica Sinica*, 6, 733–759.
- Gelman, A. and Rubin, D. B. (1992), "Inference from iterative simulation using multiple sequences," *Statistical Science*, 7, 457–511.
- Geman, S. and Geman, D. (1984), "Stochastic relaxation, Gibbs distributions, and the Bayesian restoration of images," *IEEE Transactions on Pattern Analysis and Machine Intelligence*, PAMI-6, 721–741.
- Genz, A. S., Meyer, M. R., Lumley, T., and Maechler, M. (2007), "The adapt Package. R package version 1.0-4," .
- Gilks, W. and Wild, P. (1992), "Adaptive rejection sampling for Gibbs sampling," *Applied Statistics*, 41, 337–348.
- Gilks, W. R., Thomas, A., and Spiegelhalter, D. J. (1994), "A Language and Program for Complex Bayesian Modelling," *Journal of the Royal Statistical Society. Series D (The Statistician)*, 43, 169–177, ArticleType: primary_article / Issue Title: Special Issue: Conference on Practical Bayesian Statistics, 1992 (3) / Full publication date: 1994 / Copyright 1994 Royal Statistical Society.
- Gopalaswamy (2012), "Missing," *Missing*, missing.
- Gopalaswamy, A. M., Royle, A. J., Hines, J., Singh, P., Jathanna, D., Kumar, N. S., and Karanth, K. U. (2011), *A Program to Estimate Animal Abundance and Density using Spatially-Explicit Capture-Recapture*, r package version 1.0.4.
- Hahn, T., Bouvier, A., and Kieu, K. (2011), "Package 'R2Cuba' R package version 1.0-6," .
- Hastings, W. (1970), "Monte Carlo sampling methods using Markov chains and their applications," *Biometrika*, 57, 97–109.
- Hawkins, C. and Racey, P. (2005), "Low population density of a tropical forest carnivore, *Cryptoprocta ferox*: implications for protected area management," *Oryx*, 39, 35–43.
- Hestbeck (1991), "Missing," *Missing*, Missing, Missing.
- Higdon, D. (1998), "A process-convolution approach to modelling temperatures in the North Atlantic Ocean," *Environmental and Ecological Statistics*, 5, 173–190.
- (2002), "Space and Space-Time Modeling using Process Convolutions," in *Quantitative methods for current environmental issues*, eds. Anderson, C., Barnett, V., Chatwin, P., and El-Shaarawi, A., Springer Verlag, p. 37.
- Huggins, R. M. (1989), "On the statistical analysis of capture experiments," *Biometrika*, 76, 133.
- Hurlbert, S. (1984), "Pseudoreplication and the design of ecological field experiments," *Ecological monographs*, 54, 187–211.
- Illian (2008a), "Missing," *Missing*, Missing.
- Illian, J. (2008b), *Statistical analysis and modelling of spatial point patterns*, Wiley-Interscience.
- Ivan, J. (2012), "Density, demography, and seasonal movements of snowshoe hares in central Colorado," Ph.D. thesis, COLORADO STATE UNIVERSITY.

- 6728 Jackson, R., Roe, J., Wangchuk, R., and Hunter, D. (2006), “Estimating Snow
6729 Leopard Population Abundance Using Photography and Capture-Recapture
6730 Techniques,” *Wildlife Society Bulletin*, 34, 772–781.
- 6731 Johnson (2010), “A Model-Based Approach for Making Ecological Inference from
6732 Distance Sampling Data,” *Biometrics*, 66, 310318.
- 6733 Johnson, D. (1999), “The insignificance of statistical significance testing,” *The jour-
6734 nal of wildlife management*, 763–772.
- 6735 Karanth, K. U. (1995), “Estimating tiger *Panthera tigris* populations from camera-
6736 trap data using capture–recapture models,” *Biological Conservation*, 71, 333–338.
- 6737 Kelly, M., Noss, A., Di Bitetti, M., Maffei, L., Arispe, R., Paviolo, A., De Angelo,
6738 C., and Di Blanco, Y. (2008), “Estimating puma densities from camera trapping
6739 across three study sites: Bolivia, Argentina, and Belize,” *Journal of Mammalogy*,
6740 89, 408418.
- 6741 Kendall (1997), “Missing,” *Missing*, missing.
- 6742 Kéry, M. (2010), *Introduction to WinBUGS for Ecologists: Bayesian Approach to
6743 Regression, ANOVA, Mixed Models and Related Analyses*, Academic Press.
- 6744 Kéry, M., Gardner, B., Stoeckle, T., Weber, D., and Royle, J. A. (2010), “Use of
6745 Spatial Capture-Recapture Modeling and DNA Data to Estimate Densities of
6746 Elusive Animals,” *Conservation Biology*, 25, 356–364.
- 6747 Kéry, M., Royle, J., and Schmid, H. (2005), “Modeling avian abundance from
6748 replicated counts using binomial mixture models,” *Ecological Applications*, 15,
6749 1450–1461.
- 6750 Kery, M. and Schaub, M. (2011), *Bayesian Population Analysis Using WinBugs*,
6751 Academic Press.
- 6752 King, R. (2009), “Missing,” *missing*, Missing.
- 6753 — (missing), “Missing,” *missing*, Missing.
- 6754 Kumar (missing), “Unpublished data,” .
- 6755 Kuo, L. and Mallick, B. (1998), “Variable selection for regression models,”
6756 *Sankhy{\=a}: The Indian Journal of Statistics, Series B*, 65–81.
- 6757 Laird, N. M. and Ware, J. H. (1982), “Random-effects models for longitudinal
6758 data,” *Biometrics*, 963–974.
- 6759 Langtimm (2010), “Missing,” *Missing*, missing.
- 6760 Le Cam, L. (1990), “Maximum likelihood: an introduction,” *International Statis-
6761 tical Review/Revue Internationale de Statistique*, 153–171.
- 6762 Lewin-Koh, N. J., Bivand, R., contributions by Edzer J. Pebesma, Archer, E.,
6763 Baddeley, A., Bibiko, H.-J., Dray, S., Forrest, D., Friendly, M., Giraudoux, P.,
6764 Golicher, D., Rubio, V. G., Hausmann, P., Hufthammer, K. O., Jagger, T.,
6765 Luque, S. P., MacQueen, D., Niccolai, A., Short, T., Stabler, B., and Turner,
6766 R. (2011), *maptools: Tools for reading and handling spatial objects*, r package
6767 version 0.8-10.
- 6768 Link, W. A. (2003), “Missing,” *missing*, missing.
- 6769 Link, W. A. and Barker, R. J. (2009), *Bayesian Inference: With Ecological Appli-
6770 cations*, London, UK: Academic Press.

- 6771 Liu and Wu (1999), "Parameter expansion for data augmentation," *J Am Stat*
6772 *Assoc*, 94, 1264–1274.
- 6773 MacEachern, S. and Berliner, L. (1994), "Subsampling the Gibbs sampler," *Amer-*
6774 *ican Statistician*, 188–190.
- 6775 MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., and
6776 Langtimm, C. A. (2002), "Estimating site occupancy rates when detection prob-
6777 abilities are less than one," *Ecology*, 83, 2248–2255.
- 6778 Mackenzie, D. I. and Royle, J. (2005), "Designing occupancy studies: general advice
6779 and allocating survey effort," *Journal of Applied Ecology*, 42, 1105–1114.
- 6780 Magoun, A. J., Long, C. D., Schwartz, M. K., Pilgrim, K. L., Lowell, R. E., and
6781 Valkenburg, P. (2011), "Integrating motion-detection cameras and hair snags for
6782 wolverine identification," *The Journal of Wildlife Management*, 75, 731–739.
- 6783 McCarthy, M. A. (2007), *Bayesian Methods for Ecology*, Cambridge: Cambridge
6784 University Press.
- 6785 McCullagh, P. and Nelder, J. (1989), *Generalized linear models*, Chapman &
6786 Hall/CRC.
- 6787 Metropolis, N., Rosenbluth, A., Rosenbluth, M., Teller, A., Teller, E., et al. (1953),
6788 "Equation of state calculations by fast computing machines," *The journal of*
6789 *chemical physics*, 21, 1087–1092.
- 6790 Metropolis, N. and Ulam, S. (1949), "The Monte Carlo method," *Journal of the*
6791 *American Statistical Association*, 44, 335–341.
- 6792 Millar, R. (2009), "Comparison of hierarchical Bayesian models for overdispersed
6793 count data using DIC and Bayes' Factors," *Biometrics*, 65, 962–969.
- 6794 Mollet, P., Kery, M., Gardner, B., Pasinelli, G., and A, R. J. (2012), "Population
6795 size estimation for capercaillie (*Tetrao urogallus* L.) using DNA-based individual
6796 recognition and spatial capture-recapture models," *missing*, missing, missing.
- 6797 Neal, R. (2003), "Slice sampling," *Annals of Statistics*, 31, 705–741.
- 6798 Nelder, J. and Wedderburn, R. (1972), "Generalized linear models," *Journal of the*
6799 *Royal Statistical Society. Series A (General)*, 370–384.
- 6800 Norris III, J. L. and Pollock, K. H. (1996), "Nonparametric MLE under two closed
6801 capture-recapture models with heterogeneity," *Biometrics*, 639–649.
- 6802 O'Connell, A. F., Nichols, J. D., and Karanth, U. K. (2010), *Camera traps in*
6803 *animal ecology: Methods and analyses*, Springer.
- 6804 Overton, W. and Stehman, S. (1995), "The Horvitz-Thompson theorem as a uni-
6805 fying perspective for probability sampling: with examples from natural resource
6806 sampling," *American Statistician*, 261–268.
- 6807 Pebesma, E. and Bivand, R. (2011), *Package 'sp'*, r package version 0.9-91.
- 6808 Pledger, S. (2000), "Unified maximum likelihood estimates for closed capture-
6809 recapture models using mixtures," *Biometrics*, 434–442.
- 6810 Plummer, M. (2003), "JAGS: A program for analysis of Bayesian graphical models
6811 using Gibbs sampling," in *Proceedings of the 3rd International Workshop on*
6812 *Distributed Statistical Computing (DSC 2003)*. March, pp. 20–22.
- 6813 — (2009), "rjags: Bayesian graphical models using mcmc. R package version 1.0.

- 3-12," .
- (2011), *rjags: Bayesian graphical models using MCMC*, r package version 3-5.
- Plummer, M., Best, N., Cowles, K., and Vines, K. (2006), "CODA: Convergence Diagnosis and Output Analysis for MCMC," *R News*, 6, 7–11.
- R.E., R., Royle, J., Desimone, R., Schwartz, M., Edwards, V., Pilgrim, K., and McKelvey, K. (2012), "Estimating abundance of mountain lions from unstructured spatial samples," .
- Robert, C. P. and Casella, G. (2004), *Monte Carlo statistical methods*, New York, USA: Springer.
- (2010), *Introducing Monte Carlo Methods with R*, New York, USA: Springer.
- Roberts, G. O. and Rosenthal, J. S. (1998), "Optimal scaling of discrete approximations to Langevin diffusions," *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 60, 255–268.
- Royle, J. (2006), "Site occupancy models with heterogeneous detection probabilities," *Biometrics*, 62, 97–102.
- (2009), "Analysis of capture-recapture models with individual covariates using data augmentation," *Biometrics*, 65, 267–274.
- Royle, J. and Dorazio, R. (2006), "Hierarchical models of animal abundance and occurrence," *Journal of Agricultural, Biological, and Environmental Statistics*, 11, 249–263.
- (2008), *Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities*, Academic Press.
- (2010), "Missing," *Missing*, missing, missing.
- (2011), "Missing," *Missing*, missing, missing.
- Royle, J., Dorazio, R., and Link, W. (2007), "Analysis of multinomial models with unknown index using data augmentation," *Journal of Computational and Graphical Statistics*, 16, 67–85.
- Royle, J. and Dubovsky, J. (2001), "Modeling spatial variation in waterfowl band-recovery data," *The Journal of wildlife management*, 726–737.
- Royle, J., Karanth, K., Gopalaswamy, A., and Kumar, N. (2009), "Bayesian inference in camera trapping studies for a class of spatial capture-recapture models," *Ecology*, 90, 3233–3244.
- Royle, J. and Link, W. (2006), "Generalized site occupancy models allowing for false positive and false negative errors," *Ecology*, 87, 835–841.
- Royle, J. and Nichols, J. (2003), "Estimating abundance from repeated presence-absence data or point counts," *Ecology*, 84, 777–790.
- Royle, J. A. (2004a), "Generalized estimators of avian abundance from count survey data," *Animal Biodiversity and Conservation*, 27, 375–386.
- (2004b), "N-mixture models for estimating population size from spatially replicated counts," *Biometrics*, 60, 108–115.
- (2008), "Modeling individual effects in the Cormack–Jolly–Seber model: a state-space formulation," *Biometrics*, 64, 364–370.
- (2010), "missing," *missing*, missing.

- 6857 Royle, J. A., Converse, S., and Link, W. (2011a), “Data augmentation for struc-
6858 tured populations,” *unpublished*.
- 6859 Royle, J. A., Dawson, D. K., and Bates, S. (2004), “Modeling abundance effects in
6860 distance sampling,” *Ecology*, 85, 1591–1597.
- 6861 Royle, J. A., Kéry, M., and Guélat, J. (2011b), “Spatial capture-recapture models
6862 for search-encounter data,” *Methods in Ecology and Evolution*, 1–10.
- 6863 Royle, J. A., Magoun, A. J., Gardner, B., Valkenburg, P., and Lowell, R. E. (2011c),
6864 “Density estimation in a wolverine population using spatial capture–recapture
6865 models,” *The Journal of Wildlife Management*, 75, 604–611.
- 6866 Royle, J. A. and Young, K. V. (2008), “A Hierarchical Model For Spatial Capture-
6867 Recapture Data,” *Ecology*, 89, 2281–2289.
- 6868 Sanathanan, L. (1972), “Estimating the size of a multinomial population,” *The*
6869 *Annals of Mathematical Statistics*, 142–152.
- 6870 Schofield and Barker (missing), “Missing,” *Missing*, missing.
- 6871 Sepúlveda, M., Bartheld, J., Monsalve, R., Gómez, V., and Medina-Vogel, G.
6872 (2007), “Habitat use and spatial behaviour of the endangered Southern river ot-
6873 ter (*Lontra provocax*) in riparian habitats of Chile: conservation implications,”
6874 *Biological Conservation*, 140, 329–338.
- 6875 Sillett (2011), “Missing,” *Missing*, missing.
- 6876 Simons, T. R., Pollock, K. H., Wettroth, J. M., Alldredge, M. W., Pacifici, K., and
6877 Brewster, J. (2009), “Sources of Measurement Error, Misclassification Error, and
6878 Bias in Auditory Avian Point Count Data,” in *Modeling Demographic Processes*
6879 *In Marked Populations*, eds. Thomson, D. L., Cooch, E. G., and Conroy, M. J.,
6880 Boston, MA: Springer US, vol. 3, pp. 237–254.
- 6881 Spiegelhalter, D., Thomas, A., Best, N., and Lunn, D. (2003), *WinBUGS User*
6882 *Manual Version 1.4*.
- 6883 Spiegelhalter, D. J., Best, N. G., Carlin, B. P., and Van Der Linde, A. (2002),
6884 “Bayesian measures of model complexity and fit,” *Journal of the Royal Statistical*
6885 *Society. Series B, Statistical Methodology*, 583–639.
- 6886 Stabler, B. (2006), *shapefiles: Read and Write ESRI Shapefiles*, r package version
6887 0.6.
- 6888 Sturtz, S., Ligges, U., and Gelman, A. (2005), “R2WinBUGS: A Package for Run-
6889 ning WinBUGS from R,” *Journal of Statistical Software*, 12, 1–16.
- 6890 Su, Y.-S. and Yajima, M. (2011), *R2jags: A Package for Running jags from R*, r
6891 package version 0.02-17.
- 6892 Tanner, M. A. and Wong, W. H. (1987), “The calculation of posterior distributions
6893 by data augmentation,” *J Am Stat Assoc*, 82, 528–540.
- 6894 Thomas, A., O’Hara, B., Ligges, U., and Sturtz, S. (2006), “Making BUGS Open,”
6895 *R News*, 6, 12–17.
- 6896 Trolle, M. and Kéry, M. (2005), “Camera-trap study of ocelot and other secretive
6897 mammals in the northern Pantanal,” *Mammalia*, 69, 409–416.
- 6898 Tyre, A. J., Tenhumberg, B., Field, S. A., Niejalke, D., Parris, K., and Possing-
6899 ham, H. P. (2003), “Improving precision and reducing bias in biological surveys:

- 6900 estimating false-negative error rates,” *Ecological Applications*, 13, 1790–1801.
- 6901 Wegan (missing), “missing,” *missing*, missing.
- 6902 Wolpert, R. L. and Ickstadt, K. (1998), “Poisson/gamma random field models for
- 6903 spatial statistics,” *Biometrika*, 85, 251–267.
- 6904 Yang, H. C. and Chao, A. (2005), “Modeling Animals’ Behavioral Response by
- 6905 Markov Chain Models for Capture–Recapture Experiments,” *Biometrics*, 61,
- 6906 1010–1017.
- 6907 Zuur, A., Ieno, E., Walker, N., Saveliev, A., and Smith, G. (2009), *Mixed effects*
- 6908 *models and extensions in ecology with R*, Springer Verlag.

INDEX

6909 iiiiiii HEAD
6910 bracket notation, 12 =====
6911 bracket notation, 8 llllllll b02246e5a1615f222c76f935a039d649653aaf3

INDEX

- 6912 iiiiiii HEAD
- 6913 bracket notation, 12 =====
- 6914 bracket notation, 8 iiii b02246e5a1615f2222c76f935a039d649653aaf3