

Marc Kéry
J. Andrew Royle



APPLIED HIERARCHICAL MODELING IN ECOLOGY

Analysis of distribution, abundance and
species richness in R and BUGS

Volume 1
Prelude and Static Models



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Volume 1

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For Jim Nichols, who changed the way in which we think about Ecology

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PART

MODELS FOR STATIC
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MODELING ABUNDANCE WITH COUNTS OF UNMARKED INDIVIDUALS IN CLOSED POPULATIONS: BINOMIAL N -MIXTURE MODELS

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6.1 INTRODUCTION TO THE MODELING OF ABUNDANCE

This chapter, and indeed much of this book, is about the modeling of abundance. Abundance, or local population size, refers to the number of individuals at some place and time. We typically denote abundance by N_{it} , where i indexes space (the place) and t is an index for time. Surely, abundance must be the single most important state variable in all of ecology. This is nicely illustrated by the fact that several influential ecology textbooks have “abundance” in their title (e.g., Andrewartha and Birch, 1954; Krebs, 2009). This focus on N in ecology and its applications is certainly not unnatural. If you think of a population as analogous to your bank account, then a natural first question about the latter is “How much money do I have?” and similarly, the first question in ecology is likely to be “How many are there?”

We saw in Chapter 1 that fundamentally both abundance and distribution, the other major state variable in ecology (Krebs, 2009), are simply areal summaries of an underlying point pattern. Animals and plants are small at the scale of essentially any study area, hence they can be treated approximately as points. Then, abundance is the number of such points in the pattern, while occurrence z is an indicator for a greater than zero abundance (i.e., $z = I(N > 0)$; see Chapter 10). At a fundamental level, we could therefore model the number and location of every individual within a study area. Models for abundance at this most disaggregated level are called spatial point pattern (or process) models (Illian et al., 2008; Wiegand and Moloney, 2014), and there is much recent interest in this powerful class of models in ecology (Aarts et al., 2012; Dorazio, 2012, 2014; Fithian and Hastie, 2013; Renner and Warton, 2013; Renner et al., 2015). However, these models require more expensive data (i.e., location data), and are substantially more complex both conceptually and practically (i.e., to fit), than simpler models for areal aggregates of point patterns. Furthermore, it is not straightforward to describe a measurement error process for false-negative errors, nor to model temporal dynamics (see also Section 10.1). Hence, we see the more complicated point pattern models as complementary to the abundance models covered in our book, and indeed the two can be integrated in a single model (Dorazio, 2014). In addition, the new class of spatial capture-recapture (SCR) models (Efford, 2004; Borchers and Efford, 2008; Royle and Young, 2008; Royle et al., 2014) represents point process models; see Royle et al. (2011) for an example of such a model in a meta-population context. We present such models in Chapter 24 in volume 2.

When we count animals or plants, we *measure abundance*: a count C is a measurement of abundance. When measuring abundance, there are exactly two possible types of *measurement error*: (1) we can overlook or otherwise fail to detect an individual, or (2) we can count an individual multiple times or erroneously add some other species in the count (species misidentification). The first represents a false-negative (or detection) error and leads to a negative bias in the count relative to abundance, while the last two represent false-positive errors and lead to a positive bias in the count relative to abundance. These are the most fundamental types of errors with any measurement of abundance. There are other sources of errors; e.g., you may want to study the size of a population of territory-holding adults of some species, but may be unable to distinguish juveniles from adults or territorial from transient individuals. However, if you really cannot distinguish them, then in a sense this is not an error, but you are simply asking for too much. You need to redefine your N to encompass juveniles, adults, locals, and transients alike. Thus, this is a problem of how you define N . Perhaps you can come up with some method or data collection protocol that enables you to separate out those demographic classes. Regardless, we do not think of this kind of error as comparable to the two fundamental types of

abundance measurement errors, which always affect your measurements once you have defined what you mean by N .

Over literally centuries, a large number of models, methods, and associated sampling designs have been developed that deal with one of the two kinds of abundance measurement errors: the one represented by imperfect detection—i.e., false-negative errors. Examples include the treatises by Otis et al. (1978), Seber (1982), Williams et al. (2002), Borchers et al. (2002), Royle and Dorazio (2008), King et al. (2009), McCrea and Morgan (2014), and Royle et al. (2014). Conceptually, almost all methods of estimating abundance in a closed (i.e., static) population that account for false-negative errors consist of obtaining an estimate of the fraction of individuals that are detected (p). Intuitively, it is clear that with a count C and an estimate of that detection probability, \hat{p} , we can estimate abundance N as the ratio of C over \hat{p} (i.e., by the canonical abundance estimator, Williams et al., 2002). Most approaches to estimating p in the context of abundance require capture-recapture data—i.e., repeated observations of naturally or artificially marked individuals. Natural marks may be distinctive feather, fur or general color patterns, or genetic identity. Artificial marks include rings (called “bands” west of the Atlantic), PIT transponders, or many other marking methods that allow one to unambiguously determine the identity of an individual that is physically captured or that can be observed otherwise in such a way as to being able to record the mark. Typically, capture-recapture data are “expensive” data, because they may require physical capture of the animals and sometimes also the application of complex and expensive lab analysis methods such as microsatellite analysis. In addition, the handling of the animals may be risky in the case of rare or endangered species.

In the vast majority of studies of abundance, we do not have a single site, but multiple sites, and the interest is then in modeling variability in abundance among these sites and in explaining that variability by measured covariates or perhaps by hidden structure via random effects. Of course, the challenges of measuring N are compounded in the study of a “meta-population”—that is, when we have a collection of multiple sites that we want to compare in terms of their N . (In this book, we use the term *meta-population* rather loosely to refer to all individuals that live at a collection of sites, and to denote this we prefer to write the hyphen. Sometimes we use the term *site-structured population* interchangeably.)

This chapter deals with an appealing modeling framework and data collection protocol known as the N -mixture model or binomial-Poisson mixture model (Royle, 2004b); see Dénes et al. (2015) for a recent overview. In this model class, all that is required to estimate detection probability and abundance are counts of unmarked individuals that are replicated in two dimensions: there must be multiple sites and replicate observations (i.e., counts) for at least some of these sites. No individual recognition is required, but we must avoid counting the same individual twice within a single observation period. Such data are usually “cheap” to obtain compared with typical capture-recapture (though not necessarily when compared with distance sampling data; see Chapters 8–9). Therefore, this modeling framework and its associated data collection protocol may enable you to conduct inference about abundance at larger spatial or temporal scales than what you might be able to do with a more typical capture-recapture or distance sampling protocols.

As already shown in Chapters 1, 2, and 4, the N -mixture model is an HM that combines one submodel for the latent state, abundance N , with another submodel for the actual observations C that is conditional on N . The observation component of the model is usually the same old binomial distribution that forms the backbone of practically all of capture-recapture modeling, while the model for the latent abundance state is typically a Poisson, which is the workhorse model in statistics for abundance.

Often, we follow a meta-population over time, thereby adding a temporal dimension (t) to abundance; i.e., we have an interest in explaining N_{it} —that is, explaining spatiotemporal patterns in N . For the most part and with two small exceptions in Sections 6.12, 6.14 and 9.5–9.7, we defer the modeling of the temporal dimension of abundance to Chapters 12–14 in volume 2 and focus on static models for a meta-population observed at a single point in time. Note, however, that the temporal dimension in abundance can be accommodated by fitting a static model that is stratified by time (or, equivalently, simply fitting the model separately for each time point; Dodd and Dorazio, 2004). For instance, in a single model we could analyze data from a breeding bird survey conducted over multiple years (= breeding periods) and simply fit separate parameters for every year. In addition, you may then constrain the year-specific parameters to estimate a linear trend (Kéry et al., 2009; Zellweger-Fischer et al., 2010; Fujisaki et al., 2011); also see Chapter 12.

6.2 AN EXERCISE IN HIERARCHICAL MODELING: DERIVATION OF BINOMIAL N -MIXTURE MODELS FROM FIRST PRINCIPLES

One of the neatest things about HMs is that they *invite* you to build your own statistical models, exactly according to how *you* perceive the stochastic process *you* are interested in, for *your* data and *your* questions. You can build statistical models from first principles, by thinking about the processes that underlie the observed data set. Let us look at how replicated count data (C) typically arise as a combination of two processes, one ecological and one observational. In this section and the next, we show a variant of what we have already done in more detail in Chapter 4. But here we do this specifically to introduce the binomial N -mixture model in its simplest incarnation, to provide the gentlest possible introduction to this model. To motivate the N -mixture model, ask yourself the following questions:

1. Suppose you knew the value of abundance (N) for some species at each of 100 sites—e.g., 2, 5, 0, 2, 0, ...—how would you describe this spatial variation? Or, in other words: what is a customary statistical distribution to describe the mean and the spatial variability of N ?
2. Assume that we wanted to acknowledge the presence of measurement error of the nondetection kind—i.e., permit the observed counts C to usually be less than abundance N due to imperfect detection. For instance, at some hypothetical site 2 with $N = 5$, we might obtain the following *repeated measurements* of abundance N : 4, 2, 4, 3, ... What would be a useful starting point to model the temporal variability of these *measurements* of N ?

First, most people, when confronted with the kind of data described in (1), would start with a Poisson distribution to model the spatial variation in abundance N . The Poisson distribution is the basic building block for modeling abundance (Royle and Dorazio, 2008). By adding covariate effects, zero inflation, or other latent structure (random effects), a Poisson model confers considerable flexibility to capture a wide variety of patterns in N (e.g., see Cressie et al., 2009; Zuur et al., 2012, and also Chapter 12 in volume 2). Second, knowing that there are N individuals at a site exposed to detection and that the detection probability is potentially less than 1 would lead most people to choose a binomial distribution to describe the temporal variation in the counts at a specific site. The binomial distribution is the canonical description of an observation process that contains false-negative detection error only. Again, GLM-type modeling (possibly including latent effects) of the binomial success parameter (detection probability) yields great flexibility in this model.

Excitingly, we have just reinvented the basic binomial N -mixture model from first principles! First, we have chosen the Poisson distribution as a description of the ecological (or state) process that

distributes individuals in space and thus creates the latent abundance state N . Second, we have chosen the binomial distribution as a description of the observation process, where we typically have a special kind of *measurement error*, one that does not cancel out but instead leads to observations (counts C) that are biased with respect to the measured quantity (abundance N , unless we do a large number of repeated measurements; see Exercise 2). Here is the simplest binomial N -mixture model written in algebra:

1. State process: $N_i \sim \text{Poisson}(\lambda)$
2. Observation process: $C_{ij}|N_i \sim \text{Binomial}(N_i, p)$

Here, N_i is the latent abundance state at site i ($i = 1, \dots, M$) and λ is the expected abundance—i.e., the mean abundance over all sites (sampled or not). C_{ij} is the count at site i during survey j ($j = 1, \dots, J$), and p is the per-individual detection probability.

The N -mixture model is a natural, hierarchical extension of the Poisson GLM. We use the Poisson GLM as the base model for N , but we regard N as a latent variable—i.e., as unobserved or only partially observed. We augment the Poisson GLM with a conditional model that describes how the observations C_{ij} are related to the latent variable N_i . The name, binomial mixture model, stems from the fact that the likelihood is a mixture of binomials each with a different sample size N . The resulting model is also called a binomial/Poisson mixture model. It is an HM consisting of two linked GLMs; a Poisson regression for the spatial variation in abundance and a binomial regression (a.k.a. logistic regression) for the variation of the observed counts at specific sites. Recognizing these two GLMs, we can immediately start doing all the things that we customarily do with GLMs, especially modeling structure in the two parameters (which then need to be indexed, λ_i, p_{ij}) as linear or other functions of covariates via a log and a logit link function, respectively. Other possibilities include the introduction of random effects to account for latent structure or correlations.

To ensure estimable parameters in the N -mixture model, we need data that are replicated both in space (i.e., $M > 1$) and in time (i.e., $J > 1$) (but see Section 6.12 on time-for-space substitution).

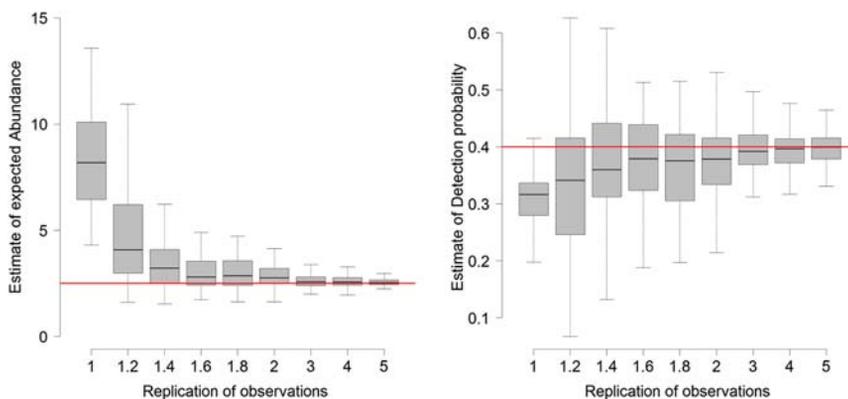


FIGURE 6.1

Effects of temporal replication in the N -mixture model on the estimators of expected abundance (λ) and detection probability (p) in a simulated example with 150 sites, $\lambda = 2.5$ and $p = 0.4$ (red lines), and no covariates. Replication is expressed as the average number of replicate surveys per site; e.g., 1.2 means that 20% of sites have two replicates and 80% only one. Each boxplot summarizes 100 simulated data sets.

Unreplicated data result in large biases (Figure 6.1), but even a small degree of replication improves the quality of estimators considerably (see also Knape and Korner-Nievergelt, 2015). You can easily repeat such a simulation for *your* sample sizes and the expected abundance and detection of *your* favorite species (see Section 6.6 for a template). It is hard to give general advice on how much replication is required to obtain reasonable estimates, but typically the number of sites (M) should be greater than 20, and you can very easily ascertain how good estimates get with simulation (see Section 6.6). Importantly, the number of temporal replicates (J) need only be two or more for *some*, but not necessarily for all sites. Typical ecological data sets are unbalanced in many ways, and most data sets to which we have applied N -mixture models did not have the same number of replicate surveys at all sites and times. The information about detection probability in the N -mixture model comes from the variability of repeated counts at a site, with more variability suggesting smaller p . In fact, the correlation coefficient among repeated measurements is a moment estimator of p when parameters are constant (Royle, 2004a). Thus, when our data set contains sites with replicated counts and without, then information about p will come from the sites with replication, and it will be propagated to the sites without replication. This means that the sites without replicated counts should constitute a random sample among the total number of sites. If this is not the case, the estimate of p may be based on a biased sample of sites with respect to all sites about which we would like to make inferences. This may lead to biased parameter estimates.

Some key assumptions of the N -mixture model, typical violations, and ways to mitigate them are:

1. *Closure assumption*: We assume that all within-site variation in counts C is attributable to detection probability p . When all counts at a site are constant, detection probability will be estimated at 1 (unless all counts are 0). So if N varies during a period when closure is assumed and the closure assumption is violated, the variability attributed to the binomial part of the model will be overstated. This will lead to underestimated p and overestimated N (see Section 6.7). Some lack of closure may not be disastrous, and one may then simply have to change the interpretation of the abundance parameter (λ) to have a superpopulation meaning: rather than the number of individuals that *permanently* reside within a site, λ will describe the total number of individuals ever associated with a site during a study period. This is analogous to site-occupancy models where random temporary emigration leads to a redefinition of the occupancy parameter from the probability of permanent occupation to the probability of use (see Section 10.2). Also, if you are sampling at two nested temporal scales, with closure satisfied among the secondary samples (i.e., when you have a robust design), then you can use multiscale N -mixture models to model the superpopulation size and temporary emigration jointly (Section 6.14). Some information about temporary emigration induced by within-territory movement may also be obtained from distance information (Johnson et al., 2014).
2. *No false-positive errors*: Implicit in the adoption of the binomial distribution as a description of the measurement error for abundance is the assumption that there are no false-positives. That is, we must not count another species as our target species, and we must not count the same individual multiple times during a single occasion. This assumption is required for the binomial to be an adequate description of the observation process. If the biology of a study species and/or the sampling protocol suggests substantial numbers of false-positive errors, the traditional N -mixture model is *not* an appropriate framework for inference about abundance. One example of this would be species with large flocks, where it would be hard to avoid double counts when measuring the size of flocks (plus independence of detection, mentioned next, would be violated). One possible way forward, however, might be a Poisson/Poisson mixture model (see Section 6.13.2).

3. *Independence of detection*: Similarly, implicit in the binomial distribution as a description of the observation process is that individuals are detected independently from each other. If they travel in pairs, groups, or flocks, detection of one individual will make it more likely that other group members are also detected, and the standard N -mixture model will no longer be an adequate representation of the observation process underlying the counts. A possible way forward might be the choice of a beta-binomial distribution for the observation process; see Martin et al. (2011) and Dorazio et al. (2013). Another way that this assumption may be violated is by density-dependent detection; for instance, if individual birds sing more frequently at higher density (Warren et al., 2013). See also our comments in [Section 6.15](#).
4. *Homogeneity of detection among N_i individuals*: The N -mixture model uses as input not individual detection data, but simple counts of unique individuals. That is, the data distinguish sites i and sampling occasions j , but we do *not* keep track of the individuals in the counts C_{ij} . Hence, with two replicate counts at a site, such as 5 and 3, we have no way knowing whether the total number of individuals detected was 5, 6, 7, or 8. The individual ID is lost in the replicated count data, hence there is an implicit assumption that all N_i individuals present at i have an identical detection probability p_{ij} at survey j . Clearly, this can never be exactly true. For instance, this assumption probably offends all distance samplers (Chapters 8 and 9), whose fundamental assumption is that individuals closer to an observer are more easily detectable than individuals farther away (Efford and Dawson, 2009). The N -mixture model averages over such distance-related or indeed any other detection heterogeneity among the N_i individuals during occasion j . The effect of this can likely be deduced from the “second law of capture-recapture,” which says that unmodeled detection heterogeneity will always lead to a negative bias in N (the first “law” is that things get harder as p gets smaller; see [Section 6.6](#)). If distance-related detection heterogeneity and its effects on N are a big concern, we may have to use distance sampling (Chapters 8 and 9) or spatial capture-recapture (SCR; Royle et al., 2014) for abundance estimation. We note, though, that in our small simulation study in [Section 6.7](#) individual heterogeneity in detection probability did not seem to bias the abundance estimator from the N -mixture model, so perhaps more detailed investigations in this respect would be interesting.
5. *Parametric modeling assumptions*: The model makes specific distributional assumptions and if they deviate substantially from the true processes that generated the data set, biased estimators may result. These assumptions can and should be tested using conventional goodness-of-fit (GoF) techniques such as parametric bootstrap or posterior predictive checks (see Sections 2.4.3, 2.8.2, and 6.8). We note, though, that these techniques are much less well understood for HMs than for flat or nonhierarchical models.

6.3 SIMULATION AND ANALYSIS OF THE SIMPLEST POSSIBLE N -MIXTURE MODEL

We first illustrate the model in the simplest possible setting, with constant expected abundance and detection ($\lambda = 2.5$, $p = 0.4$), for a sample size of $M = 150$ sites and $J = 2$ repeated measurements of abundance. You will recognize that we have already shown exactly the same data-generation process in Chapter 4 for a more complex binomial N -mixture model, but without explicitly focusing on this model. Here, we simulate data in R and fit the model, using ML with `unmarked` and Bayesian inference in BUGS. As so often, we use data simulation to help explaining a model in the first part of this section.

```

# Choose sample sizes and prepare observed data array C
set.seed(24)          # So we all get same data set
M <- 150              # Number of sites
J <- 2                # Number of abu. measurements per site (rep. counts)
C <- matrix(NA, nrow = M, ncol = J) # to contain the obs. data

# Parameter values
lambda <- 2.5        # Expected abundance
p <- 0.4              # Probability of detection (per individual)

# Generate local abundance data (the truth)
N <- rpois(n = M, lambda = lambda)

# Conduct repeated measurements (generate replicated counts)
for(j in 1:J){
  C[,j] <- rbinom(n = M, size = N, prob = p)
}

# Look at data
# The truth ....
table(N)              # True abundance distribution
N
  0  1  2  3  4  5  6  7  8  9
11 37 39 37 10 10 3 1 1 1
sum(N)                # True total population size at M sites
[1] 358
sum(N>0)              # True number of occupied sites
[1] 139
mean(N)               # True mean abundance (estimate of lambda)
[1] 2.386667

# ... and the observations
table(apply(C, 1, max)) # Observed abundance distribution (max count)
  0  1  2  3  4
30 57 45 15 3
sum(apply(C, 1, max))  # Observed total population size at M sites
[1] 204
sum(apply(C, 1, max)>0) # Observed number of occupied sites
[1] 120
mean(apply(C, 1, max)) # Observed mean "relative abundance"
[1] 1.36

head(cbind(N=N, count1=C[,1], count2=C[,2])) # First 6 sites
  N count1 count2
[1,] 2      0      1
[2,] 1      1      0
[3,] 3      0      0
[4,] 2      0      1
[5,] 3      1      2
[6,] 5      3      3

```

Thus, in our simulation, the species occurs at 139 sites with a total of 358 individuals, but is detected at only 120 sites, and the maximum counts at each site add up to 204. Thus, the observed

“relative mean abundance” is 1.36, rather than 2.39, the true mean abundance in the M sampled sites, or 2.5 in the statistical population of sites from which we sampled 150. The overall measurement error at an occupancy level is therefore $(139 - 120)/139 \approx -14\%$ and at the abundance level, $(358 - 204)/358 \approx -43\%$. Among the first six sites, all are occupied, and under the assumption of no false-positives, we can only obtain counts $\leq N$. We undercount (i.e., $\max(C_i) < N_i$) at all sites except for site 2; indeed, at site 3 we fail to detect any of the three individuals present. Since our model has constant parameters, the correlation coefficient among repeated measurements should be approximately equal to p (Royle, 2004a); let us check this.

```
cor(C)[1,2]
[1] 0.4023582 # Note excellent agreement with value of p
```

We use unmarked function `pcount` to fit the N -mixture model for replicated counts.

```
library(unmarked) # Load package
umf <- unmarkedFramePCount(y = C) # Create um data frame
summary(umf) # Summarize
(fm1 <- pcount(~1 ~1, data = umf)) # Fit model: get estimates on link scale
backTransform(fm1, "state") # Get estimates on natural scale
backTransform(fm1, "det")
```

```
Call:
pcount(formula = ~1 ~1, data = umf)
```

```
Abundance:
  Estimate    SE      z    P(>|z|)
    0.981  0.191  5.14  2.74e-07
```

```
Detection:
  Estimate    SE      z    P(>|z|)
   -0.565  0.298  -1.89  0.0582
```

```
AIC: 754.4465
```

```
Backtransformed linear combination(s) of Abundance estimate(s)
  Estimate    SE  LinComb (Intercept)
    2.67  0.509    0.981            1
```

```
Backtransformed linear combination(s) of Detection estimate(s)
  Estimate    SE  LinComb (Intercept)
    0.363  0.0689  -0.565            1
```

Next, a Bayesian analysis of the model with JAGS.

```
# Bundle and summarize data set
win.data <- list(C = C, M = nrow(C), J = ncol(C))
str(win.data) # Look at data

# Specify model in BUGS language
sink("model1.txt")
cat("
model {
```

```

# Priors
lambda ~ dgamma(0.001, 0.001)
p ~ dunif(0, 1)
# Likelihood
for (i in 1:M) {
  N[i] ~ dpois(lambda)      # State model
  for (j in 1:J) {
    C[i,j] ~ dbin(p, N[i])  # Observation model
  }
}
",fill = TRUE)
sink()

# Initial values
Nst <- apply(C, 1, max)      # Avoid data/model/inits conflict
inits <- function(){list(N = Nst)}

# Parameters monitored
params <- c("lambda", "p")

# MCMC settings
ni <- 25000 ; nt <- 20 ; nb <- 5000 ; nc <- 3

# Call JAGS (ART 1 min) and summarize posteriors
library(jagsUI)
fm2 <- jags(win.data, inits, params, "model1.txt", n.chains=nc, n.thin=nt, n.iter=ni,
  n.burnin=nb)
print(fm2, dig=3)

```

	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff
lambda	2.829	0.659	1.969	2.692	4.600	FALSE	1	1.010	1996
p	0.356	0.068	0.210	0.358	0.478	FALSE	1	1.002	3000

We get similar estimates from likelihood and Bayesian inference. To finish this section, note the striking similarity of an HM when written in algebra, in R when simulating the data, and in the BUGS language when fitting the model (Table 6.1). Hence, when you know how to write a model in algebra, you are almost there at fitting it in BUGS, and algebra, data simulation in R or possibly other computer languages, and the BUGS language are similarly precise and useful ways of describing and understanding an HM.

Table 6.1 Model descriptions in terms of algebra, data simulation in R, and in the BUGS language. See Table 10.1 for the analogous scheme in the case of the occupancy model.

	Algebraic Description	R Data Simulation	BUGS Model Statement
State model	$N_i \sim \text{Poisson}(\lambda)$	<code>N <- rpois(M, lambda)</code>	<code>N[i] ~ dpois(lambda)</code>
Obs. model	$y_{ij} N_i \sim \text{Binomial}(N_i, p)$	<code>y[,j] <- rbinom(M,N,p)</code>	<code>y[i,j] ~ dbin(p, N[i])</code>

6.4 A SLIGHTLY MORE COMPLEX N -MIXTURE MODEL WITH COVARIATES

The model in the previous section is rarely directly useful and we went through it mainly for conceptual reasons: to explain the basics of this HM. In practice, we will virtually always have covariates whose effects on abundance and/or detection we want to model. We illustrate this by simulating another data set, analyzing it, making predictions, and showing bootstrap error estimation. We illustrate one model with BUGS, but work mostly with `unmarked`. We simulate data under the following model:

$$N_i \sim \text{Poisson}(\lambda_i), \text{ with } \log(\lambda_i) = \beta_0 + \beta_1 * \text{vegHt}_i$$

$$C_{ij}|N_i \sim \text{Binomial}(N_i, p_{ij}), \text{ with } \text{logit}(p_{ij}) = \alpha_0 + \alpha_1 * \text{wind}_{ij}$$

Hence, expected abundance (λ) is affected by a site covariate (vegetation height), and detection probability is affected by a sampling or observational covariate (wind speed). You will note that much of this section is very similar to Section 10.3 for a similar HM for modeling presence/absence instead of abundance, the site-occupancy model. We do this on purpose to emphasize the strong structural similarity of the two.

```
# Choose sample sizes and prepare observed data array y
set.seed(1)           # So we all get same data set
M <- 100              # Number of sites
J <- 3                # Number of repeated abundance measurements
C <- matrix(NA, nrow = M, ncol = J) # to contain the observed data

# Create a covariate called vegHt
vegHt <- sort(runif(M, -1, 1)) # sort for graphical convenience

# Choose parameter values for abundance model and compute lambda
beta0 <- 0            # Log-scale intercept
beta1 <- 2            # Log-scale slope for vegHt
lambda <- exp(beta0 + beta1 * vegHt) # Expected abundance
plot(vegHt, lambda, type = "l", lwd = 3) # Expected abundance

# Draw local abundance and look at data so far
N <- rpois(M, lambda)
points(vegHt, N)      # Add realized abundance to plot
table(N)
N
 0  1  2  3  4  5  6  8  9
35 24 12  7  9  5  4  3  1

# Plot the true system state (Figure 6.2, left)
par(mfrow = c(1, 3), mar = c(5, 5, 2, 2), cex.axis = 1.5, cex.lab = 1.5)
plot(vegHt, N, xlab = "Vegetation height", ylab = "True abundance (N)", frame = F, cex = 1.5)
lines(seq(-1, 1, , 100), exp(beta0 + beta1 * seq(-1, 1, , 100)), lwd = 3, col = "red")
```

Figure 6.2 (left) shows how the relationship between expected abundance and `vegHt` translates into a realized abundance pattern. In real life, both expected abundance (λ) and realized abundance (N) will usually be latent; i.e., neither will be directly observable, the former because it is an abstract construct

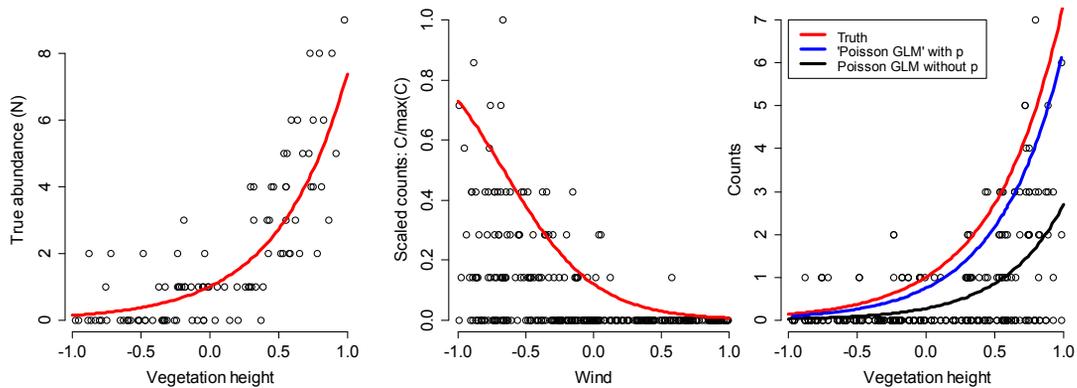


FIGURE 6.2

Left: The relationship between abundance and vegetation height (red line: expected abundance λ ; circles: realized abundance N). Middle: The relationship between detection probability and wind speed (red line); circles are the scaled observed counts (by division with the maximum count). Right: Comparison between the true abundance–covariate relationship (red), and its estimate under the N -mixture model (blue) and a simple Poisson regression (black); circles represent the observed counts of each site.

(a parameter), and the latter because of measurement error. Although observable in principle, N is thus typically a latent variable, too. We simulate this next and assume that detection probability p depends on wind speed in a logit-linear relationship described by intercept -2 and slope -3 , and that we make $J = 3$ repeated abundance measurements at each site (Figure 6.2, middle). We scale the counts in Figure 6.2 (middle) by dividing each by the maximum count to make the abundance measurements more directly comparable with detection probability.

```
# Create a covariate called wind
wind <- array(runif(M * J, -1, 1), dim = c(M, J))

# Choose parameter values for measurement error model and compute detectability
alpha0 <- -2 # Logit-scale intercept
alpha1 <- -3 # Logit-scale slope for wind
p <- plogis(alpha0 + alpha1 * wind) # Detection probability
# plot(p ~ wind, ylim = c(0,1)) # Look at relationship

# Take J = 3 abundance measurements at each site
for(j in 1:J) {
  C[,j] <- rbinom(M, N, p[,j])
}

# Plot observed data and effect of wind on det. probability (Figure 6.2, middle)
plot(wind, C/max(C), xlab="Wind", ylab="Scaled counts: C/max(C)", frame = F, cex = 1.5)
lines(seq(-1,1,100), plogis(alpha0 + alpha1*seq(-1,1,100)), lwd=3, col="red")
```

It is instructive to compare the expected and realized abundance and the replicated abundance measurements; make sure you really understand what they all mean.

```
# Expected (lambda) and realized abundance (N) and measurements (C)
cbind(lambda=round(lambda,2), N=N, C1=C[,1], C2=C[,2], C3=C[,3])
      lambda N C1 C2 C3
[1,]  0.14 0  0  0  0
[2,]  0.15 0  0  0  0
[3,]  0.17 0  0  0  0
[4,]  0.17 2  1  0  0
[5,]  0.18 0  0  0  0
[ output truncated]
[91,]  4.49 6  2  2  4
[92,]  4.50 4  3  3  0
[93,]  4.80 2  0  0  0
[94,]  4.92 8  3  0  7
[95,]  5.12 4  1  3  2
[ output truncated]
```

Next, we use the *N*-mixture model to analyze these data using `unmarked` and `BUGS`. We start with `unmarked`. We also illustrate the fitting of two factors that are unrelated to the data (because the response was not generated with their effects “built in”): `time` will index the first through the third survey, while `hab` will contrast three imaginary habitat types.

```
# Create factors
time <- matrix(rep(as.character(1:J), M), ncol = J, byrow = TRUE)
hab <- c(rep("A", 33), rep("B", 33), rep("C", 34)) # assumes M = 100
```

We first package the data into an `unmarked` frame, noting the difference between site covariates (indexed by site only) and sampling or observational covariates (indexed by site and survey).

```
# Load unmarked, format data in unmarked data frame and summarize
library(unmarked)
umf <- unmarkedFramePCount(
  y = C, # Counts matrix
  siteCovs = data.frame(vegHt = vegHt, hab = hab), # Site covariates
  obsCovs = list(time = time, wind = wind)) # Observation covs
summary(umf)
unmarkedFrame Object

100 sites
Maximum number of observations per site: 3
Mean number of observations per site: 3
Sites with at least one detection: 47

Tabulation of y observations:
  0  1  2  3  4  5  6  7 <NA>
214 43 19 17  2  3  1  1  0
```

```

Site-level covariates:
  vegHt      hab
Min.   :-0.97322  A:33
1st Qu.:-0.35384  B:33
Median :-0.02438  C:34
Mean   : 0.03569
3rd Qu.: 0.53439
Max.   : 0.98381

Observation-level covariates:
time      wind
1:100 Min.   :-0.99633
2:100 1st Qu.:-0.54111
3:100 Median :-0.10469
      Mean   :-0.03803
      3rd Qu.: 0.44824
      Max.   : 0.99215

# Fit model and extract estimates
# linear model for p follows first tilde, then comes linear model for lambda
summary(fm.Nmix1 <- pcount(~wind~vegHt, data=umf, control=list(trace=T, REPORT=1)))

Abundance (log-scale):
      Estimate      SE      z      P(>|z|)
(Intercept) -0.294  0.191 -1.53  1.25e-01
vegHt        2.141  0.271  7.91  2.53e-15

Detection (logit-scale):
      Estimate      SE      z      P(>|z|)
(Intercept) -1.73  0.254 -6.83  8.27e-12
wind         -4.22  0.529 -7.97  1.61e-15

AIC: 333.3263
Number of sites: 100
optim convergence code: 0
optim iterations: 37
Bootstrap iterations: 0

Warning message:
In pcount(~wind~vegHt, data = umf, control = list(trace = TRUE, :
  K was not specified and was set to 107.

```

Here K is the upper summation limit for the summation over the random effects in the integrated likelihood (Royle, 2004b, p. 110). In `unmarked`, the default choice of K is the maximum observed count plus 100. This should normally be enough, but some sensitivity analysis may be useful (e.g., by setting K as 200 plus the maximum count). For small data sets, there may be identifiability problems that can be diagnosed by estimates of λ that keep increasing when K is made larger (Couturier et al., 2013; Dennis et al., 2015a).

In `unmarked`, we may choose three alternative abundance models: the Poisson (default), negative binomial (NB) (Royle, 2004b), and zero-inflated Poisson (ZIP) (see Section 3.3.4; Wenger and

Freeman, 2008). We can compare them by AIC or a likelihood ratio test (LRT). Not surprisingly, given our way of data simulation, the Poisson comes out best.

```
fm.Nmix2 <- pcount(~wind~vegHt, data=umf, mixture="NB",
  control=list(trace=TRUE, REPORT=5))
fm.Nmix3 <- pcount(~wind~vegHt, data=umf, mixture="ZIP",
  control=list(trace=TRUE, REPORT=5))
cbind(AIC.P=fm.Nmix1@AIC, AIC.NB=fm.Nmix2@AIC, AIC.ZIP=fm.Nmix3@AIC)
      AIC.P   AIC.NB AIC.ZIP
[1,] 333.3263 335.3284 335.327
```

The parameters of the linear model are defined on the log scale for abundance and on the logit scale for detection. Neither is a scale most of us like to think in, so to make better sense of what the parameter estimates mean, we can make predictions of λ and p for specified values of the covariates. The function `predict` uses the delta rule to compute SEs and 95% CIs (see Section 2.4.3).

```
# Predictions of lambda for specified values of vegHt, say 0.2 and 2.1
newdat <- data.frame(vegHt=c(0.2, 1.1))
predict(fm.Nmix1, type="state", newdata=newdat, append=T)
  Predicted      SE      lower      upper  vegHt
1   1.14387 0.1747408 0.8479004  1.543152    0.2
2   7.85632 1.4894445 5.4180585 11.391861    1.1

# ... or of p for values of wind of -1 to 1
newdat <- data.frame(wind=seq(-1, 1, , 5))
predict(fm.Nmix1, type="det", newdata=newdat, append=T)
  Predicted      SE      lower      upper  wind
1 0.922954766 0.033547623 0.8261414764 0.96794900 -1.0
2 0.592735702 0.065419999 0.4611115369 0.71227136 -0.5
3 0.150253394 0.032371147 0.0971288099 0.22518741  0.0
4 0.021030714 0.009093726 0.0089579531 0.04857659  0.5
5 0.002603173 0.001772162 0.0006844676 0.00984741  1.0
```

We can compute the expected values of the expected abundance λ and of detection probability p for the actual data set (i.e., for the specific, observed values of the `vegHt` and `wind` covariates). For the detection model, predictions are produced for each of (here) 300 observations. Predictions for the three surveys at site 1 are in rows 1–3 (i.e., `p.hat[1:3,1]` below, and *not* in rows 1, 101, and 201 as one might perhaps think).

```
# Predict lambda and detection for actual data set
(lambda.hat <- predict(fm.Nmix1, type="state")) # lambda at every site
(p.hat <- predict(fm.Nmix1, type="det"))       # p during every survey
```

To visualize the covariate relationships in general, it is best to predict for a new data frame with a suitable range of covariate values.

```
# Predict lambda and detection as function of covs
newdat <- data.frame(vegHt=seq(-1, 1, 0.01))
pred.lam <- predict(fm.Nmix1, type="state", newdata=newdat)
newdat <- data.frame(wind=seq(-1, 1, 0.1))
pred.det <- predict(fm.Nmix1, type="det", newdata=newdat)
```

We may summarize the analysis by plotting the observed data, the true data-generating values, and the estimated relationship between expected abundance (i.e., λ) and `vegHt` under the N -mixture model (a hierarchical Poisson regression that does account for imperfect detection p) and under a nonhierarchical Poisson regression that does not account for p and therefore only models an index of abundance (Johnson, 2008) (Figure 6.2, right). We see that ignoring imperfect detection leads to (1) underestimation of abundance and (2) a bias toward zero of the regression coefficient of `vegHt`.

```
# Fit detection-naive GLM to counts and plot comparison (Figure 6.2, right)
summary(fm.glm <- glm(c(C) ~ rep(vegHt, 3), family=poisson)) # p-naive model
matplot(vegHt, C, xlab="Vegetation height", ylab="Counts", frame = F, cex = 1.5, pch = 1,
        col = "black")
lines(seq(-1,1,.1,100), exp(beta0 + beta1* seq(-1,1,.1,100)), lwd=3, col = "red")
curve(exp(coef(fm.glm)[1]+coef(fm.glm)[2]*x), -1, 1, type="l", lwd=3, add=TRUE)
lines(vegHt, predict(fm.Nmix1, type="state")[,1], col = "blue", lwd = 3)
legend(-1, 7, c("Truth", "'Poisson GLM' with p", "Poisson GLM without p"), col=c("red",
"blue", "black"), lty = 1, lwd=3, cex = 1.2)
```

Predictions of λ represent an estimate of the expected abundance in a comparable site that has the chosen values of covariates. But we can also use the model to provide us with an estimate of abundance at the studied sites—i.e., for the realized abundance N_i . In the frequentist analysis, site-specific abundance, the random effect N_i , is lost by the summation over all possible states up to K (see above) of N_i in forming the integrated likelihood. We can obtain estimates of these random effects by application of the function `ranef`. This applies Bayes' rule for a conditional estimate of abundance N_i , given the model parameters and the observed data \mathbf{y}_i . That is, the function obtains the *best unbiased prediction* (BUP) of the random effects N_i as $\hat{N}_i = E(N_i|\mathbf{y}_i, \lambda)$, with $\hat{\lambda}$ used in place of λ (Royle, 2004a), based on the posterior distribution of N_i :

$$p(N_i|\mathbf{y}_i, \lambda_i, p_i) = \frac{f(\mathbf{y}_i|N_i, p_i)g(N_i|\lambda_i)}{q(\mathbf{y}_i|\lambda_i, p_i)}$$

Here, $f(\mathbf{y}_i|N_i, p_i)$ is the likelihood of the data y_{ij} , $g(N_i|\lambda_i)$ the prior for N_i , and $q(\mathbf{y}_i|\lambda_i, p_i)$ denotes the probability of the observed data, given the values of λ_i and p_i . The function `ranef` yields the results of this for each site.

```
ranef(fm.Nmix1)
      Mean Mode 2.5% 97.5%
[1,] 0.037770455 0 0 1
[2,] 0.001489541 0 0 0
[3,] 0.081963672 0 0 1
[4,] 1.040688154 1 1 2
[5,] 0.021773600 0 0 0
[ . . . ]
[91,] 4.075543688 4 4 5
[92,] 3.539540712 3 3 5
[93,] 1.969791630 1 0 5
[94,] 7.765449990 7 7 10
[95,] 4.280652414 4 3 7
[ . . . ]
```

To clarify the above expression, we here do the same “by hand.”

```
# calculate lambda.hat: exp(a0 + a1*vegHt)
lambda.hat <- predict(fm.Nmix1, type="state")[,1]

# calculate p.hat: plogis(b0 + b1*wind)
p.hat <- matrix(predict(fm.Nmix1, type="det")[,1], ncol=ncol(C), byrow=TRUE)

Ngrid <- 0:(100+max(umf@y, na.rm = TRUE))
posterior <- matrix(NA, nrow=nrow(C), ncol=length(Ngrid))
bup2 <- array(NA, dim = M)

for(i in 1:nrow(C)){ # Loop over sites
  # Compute prior using MLE
  gN <- dpois(Ngrid, lambda.hat[i])
  gN <- gN/sum(gN)

  # Compute likelihood for each possible value of N
  fy <- rep(NA, length(Ngrid))
  for(j in 1:length(Ngrid)){
    fy[j] <- prod(dbinom(C[i,], Ngrid[j], p.hat[i,]))
  }

  # Compute marginal of y. for denominator of Bayes rule
  qy <- sum(fy * gN)

  # Posterior
  posterior[i,] <- fy * gN / qy

  # N can't be less than max(C)
  if(max(C[i,] > 0))
    posterior[i,0:max(C[i,])]<- 0

  # Compute posterior mean (BUP)
  bup2[i] <- sum(posterior[i,] * Ngrid)
}

# Compare BUPs with true N and counts for first and last 5 sites
(bup1 <- bup(ranef(fm.Nmix1)))
cbind(N=N, count1=C[,1], count2=C[,2], count3=C[,3], BUP1=bup1, BUP2=bup2)[c(1:5,
91:95),]

```

	N	count1	count2	count3	BUP1	BUP2
[1,]	0	0	0	0	0.037770455	0.037770455
[2,]	0	0	0	0	0.001489541	0.001489541
[3,]	0	0	0	0	0.081963672	0.081963672
[4,]	2	1	0	0	1.040688154	1.040688154
[5,]	0	0	0	0	0.021773600	0.021773600
[6,]	6	2	2	4	4.075543688	4.075543688
[7,]	4	3	3	0	3.539540712	3.539540712
[8,]	2	0	0	0	1.969791630	1.969791630
[9,]	8	3	0	7	7.765449990	7.765449990
[10,]	4	1	3	2	4.280652414	4.280652414

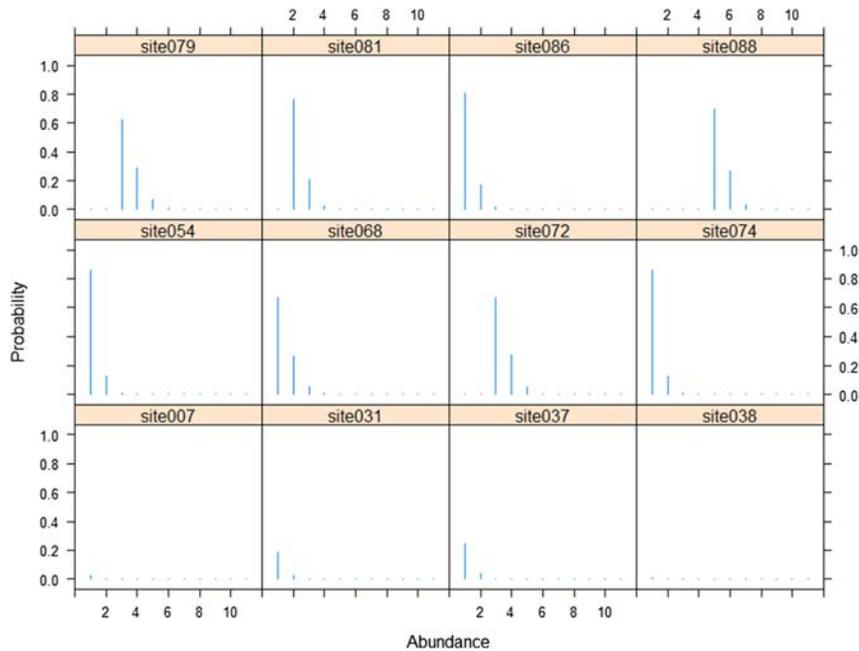


FIGURE 6.3

Estimated conditional posterior distributions of local abundance at a random selection of sites. The *best unbiased prediction* (BUP) is the mean of these distributions.

We can plot the empirical posterior distributions of N , shown here for a random sample of 12 sites (Figure 6.3).

```
plot(ranef(fm.Nmix1), xlim=c(0,12))[sort(sample(1:100, 12))]
```

These estimates are approximations, because their uncertainty does not incorporate the uncertainty stemming from the fact that the parameters had to be estimated. In contrast, the Bayesian estimates of N using BUGS (see later) are exact except for Monte Carlo error inherent in the MCMC analysis. We could also compute functions of the BUPs, for example, to estimate the combined population size in groups of sites (for instance, in habitats of type A, B and C) or over all of them (Lyons et al., 2012). The uncertainty around such derived quantities could be bootstrapped; see Section 10.4 for the analogous problem of estimating the number of occupied sites under an occupancy model.

We will next quickly illustrate the fitting of linear models involving factors inside an N -mixture model. We fit models in the “means parameterizations,” where the parameters for the levels of the factors have the direct meaning of the means for each factor level (see Section 3.2.1). The linear models underlying these two models are called “main-effects analysis of covariance (ANCOVA)” and “interaction-effects ANCOVA” in other fields (Kéry, 2010; Section 3.2.2). For a factor A and a continuous covariate x , these linear models could be denoted “ $A + x$ ” and “ $A * x$,” respectively.

```
# Main-effects ANCOVA: additive effects of factor and covariate
summary(fm.Nmix2 <- pcount(~ wind+time-1 ~ vegHt+hab-1, data=umf))
```

```
# Interaction-effects ANCOVA: multiplicative effects of factor and covariate
summary(fm.Nmix3 <- pcount(~ wind*time-1-wind ~ vegHt*hab-1-vegHt, data=umf))

# Get predictions for factor levels at average values of covariates
newdat <- data.frame(vegHt=0, hab = c("A", "B", "C"))
predict(fm.Nmix2, type="state", newdata=newdat, appendData = T) # for abundance
  Predicted      SE    lower    upper vegHt  hab
1 0.5527982 0.3188844 0.1784624 1.712326    0    A
2 0.7692908 0.1908027 0.4731208 1.250861    0    B
3 0.9158200 0.3858810 0.4010108 2.091530    0    C

newdat <- data.frame(time = c("1", "2", "3"), wind = 0)
predict(fm.Nmix3, type="det", newdata=newdat, appendData = T) # for detection
  Predicted      SE    lower    upper time wind
1 0.2066560 0.06272938 0.10957280 0.3554218    1    0
2 0.1355945 0.04862346 0.06504282 0.2612868    2    0
3 0.1184702 0.04544869 0.05416939 0.2397505    3    0
```

A little confusingly, to get predictions only for selected levels of a factor such as habitat, you need to add *all* the levels (in the correct order!) to your factor in `newdata`:

```
newdat <- data.frame(vegHt=seq(0, 2 ,by=0.1), hab = factor("A", levels = c("A", "B", "C")))
predict(fm.Nmix2, type="state", newdata=newdat, appendData = T)
```

Model selection can be done using the AIC (see above) or by a likelihood ratio test.

```
LRT(fm.Nmix3, fm.Nmix1)
  Chisq DF Pr(>Chisq)
1 6.235671 8 0.6208518
```

In summary, `unmarked` gives us considerable flexibility in fitting a wide range of *N*-mixture models quickly and reliably, and makes available to us all the convenience of likelihood inference (e.g., tests and AIC). Despite the name of the model-fitting function (`pcount`), and even some published analyses that call this model “*the point count model*,” applications of the binomial mixture model are of course *not* restricted to point count data. Instead, any kind of replicated counts for any reasonably well-defined spatial sampling units may be adequate for this model; e.g., counts along linear transects (Kéry et al., 2009), or areal counts with or without defined transects (Kéry et al., 2005b; Lyons et al., 2012); see also [Figure 6.8](#).

We conclude this section with an illustration of BUGS fitted to the last one of these models, the one with an interaction-effects ANCOVA linear model structure. We do not need to add time into the data bundle, because we can use the column dimension of the two-dimensional data array containing the counts to specify models with seasonal variation in detection probability. We add four types of derived quantities: the number of occupied sites in the sample of 100 study sites (N_{occ}), the total population size (N_{total}), the habitat-specific total population size (N_{hab}), and predictions of expected abundance and of detection for a range of values of the covariates `vegHt` and `wind`, respectively, for which we provide two sets of evenly spaced covariate values (X_{vegHt} , X_{wind}). We defer until later the fitting of alternative abundance models; e.g., the Poisson-lognormal (PLN), negative-binomial (NB), and zero-inflated Poisson (ZIP) (see [Section 6.10](#)).

One of the greatest things about a Bayesian analysis is the ease with which we can do calculations on latent variables, and in general make inferences about derived quantities or functions of parameters, with full propagation of all uncertainty involved in its computation via the posterior distribution (see also Sauer and Link, 2002, for a neat example). In our example we emphasize inference about functions of site-specific abundance N : the number of occupied sites (N_{occ}), the total abundance across all M sites (N_{total}), total abundance in the three habitat types (N_{hab}), as well as predictions of λ and p for a range of values of the `vegHt` and `wind` covariates, for each level of the two factors in the model.

As another, fairly crazy example of such derived quantities, suppose that a famous theoretical ecologist has just come up with a sophisticated theory about the extinction risk of metapopulations. His theory predicts that our metapopulation would go extinct if 75% or more of all patches had only two or fewer individuals. Is it possible to estimate the extinction probability of our metapopulation? It turns out that in a Bayesian analysis this is really simple: in the BUGS model, we simply define a statistic that codes for the desired condition, add it up over the M sites and then obtain posterior samples for this latter quantity. So as one solution to this difficult problem, we could add the following lines in the model:

```
critical[i] <- step(2-N[i])      # yields 1 whenever N is less or equal to 2
N.critical <- sum(critical[])   # Number of sites with critical size
```

Thus, whenever N_i is less than or equal to 2, the indicator `critical` evaluates to 1, and `N.critical` tallies the number of populations for which this is the case.

```
# Bundle data
win.data <- list(C = C, M = nrow(C), J = ncol(C), wind = wind, vegHt = vegHt,
hab = as.numeric(factor(hab)), XvegHt = seq(-1, 1, , 100), Xwind = seq(-1, 1, , 100) )
str(win.data)

# Specify model in BUGS language
cat(file = "model2.txt", "
model {
# Priors
for(k in 1:3){
      alpha0[k] ~ dunif(-10, 10)   # Loop over 3 levels of hab or time factors
      alpha1[k] ~ dunif(-10, 10)   # Detection intercepts
      beta0[k] ~ dunif(-10, 10)    # Detection slopes
      beta1[k] ~ dunif(-10, 10)    # Abundance intercepts
      beta2[k] ~ dunif(-10, 10)    # Abundance slopes
}

# Likelihood
# Ecological model for true abundance
for (i in 1:M){
  N[i] ~ dpois(lambda[i])
  log(lambda[i]) <- beta0[hab[i]] + beta1[hab[i]] * vegHt[i]
  # Some intermediate derived quantities
  critical[i] <- step(2-N[i])      # yields 1 whenever N is 2 or less
  z[i] <- step(N[i]-0.5)          # Indicator for occupied site
  # Observation model for replicated counts
  for (j in 1:J){
    C[i,j] ~ dbin(p[i,j], N[i])
    logit(p[i,j]) <- alpha0[j] + alpha1[j] * wind[i,j]
  }
}
}
```

```

# Derived quantities: functions of latent variables and predictions
Nocc <- sum(z[]) # Number of occupied sites among sample of M
Ntotal <- sum(N[]) # Total population size at M sites combined
Nhab[1] <- sum(N[1:33]) # Total abundance for sites in hab A
Nhab[2] <- sum(N[34:66]) # Total abundance for sites in hab B
Nhab[3] <- sum(N[67:100]) # Total abundance for sites in hab C
for(k in 1:100){ # Predictions of lambda and p ...
  for(level in 1:3){ # ... for each level of hab and time factors
    lam.pred[k, level] <- exp(beta0[level] + beta1[level] * XvegHt[k])
    logit(p.pred[k, level]) <- alpha0[level] + alpha1[level] * Xwind[k]
  }
}
N.critical <- sum(critical[]) # Number of populations with critical size
})

# Initial values
Nst <- apply(C, 1, max)+1 # Important to give good inits for latent N
inits <- function() list(N = Nst, alpha0 = rnorm(3), alpha1 = rnorm(3), beta0 = rnorm(3),
beta1 = rnorm(3))

# Parameters monitored
params <- c("alpha0", "alpha1", "beta0", "beta1", "Nocc", "Ntotal", "Nhab",
"N.critical", "lam.pred", "p.pred") # could also estimate N, bayesian
counterpart to BUPs before: simply add "N" to the list

# MCMC settings
nc <- 3 ; ni <- 22000 ; nb <- 2000 ; nt <- 10

# Call JAGS, time run (ART 1 min) and summarize posteriors
library(jagsUI)
system.time(out <- jags(win.data, inits, params, "model2.txt", n.chains = nc,
n.thin = nt, n.iter = ni, n.burnin = nb, parallel = TRUE))
traceplot(out, param = c('alpha0', 'alpha1', 'beta0', 'beta1', 'Nocc', 'Ntotal',
'Nhab', 'N.critical'))
print(out, 2)

```

	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff
alpha0[1]	-1.41	0.40	-2.23	-1.39	-0.67	FALSE	1.00	1.00	6000
alpha0[2]	-1.92	0.43	-2.82	-1.89	-1.15	FALSE	1.00	1.00	6000
alpha0[3]	-2.08	0.45	-3.01	-2.07	-1.26	FALSE	1.00	1.00	6000
alpha1[1]	-3.65	0.83	-5.43	-3.59	-2.21	FALSE	1.00	1.00	6000
alpha1[2]	-4.76	0.93	-6.76	-4.71	-3.13	FALSE	1.00	1.00	6000
alpha1[3]	-5.01	0.98	-7.09	-4.94	-3.29	FALSE	1.00	1.00	2789
beta0[1]	-3.75	1.87	-7.91	-3.55	-0.56	FALSE	0.99	1.01	361
beta0[2]	-0.35	0.28	-0.93	-0.34	0.16	TRUE	0.90	1.00	6000
beta0[3]	-0.36	0.52	-1.41	-0.36	0.64	TRUE	0.75	1.00	975
beta1[1]	-2.89	2.52	-8.10	-2.82	1.83	TRUE	0.88	1.01	457
beta1[2]	2.04	1.24	-0.33	2.03	4.50	TRUE	0.95	1.00	6000
beta1[3]	2.24	0.69	0.88	2.24	3.61	FALSE	1.00	1.00	825
Nocc	57.53	2.98	52.00	57.00	64.00	FALSE	1.00	1.00	6000

```

Ntotal      141.76 12.90 122.00 140.00 173.00      FALSE 1.00 1.00 4873
Nhab[1]     6.45  2.06  4.00  6.00  12.00      FALSE 1.00 1.00 1965
Nhab[2]    28.17  4.22 22.00 28.00  38.00      FALSE 1.00 1.00 6000
Nhab[3]   107.13 10.06 92.00 106.00 131.00      FALSE 1.00 1.00 6000
N.critical  76.43  2.45 71.00 77.00  81.00      FALSE 1.00 1.00 6000
[ output truncated ]

```

Hence, the number of occupied sites (N_{occ}) is estimated at 57.5 (CRI 52–64), the total abundance across all M sites (N_{total}) at 141.8 (CRI 122–173), and the habitat-specific total abundance at 6.45 (CRI 4–12) in habitat A, 28.2 (CRI 22–38) in habitat B, and 107.1 (CRI 92–131) in habitat C. Finally, the number of sites with critical population size (i.e., two or fewer individuals) is estimated at 76.4 (CRI 71–81); see Figure 6.4.

```

plot(table(out$sims.list$N.critical), xlab="Number of populations with critical size",
ylab="Frequency", frame = F) # Produces plot 6.4
abline(v = 74.5, col = "red", lwd = 3)

```

Our estimate of the metapopulation extinction risk is simply the proportion of MCMC samples for which $N_{critical} \geq 75$.

```

(metapop.extinction.risk <- mean(out$sims.list$N.critical > 74))
[1] 0.8008333

```

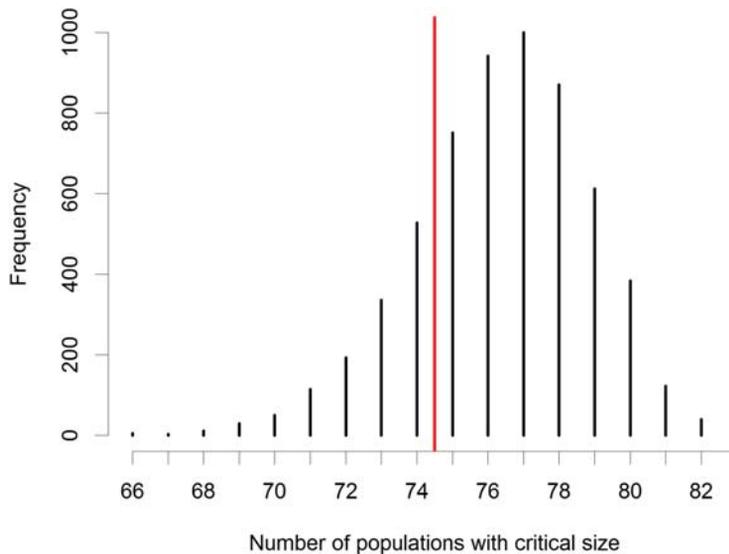
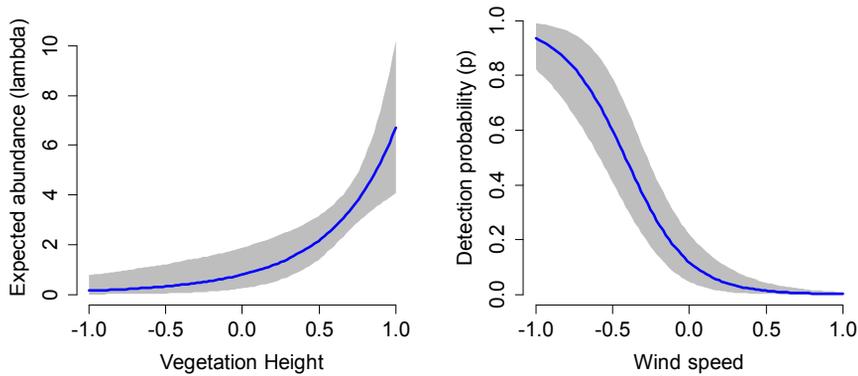


FIGURE 6.4

Example of a crazy derived variable in a Bayesian analysis: the posterior distribution of the number of populations that meet some hypothetical extinction threshold (here, two or fewer individuals), and the imaginary critical number (red line, 75) of such populations at which the metapopulation is going extinct. The metapopulation extinction risk is the relative mass to the right of the red line and amounts to about 80%.

**FIGURE 6.5**

Predictions of expected abundance (λ) in habitat type C (left), and detection probability (p) for occasion 3 (right) (posterior means and 95% CRIs are shown).

Hence, the future is not bright for our metapopulation... let us produce some plots to illustrate the covariate relationships for one of the levels of the two factors (Figure 6.5).

```
par(mfrow = c(1,2), mar = c(5,5,3,2), cex.axis = 1.5, cex.lab = 1.5)
X <- seq(-1, 1, , 100)
plot(X, out$summary[219:318,1], xlab = "Vegetation Height", ylab = "Expected abundance
(lambda)", ylim = c(0, 11), frame = F, type = "l")
polygon(c(X, rev(X)), c(out$summary[219:318,3], rev(out$summary[219:318,7])),
col = "gray", border = F)
lines(X, out$summary[219:318,1], lty = 1, lwd = 3, col = "blue")
plot(X, out$summary[519:618,1], xlab = "Wind speed", ylab = "Detection probability (p)",
ylim = c(0, 1), frame = F, type = "l")
polygon(c(X, rev(X)), c(out$summary[519:618,3], rev(out$summary[519:618,7])),
col = "gray", border = F)
lines(X, out$summary[519:618,1], lty = 1, lwd = 3, col = "blue")
```

Thus, when fitting the model with the BUGS language, you have all the power and flexibility of the Bayesian approach to inference and the BUGS engines at your fingertips (see Sections 6.9 and 10.6 for easy implementation, in BUGS, of complex linear models using design matrices).

6.5 A VERY GENERAL DATA SIMULATION FUNCTION FOR *N*-MIXTURE MODELS: `simNmix`

In Section 4.3, we met a function that generates data under a binomial mixture model with covariates in both abundance and detection. Here, we introduce a much more general function that we have written to simulate data under both binomial and multinomial *N*-mixture models (Chapter 7), `simNmix`, which is in the applied hierarchical modeling (AHM) package. The default arguments are the following:

```
simNmix(nsite = 267, nvisit = 3, mean.theta = 1, mean.lam = 2, mean.p = 0.6,
area = FALSE, beta1.theta = 0, beta2.theta = 0, beta3.theta = 0, beta2.lam = 0,
```

```

beta3.lam=0, beta4.lam=0, beta3.p=0, beta5.p=0, beta6.p=0,
beta.p.survey=0, beta.p.N=0, sigma.lam=0, dispersion=10, sigma.p.site=
0, sigma.p.visit=0, sigma.p.survey=0, sigma.p.ind=0, Neg.Bin=FALSE,
open.N=FALSE, show.plot=TRUE)

```

The default settings create an “MHB-type” of data set (267 sites, three replicate visits) under the simplest *N*-mixture model (see Section 6.3) with constant expected abundance ($\lambda = 2$) and detection ($p = 0.6$). Switching on some “toggles” such as `area`, `Neg.Bin`, and `open.N`, and choosing covariate coefficients and random effects SDs other than zero, permit generation of data sets under a large number of models, including different mixture distributions for abundance (Poisson, ZIP, PLN, ZIP-lognormal, negative binomial, zero-inflated NB), varying area of sites (which might then lead to an analysis with offset; see Section 3.3.2), violation of the closure assumption, and a large number of possible types of “overdispersion” (OD). One of the most general model types under which data sets can be generated is a zero-inflated PLN *N*-mixture model with covariates in suitability probability, expected abundance, and detection probability, and with OD in `logit(detection)` due to sites, surveys, visits, and individuals:

Suitability (or zero-inflation) model

$$s_i \sim \text{Bernoulli}(\theta_i)$$

$$\text{logit}(\theta_i) = \alpha_{0,\theta} + \text{beta1.theta} * \text{Xsite1}_i + \text{beta2.theta} * \text{Xsite2}_i + \text{beta3.theta} * \text{Xsite3}_i$$

Abundance model (given suitability)

$$N_i | s_i \sim \text{Poisson}(s_i * \lambda_i)$$

$$\log(\lambda_i) = \log(A_i) + \alpha_{0,\lambda} + \text{beta2.lam} * \text{Xsite2}_i + \text{beta3.lam} * \text{Xsite3}_i + \text{beta4.lam} * \text{Xsite4}_i + \text{eta.lam.site}_i$$

Detection model (given abundance)

$$C_{ij} | N_i \sim \text{Binomial}(N_i, p_{ij})$$

$$\text{logit}(p_{ij}) = \alpha_{0,p} + \text{beta3.p} * \text{Xsite3}_i + \text{beta5.p} * \text{Xsite5}_i + \text{beta6.p} * \text{Xsite6}_i + \text{beta.p.survey} * \text{Xsurvey}_{ij} \\ + \text{beta.p.N} * N_i.\text{centered}_i + \text{eta.p.site}_i + \text{eta.p.visit}_j + \text{eta.p.survey}_{ij} + \text{eta.p.ind}_n$$

“Overdispersion” models

$$\text{eta.lam.site}_i \sim \text{Normal}(0, \text{sigma.lam}^2)$$

Abundance site random effects in `log(λ)`

$$\text{eta.p.site}_i \sim \text{Normal}(0, \text{sigma.p.site}^2)$$

Detection site random effects in `logit(p)`

$$\text{eta.p.visit}_j \sim \text{Normal}(0, \text{sigma.p.visit}^2)$$

Detection visit random effects in `logit(p)`

$$\text{eta.p.survey}_{ij} \sim \text{Normal}(0, \text{sigma.p.survey}^2)$$

Detection site/survey random effects in `logit(p)`

$$\text{eta.p.ind}_n \sim \text{Normal}(0, \text{sigma.p.ind}^2)$$

Detection individual random effects in `logit(p)`

This model describes three major, linked random variables, two latent and one observed: s_i denotes whether site i is suitable ($s_i = 1$) or not ($s_i = 0$; this is the zero-inflation part), $N_i | s_i$ is the abundance at site i given that site i is suitable, $C_{ij} | N_i$ denotes the observed counts at site i during replicate j given local abundance N_i , `Xsite1` through `Xsite6` are site-level covariates, and `Xsurvey` is an observational covariate. Coefficients of these covariates have names that start with `beta` and include as a suffix `theta`, `lam`, or `p` to indicate whether they are in the suitability (`theta`), abundance (`lambda`), or detection (`p`) model. Two covariates may affect more than one level in the model: `Xsite2` can affect both suitability and abundance via the coefficients `beta2.theta`, `beta2.lam`, and `Xsite3` can affect all three via coefficients `beta3.theta`, `beta3.lam`, and `beta3.p`. Covariate `N.centered` allows for a logarithmic relationship between local abundance and detection probability—i.e., for density-dependent detection probability. A_i is the area of a site; hence, unless $A = 1$ (the default when `area = FALSE`), the log of the supplied area will be used as an offset in the linear predictor of the abundance model; see below for an example. All `eta` terms are random

effects that vary by what their name and their subscript says—i.e., by site, visit (= occasion), or site/visit (= survey). They are draws from separate zero-mean normal distributions with SDs that are selected as a function argument.

The last set of random effects, *eta.p.ind_n*, is specific to the n individuals ($n = 1, \dots, N_{\text{total}}$) occurring anywhere at the studied sites; i.e., it lets us simulate data under what is known as model M_n in the capture-recapture literature (Otis et al., 1978, Williams et al., 2002; Royle and Dorazio, 2008; King et al., 2009; see also Section 7.8.3). We introduce such individual effects by simulating the data *at the level of each individual*. To obtain the simulated count C_{ij} , we sum up the observed individuals for each site and visit. Therefore, function `simNmix` yields the individual-level detection histories for all individuals, including those that were never detected. These individual detection histories can be aggregated for the observed individuals and analyzed using multinomial mixture models (see Chapter 7), or aggregated to counts and analyzed using binomial mixture models.

Setting `Neg.Bin = TRUE` will generate data with an NB distribution for abundance, with dispersion equal to the `dispersion` argument. As another overdispersed alternative to a Poisson, we can choose a PLN distribution by setting `sigma.lam` to a nonzero value.

With `open.N = TRUE`, data are simulated under one specific form of an open-population model, where N in the first occasion is drawn from the specified distribution, and for all further occasions j we have $N_{ij} \sim \text{Poisson}(N_{i(j-1)})$. Data sets generated with this setting can be used to study the effects of a (fairly serious) violation of the closure assumption. With `open.N = TRUE`, we must have `sigma.p.ind = 0` and `nvisit > 1`.

Argument `show.plot` determines whether to show plots that visualize the data-generating processes including the final data. These should help you understand the effects of different settings for the function arguments. You must browse through the plots by pressing the Enter key; hence when running simulations, you should set `show.plot = FALSE`.

```
# Execute function and inspect results
data <- simNmix()                                # Default arguments
data <- simNmix(show.plot = FALSE)              # Default args, no plots
set.seed(24)
str(data <- simNmix(nsite = 267, nvisit = 3, mean.theta = 1, mean.lam = 2,
  mean.p = 0.6, area = FALSE, beta1.theta = 0, beta2.theta = 0, beta3.theta = 0,
  beta2.lam = 0, beta3.lam = 0, beta4.lam = 0, beta3.p = 0, beta5.p = 0, beta6.p =
  0, beta.p.survey = 0, beta.p.N = 0, sigma.lam = 0, dispersion = 10, sigma.p.site
  = 0, sigma.p.visit = 0, sigma.p.survey = 0, sigma.p.ind = 0, Neg.Bin = FALSE,
  open.N = FALSE, show.plot = TRUE))           # All default args explicit
```

The object to which the function output is assigned first repeats the values of all function arguments, followed by most things created along the way, to generate the main output, the individual detection history matrix (DH) and the replicated counts (C).

```
List of 44
 $ nsite      : num 267
 [Output truncated: values of all function arguments ]
 $ site.cov   : num [1:267, 1:6] -0.8297 -1.1004 0.8169 0.0756 0.6505 ...
 .. attr(*, "dimnames")=List of 2
 ...$ : NULL
 ...$ : chr [1:6] "cov1" "cov2" "cov3" "cov4" ...
 $ survey.cov : num [1:267, 1:3] -1.209 1.111 -1.359 0.993 -1.304 ...
 $ log.lam    : num [1:267] 0.693 0.693 0.693 0.693 0.693 ...
```

```

$ s      : int [1:267] 1 1 1 1 1 1 1 1 1 1 ...
$ N      : int [1:267] 4 2 4 4 1 2 0 3 2 0 ...
$ p      : num [1:267, 1:3, 1:7] 0.6 0.6 0.6 0.6 0.6 0.6 NA ...
$ DH     : int [1:267, 1:3, 1:7] 1 1 0 1 1 1 NA 0 1 NA ...
$ N.open : logi NA
$ C      : int [1:267, 1:3] 4 2 2 1 1 2 0 0 2 0 ...
[ more truncated output ]
$ Ntotal : int 507
$ summax  : int 422

```

The function defaults to the simplest possible *N*-mixture model with constant λ and p . By changing some default arguments, you can generate data under an extremely wide variety of models, as we will now show (we will omit default arguments and only set the arguments required for the stated kind of data-generating model). For the most complex models and large sample sizes, function execution may easily take 10–20 s, and you can ignore the warnings. We start our illustration with a few simple variants of the default Null model.

```

str(data <- simNmix())                # Null data-generating model
str(data <- simNmix(mean.theta = 0.60)) # ZIP with 40% structural zeroes
str(data <- simNmix(sigma.lam = 1))    # Poisson-lognormal (PLN) mixture
str(data <- simNmix(Neg.Bin = TRUE))   # Negative-binomial mixture
str(data <- simNmix(mean.theta = 0.6, sigma.lam = 1)) # Zero-inflated PLN
str(data <- simNmix(mean.theta = 0.6, Neg.Bin = TRUE)) # Zero-infl. NegBin
str(data <- simNmix(mean.p = 1))       # Perfect detection (p = 1)
str(data <- simNmix(mean.theta = 0.6, mean.p = 1))   # ZIP with p = 1
str(data <- simNmix(sigma.lam = 1, mean.p = 1))      # PLN with p = 1

```

Other simple variants of the default model include the following.

```

areas <- runif(267, 1, 2)                # Generate vector with site area
str(data <- simNmix(nsite = 267, area = areas)) # Sites with variable area
str(data <- simNmix(nvisit = 1))         # Only one visit
str(data <- simNmix(sigma.p.site = 1))   # Random site effects in p
str(data <- simNmix(sigma.p.visit = 1))  # Random visit (= time) effects in p
str(data <- simNmix(sigma.p.survey = 1)) # Random site-by-visit effects in p
str(data <- simNmix(sigma.p.ind = 1))    # Random individual effects in p
str(data <- simNmix(mean.theta = 0.5, beta1.theta = 1)) # Site cov 1 in suitability
str(data <- simNmix(beta2.lam = 1))      # Site covariate 2 in abundance process
str(data <- simNmix(beta3.p = 1))       # Site covariate 3 in detection process
str(data <- simNmix(beta.p.N = 1))       # Positive density-dep. in p
str(data <- simNmix(beta.p.N = -1))     # Negative density-dep. in p
# Same covariate in suitability and abundance (see Phillips & Elith, Ecology, 2014)
str(data <- simNmix(mean.theta = 0.5, beta2.theta = 1, beta2.lam = -1))
# Same covariate in abundance and detection (see Kéry, Auk, 2008)
str(data <- simNmix(beta3.lam = 1, beta3.p = -1))
# Same covariate in all three levels of model (ouch!)
str(data <- simNmix(mean.theta = 0.5, beta3.theta = 1, beta3.lam = 1, beta3.p = -1))

```

Site covariates 2 and 3 may be chosen to affect both the suitability and the abundance processes, and sometimes one sees people fit such models to data. We suspect that identifiability in this case is due

exclusively to the strict assumption about the link transformation (logit and log, respectively) and thus, that this estimation problem is analogous to that of estimating N -mixture or site-occupancy models from unreplicated data (Knapé and Korner-Nievergelt, 2015).

```
# Use unmarked to fit some models to these data sets
cov <- data$site.cov
summary(umf <- unmarkedFramePCount(
  y=data$C, siteCovs=data.frame(cov1=cov[,1], cov2=cov[,2], cov3=cov[,3],
    cov4=cov[,4], cov5=cov[,5], cov6=cov[,6], area = data$area),
  obsCovs = list(survey.cov = data$survey.cov)))
summary(fm <- pcount(~1 ~1, umf))
summary(fm <- pcount(~1 ~1, umf, mixture = "ZIP"))
summary(fm <- pcount(~1 ~1, umf, mixture = "NB"))
summary(fm <- pcount(~cov1+cov2+cov3 ~ cov1+cov2+cov3, umf))
```

It would be straightforward to extend this function—e.g., to add other mixture distributions, more covariate effects including polynomial terms and their interactions, factors (categorical explanatory variables), or an individual covariate such as mass that affects the detection probability of each individual. Similarly, increased ecological realism could be included by shooting missing values in the resulting observed data—for instance, to emulate surveys that were not conducted.

6.6 STUDY DESIGN, BIAS, AND PRECISION OF THE BINOMIAL N -MIXTURE MODEL ESTIMATOR

As for many HMs, there is substantial scope for investigations about optimal sampling design. Some work has been done for occupancy models (e.g., MacKenzie and Royle, 2005; Bailey et al., 2007; Guillera-Aroita et al., 2010, 2014; Sanderlin et al., 2014; Ellis et al., 2015), but hardly anything has been published so far for N -mixture models (McIntyre et al., 2012; Yamaura, 2013; Yamaura et al., in press). A basic design question with practical importance is how many sites have to be visited or how many visits have to be conducted in order to obtain estimates of some desired quality. A related question is whether it is better to invest more in replicate sites or replicate visits. Both are best answered with simulation.

Further, while in principle, with decent data, the parameters of the N -mixture model may be estimated well, the quality of the estimates naturally depends on the sample size (number of sites, number of replicates) and on the magnitude of the parameters λ and p . For small sample sizes, the widely proclaimed unbiasedness of MLEs is lost (Le Cam, 1990), and it is not clear when this happens. In addition, there may be problems with the identifiability of the parameters for small samples or certain parameter values (Couturier et al., 2013; Dennis et al., 2015a). Simulation can give you extremely valuable insight, for exactly *your* sample sizes and presumed parameter values; the latter may come from previous studies, similar species or be based on expert opinion.

Here is a small simulation study that shows how the quality of estimates for particular scenarios (sample sizes, parameter values) can very easily be ascertained by simulation. In our example, we do this for the simplest N -mixture model, but such a simulation can easily be extended to more complex models (for instance, see the next section for a slightly more complex model). Also, see Section 10.7 for the analogous study with the site-occupancy model. Specifically, we want to know how bias and precision of the abundance estimator is affected by three factors: number of sites, number of visits, and

detection probability (p). In our simulation, we treat the former two as factors (with three levels) and the latter as akin to a continuous explanatory variable by varying p continuously between 0.01 and 0.99.

```
# Define simulation settings and arrays for sim results
simreps <- 1000          # Simulate and analyse 1000 data sets
nsites <- c(20, 120, 250) # Levels for nsites factor
nreps <- c(2, 5, 10)    # Levels of nrep factor
estimates <- array(NA, dim=c(2, simreps, 3, 3))

# Fill p with random numbers between 0.01 and 0.99
p <- array(runif(n=simreps*3*3, 0.01, 0.99), dim=c(simreps, 3, 3))

# Launch simulation (takes about 6.3 hours)
for(s in 1:3){          # Loop over levels of nsites factor
  for(r in 1:3){        # Loop over levels of nreps factor
    for(i in 1:simreps){ # Simulate and analyse 1000 data sets
      cat("*** Simrep number", i, "***\n")
      data <- simNmix(nsites=nsites[s], nvisit=nreps[r], mean.lam = 5,
        mean.p=p[i,s,r], show.plot = F)          # Generate data set
      umf <- unmarkedFramePCount(y = data$C)      # Bundle data for unmarked
      fm <- pcount(~1 ~1, umf)                   # Fit model
      estimates[,i,s,r] <- coef(fm)              # Save estimates
    }
  }
}

# Visualization
par(mfrow=c(3,3), mar=c(4.5,4.5,2,2), cex.lab=1.5, cex.axis=1.3)
for(s in 1:3){          # Loop over nsites
  for(r in 1:3){        # Loop over nreps
    plot(p[,s,r], exp(estimates[1, ,s,r]), xlab="Detection probability",
      ylab="lambda_hat", main="", ylim=c(0, 75), frame=F)
    text(0.75, 60, paste("M = ", nsites[s], ", J = ", nreps[r], sep=""),
      cex=1.5)
    abline(h=5, col="red", lwd=2)
    lines(smooth.spline(exp(estimates[1, ,s,r])~p[,s,r]), col="blue", lwd=2)
  }
}
```

Figure 6.6 shows that there is considerable variation in the quality of the N -mixture model estimates: higher numbers of sites (M), visits (J), and values of detection probability are all beneficial for the quality of the estimates, and the effects of these factors interact. We can clearly recognize the “first law of capture-recapture”: that things become more difficult when p gets small. The range of p over which we can expect unbiased estimates of λ (where the red and blue lines coincide) varies from 0.7–1 in the least information-rich scenario (20 sites surveyed twice) to essentially 0.1–1 for the most information-rich scenario (250 sites with 10 surveys each). We also note that for small values of M , J , and p , we get a higher incidence of “freak” estimates, where λ is estimated at some very large value.

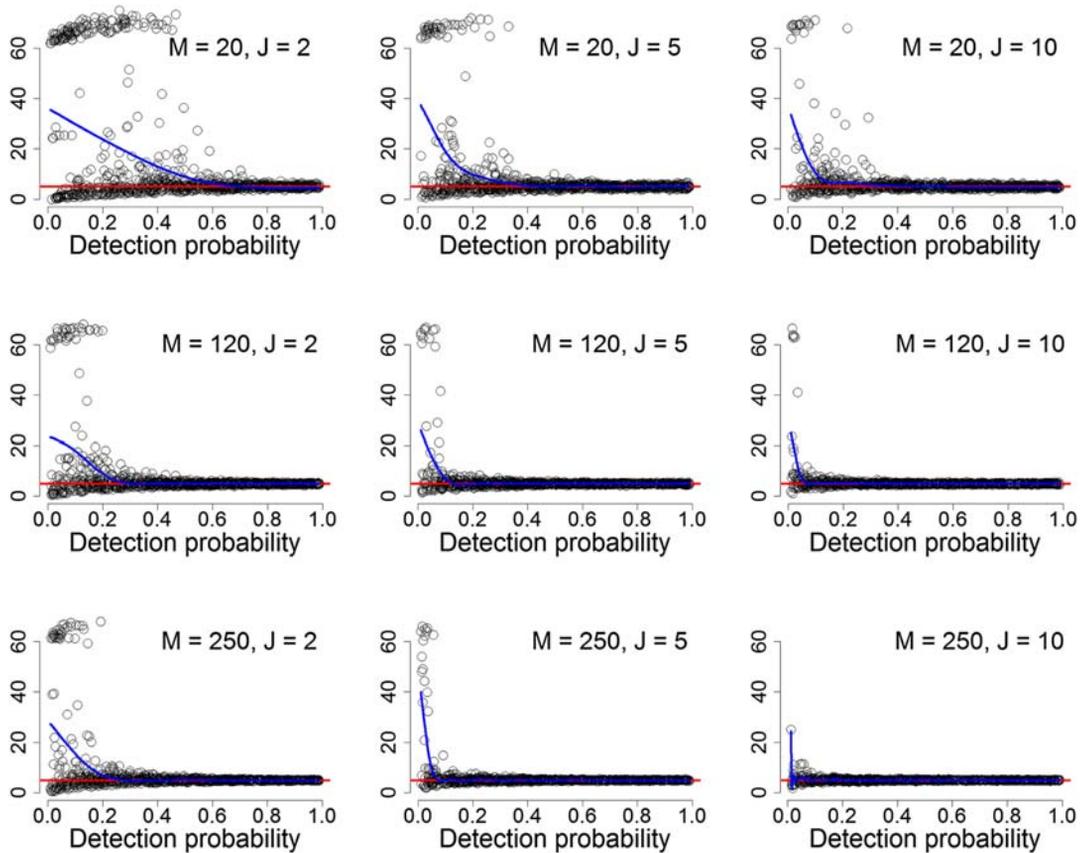


FIGURE 6.6

Yes, it is *that* easy to determine the required sample size for your study: simply simulate data sets where you vary the factors you are interested in, fit the model, and compare the estimates with the known truth. Then, choose the sample size that gives the desired quality of the estimates of the important parameters. Here are results from simulating/analyzing a total of 9000 data sets where we simultaneously varied two factors with three levels each (number of sites M and number of replicate surveys J) and detection probability p (continuously from 0.01 to 0.99). The red line shows truth ($\lambda = 5$), and the blue line is a smoothing spline fit to the estimates.

In the range of p where there are no such outliers, the N -mixture estimator appears unbiased, since the mean of the estimates (blue line) agrees well with the truth (red line).

These results are qualitatively identical to what we find for the occupancy model in Section 10.7. Computation time is much greater for the N -mixture models, but we never obtained crashes associated with a singular Hessian matrix. We could run this simulation with BUGS (and wait for a much *longer* time still) and would presumably observe a “regularizing” effect of the use of the posterior mean as a point estimator as we do in Section 10.7—i.e., observe fewer or no high, freak estimates.

6.7 STUDY OF SOME ASSUMPTION VIOLATIONS USING FUNCTION

`simNmix`

Using simulation, it is also straightforward to study effects of assumption violations: we simply simulate data that include some extra feature such as random effects at some level or lack of closure, and then we analyze the data using a model that assumes the absence of these effects. The presence of an important effect in the data generation and its absence in the analysis model represents an assumption violation in the model. We illustrate this next. Two assumptions of the basic N -mixture models are population closure and the absence of unmodeled heterogeneity in λ and p . To test for the effects of a violation of these assumptions, we use function `simNmix` to generate six data sets with the following basic settings:

```
mean.lam = exp(1), mean.p = 0.5, beta2.lam = 1, beta3.p = 1, beta.p.survey = 1
```

That is, mean expected abundance is 2.71, mean detection is 0.5, and the slopes of the expected abundance on covariate 2, and of detection probability on covariate 3 and on the survey covariate are all equal to 1. In addition, data sets 1–5 contain one type of heterogeneity that can be created by setting the following arguments to a value of 1: `sigma.lam` (creating site random effects in abundance) and, for random effects in detection, `sigma.p.site` (site random effects), `sigma.p.visit` (occasion random effects), `sigma.p.survey` (random effects of site-by-occasion), or `sigma.p.ind` (random effects for each individual). For data set 6, we set `open.N = TRUE` and do not add any heterogeneity. We then use unmarked to fit a model that is correct in terms of the covariate structure but ignores the extra heterogeneity or openness. We repeat this for 1000 data sets. Code for case 6 (lack of closure) is shown here. This section builds partly upon Tanadini (2010).

```
simreps <- 1000 # Number of data sets created/analysed
MLE <- array(dim = c(5, simreps)) # Array to hold MLEs

for(i in 1:simreps){ # Create and analyse 1000 data sets
  cat("*** Simrep number", i, "***\n")
  # Create data set with some extra (here: open populations)
  data <- simNmix(mean.lam=exp(1), mean.p=0.5, beta2.lam=1,
    beta3.p=1, beta.p.survey=1, open.N=TRUE, show.plot=F)
  # Analyze data set with standard model (here: assuming closure)
  umf <- unmarkedFramePCount(y=data$C, siteCovs =
    data.frame(cov2=data$site.cov[,2], cov3=data$site.cov[,3]),
    obsCovs = list(survey.cov = data$survey.cov))
  fm <- pcount(~cov3+survey.cov ~cov2, umf, se = F)
  # Save MLEs
  MLE[,i] <- coef(fm)
}
```

Each type of assumption violation induced bias in some of the five estimated parameters, but not every parameter estimate was affected equally, or indeed at all (Table 6.2). With unmodeled site heterogeneity in abundance, we overestimated mean abundance by 50%, and detection and the slope of the observational covariate by 14%, but the slope estimates of the two site covariates on abundance and detection remained unbiased. Interestingly, Dorazio et al. (2008) found that when a model with lognormal Poisson abundance is assumed, but the site-specific heterogeneity in abundance has a more complex form, then abundance is also overestimated.

Table 6.2 Effects of six types of assumption violations on N -mixture model estimators. The first five effects are associated with unmodeled heterogeneity in the form of normal random effects in either $\log(\lambda)$ or $\text{logit}(p)$, while the sixth case is lack of closure without any heterogeneity. For detection (p), slope 1 is for a site covariate and slope 2 for a sampling covariate. Mean and 2.5–97.5% percentiles are given for 1000 data sets that were simulated in every case.

Parameter	λ (Int.)	λ (Slope)	p (Int.)	p (Slope 1)	p (Slope 2)
True Value	2.71	1	0.5	1	1
Type of Assumption Violation					
(1) lambda site heterogeneity	4.04 (3.27–5.02)	0.99 (0.80–1.22)	0.57 (0.49–0.64)	1.02 (0.79–1.26)	1.14 (0.99–1.30)
(2) p site heterogeneity	2.60 (2.26–2.93)	1.00 (0.91–1.10)	0.52 (0.47–0.58)	0.84 (0.66–1.00)	0.89 (0.77–1.03)
(3) p occasion heterogeneity	3.76 (2.53–12.02)	1.01 (0.94–1.09)	0.40 (0.09–0.69)	0.81 (0.36–1.06)	0.77 (0.34–1.04)
(4) p survey heterogeneity	3.15 (2.77–3.64)	1.02 (0.94–1.10)	0.41 (0.35–0.46)	0.76 (0.63–0.90)	0.71 (0.60–0.85)
(5) p individual heterogeneity	2.62 (2.33–2.93)	1.00 (0.92–1.08)	0.52 (0.48–0.57)	0.86 (0.75–0.98)	0.89 (0.79–1.00)
(6) Open N (no closure)	9.03 (3.34–16.80)	1.01 (0.91–1.12)	0.20 (0.03–0.49)	0.00 (–0.08–0.08)	0.00 (–0.08–0.08)

Unmodeled site heterogeneity in detection leads to a slight underestimation of abundance, and attenuation (a pull toward zero) of both detection covariate slope estimates. Occasion-specific heterogeneity in detection induced a 39% overestimation of abundance, and bias in detection and attenuation in the estimate of both detection covariates. With survey-specific heterogeneity in detection, abundance was overestimated by 16%, detection underestimated, and both detection covariate estimates attenuated. Unmodeled detection heterogeneity at the level of the individual induced only a negligible bias in abundance and attenuation in the slopes of the detection covariate estimates. This is surprising in view of the “second law of capture-recapture”, which says that unmodelled detection heterogeneity at the individual level induces a negative bias in the abundance estimator. Not surprisingly, the strong violation of the closure assumption represented by setting argument `open.N` to `TRUE` leads to strong positive bias in abundance, strong negative bias in detection, and maximal attenuation of the detection covariate estimates. Surprisingly, the slope of the single abundance covariate remained effectively unbiased over all scenarios tested, while estimates of the slopes of detection covariates were typically attenuated.

Obviously, this is not an exhaustive simulation for the study of the effects of assumption violations on the estimators of the binomial N -mixture model. However, it does yield some important insights. Moreover, it shows how this topic can be addressed in a very straightforward way using simulation.

Thus, there is an interest in getting right the main structures in the data and minimizing unexplained heterogeneity by use of covariates or by accommodating heterogeneity by additional random effects in the model. With the exception of individual heterogeneity (case 5), all forms of heterogeneity studied in this section may easily be specified in BUGS. For instance, occasion- and survey-specific detection heterogeneity can be coded by adding into the linear predictor for detection extra terms like `eta[j]` or `eta[i, j]` and then specifying a zero-mean normal prior for `eta` with an SD that is estimated; see Kéry et al. (2009), Zellweger-Fischer et al. (2011) and Sections 6.11, 7.6.3, and 7.8.4 for examples.

Openness can be accommodated by moving to a dynamic N -mixture model (see Chapters 12–14 in volume 2). The risk of bias for an ill-specified model emphasizes the importance of goodness-of-fit (GoF), which we cover next.

6.8 GOODNESS-OF-FIT (GoF)

The essence of GoF testing lies in comparing the observed data, or some function thereof, with the analogous quantity that we would expect to see under the model using some discrepancy measure. Ideally, this latter should be chosen such that it indicates a particular breakdown of the model that is relevant to *you*, because it affects *your* intended use of the model. For instance, it could be the observed and expected maximum response if you are interested in predicting extremes (Gelman et al., 1996). In addition, residual diagnostics should be used more often, since they can point out more specifically *where* a model fits and where it does not, and this may suggest ways to improve our model. However, most of the time, we simply calculate a single number that gives a combined measure of the discrepancy between the data and what the model says the data should look like. Typical examples of such statistics are Chi-square, sum of squares, or Freeman–Tukey, and these may be bootstrapped in a non-Bayesian analysis, or their posterior predictive distributions may be used in a Bayesian analysis (Sections 2.8.2 and 5.10).

We illustrate such a GoF test with N -mixture models, using again the function `simNmix`. We could directly use function `parboot` in `unmarked` to conduct a parametric bootstrap for a fit statistic of our choice, but instead use the wrapper function `Nmix.gof.test` in the R package `AICcmodavg`, which bootstraps a Chi-square statistic (Mazerolle, 2015). We illustrate with simulated data that represent different kinds of assumption violations with respect to the analyzing model. We start with the “true model” and repeat the exercise nine times to give you an idea of the sampling error in p -values from a GoF test. For illustration, we run only 100 bootstrap replicates, but for a “real” analysis, you should perhaps run at least 1000.

```
# Case 1: Test GoF of correct model
library(AICcmodavg)
par(mfrow = c(3,3))
for(i in 1:9){
  data <- simNmix(show.plot = F)           # Create data set
  fm <- pcount(~1~1, unmarkedFramePCount(y = data$C)) # Fit model
  pb.gof <- Nmix.gof.test(fm, nsim = 100)  # 100 bootstrap reps
}
```

Next, we look at the following assumption violations: in abundance, zero inflation, lognormal extra-Poisson dispersion, and an unmodeled site covariate, and in detection probability, logit-normal extra-binomial dispersion, and an unmodeled site or observational covariate. We run nine cases for each, with decreasing magnitudes of the assumption violation. When you execute the following code, you can observe how the GoF test statistic will come down *on average*, but that there is substantial sampling error.

```
# Case 2: Simulate data with zero inflation and analyse without
val.range <- seq(0.1, 1, ,9)           # Much to no zero-inflation
for(i in 1:9){
  data <- simNmix(mean.theta = val.range[i], show.plot = F)
  fm <- pcount(~1~1, unmarkedFramePCount(y = data$C)) # Fit model
  pb.gof <- Nmix.gof.test(fm, nsim = 100)
}
```

```

# Case 3: Extra-Poisson dispersion in lambda
val.range <- seq(1, 0,,9)      # Some to no extra-Poisson dispersion
for(i in 1:9){
  data <- simNmix(sigma.lam = val.range[i], show.plot = F)
  fm <- pcount(~1 ~1, unmarkedFramePCount(y = data$C))  # Fit model
  pb.gof <- Nmix.gof.test(fm, nsim = 100)
}

# Case 4: Site covariate in lambda
val.range <- seq(3, 0,,9)      # Strong to no effect of covariate
for(i in 1:9){
  data <- simNmix(beta3.lam = val.range[i], show.plot = F)
  fm <- pcount(~1 ~1, unmarkedFramePCount(y = data$C))  # Fit model
  pb.gof <- Nmix.gof.test(fm, nsim = 100)
}

# Case 5: Extra-binomial dispersion in p (survey random effect)
val.range <- seq(1, 0,,9)      # Strong to no effect extra-dispersion
for(i in 1:9){
  data <- simNmix(sigma.p.survey = val.range[i], show.plot = F)
  fm <- pcount(~1 ~1, unmarkedFramePCount(y = data$C))  # Fit model
  pb.gof <- Nmix.gof.test(fm, nsim = 100)
}

# Case 6: Site covariate in p
val.range <- seq(3, 0,,9)      # Strong to no covariate effect
for(i in 1:9){
  data <- simNmix(beta3.p = val.range[i], show.plot = F)
  fm <- pcount(~1 ~1, unmarkedFramePCount(y = data$C))  # Fit model
  pb.gof <- Nmix.gof.test(fm, nsim = 100)
}

# Case 7: Observational covariate in p
val.range <- seq(3, 0,,9)      # Strong to no covariate effect
for(i in 1:9){
  data <- simNmix(beta.p.survey = val.range[i], show.plot = F)
  fm <- pcount(~1 ~1, unmarkedFramePCount(y = data$C))  # Fit model
  pb.gof <- Nmix.gof.test(fm, nsim = 100)
}

```

The above simulation code may be valuable for you to gain an intuition into the working of such a GoF test and seems to suggest a decent sensitivity of our bootstrapped Chi-square statistic to most kinds of assumption violations. You could build on it to do a simulation study for gauging test sensitivity to certain kinds of assumption violations that are important to you.

With your real data sets, in addition to running a GoF test, we emphasize the usefulness of doing residual checks to highlight places *where* the model does not fit. For an unmarked fitted model object `fm` you can extract residuals by typing `residuals(fm)`. Plotting residuals against predicted values or covariates can help determine why lack of fit is occurring and whether additional structure (e.g., additional covariates) should be added to help remedy lack of fit (ver Hoef

and Boveng, 2015). Finally, if despite your best efforts you do not succeed in building a model that passes your GoF test, you have at least three options: (1) you can discard the data set and claim it is unanalyzable, (2) you can look for an entirely different type of model (and then test GoF again), or (3) you can stick to the nonfitting model in the hope that the lack of fit is inconsequential for your intended use of the model, and because it may still be the best (or only) model you can think of.

But perhaps you may assume that the lack of fit detected is simply unstructured noise (i.e., from over-dispersion (OD)), such that the mean structure of the model is correct but the variance is too large, something extremely common in count data (Lee and Nelder, 2000; ver Hoef and Boveng, 2007). One approach to accounting for OD is to estimate its magnitude—e.g., by dividing the observed Chi-square statistic by the mean of simulated values as an OD parameter (\hat{c}), and then multiplying the variance–covariance matrix by \hat{c} (MacKenzie and Bailey, 2004; McKenny et al., 2006; Johnson et al., 2010). Such an accommodation for up to moderate amounts of lack of fit (e.g., for \hat{c} up to 4, Mazerolle, 2015) is similar to what is commonly done for capture-mark-recapture models in program MARK, and widely used in Cormack-Jolly-Seber survival models (White and Burnham, 1999). See Sections 6.9 and 7.9.3 for illustrations in the context of HMs.

We go on to illustrate the use of posterior predictive checking for GoF when you fit an N -mixture model in a Bayesian analysis. Remember that at each iteration of the MCMC algorithm we randomly draw a new data set using the very model used to analyze the data set at hand and with the particular draws from the posterior distribution of all its parameters. For both the actual and the replicated (“perfect”) data sets, we then compare some discrepancy measure between data and model. Then, we compare the posterior distributions of the two discrepancy statistics in a plot or by summarizing with a Bayesian p -value (Sections 2.8.2 and 5.10). We write the code for the simplest N -mixture model such that you can feed into it all types of data sets as created above and see whether a posterior predictive check based on a Chi-square discrepancy can pick up the known assumption violations. We illustrate with a data set that contains lognormal extra-Poisson dispersion in λ with `sigma.lam = 0.5` (case 3 above). We add a small constant (ϵ) to the denominator of the Chi-square discrepancy in the BUGS code to avoid any division by zero.

```
# Bundle and summarize data set
str( win.data <- list(C = data$C, M = nrow(data$C), J = ncol(data$C), e = 0.001))

# Specify model in BUGS language
sink("model.txt")
cat("
model {
# Priors
  lambda ~ dgamma(0.001, 0.001)
  p ~ dunif(0, 1)
# Likelihood
  for (i in 1:M) {
    N[i] ~ dpois(lambda)      # State model
    for (j in 1:J) {
      C[i,j] ~ dbin(p, N[i]) # Observation model
    }
  }
}
```

```

# Posterior predictive distributions of chi2 discrepancy
for (i in 1:M) {
  for (j in 1:J) {
    C.sim[i,j] ~ dbin(p, N[i]) # Create new data set under model
    e.count[i,j] <- N[i] * p # Expected datum
    # Chi-square discrepancy for the actual data
    chi2.actual[i,j] <- pow((C[i,j]-e.count[i,j]),2) / (e.count[i,j]+e)
    # Chi-square discrepancy for the simulated ('perfect') data
    chi2.sim[i,j] <- pow((C.sim[i,j]-e.count[i,j]),2) / (e.count[i,j]+e)
    # Add small value e to denominator to avoid division by zero
  }
}
# Add up individual chi2 values for overall fit statistic
fit.actual <- sum(chi2.actual[,]) # Fit statistic for actual data set
fit.sim <- sum(chi2.sim[,]) # Fit statistic for a fitting model
c.hat <- fit.actual / fit.sim # c-hat estimate
bpv <- step(fit.sim-fit.actual) # Bayesian p-value
}
", fill = TRUE)
sink()

# Do other preps and run model with JAGS
inits <- function(){list(N = apply(data$C, 1, max)+1)}
params <- c("lambda", "p", "fit.actual", "fit.sim", "c.hat", "bpv")
ni <- 2500 ; nt <- 2 ; nb <- 500 ; nc <- 3
fm <- jags(win.data, inits, params, "model.txt", n.chains = nc, n.thin = nt, n.iter = ni,
  n.burnin = nb)
print(fm, dig = 3)

```

	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff
lambda	2.027	0.100	1.833	2.026	2.222	FALSE	1	1.000	3000
p	0.682	0.019	0.643	0.682	0.719	FALSE	1	1.000	3000
fit.actual	228.371	9.673	211.787	227.563	248.952	FALSE	1	1.001	1395
fit.sim	210.795	16.266	180.604	210.388	243.751	FALSE	1	1.000	3000
c.hat	1.087	0.061	0.977	1.084	1.213	FALSE	1	1.000	3000
bpv	0.070	0.255	0.000	0.000	1.000	TRUE	1	1.001	3000

For this realization of the random process represented by our data simulation process, doing a posterior predictive check based on a Chi-square discrepancy does not quite pick up the lack of fit here (i.e., the mismatch between the data-generating and the data-analyzing models): `c.hat` is estimated at only a little more than 1, and the Bayesian p -value of 0.070 almost suggests a fitting model.

We use our function `ppc.plot` to produce four plots that summarize the results from the Bayesian GoF test using posterior predictive distributions of the Chi-square discrepancy in this section (Figure 6.7). We see that the “lack-of-fit ratio,” or `c.hat`, is estimated at 1.09, and that there is a 23% chance of observing a value of the test statistic that is more extreme than the one for the observed data set. A fitting model has a Bayesian p -value around 0.5 and a model that does not fit has a p -value close to or equal to 0 or 1. However, there are no rules to decide on a threshold value that distinguishes a fitting from a nonfitting model.

```
ppc.plot(fm) # Produces Figure 6.7
```

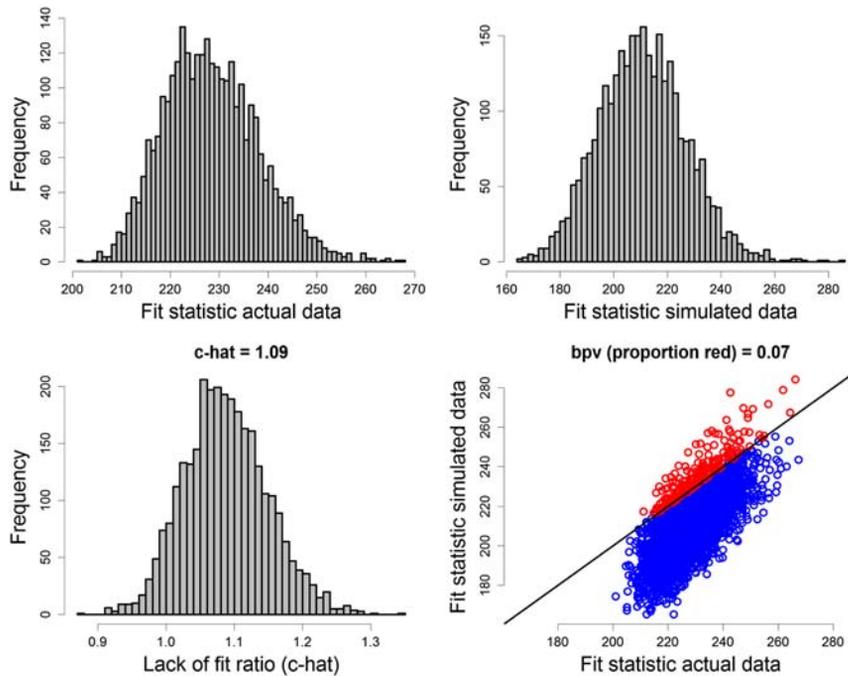


FIGURE 6.7

Results from a posterior predictive check of GoF (based on Chi-square discrepancy) for simulated data under an N -mixture model variant. Marginal posterior distributions are given for the test statistic for the actual and simulated data (top), and for their ratio (\hat{c}). Bottom right shows the joint posterior distribution of the fit statistics, with the proportion of the posterior mass above the 1:1 line (colored red) representing the value of the Bayesian p -value (bpv).

GoF relies on comparing expected and observed values. Link and Barker (2010, pp. 194–197) show a two-level posterior predictive check for a model that looks almost like a variation of an N -mixture model, except that both the Poisson and the binomial random variables are observed, so they can check for the fit of both model parts. This is not possible in the N -mixture model where the Poisson random variable is latent. See Section 7.9.3 for how we attempt to do this in a multinomial mixture model and Section 10.8 for GoF assessment in the related occupancy model. Despite its importance, GoF analysis is underdeveloped for HMs and some things we describe here should be understood as tentative. This is an area where more research is needed.

6.9 ABUNDANCE MAPPING OF SWISS GREAT TITS WITH unmarked

In this section, we use counts of great tits (Figure 4.1) collected in the Swiss breeding bird survey MHB from 2013. The Swiss common breeding bird survey MHB (Monitoring Häufige Brutvögel; Schmid et al., 2004) is based on a sample of 267 1-km² quadrats that are laid out as a grid over Switzerland, which has

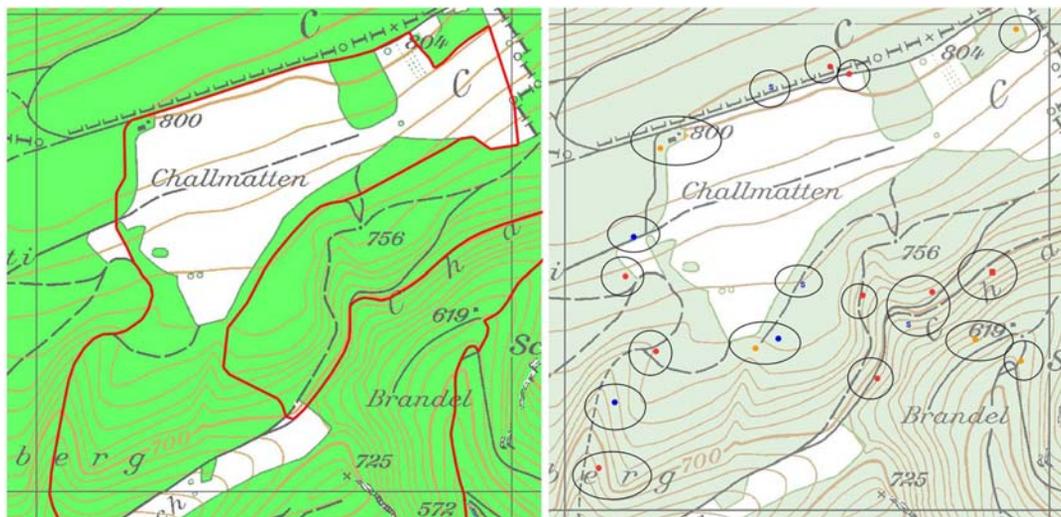


FIGURE 6.8

Example of a survey quadrat in the Swiss common breeding bird survey MHB with the surveyed transect route shown in red (left). Forest is shown in green and elevation in meters. Only the 4.0 km of transect and the birds inside the 1-km² quadrat are surveyed. Right: Combined survey data for the great tit *Parus major* in 2010. Dots represent detection locations, with colors indicating occasions 1–3, and ellipses are the putative territories.

an area a little over 41,000 km². Experienced volunteers survey a quadrat-specific, irregular transect route whose length varies from 1–9 km (mean 5.1); see Figure 6.8 (left) for an example. Each transect is surveyed three times during the breeding season (mid-April until early July) using the territory mapping method (Bibby et al., 2000). High-lying quadrats (above the tree line) are surveyed only twice. Surveys start at dawn and last for four hours on average (SD = 1 h). Observers record the location of each individual of each identified species on a map. Afterward, putative territories are determined based on the clustering of observations and for isolated records, based on the knowledge of typical territory sizes of each species (Figure 6.8, right). Here, we analyze quadrat counts of the number of great tit territories (y_{ij}) in quadrat i during survey j in 2013. We load a data set that contains MHB counts of all six Swiss tit species from 2004–2013. Virtually all quadrats are surveyed annually, but survey-specific counts are currently available for only a subset of quadrats that increases over the years. The data set includes site coordinates and covariates for elevation (m), forest cover (%), and route length (km), and as observational covariates the date (day 1 = April 1) and duration (min) of every survey.

The goals of our analysis are threefold:

1. Identify environmental factors that affect the abundance of Swiss great tits,
2. Produce a Swiss map of great tit abundance in 2013, and
3. Estimate the size of the Swiss population of great tits in 2013.

We use `unmarked` to obtain MLEs for the following HM:

1. Model for quadrat population size (state process model):

$$N_i \sim \text{Poisson}(\lambda_i)$$

$$\log(\lambda_i) = \beta_0 + \text{covariate effects}$$

2. Measurement error model (observation model):

$$y_{ij}|N_i \sim \text{Binomial}(N_i, p_{ij})$$

$$\text{logit}(p_{ij}) = \alpha_0 + \text{covariate effects}$$

Route length varies by quadrat and it is likely that quadrats with longer routes are covered more thoroughly than quadrats with shorter routes. To account for such variable coverage bias, we use the inverse of route length as a covariate on abundance, as did Royle and Dorazio (2006) and Royle et al. (2007b); see also Section 7.9. The idea is that the “exposed population,” say, N_i , for a quadrat i with a given route location and length L is less than the actual population in the quadrat, say M_i , but as L goes to infinity, the quadrat becomes saturated with sampling effort and N_i goes to M_i .

Hence, the new quadrat population size model is

$$M_i \sim \text{Poisson}(\lambda_i)$$

$$\log(\lambda_i) = \beta_0 + \text{covariate effects}$$

$$N_i|M_i \sim \text{Binomial}(M_i, \phi(L_i))$$

where we model $\phi(L_i) = \exp(-\beta_5/L_i)$. Under this model the marginal distribution of N_i is

$$N_i \sim \text{Poisson}(\mu_i), \text{ with}$$

$$\mu_i = \phi(L_i)\lambda_i, \text{ and hence}$$

$$\log(\mu_i) = \beta_0 + \text{covariate effects} - \beta_5(1/L_i).$$

This means that we use inverse route length to account for $N_i \rightarrow M_i$ as L_i increases. For making predictions we set $1/L_i = 0$ (or possibly to any other route length). The prediction then applies to saturation sampling effort—i.e., to a 1-km² quadrat that is 100% covered (and quite possibly more than that; see Section 6.10).

We will consider two additional models for abundance, the NB and the ZIP distributions, both generalizations of a Poisson model. The NB model is a mixture of a Poisson and a gamma distribution (Lee and Nelder, 2000). Marginally, we have $N_i \sim \text{NegBin}(\mu_i, \alpha)$; here, α is the dispersion parameter, called “size” in R (we estimate $\log(\alpha)$ in `unmarked`). The variance of N is $\mu + \mu^2/\alpha$, so lower values of α imply higher variance and with $\alpha = \infty$ (or in practice with $\alpha \approx 100$) we are back to a Poisson. The ZIP model can be described by adding another hierarchical layer to our hierarchical model, which we can imagine describes the binary suitability of a site, with $w_i = 1$ denoting a suitable site and $w_i = 0$ one that is not suitable and that must therefore have zero abundance. The ZIP model in `unmarked` is this:

$$w_i \sim \text{Bernoulli}(1 - \phi) \quad \text{“Suitability” part of model}$$

$$N_i \sim \text{Poisson}(w_i\lambda_i) \quad \text{“Abundance” part of model}$$

Hence, the “zero-inflation parameter” ϕ here denotes the expected proportion of *unsuitable* sites that produce structural zero counts because they cannot be occupied by a species in principle. When $\phi = 0$, all sites are suitable in principle and we are back to a standard Poisson. The mean of a ZIP random variable is $(1 - \phi_i)\lambda_i$ (we will use this for prediction later). We could alternatively parameterize this model with $w_i \sim \text{Bernoulli}(\phi)$; now ϕ represents the expected proportion of *suitable* sites for which N has a standard Poisson distribution.

In *unmarked*, the zero-inflation or “suitability” part of the model cannot be modeled as a function of covariates, and sometimes there may be reasons for wanting to do so. However, there are several important, and we believe only little-known, caveats. First of all, fitting the same covariates in both the suitability and the abundance parts of the model results in a kind of borderline identifiability that is due exclusively to the critical parametric assumptions of the model (Ghosh et al., 2012). Arguably, this case is analogous to estimating abundance and detection from unreplicated count data (Knappe and Korner-Nievergelt, 2015). Hence, we would try to avoid whenever possible using identical covariates in the suitability and the abundance parts of a ZIP model. The second reason for why we think you ought to be cautious with the use of ZIP models with covariates in the zero-inflation part is more philosophical. At many places (e.g., in Chapters 1 and 10), we stress the unity of abundance and distribution: species occurrence is simply an information-reduced summary of species abundance. Adopting elaborate covariate models for both the suitability and the abundance parts of a ZIP model seems to us to obscure this important conceptual point. It does not seem to be conducive to clear thinking either about the concepts of distribution and abundance, or about the factors governing spatial variation in the fundamental quantity, which is abundance. Notwithstanding, if you really, *really* feel you *must* put covariates also in the suitability part of the model, then you can do this fairly easily in BUGS and use code in [Section 6.10](#) as a template.

In the ensuing analysis of great tits with *unmarked*, we will follow a four-step work flow: (1) setup of analysis, (2) model fitting, (3) GoF, model criticism, and model selection, and (4) analysis of results (especially the forming of predictions).

6.9.1 SETUP OF THE ANALYSIS

We read the file containing the counts of six Swiss tit species between 2004 and 2013, select the great tit data, and do some preliminaries.

```
tits <- read.table("SwissTits_mhb_2004_2013.csv", header = T, sep = ";")
show(tits)                # Look at data
str(tits)                 # Overview of data file

table(tits$latname)      # Available species (Latin short)
PARATE PARCAE PARCRI PARMAJ PARMON PARPAL
  267    267    267    267    267    267

table(tits$name)        # Same in English
Blue tit Coal tit Crested tit Great tit Marsh tit Willow tit
  267    267    267    267    267    267

# Select Great tit and covariate data from 2013 and
# drop 4 sites not surveyed in 2013
tits <- tits[tits$latname == "PARMAJ",]           # Get great tit data
NA.sites <- which(apply(is.na(tits[,41:43]), 1, sum) == 3) # Unsurveyed sites
tits <- tits[-NA.sites,]                         # Drop them
```

```

y <- cbind(tits$count131,tits$count132, tits$count133)      # Counts
date <- cbind(tits$date131,tits$date132, tits$date133)    # Survey date
dur <- cbind(tits$dur131,tits$dur132, tits$dur133)        # Survey duration

# Plot observed data: counts vs survey date (Figure 6.9)
matplot(t(date), t(y), type = "l", lwd = 3, lty = 1, frame = F, xlab = "Survey date
(1 = April 1)", ylab = "Count of Great Tits")

# Load unmarked, create unmarked data frame and inspect result
library(unmarked)
time <- matrix(rep(as.character(1:3), nrow(y)), ncol = 3, byrow = TRUE)
umf <- unmarkedFramePCount(y = y, siteCovs=data.frame(elev=scale(tits["elev"]),
forest=scale(tits["forest"]), iLength=1/tits["rlength"]),
obsCovs=list(time = time, date = scale(date), dur = scale(dur)))
summary(umf)                                               # Summarize unmarked data frame
summary(apply(y, 1, max, na.rm = TRUE))                   # Summarize max counts

```

On executing this code, we are reminded that we have data from 263 sites, with up to 3 and on average 2.83 surveys per site. Great tits were detected at 191 sites, and counts ranged from 0–41 per survey. We also discover that the maximum count per site, a simplistic estimator of local abundance that ignores imperfect detection, ranges from 0–41, with an average of 8.4. We also see that counts seem to decline over the course of the season (Figure 6.9).

6.9.2 MODEL FITTING

We now fit our *N*-mixture model and explore different structures in the deterministic and the stochastic parts of the HM. Specifically, we investigate different covariate structures in abundance and detection,

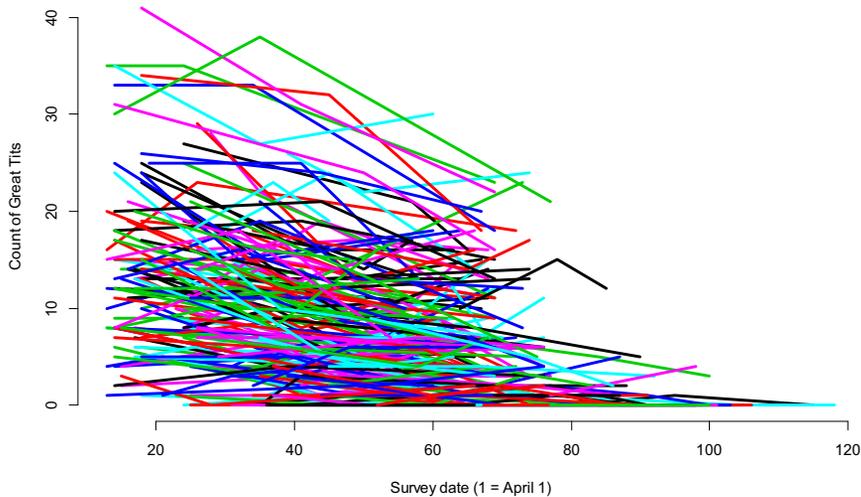


FIGURE 6.9

Time series of counts of great tits in 263 1-km² quadrats surveyed in 2013 as part of the Swiss breeding bird survey MHB.

and three different mixture distributions for abundance. To select a parsimonious covariate structure, we start with a highly parameterized model with a Poisson mixture and use backwards elimination guided by p -values and AIC scores. We start this process for the detection submodel and then proceed to the abundance submodel.

In the most complex abundance model, we fit the interactions of linear and quadratic effects of elevation and forest cover, as well as the main effect of the reciprocal of route length. In the detection model, we start with linear and quadratic effects and interactions of three continuous covariates (site elevation, and survey date and duration). We also fit main effects of the factor “time” (or occasion, representing the first, second, and third surveys), which accommodates temporal effects that are not captured by the continuous covariates survey date and duration.

```
fm1 <- pcount(~(elev+I(elev^2)) * (date+I(date^2)) * (dur+I(dur^2)) + time-1
             ~ (elev+I(elev^2)) * (forest+I(forest^2)) + iLength,
             umf, control=list(trace=TRUE, REPORT=5))
summary(fm1) ; fm1@AIC
```

We first ensure that there are no identifiability issues and that the summation limit in the likelihood evaluation (K) is high enough at its default by refitting the model with $K = 500$ (Couturier et al., 2013; Dennis et al., 2015a). (Note the use of the `formula` slot in the fitted model object to simplify the definition of an identical covariate structure in two model fits.)

```
fm1.K500 <- pcount(fm1@formula, umf, control=list(trace=T, REPORT=5), K = 500)
summary(fm1.K500) ; fm1.K500@AIC
```

We find identical AIC scores of 3701.771, and hence the default K was sufficient. Looking at the estimates of model 1, we observe that none of the eight three-way interactions are significant (their p -values range from 0.28 to 0.96), so we drop them all and refit the model. We are using model selection rather informally here. Normally, we would drop only one term at a time, and use likelihood ratio rather than Wald tests as a formal significance test in a GLM or an HM. We use solutions from the earlier model as starting values for the next. This speeds up convergence and sometimes may even be necessary to find the MLEs at all. Of course, when doing this, you should take care to check the ordering of the coefficients so that they correspond to the terms in the current model. When your current model has, say, one more coefficient than the one whose solutions you used to provide starting values, then you may have to fill in an NA or some reasonable value at the right place.

```
fm2 <- pcount(~(elev+I(elev^2)) * (date+I(date^2)) * (dur+I(dur^2)) + time-1
             - elev:date:dur - elev:date:I(dur^2) - elev:I(date^2):dur
             - elev:I(date^2):I(dur^2) - I(elev^2):date:dur - I(elev^2):date:I(dur^2)
             - I(elev^2):I(date^2):dur - I(elev^2):I(date^2):I(dur^2)
             ~ (elev+I(elev^2)) * (forest+I(forest^2))
             + iLength, starts = coef(fm1)[1:31],
             umf, control=list(trace=TRUE, REPORT=5))
summary(fm2) # AIC = 3695.792
```

In `fm2`, the two-way interactions between quadratic terms ($I(elev^2):I(date^2)$, $I(elev^2):I(dur^2)$ and $I(date^2):I(dur^2)$) have p -values between 0.33 and 0.89, so we remove all three at once.

```
fm3 <- pcount(~(elev+I(elev^2)) * (date+I(date^2)) * (dur+I(dur^2)) + time-1
  - elev:date:dur - elev:date:I(dur^2) - elev:I(date^2):dur
  - elev:I(date^2):I(dur^2) - I(elev^2):date:dur - I(elev^2):date:I(dur^2)
  - I(elev^2):I(date^2):dur - I(elev^2):I(date^2):I(dur^2)
  - I(elev^2):I(date^2) - I(elev^2):I(dur^2) - I(date^2):I(dur^2)
  ~ (elev+I(elev^2)) * (forest+I(forest^2))
  + iLength, starts = coef(fm2)[-c(23, 27, 31)],
  umf, control=list(trace=TRUE, REPORT=5))
summary(fm3) # AIC = 3691.184
```

From fm3, we drop the interactions `elev:I(date^2)` and `I(date^2):dur`, with p -values of 0.92 and 0.54, respectively.

```
fm4 <- pcount(~(elev+I(elev^2)) * (date+I(date^2)) * (dur+I(dur^2)) + time-1
  - elev:date:dur - elev:date:I(dur^2) - elev:I(date^2):dur
  - elev:I(date^2):I(dur^2) - I(elev^2):date:dur - I(elev^2):date:I(dur^2)
  - I(elev^2):I(date^2):dur - I(elev^2):I(date^2):I(dur^2)
  - I(elev^2):I(date^2) - I(elev^2):I(dur^2) - I(date^2):I(dur^2)
  - elev:I(date^2) - I(date^2):dur
  ~ (elev+I(elev^2)) * (forest+I(forest^2))
  + iLength, starts = coef(fm3)[-c(21, 28)],
  umf, control=list(trace=TRUE, REPORT=5))
summary(fm4) # AIC = 3687.565
```

At this point, respecting the rules of marginality (that main effects contained in a significant interaction must be kept in a model, etc.; McCullagh and Nelder, 1989; also see Section 3.2.4), we cannot simplify the detection model anymore, so we turn to the abundance model now, where we first drop the two-way interactions `elev2:forest2` and `elev2:forest` with $p = 0.30$ and $p = 0.42$.

```
fm5 <- pcount(~(elev+I(elev^2)) * (date+I(date^2)) * (dur+I(dur^2)) + time-1
  - elev:date:dur - elev:date:I(dur^2) - elev:I(date^2):dur
  - elev:I(date^2):I(dur^2) - I(elev^2):date:dur - I(elev^2):date:I(dur^2)
  - I(elev^2):I(date^2):dur - I(elev^2):I(date^2):I(dur^2)
  - I(elev^2):I(date^2) - I(elev^2):I(dur^2) - I(date^2):I(dur^2)
  - elev:I(date^2) - I(date^2):dur
  ~ (elev+I(elev^2)) * (forest+I(forest^2)) + iLength
  - I(elev^2):forest - I(elev^2):I(forest^2),
  starts = coef(fm4)[-c(9:10)],
  umf, control=list(trace=TRUE, REPORT=5))
summary(fm5) # AIC = 3686.094
```

The term `elev:I(forest^2)` has $p = 0.09$, so we try to drop it, but on doing so, the AIC goes up by 1 unit. Hence, we retain model 5 as our final model of the covariate structure. Next, we decide on an appropriate variance structure by comparing Poisson, NB, and ZIP (Wenger and Freeman, 2008) mixtures.

```
# Negative binomial (NB) mixture
fm5NB <- pcount(fm5@formula, starts = c(coef(fm5), 0),
  umf, control=list(trace=TRUE, REPORT=5), mixture = "NB")
summary(fm5NB) # AIC = 3181.046
```

```
# Zero-inflated Poisson (ZIP) mixture
fm5ZIP <- pcount(fm5@formula, starts = c(coef(fm5),0),
  umf, control=list(trace=TRUE, REPORT=5), mixture = "ZIP")
summary(fm5ZIP) # AIC = 3636.058
```

These models predict quite different average abundances and detection errors. In fact, under the NB mixture, mean abundance is estimated twice as high as under the two Poisson and ZIP models, and, consequently, the mean detection probability during occasions 1–3 is estimated to be much lower as well. Hence, our decision about which variance structure is most appropriate will really matter for our population assessment of the great tits in Switzerland.

```
cbind(rbind("Poisson" = exp(coef(fm5)[1]), "NegBin" = exp(coef(fm5NB)[1]), "ZIP"
= exp(coef(fm5ZIP)[1])), rbind(plogis(coef(fm5)[15:17]),
plogis(coef(fm5NB)[15:17]), plogis(coef(fm5ZIP)[15:17])))

      lam(Int)  p(time1)  p(time2)  p(time3)
Poisson 14.45832 0.6286573 0.5303886 0.4513780
NegBin  31.14023 0.3076560 0.2581500 0.2177134
ZIP     15.74359 0.5934831 0.4955699 0.4188714
```

In addition, the ZIP model estimates that `plogis(coef(fm5ZIP)[25])`, or about 8%, of all sites are not suitable for great tits in principle, while the NB model estimates the dispersion parameter α at `exp(coef(fm5NB)[25])`, or about 2. (As often, you have to execute all this code to see this.)

6.9.3 MODEL CRITICISM AND GoF

The NB is favored by AIC by a very large margin, followed by the ZIP ($\Delta\text{AIC} = 455$) and the Poisson ($\Delta\text{AIC} = 505$). We run a parametric bootstrap GoF test on a Chi-square discrepancy...

```
library(AICcmodavg)
system.time(gof.P <- Nmix.gof.test(fm5, nsim=100)) # 65 min
system.time(gof.NB <- Nmix.gof.test(fm5NB, nsim=100)) # 131 min
system.time(gof.ZIP <- Nmix.gof.test(fm5ZIP, nsim=100)) # 69 min
gof.P ; gof.NB ; gof.ZIP # print results
```

... and find that none of the models formally passes the GoF test, with the magnitude of overdispersion (OD, \hat{c}) ranging from 3.82 (Poisson), to 2.47 (ZIP) and to 1.79 (NB). This is disappointing, but before we discard the data set and declare it unanalyzable, we want to see whether there are any patterns in this lack of fit by investigating the residuals of each model. Perhaps we can treat this lack of fit simply as unstructured OD and then adjust for it by inflating the uncertainty around the estimates? We start by using our AHM function `plot.Nmix.resi` to graph the fitted values (i.e., the expected value of each datum) vs. the observed data and the residuals vs. the fitted values under each model (Figure 6.10). It can also be useful to directly compare data, fitted values, and residuals.

```
# Look at data, fitted values and residuals and produce plots
print(cbind(y, fitted(fm5), residuals(fm5)), 2) # For Poisson model
plot.Nmix.resi(fm5, fm5NB, fm5ZIP) # Produces Figure 6.10
```

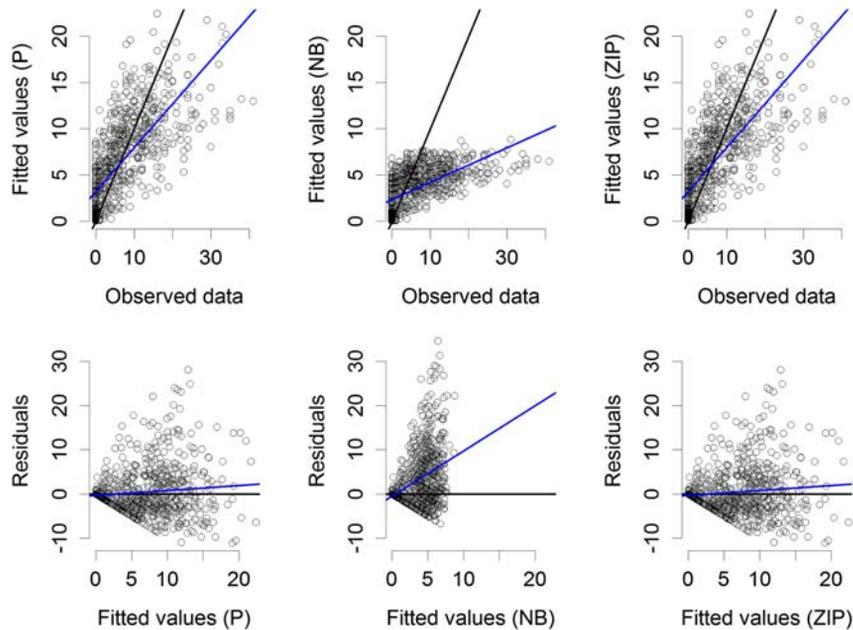
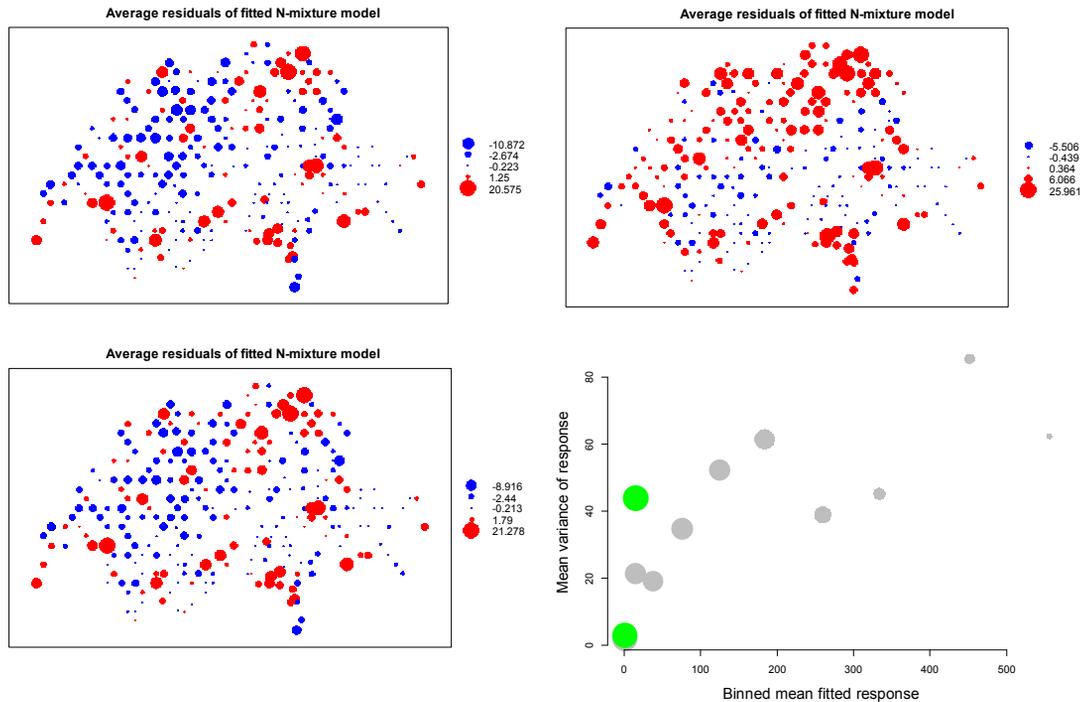


FIGURE 6.10

Residual diagnostics for the three *N*-mixture models fitted to the 2013 Swiss great tit counts. Top: Fitted values (= expected data) versus observed counts; the black line shows a 1:1 relationship and the blue line is the linear regression line of best fit. Bottom: Residuals versus fitted values (black line denotes a zero residual and the blue line is the linear regression line).

Surprisingly, we find a much better agreement between observed and expected data under the Poisson and ZIP models than under the NB. For the two former, fitted values cluster almost symmetrically around the 1:1 line of correspondence, while for the NB model, fitted values are much too small for a large range of observed data (Figure 6.10, top). When plotting residuals against fitted values (Figure 6.10, bottom), we find more or less symmetry of positive and negative residuals for the Poisson and ZIP models; this is shown by the blue regression line that essentially covers the black zero line. In contrast, there is a preponderance of positive residuals in the NB model; this is emphasized by the strong mismatch of the blue and the black lines. Accordingly, the root mean square error (RMSE) is about 40% larger for the NB than for the Poisson and ZIP mixtures.

```
# Compute RMSE for all three models
(RMSEP <- sqrt(mean((y - fitted(fm5))^2, na.rm = TRUE))) # Poisson
(RMSENB <- sqrt(mean((y - fitted(fm5NB))^2, na.rm = TRUE))) # NB
(RMSEZIP <- sqrt(mean((y - fitted(fm5ZIP))^2, na.rm = TRUE))) # ZIP
[1] 5.18944
[1] 7.139032
[1] 5.228797
```

**FIGURE 6.11**

Maps of the residuals (averaged over replicate surveys) under the AIC-best Poisson, NB, and ZIP *N*-mixture models for Swiss great tits in 2013, and of the mean variance of the response vs. the mean fitted response (bottom right) under the Poisson (gray) and the NB (green) models.

To investigate any spatial structure in the lack of fit of the three models, we use our AHM function `map.Nmix.resi` to produce a map of the residuals (averaged over occasions; Figure 6.11). We see less spatial structure (local pockets of high or low values) in the residuals of the Poisson and the ZIP models, and more such pattern, and more consistently positive residuals, for the NB model.

```
map.Nmix.resi(fm5)           # Map of average residuals for Poisson model
map.Nmix.resi(fm5NB)        # Map of average residuals for NB model
map.Nmix.resi(fm5ZIP)       # Map of average residuals for ZIP model
```

As a final check on model adequacy, we plot the squared residuals against the fitted values, to investigate the variance/mean structure in the data (ver Hoef and Boveng, 2007; code not shown). Under the Poisson models, the variance should be equal to the mean, while the NB stipulates a quadratic variance/mean relationship. We produce plots that show the means for suitably chosen bins, to smooth out the ruggedness in the raw data (Figure 6.11, bottom right).

We see some scatter and only few points for the NB, but the variance/mean relationship seems much better described by a straight line than by a quadratic curve. This indicates a constant degree of OD rather than an NB error structure (Lee and Nelder, 2000; ver Hoef and Boveng, 2007).

Hence, we feel much more comfortable to base our inference about the abundance of Swiss great tits on one of the two Poisson models than on the NB. The NB predicts almost twice as many great tits as do Poisson or ZIP; and this discrepant behavior of the NB is consistent with earlier observations (Kéry et al., 2005b; ver Hoef and Boveng, 2007; Joseph et al., 2009). In addition, the residual diagnostics for the Poisson and ZIP models look much better than those of the NB, intriguingly despite the much better fit (measured by \hat{c}) and predictive ability (measured by AIC) of the NB.

We are a little puzzled by these somewhat conflicting findings in terms of AIC, GoF, RMSE, and the graphical fit assessments for these mixture distributions. Moreover, these patterns appear to be quite common and not restricted to the great tit data at all. In many of our own analyses, the NB clearly won in terms of AIC over the Poisson and ZIP mixtures, yet it predicted unrealistic levels of abundance. Thus, we often observe the “good fit/bad prediction dilemma” with binomial N -mixture models and suggest caution when using an NB, even when it is greatly favored by AIC, *especially* when it produces substantially higher abundance estimates than a Poisson or ZIP model. Overall, we repeat our call for more study of the topics of GoF and model selection in N -mixture and similar hierarchical models.

6.9.4 ANALYSIS OF RESULTS

Overdispersion (OD) due to unmodeled covariates or ignored dependency structures is very common in analyses of count data (ver Hoef and Boveng, 2007). We could not find strong patterns in the residuals of the Poisson and the ZIP models. Hence, we now assume that the lack of fit revealed by the GoF tests is simply additional noise, and we want to correct for it by adjusting upwards the uncertainty statements (SEs, CIs) in our inference (e.g., Johnson et al., 2010). This can be done by multiplying the variance–covariance matrix by the estimate of \hat{c} under the ZIP model (e.g., where it is 2.47), which we prefer over the simple Poisson for its better result in the GoF test. All three main goals of our analysis require us to predict abundance over a range of covariate values. We will thus use the ZIP model for making these predictions, but adjust the prediction uncertainty for an OD factor (\hat{c}) of 2.47.

A little confusingly, there are currently three functions in `unmarked` and `AICcmodavg` to form predictions for an N -mixture model: `predict`, `predictSE`, and `modavgPred`. We here give an overview of the working of these functions because prediction is extremely important in statistical practice and yet is often felt to be confusing. For illustration, we predict λ along an elevational gradient from 200–2250 m and p for survey date from April 1 to the end of June (days 1–90). The values of all other covariates are set at their average and for the time factor in p , we choose the middle occasion 2. We define two data frames for use in the predictions below.

```
# Two new data sets for prediction: for lambda and for p (200 data points each)
lamNewData <- data.frame(elev = (seq(200, 2250, ,200) - mean(tits[, "elev"])) /
  sd(tits[, "elev"]), forest = 0, iLength = 1/5.1)
pNewData <- data.frame(elev = 0, time = factor("2", levels = c("1", "2", "3")),
  dur = 0, date = (seq(1, 90, ,200) - mean(date, na.rm = T)) / sd(date, na.rm = T))
```

We have three options to produce predictions (although it is likely that future versions of `unmarked` and `AICcmodavg` will have more functionality in this respect):

1. Function `predict` in `unmarked` yields point predictions with SEs and 95% CIs for λ and p for Poisson and NB mixtures, but for ZIP mixtures currently only gives point estimates (though we have a beta version of the function in the `AHM` package that gives SEs and CIs for the ZIP as well). Function `predict` cannot inflate SEs and CIs to accommodate an OD correction factor.

```
# Predictions for lambda and p, with SE and CIs, but no overdispersion
predict(fm5, type="state", newdata=lamNewData) # Poisson model
predict(fm5, type="det", newdata=pNewData)
predict(fm5NB, type="state", newdata=lamNewData) # NegBin model
predict(fm5NB, type="det", newdata=pNewData)
predict(fm5ZIP, type="state", newdata=lamNewData) # ZIP
predict(fm5ZIP, type="det", newdata=pNewData)
```

2. Function `predictSE` in package `AICcmodavg` produces point predictions and SEs for ZIP mixtures, but currently no CIs, and allows specification of an OD correction \hat{c} , which is used to inflate the SEs. Only predictions of λ are currently available and only on the response, but not the link scale.

```
# Predictions for lambda only, incl. SE and CIs, with overdispersion
predictSE(fm5ZIP, newdata=lamNewData, print.matrix = TRUE, type="response",
parm.type = "lambda", c.hat = 2.47)
```

3. Function `modavgPred` in `AICcmodavg` can be tricked into producing point predictions with SEs and 95% CIs by providing a candidate list with a single model only. As of August 2015, no CIs are available, though for some cases 95% CIs can be obtained by adding/subtracting twice the SEs from the point estimates on the link scale and then applying the inverse link transformation.

```
# Predictions for lambda and p, incl. SE and with overdispersion, but no CIs
# Poisson model, for natural and for link scale of both lambda and p
modavgPred(cand.set = list(fm5), newdata=lamNewData, parm.type = "lambda", type
= "response", c.hat = 3.82)
modavgPred(cand.set = list(fm5), newdata=lamNewData, parm.type = "lambda", type
= "link", c.hat = 3.82) # Could be used to get 95% CIs
modavgPred(cand.set = list(fm5), newdata=pNewData, parm.type = "detect", type =
"response", c.hat = 3.82)
modavgPred(cand.set = list(fm5), newdata=pNewData, parm.type = "detect", type =
"link", c.hat = 3.82) # Could be used to get 95% CIs

# NegBin model, for natural and for link scale of both lambda and p
modavgPred(cand.set = list(fm5NB), newdata=lamNewData, parm.type = "lambda",
type = "response", c.hat = 1.79)
modavgPred(cand.set = list(fm5NB), newdata=lamNewData, parm.type = "lambda",
type = "link", c.hat = 1.79) # Could be used to get 95% CIs
```

```

modavgPred(cand.set = list(fm5NB), newdata=pNewData, parm.type = "detect",
type = "response", c.hat = 1.79)
modavgPred(cand.set = list(fm5NB), newdata=pNewData, parm.type = "detect",
type = "link", c.hat = 1.79) # Could be used to get 95% CIs

# ZIP model, for natural and for link scale of both lambda and p
modavgPred(cand.set = list(fm5ZIP), newdata=lamNewData, parm.type = "lambda",
type = "response", c.hat = 2.47)
modavgPred(cand.set = list(fm5ZIP), newdata=lamNewData, parm.type = "lambda",
type = "link", c.hat = 2.47) # Not yet implemented (August 2015)
modavgPred(cand.set = list(fm5ZIP), newdata=pNewData, parm.type = "detect", type =
"response", c.hat = 2.47)
modavgPred(cand.set = list(fm5ZIP), newdata=pNewData, parm.type = "detect", type =
"link", c.hat = 2.47) # this works, so we could get 95% CIs

```

Our model enables us to gauge coverage bias in the MHB survey: i.e., of the proportion of the nominal sample area, represented by the 1-km² sample plot, that is actually covered by the survey route. We specify a relationship between the size of the exposed population within a nominal 1-km² sample plot and a saturation population that is informed by variation in route length and estimate a coefficient of the reciprocal of route length of -1.3412 . We first form predictions of λ for this crucial relationship to see how it looks (Figure 6.12).

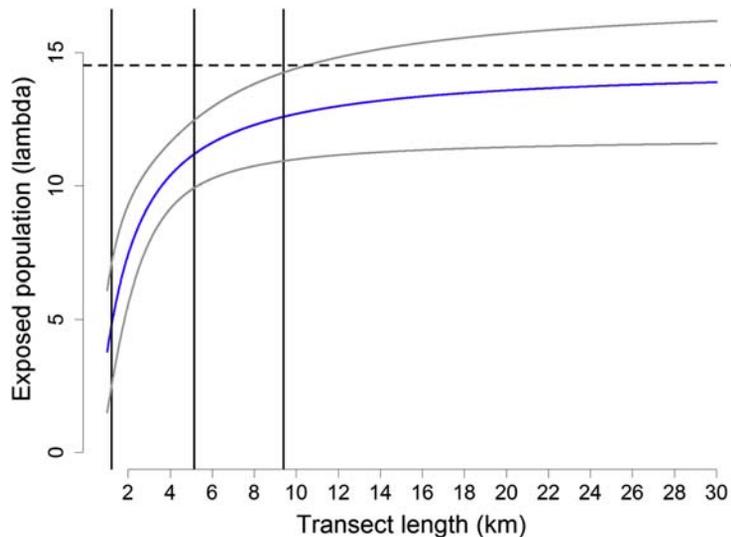


FIGURE 6.12

Estimated relationship (with 1-SE bounds) between the expected numbers of great tit territories (λ) that are exposed to detection by a 1-km² quadrat as a function of transect length. Vertical black lines show the minimum, mean, and maximum route lengths in the Swiss MHB (1.2, 5.1, and 9.4, respectively). The associated exposed population represents 33%, 77%, and 87% of the exposed population at saturation sampling (horizontal dashed line), when a hypothetical route of length infinity is squeezed into the 1-km² sampling quadrat.

```

rlength <- seq(1, 30, 0.01)          # Vary route length from 1 to 30 kms
newData <- data.frame(elev=0, forest=0, iLength=1/rlength)
pred <- predictSE(fm5ZIP, parm.type="lambda", newdata=newData, c.hat = 2.47)
par(mar = c(5,5,3,2), cex.lab = 1.5, cex.axis = 1.3)
plot(rlength, pred[[1]], type = "l", lwd = 3, col = "blue", frame = F, xlab =
"Transect length (km)", ylab = "Exposed population (lambda)", ylim = c(0, 16), axes = F)
axis(1, at = seq(2,30,2))          ; axis(2)
abline(v = c(1.2, 5.135, 9.4), lwd = 2)
matlines(rlength, cbind(pred[[1]]-pred[[2]], pred[[1]]+pred[[2]]), type = "l",
lty = 1, lwd = 2, col = "gray")

```

By doing the prediction with the value for `iLength` set at 0, we compute the expected abundance of great tits at saturation sampling (i.e., with infinite route length). We do this and add this value to the plot.

```

sat.pred <- predictSE(fm5ZIP, parm.type="lambda", newdata=data.frame(elev=0, forest=0,
iLength=0), c.hat = 2.47)
abline(h = sat.pred$fit, lwd = 2, lty = 2)

# Inspect the numbers
print(cbind("Route length" = rlength, "Exp. pop" = pred[[1]], "Rel. exp. pop" = pred[[1]] /
sat.pred$fit), 3)

```

We estimate a relative expected population size of 77% for the average route length of 5.1 km. This percentage rises to 87% for the maximum route length of 9.4, and to 91%, 94%, and 95% at route lengths of 15, 20, and 25 km, respectively. By setting the value of `iLength` to zero, we estimate the expected size of the local great tit population at saturation sampling effort—i.e., λ under the assumption that we survey a route of length infinity within each 1-km² sample quadrat. For all other covariates, we predict at their average value—i.e., at zero—since they were standardized in the analysis. For the time factor, we choose the middle level 2; i.e., we predict for occasion 2. As said above, we cannot currently produce 95% CIs easily for ZIP models with OD, and hence we compute intervals of ± 1 SE.

```

# Create covariate vectors for prediction and standardise as in analysis
ep.orig <- seq(200, 2250, length.out=100)    # Elevation between 200 and 2250 m
(elev.mean <- mean(tits[,"elev"]))
(elev.sd <- sd(tits[,"elev"]))
ep <- (ep.orig - elev.mean) / elev.sd        # Standardized for prediction
fp.orig <- seq(0, 100, length.out=100)      # Forest cover between 0 and 100%
(forest.mean <- mean(tits[,"forest"]))
(forest.sd <- sd(tits[,"forest"]))
fp <- (fp.orig - forest.mean) / forest.sd    # Standardised for prediction
date.orig <- seq(1, 90, length.out=100)     # Survey date from 1 April - 1 July
(date.mean <- mean(date, na.rm = TRUE))
(date.sd <- sd(date, na.rm = TRUE))
datep <- (date.orig - date.mean) / date.sd   # Standardised for prediction
dur.orig <- seq(90, 420, length.out=100)    # Survey duration from 90 - 420 min
(dur.mean <- mean(dur, na.rm = TRUE))
(dur.sd <- sd(dur, na.rm = TRUE))
durp <- (dur.orig - dur.mean) / dur.sd      # Standardised for prediction

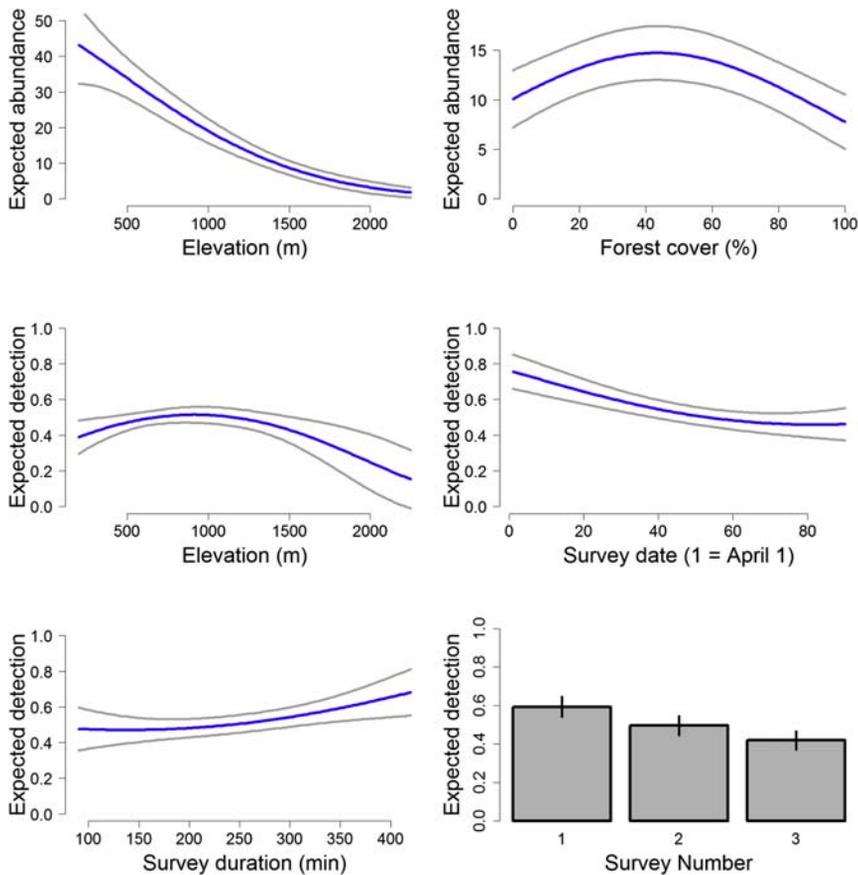
```

```

# Do predictions along single covariate gradient
newData1 <- data.frame(elev=ep, forest=0, iLength=0, date=0, dur=0, time =
  factor("2", levels = c("1", "2", "3")))
pred1 <- predictSE(fm5ZIP, newdata=newData1, c.hat = 2.47)
pred2 <- modavgPred(cand.set = list(fm5ZIP), newdata=newData1, parm.type =
  "detect", type = "response", c.hat = 2.47)
newData3 <- data.frame(elev=0, forest=fp, iLength=0, date=0, dur=0, time =
  factor("2", levels = c("1", "2", "3")))
pred3 <- predictSE(fm5ZIP, newdata=newData3, c.hat = 2.47)
newData4 <- data.frame(elev=0, forest=0, iLength=0, date=datep, dur=0, time =
  factor("2", levels = c("1", "2", "3")))
pred4 <- modavgPred(cand.set = list(fm5ZIP), newdata=newData4, parm.type =
  "detect", type = "response", c.hat = 2.47)
newData5 <- data.frame(elev=0, forest=0, iLength=0, date=0, dur=durp, time =
  factor("2", levels = c("1", "2", "3")))
pred5 <- modavgPred(cand.set = list(fm5ZIP), newdata=newData5, parm.type =
  "detect", type = "response", c.hat = 2.47)
newData6 <- data.frame(elev=0, forest=0, iLength=0, date=0, dur=0,
  time = c("1", "2", "3"))
pred6 <- modavgPred(cand.set = list(fm5ZIP), newdata=newData6, parm.type =
  "detect", type = "response", c.hat = 2.47)

# Plot these predictions along single covariate gradient
par(mfrow = c(3,2), mar = c(5,5,3,2), cex.lab = 1.3, cex.axis = 1.3)
plot(ep.orig, pred1[[1]], type = "l", lwd = 2, col = "blue", xlab = "Elevation (m)",
  ylab = "Expected abundance", las = 1, ylim = c(0,50), frame = F)
matlines(ep.orig, cbind(pred1[[1]]-pred1[[2]], pred1[[1]]+pred1[[2]]), type = "l",
  lty = 1, lwd = 1, col = "gray")
plot(fp.orig, pred3[[1]], type = "l", lwd = 2, col = "blue", xlab = "Forest cover (%)",
  ylab = "Expected abundance", las = 1, ylim = c(0, 18), frame = F)
matlines(fp.orig, cbind(pred3[[1]]-pred3[[2]], pred3[[1]]+pred3[[2]]), type = "l",
  lty = 1, lwd = 1, col = "gray")
plot(ep.orig, pred2[[1]], type = "l", lwd = 2, col = "blue", xlab = "Elevation (m)",
  ylab = "Expected detection", las = 1, ylim = c(0,1), frame = F)
matlines(ep.orig, cbind(pred2[[1]]-pred2[[2]], pred2[[1]]+pred2[[2]]), type = "l",
  lty = 1, lwd = 1, col = "gray")
plot(date.orig, pred4[[1]], type = "l", lwd = 2, col = "blue", xlab = "Survey date (1 =
  April 1)", ylab = "Expected detection", las = 1, ylim = c(0,1), frame = F)
matlines(date.orig, cbind(pred4[[1]]-pred4[[2]], pred4[[1]]+pred4[[2]]), type = "l",
  lty = 1, lwd = 1, col = "gray")
plot(dur.orig, pred5[[1]], type = "l", lwd = 2, col = "blue", xlab = "Survey duration
  (min)", ylab = "Expected detection", las = 1, ylim = c(0,1), frame = F)
matlines(dur.orig, cbind(pred5[[1]]-pred5[[2]], pred5[[1]]+pred5[[2]]), type = "l",
  lty = 1, lwd = 1, col = "gray")
barplot(pred6[[1]], names.arg = c("1", "2", "3"), ylim = c(0,1),
  ylab = "Expected detection", xlab = "Survey Number")
segments(c(0.7,1.9, 3.1), pred6[[1]]-pred6[[2]], c(0.7,1.9, 3.1), pred6[[1]]+
  pred6[[2]], lwd = 2)

```

**FIGURE 6.13**

Predictions of expected abundance (λ) and detection (p) for Swiss great tits in 2013 under model `fm5Z1P` along single covariate gradients. Gray lines and black error bars show 1-SE bounds.

We see in [Figure 6.13](#) that the expected abundance of great tits in Switzerland declines strongly with altitude. Interestingly, there is an intermediate optimum forest cover at a little over 40%. Detection probability has an optimum relationship with elevation, with a maximum around 1000 m, declines over the survey season from about 0.8 to 0.4, and increases only slightly with increasing survey duration. Irrespective of these effects, detection declines from the first through the third survey.

As we stress at many places, plotting such predictions is often virtually the only way that we can understand the meaning of linear models with polynomial terms, interactions, and/or nonlinear link functions. Sometimes it can be interesting to produce predictions when we vary more than one

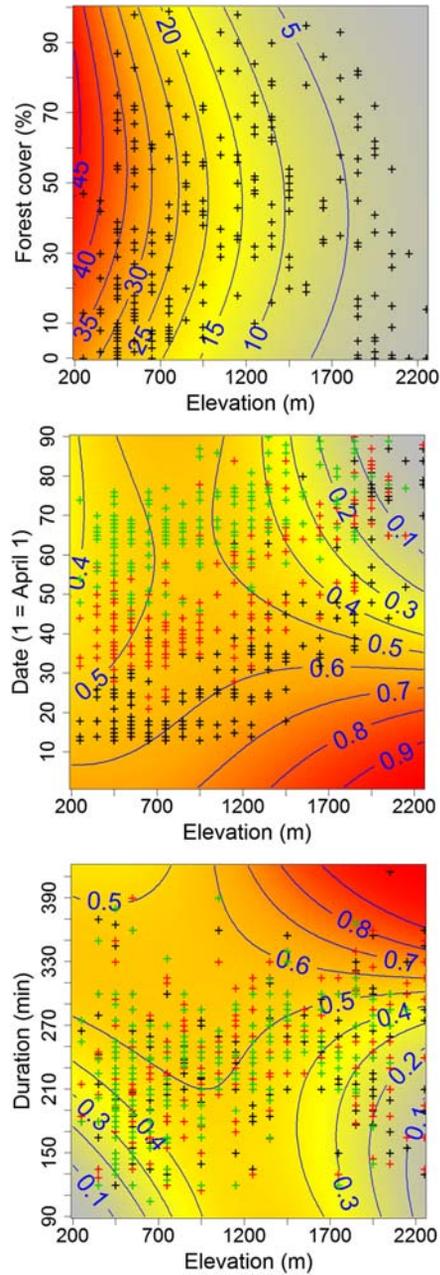


FIGURE 6.14

Bivariate predictions of expected abundance and detection when two covariates are varied simultaneously. Plus signs show values of covariates for the 263 quadrats or for every survey in 2013, with colors in the middle and bottom panels denoting surveys 1 (black), 2 (red), and 3 (green).

covariate. We illustrate this now with the joint relationship of expected abundance, forest cover, and elevation, and of expected detection, elevation, and survey date (Figure 6.14). We will not bother with prediction uncertainty now and simply use the `predict` function in `unmarked`.

```
# Make predictions along two covariate gradients
# (1) Expected abundance (lambda) for forest and elevation
pred.matrix1 <- array(NA, dim = c(100, 100))
for(i in 1:100){
  for(j in 1:100){
    newData <- data.frame(x=0, y=0, elev=ep[i], forest=fp[j], iLength=0)
    pred.matrix1[i,j] <- predict(fm5ZIP, type="state", newdata=newData)[1,1]
  }
}

# (2) Expected detection (p) for elevation and survey date
pred.matrix2 <- array(NA, dim = c(100, 100))
for(i in 1:100){
  for(j in 1:100){
    newData <- data.frame(elev=ep[i], date=datep[j], dur=0,
      time = factor("2", levels = c("1", "2", "3")))
    pred.matrix2[i,j] <- predict(fm5ZIP, type="det", newdata=newData)[1,1]
  }
}

# (3) Expected detection (p) for elevation and survey duration
pred.matrix3 <- array(NA, dim = c(100, 100))
for(i in 1:100){
  for(j in 1:100){
    newData <- data.frame(elev=ep[i], date=0, dur=durp[j],
      time = factor("2", levels = c("1", "2", "3")))
    pred.matrix3[i,j] <- predict(fm5ZIP, type="det", newdata=newData)[1,1]
  }
}

# Plot these prediction matrices
par(mfrow = c(1, 3), mar = c(5,5,2,2), cex.lab = 1.5, cex.axis = 1.5)
mapPalette <- colorRampPalette(c("grey", "yellow", "orange", "red"))

image(x=ep.orig, y=fp.orig, z=pred.matrix1, col = mapPalette(100), axes = F,
  xlab = "Elevation (m)", ylab = "Forest cover (%)")
contour(x=ep.orig, y=fp.orig, z=pred.matrix1, add = T, col = "blue", labcex = 1.5,
  lwd = 1.5)
axis(1, at = seq(min(ep.orig), max(ep.orig), by = 250))
axis(2, at = seq(0, 100, by = 10))
box()
points(tits$elev, tits$forest, pch="+", cex=1.5)

image(x=ep.orig, y=date.orig, z=pred.matrix2, col = mapPalette(100), axes = F,
  xlab = "Elevation (m)", ylab = "Date (1 = April 1)")
```

```

contour(x=ep.orig, y=date.orig, z=pred.matrix2, add=T, col="blue", labcex=1.5,
lwd=1.5)
axis(1, at = seq(min(ep.orig), max(ep.orig), by = 250))
axis(2, at = seq(10, 120, by = 10))
box()
matpoints(tits$elev, date, pch="+", cex=1.5)

image(x=ep.orig, y=dur.orig, z=pred.matrix3, col = mapPalette(100), axes = F,
xlab = "Elevation (m)", ylab = "Duration (min)")
contour(x=ep.orig, y=dur.orig, z=pred.matrix3, add=T, col="blue",
labcex=1.5, lwd=1.5)
axis(1, at = seq(min(ep.orig), max(ep.orig), by = 250))
axis(2, at = seq(90, 420, by = 20))
box()
matpoints(tits$elev, dur, pch="+", cex=1.5)

```

The panels for detection in [Figure 6.14](#) are especially interesting: they show that the relatively mild effects of survey date and duration on detection probability at the *average* of the other covariates including elevation (at 1190 m a.s.l.), and depicted in [Figure 6.13](#), are modified substantially by elevation: both effects become stronger with increasing elevation. Thus, again, forming predictions, in one or in multiple dimensions, is *the key* to understanding what complicated regression models are telling us about covariate relationships.

Let us now move to our second goal and produce abundance maps of great tits in Switzerland in 2013 ([Figure 6.15](#)). For this we will project the estimated covariate relationships for abundance onto a map of Switzerland, using the values of these covariates that are known for every 1-km² quadrat. We load the Swiss landscape data from `unmarked`.

```

data(Switzerland)      # Load Swiss landscape data in unmarked
CH <- Switzerland

```

We scale all four covariates using the same mean and sd that we used for the covariates in the analyzed data set and predict expected abundance for every Swiss km² quadrat.

```

# Predictions for lambda, with overdispersion
newData <- data.frame(elev = (CH$elev-elev.mean)/elev.sd, forest = (CH$forest-
forest.mean)/forest.sd, iLength=0, date=0, dur=0, time = factor("2",
levels = c("1", "2", "3")))
predCH <- predictSE(fm5ZIP, newdata=newData, print.matrix = TRUE, type="response",
parm.type = "lambda", c.hat = 2.47)

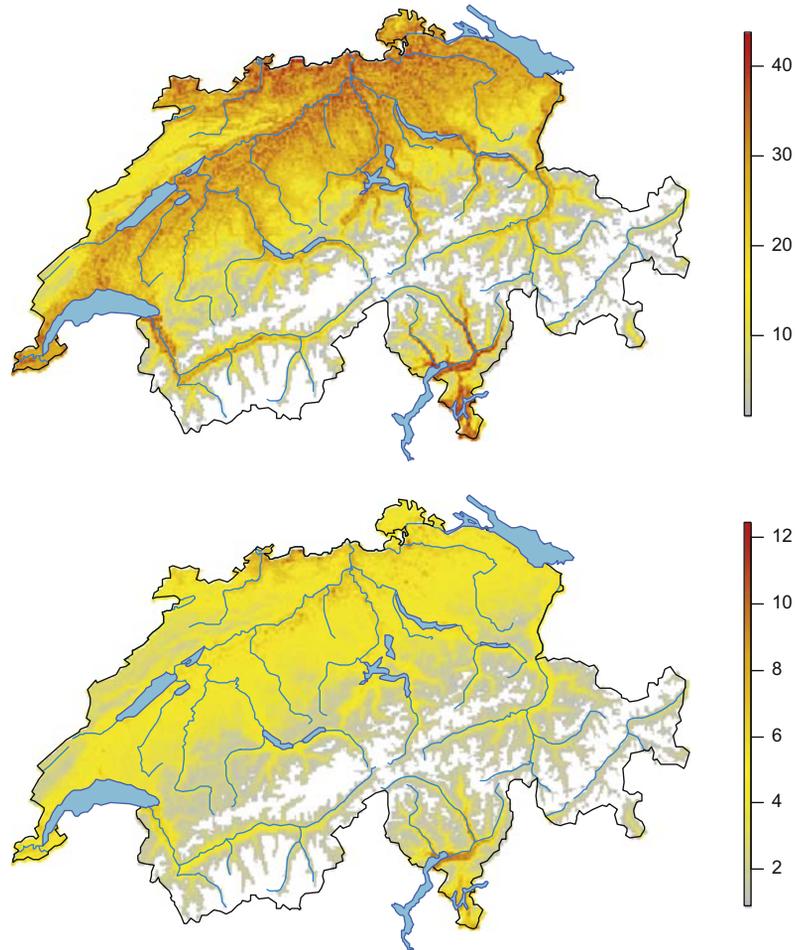
```

We check for unrealistic abundance predictions as they can occur quite frequently with linear models with a log link. We are prepared to censor any prediction greater than about 60, because a great tit density greater than that is deemed rare in Switzerland (Schmid et al., 1998). Depending on the model, freak predictions may occur and are particularly common with greater elevation. However, in our case there are none.

```

max(predCH[,1])          # Look at the max prediction --- 43.8
sum(predCH[,1] > 60)    # How many are > 60 ? --- none

```

**FIGURE 6.15**

Species distribution maps for the great tit (*Parus major*; see Figure 4.1) in Switzerland in 2013 under the best N -mixture model (fm5ZIP) for data modeled at the 1-km² scale. Top: map of point estimates (expected number of territories (λ) per 1 km²); bottom: map of prediction uncertainty (SE).

```
plot(CH$elev, predCH[,1])      # Relationship with elevation
predCH[1][predCH[1] > 60] <- 60 # Censor freak predictions (not req'd here)

# Prepare Swiss coordinates and produce rudimentary
library(raster)

# Define a new dataframe with coordinates and outcome to be plotted
PARAM1 <- data.frame(x = CH$x, y = CH$y, z = predCH[,1])
```

```

# Convert the DataFrame into a raster object
r1 <- rasterFromXYZ(PARAM1)

# Create mask for elevation (mask areas > 2250 m)
elev <- rasterFromXYZ(cbind(CH$x, CH$y, CH$elevation))
elev[elev > 2250] <- NA
r1 <- mask(r1, elev)

# Create custom color palette
mapPalette <- colorRampPalette(c("grey", "yellow", "orange", "red"))

# Map expected abundance of great tits in Switzerland in 2013
par(mfrow = c(1,2), mar = c(1,1,2,4))
plot(r1, col = mapPalette(100), axes = F, box = FALSE, main = "")

```

Although this is very rarely done in the species distribution modeling world, we should always plot the uncertainty associated with a species distribution model—e.g., as a map of the SEs or the width of 95% CIs of these predictions (see Webster et al., 2008; also see Figures 8.8 and 11.27). With a parametric statistical model, such an uncertainty assessment is easily obtained.

```

# Prepare raster with prediction SEs
r2 <- rasterFromXYZ(data.frame(x = CH$x, y = CH$y, z = predCH[,2]))
elev <- rasterFromXYZ(cbind(CH$x, CH$y, CH$elevation))
elev[elev > 2250] <- NA
r2 <- mask(r2, elev)

# Map prediction SEs of expected abundance
plot(r2, col = mapPalette(100), axes = F, box = FALSE, main = "")

```

We could also produce a map of the predicted detection probability of great tits in Switzerland (Olea and Mateo-Tomas, 2011; Kéry et al., 2013). However, the only spatially indexed covariate in detection in our model is elevation, and hence a map of predictions of detection probability does not yield much more insight into spatial variation of p than does [Figure 6.13](#). Hence, we omit a map of detection probability, but you could produce one as an exercise and use the following R code as a start.

```

# Predictions for p with overdispersion
newData <- data.frame(elev = (CH$elev - elev.mean)/elev.sd, date=0, dur=0, time =
  factor("2", levels = c("1", "2", "3")))
predCHp <- modavgPred(cand.set = list(fm5ZIP), newdata = newData, parm.type =
  "detect", type = "response", c.hat = 2.47)

```

We move on to the third goal of our analysis: come up with a formal estimate of the national population size of great tits in Switzerland. Assuming independence of quadrats, this estimate is naturally obtained by adding up, for all 1-km² quadrats in Switzerland, the predictions under our model (see [Section 6.10](#) for a discussion of this innocuous seeming assumption). We can do this easily (and exclude quadrats at >2250 m elevation—where we know there are no great tits).

```

(N <- sum(predCH[-which(CH$elev > 2250),1])) # National population size
[1] 655509.5

```

But wait, some quadrats lie mostly in lakes. So let us also exclude quadrats with >50% water.

```
out <- which(CH$water > 50 | CH$elev > 2250)
(N <- sum(predCH[-out,1])) # 'Terrestrial' population size < 2250 m elevation
[1] 618840.3
```

Hence, we estimate about 0.62 million pairs of great tits in Switzerland in 2013, right in the middle of the estimate of 500,000–700,000 pairs put forward during the last Swiss breeding bird atlas project (Schmid et al., 1998). Our estimate is conditional on the explicit assumptions of our model, which also includes our specification of an infinite route length representing saturation sampling density within a quadrat of exactly 1 km². In [Sections 6.9.5 and 6.10](#) we discuss this crucial assumption further, but for now want to obtain an estimate of the uncertainty in our Swiss population size estimate of great tits. We use the bootstrap for this. To speed up computation we do not use function `predict`, but do the required calculations “by hand.”

```
# Remind ourselves of the relevant coefficients in the model
cbind(coef(fm5ZIP)[25]) # Zero-inflation model
cbind(coef(fm5ZIP)[1:8]) # Abundance model
```

We prepare covariates for the Swiss map of elevation and forest cover that are scaled identically to those in our analysis.

```
pelev <- (CH$elev - elev.mean)/elev.sd
pforest <- (CH$forest - forest.mean)/forest.sd
```

To run a bootstrap, we must define a function that produces a national population size estimate based on the output of our model. Function `Nhat` returns three such estimates: one estimate of the national population size at elevations below 2250 m a.s.l. when water bodies and potential nonsensical high estimates are ignored (N1), another when nonsensical high estimates are censored at a biologically realistically ceiling for great tits of 60 territories (N2), and a third when we also exclude quadrats with >50% water (N3). There is a second function argument that enables us to accommodate variation in effective sampling areas associated with differences in route lengths: the default is infinite route length, corresponding to saturation density. The third argument gives the effective sample area associated with a 1-km² quadrat (see below) and is set at 1 by default.

```
Nhat <- function(fm = fm5ZIP, iLength = 0, area = 1) {
  betavec <- coef(fm)[1:8]
  DM <- cbind(rep(1,length(pelev)), pelev, pelev^2, pforest,
  pforest^2, rep(iLength,length(pelev)), pelev*pforest, pelev*pforest^2)
  pred <- exp(DM %*% betavec) * (1-plogis(coef(fm)[25])) * (1/area)
  pred2 <- pred
  N1 <- sum(pred[-which(CH$elev > 2250),]) # Drop quads > 2250 m
  pred2[pred2 > 60] <- 60 # Censor freak-high estimates
  N2 <- sum(pred2[-which(CH$elev > 2250),]) # Estimate with freaks censored
  out <- which(CH$water > 50 | CH$elev > 2250)
  N3 <- sum(pred2[-out,]) # Estimate excluding water bodies
  return(c(N1 = N1, N2 = N2, N3 = N3))
}
```

We test the function for our actual data set and recover identical point estimates to those from `predictSE`, then we launch a bootstrap with 2500 replications.

```
(Nest <- Nhat(fm5ZIP))           # For default saturation density
(Nest <- Nhat(fm5ZIP, 1/10))    # For 10 km routes
  N1      N2      N3
655509.5 655509.5 618840.3
  N1      N2      N3
573235.2 573235.2 541168.4

# Launch the bootstrap (takes about 30h)
system.time(pb.N <- parboot(fm5ZIP, Nhat, nsim = 2500, report = 5))
```

Once we are done, we focus on the bootstrapped values for `N3`, where any freak high estimates are censored at 60 and main Swiss water bodies and quadrats > 2250 m elevation are excluded, and summarize them, first by sample statistics and then in a plot (Figure 6.16).

```
bs <- pb.N@t.star[,3]          # Extract the bootstrapped vals of N3

# Sample statistics
summary(bs)
quantile(bs, prob = c(0.025, 0.975)) # Get 95% CI
> summary(bs)
  Min. 1st Qu. Median  Mean 3rd Qu.  Max.
412500 571300 617200 623300 668500 933100
```

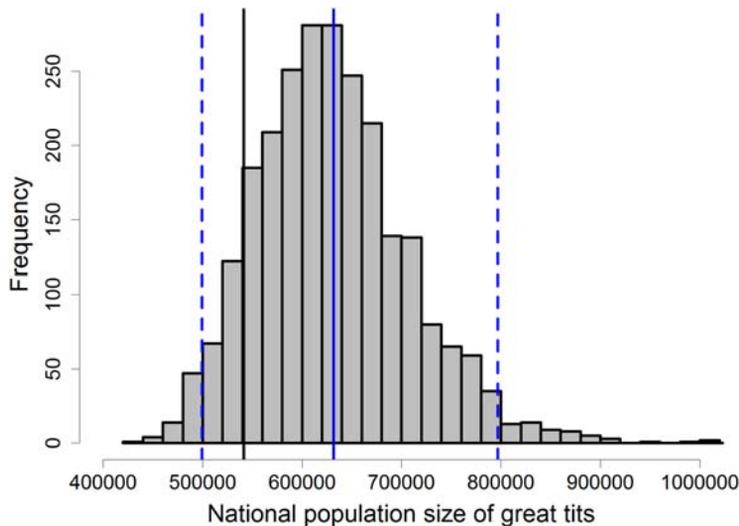


FIGURE 6.16

Bootstrapped sampling distribution of the number of pairs of great tits in Switzerland under model `fm5ZIP`. The black line shows the estimate for the actual data set and the solid blue line the mean of the 2500 bootstrap replicates. The dashed blue lines show the bootstrapped 95% CIs.

```

> quantile(bs, prob = c(0.025, 0.975))    # Get 95% CI
      2.5%      97.5%
489623.2  784803.2

# Plot (produces Fig. 6.16)
hist(bs, breaks = 100, col = "grey", xlab = "National population size of great tits",
     cex = 1.5, main = "", xlim = c(400000, 1000000))
abline(v = Nest[3], lwd = 3)
abline(v = mean(bs), lwd = 3, col = "blue")
abline(v = quantile(bs, prob = c(0.025, 0.975)), lwd = 3, col = "blue", lty = 2)

```

This bootstrap does not account for OD ($\hat{c} = 2.47$). Therefore, we next attempt to propagate this additional uncertainty into the national population total by multiplying the bootstrap SD with the square-root of \hat{c} and computing approximate 95% CIs by adding/subtracting twice that product from the mean. As a check for how reasonable this approach might be, we first use such a normal approximation to compute 95% CIs without OD, so that we can compare them with the percentile-based CIs: we see that they are pretty similar.

```

(CI1 <- quantile(bs, prob = c(0.025, 0.975)))    # Percentile-based CI
(CI2 <- c(mean(bs-2*sd(bs)), mean(bs+2*sd(bs)))) # Normal approx.-based CI

      2.5%      97.5%
489623.2  784803.2    # Percentile-based CI
473448.8  773055.6    # Normal approximation-based CI

```

Presumably, this is a reasonable approximation when the bootstrap distribution is approximately normal. We now do something analogous with an OD correction to make this interval wider, to account for the extra-uncertainty represented by OD.

```

c.hat <- gof.ZIP$c.hat.est
(CI <- c(mean(bs-2*sqrt(c.hat)*sd(bs)), mean(bs+2*sqrt(c.hat)*sd(bs))))
[1] 387673.2 858831.2

```

Hence, based on our *ad hoc* OD-correction of the CIs, we conclude that there were 388,000–859,000 pairs of great tits in Switzerland in 2013.

6.9.5 CONCLUSIONS ON THE ANALYSIS WITH unmarked

In this section, we have seen a couple of important things:

- We can use `unmarked` to flexibly fit a large range of N -mixture models for spatially and temporally replicated count data.
- We can use AIC or LRTs to tell us which model has the most support from the data; though we should never trust such numbers blindly (see comments below on the NB model).
- We can use parametric bootstrapping to compute measures of GoF, uncertainty in derived quantities such as predictions, or the total population size of Swiss great tits.
- We have looked into the calculation of predicted values of abundance or detection under the model. This is an extremely important topic, because the resulting plots are an informative way of presenting the results from such an analysis. Also, when your model contains

polynomials or interactions of covariates, we cannot usually understand what the model is telling us from staring at the parameter estimates alone. Rather, the only way to understand what the model is telling us is usually by producing a picture of the response in relation to the covariate values.

- As always, whenever we have spatially indexed covariates in an analysis, we can compute the expected value of a response such as abundance for each pixel in some region and then project these predictions, producing a map (Kéry et al., 2013). Hence, the N -mixture model is naturally also a *species distribution model*, primarily for abundance. However, we could also compute the probability of occurrence (as 1 minus the probability that $N > 0$ under the abundance model) and plot that; see Royle et al. (2005). Since there is a logical equivalence of abundance and occurrence, we can use the N -mixture model for abundance to produce a traditional map of species occurrence probability (Dorazio, 2007).
- Estimates of national population sizes are naturally obtained by predicting abundance for each pixel in the area of interest and then summing them up. Of course, if you are interested in smaller-scale totals—e.g., for certain regions or for different habitat types or other categorizations of space—then you proceed in exactly the same manner: you simply add up the predictions over the pixels in each group to obtain the total population size in each. You will see an example of this in [Section 6.11](#), where we estimate the population size of great tits per elevation band of 100 m. Parametric bootstrapping is a flexible frequentist method of obtaining uncertainty intervals for such derived quantities.
- We have seen that the Poisson mixture models did not formally fit the data based on the bootstrap GoF. This means that the observed responses were more variable than expected under the Poisson model. Allowing for extra-Poisson dispersion in the abundance part of the model by use of an NB distribution bought us a better fitting model that won the AIC contest by a very large margin, but also predicted much too high abundances, leading to the “good fit/bad prediction dilemma” fairly often observed in this model (Kéry et al., 2005b; Joseph et al., 2009). We suggest caution when using the NB distribution for abundance in binomial N -mixture models and think that using a Poisson or ZIP model with moderate lack of fit (e.g., values of c -hat less than about 4) followed by an “OD correction” may be a safer choice for inferences about abundance. At any rate, the NB seems to always predict greater or equal abundance, compared with Poisson or ZIP binomial N -mixture models (though perhaps not for multinomial mixture models; see Chapter 7). Hence, if you erroneously choose one of the latter over an NB model, you will err on the side of caution when predicting population sizes (e.g., when modeling a species of conservation concern).

This is only a relatively rough sketch of a thorough spatial analysis of the abundance of a species. For instance, in your study you may have many more covariates. Then, the model selection part may become heavier or you may want to model-average your predictions to propagate model selection uncertainty into your abundance maps and into estimates of regional or national totals. Or you may want to adopt more elaborate models—e.g., to model spatial autocorrelation (see Chapter 21) or “wiggly” covariate relationships using splines (see Section 10.14). These and many other extensions are conceptually fairly straightforward, but in some cases at least, they may require you to code up your model in BUGS.

6.10 THE ISSUE OF SPACE, OR: WHAT IS YOUR EFFECTIVE SAMPLE AREA?

Any calculation that adds site-specific estimates of local density up to a population total makes the implicit assumption that we know the precise area of each site. In the Swiss MHB a site is 1 km²—or is it really? Is this a sensible assumption? There are two potential issues: first, “holes” of unsurveyed areas inside a quadrat and second, “edge effects” represented by home ranges that sit on the quadrat boundary. Look for instance at [Figure 6.8](#): just from the location of the detected great tit territories you get a pretty good idea of where the transect route lies. Presumably, then, there were other territories away from the survey route that had a zero or at least a very low probability of being detected. This leads to “holes” in the quadrat coverage and will *reduce* the effective sample area relative to the nominal 1-km² area. In the preceding analysis, we have taken account of this effect by including into our model the relationship between the exposed population and route length.

On the other hand, clearly the sample quadrat is not an island, but simply an arbitrary square cut out from a more or less continuous landscape. Hence, it would be naive to believe that all home ranges lie either exclusively inside or exclusively outside of a quadrat; rather, some territories are likely to straddle the quadrat boundary. You can actually see one such home range near the top-right corner of the quadrat ([Figure 6.8](#), right). The presence of such edge territories will tend to make the effective sample area bigger than the 1 km² associated with the nominal MHB sample area. The shape of the effectively sampled area is more likely to resemble that of a sunflower, with petals representing edge home ranges. Both the presence and the magnitude of “holes” and of “sunflower effects” depend on the home range size of a species. Species with a small home range, such as small passerines, will range much less beyond the quadrat edge and will more likely have holes inside the quadrat than do species with a large home range such as crows or raptors, for which the sunflower effect will be more severe, but there will be fewer and smaller holes. See [Figure 6.17](#) for a schematic representation of these ideas.

As a consequence, strictly speaking we very rarely know the effective size and shape of a sampled area in continuous habitat, regardless of how authoritative we feel when we mark its boundaries on a map. And worse, both the size and the shape of the effective sampling area associated with a nominal study area will differ by species, habitat, and a multitude of potential factors that may affect the movement behavior of an organism within its home range and especially the home range size. These problems have long been known in closed population estimation (Dice, 1938; Efford and Dawson, 2012) and their knowledge has given rise to the development of the novel class of spatial capture-recapture (SCR) models (Efford, 2004; Borchers and Efford, 2008; Royle and Young, 2008; Royle et al., 2014). Only distance sampling (Chapters 8, 9, 14 and 24) and SCR models (Chapter 24) are immune to the general problems induced by the impossibility of defining the limits of a study area unequivocally. However, these methods usually require data with extra information that is more “expensive” to collect (though this cost is arguably lower for distance sampling).

In the absence of such extra information in the MHB great tit data set, we must either make assumptions about the effective sample area (for instance, in our case, that it is exactly 1 km²) or, alternatively, accept that the effective sample area is smaller than 1 km² (because the area of ‘holes’ probably exceeds that of the ‘sunflower petals’), and that our totals will be conservative; i.e., they will underestimate the true N . A third possibility is to try and accommodate space in a model, as we just showed when we adjusted for “holes,” representing incomplete sample coverage, in our great tit

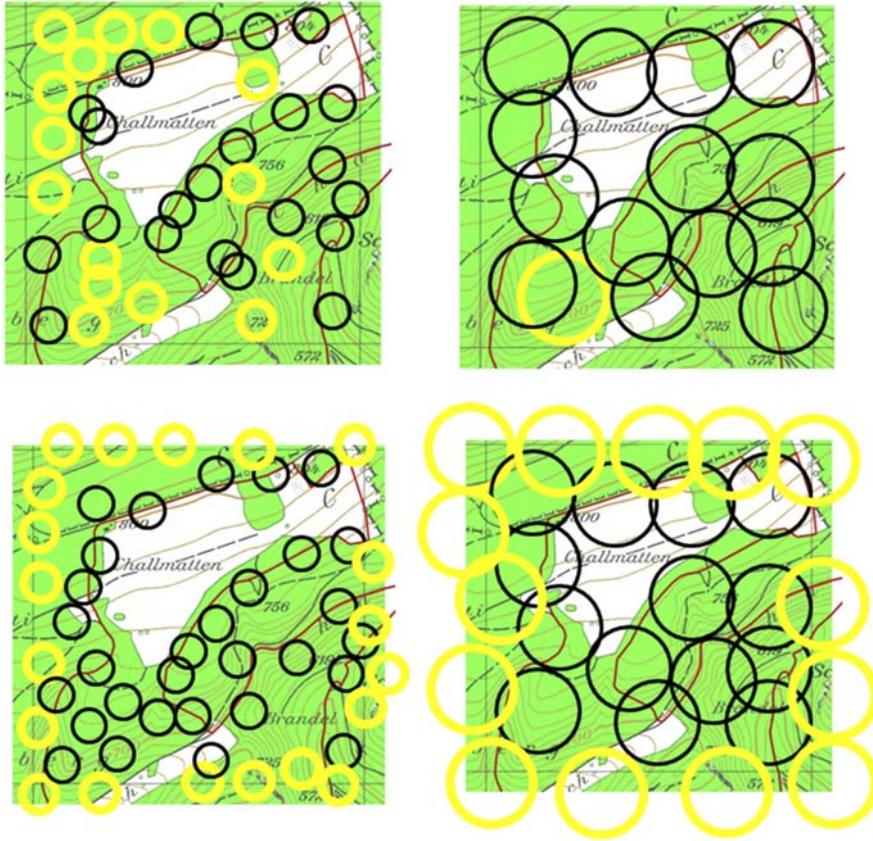


FIGURE 6.17

Schematic of “holes” (top row) and “sunflower effects” (bottom row) in biological transect surveys in continuous habitat as a function of the size of a territory or activity range (left: small territories, right: large territories). The survey route is shown in red (see [Figure 6.8](#) for more detail of this sample quadrat). For species (or study sites) where territory size is small, there are many “holes” (represented by 15 yellow territories that are unavailable for detection; top left). For large territories, the identical transect route will be associated with fewer “holes” (only one yellow territory unavailable for detection; top right). For species with small territories (bottom left), the presence of edge territories (marked yellow) will not increase the effective sample area so much as for species with large territories (bottom right).

analysis. Modeling sampling coverage as a function of a measured covariate such as route length is a useful way to correct for incomplete quadrat coverage (Royle and Dorazio, 2006; Royle et al., 2007b). On the other hand, extrapolating density to saturation coverage in the MHB almost certainly makes the effective sampling area greater than the nominal 1 km^2 . This may not be the case in the absence of adjustment for coverage bias, since the holes inside of the nominal sampling area may compensate for any extra sampled area outside—i.e., for the sunflower “petals.” In our analysis, if the effective sample area in the Swiss MHB resembles a sunflower with greater than 1 km^2 area, then regional or national

population totals obtained by adding up of estimates from adjacent quadrats represent an overestimate. Next, we try a somewhat *ad hoc* method to correct for this.

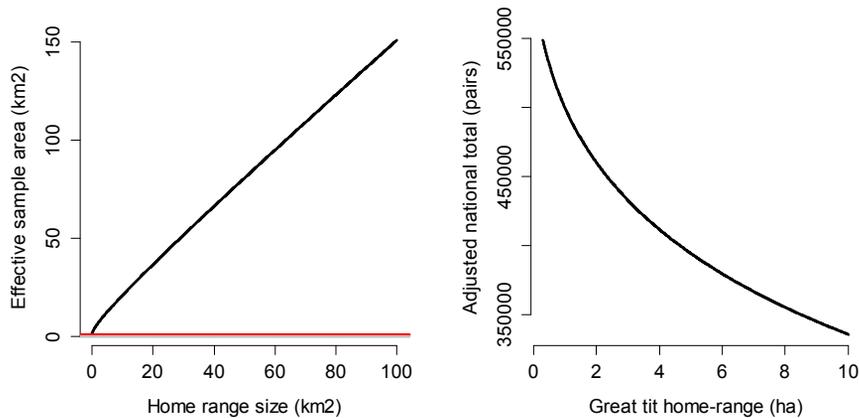
Great tit breeding home ranges in Switzerland vary from 0.3–0.5 ha in the insect-richest habitats (lowland deciduous forests), to 2–5 ha in mixed forests at medium elevations (600–800 m), and to 5–10 ha at high elevations around 1800 m (B. Naef-Daenzer, pers. comm.). Assuming circular home ranges, this corresponds to home range radii of between 31 and 178 m. Can we translate this knowledge into an “effective sample area” that adjusts for the sunflower effect? Actually, we can follow the same reasoning that folks in closed population estimation did before the advent of SCR: they added a boundary strip to the nominal sampling area of a width equal to half the diameter of an average home range (e.g., Dice, 1938; Karanth and Nichols, 1998; Karanth et al., 2006; Trolle and Kéry, 2003). For instance, for a species with a 100-m home range radius, a nominal sample area of 1 km² would then become a square with a side of length 1.2 km and an area of 1.44 km². It is instructive to plot the relationship between the average home range size of a species and the effective sample area in the MHB. Here we do the calculations for a range of home range sizes between 0.1 ha (perhaps representing *Regulus spec.*, the smallest European bird species) and about 100 km² (representing a moderate to large raptor; Figure 6.18, left).

```
AHR <- seq(0.001, 100, 0.1)      # Area home range (in km2): 0.1-100
RHR <- sqrt(AHR/pi)             # Translate to home range radius (in km)
ESA <- (1 + 2*RHR)^2            # Eff. sample area for 1km2 nominal area
par(mfrow = c(1,2), mar = c(5,5,3,2), cex.lab = 1.3, cex.axis = 1.3)
plot(AHR, ESA, xlab = "Home range size (km2)", ylab = "Effective sample area (km2)",
     type = "l", lwd = 3, frame = F)
abline(h = 1, col = "red", lwd = 3) # Nominal sample area
abline(h = 0, col = "grey", lwd = 3)
```

Using this reasoning for our great tits, home range radii of 31–178 m will translate to effective sample areas of an MHB quadrat for the great tit of 1.062²–1.356² or about 1.13–1.84 km². Hence, the quadrat population sizes associated with our saturation sampling effort can be assumed to refer to this area. Continuing this *ad hoc* argument, the expected density per 1 km² nominal sample area will correspond to a proportion between 0.54 and 0.88 of that and our quadrat-specific predictions would have to be reduced by 12–46% before they could be added up to provide a Swiss national population total. We can make that adjustment with our `Nhat` function using the argument `area`, which denotes the effective sample area.

Actually, multiplying our original estimate of 618,840 Swiss tits with `1/area` yields the same estimate, but the function argument can be useful if we want to bootstrap an uncertainty interval around it. We compute and plot the estimated national population size for a range of average home range sizes between 0.3 and 10 ha, corresponding to 1.13–1.84 km². We see a considerable reduction in our estimate of the Swiss national population size of great tits when we do this adjustment for the effective sampling area being greater than 1 km² (Figure 6.18, right). Hence, our estimate is quite sensitive to our assumptions about the size of the sampled area.

```
GT.HR <- seq(0.003, 0.1, ,1000)  # Great tit home ranges in km2
GT.rad <- sqrt(GT.HR/pi)        # Great tit home range radius (in km)
ESA.GT <- (1 + 2*GT.rad)^2      # Effective sample area for Great tit
NTOT <- numeric(length(ESA.GT)) # Adjusted national total population
```

**FIGURE 6.18**

Left: Relationship between the average size of a species' home range (assumed to be circular) and the effective sample area of a 1-km² quadrat obtained by buffering the nominal area with a strip of width equal to half the home range diameter. Gray and red lines show value of 0 and of the nominal sample area of 1 km². Right: Relationship between the adjusted Swiss national population size of great tits in 2013 and the average home range size of great tits.

```
for(i in 1:length(NTOT)){
  NTOT[i] <- Nhat(fm5ZIP, 0, ESA.GT[i])[3]
}
plot(100*GT.HR, NTOT, xlab = "Great tit home-range (ha)", ylab = "Adjusted national
total (pairs)", type = "l", lwd = 3, frame = F)
```

Our inability to unambiguously define the effective sample area and its consequences are *not* a defect of our explicit estimation approach. Rather, any nonspatial method of inference about regional or national totals would suffer similarly from this challenge—e.g., even a simple method that might multiply the average number of tit territories detected per quadrat, 8.4, by the number of quadrats summed over. Only methods that explicitly deal with space, such as distance sampling and spatial capture-recapture, are immune to this problem. Finally, note that Chandler and Royle (2013) have developed a spatial N -mixture model that estimates the parameters of an underlying spatial point pattern, representing home range or activity centers, from the spatial correlation of replicated counts in adjacent sample areas. To fit this model you need a fairly large number of sampling sites that touch each other, and hence the model would not directly be applicable to spatial grid samples as in the Swiss MHB. It might be possible, however, to subdivide, say, each 1 km² main quadrat into 25 sub-quadrats with 200 m length. Combining such data for a large number of main quadrats may provide enough information to obtain parameter estimates with reasonable precision Ramsey et al. (2015) have extended that model to “presence/absence” data.

6.11 BAYESIAN MODELING OF SWISS GREAT TITS WITH BUGS

In Section 6.11.1, we start by fitting our great tit model of choice in BUGS to compare the estimates with those from the analysis in `unmarked`. After that, we illustrate the accommodation of OD with

additional random effects in the linear predictors of abundance or detection in BUGS. You may use this analysis as a template for models with more complex random effects in BUGS generally. The coding of extra-Poisson and extra-binomial dispersion may be important in allowing for additional sources of heterogeneity and achieving a model that passes a formal GoF test. In addition, you may be interested in decomposing additional variability in expected abundance (λ) and detection probability (p). Finally, we also show how you can code “switches” in BUGS that turn some model components on or off. Finally, we give an example of the covariate modeling of a heterogeneous variance term.

6.11.1 BAYESIAN FITTING OF THE BASIC ZERO-INFLATED POISSON (ZIP) *N*-MIXTURE MODEL

We start with the Bayesian implementation of model `fm5ZIP` from [Section 6.9](#). We will provide another example of how easy it is to compute derived quantities in an MCMC-based analysis by estimating the proportion of the Swiss great tit population that lives in each 100-m elevation band between 200 and 2250 m. Elevation gradients of occurrence or abundance have always fascinated ecologists and are topical in climate change research, when fairly big changes can be expected along this dimension of species distributions. We will compute the derived quantities in R, outside of BUGS, using MCMC samples of all involved quantities, because sometimes it is easier to compute posterior samples of derived quantities after the analysis in BUGS.

```
# Prepare data for BUGS data bundle
elev <- umf@siteCovs$elev ; elev2 <- elev^2
forest <- umf@siteCovs$forest ; forest2 <- forest^2
date <- matrix(umf@obsCovs$date, ncol = 3, byrow = TRUE)
dur <- matrix(umf@obsCovs$dur, ncol = 3, byrow = TRUE)
date[is.na(date)] <- 0 ; date2 <- date^2
dur[is.na(dur)] <- 0 ; dur2 <- dur^2
iRoute <- umf@siteCovs$iLength

# Design matrix for abundance model (no intercept)
lamDM <- model.matrix(~ elev + elev2 + forest + forest2 + elev:forest +
  elev:forest2 + iRoute)[-1]
```

In the BUGS model, we add a couple of special features: (1) we add a posterior predictive GoF check, (2) we add “switches” to turn on/off specific components of the model, and (3) we simplify the fitting of the linear model for abundance by using a design matrix (see [Section 10.6](#) for more on this useful trick). “Switches” in BUGS programming can be quite useful because they allow you to fit a much larger variety of statistical models using a single BUGS model. We build three switches, `h.lam.on`, `hp.site.on`, and `hp.survey.on` (note that `h` stands for ‘heterogeneity’), to add to the model normally distributed random effects in abundance (site-specific) and in detection (site-specific or site-by-occasion specific). We discuss these switches in the next section, where we actually turn some of them on; for now, they are all turned off—i.e., set to zero.

```
# Specify model in BUGS language
sink("ZIPNmix.txt")
cat("
model {
```

```

# Specify priors
# zero-inflation/suitability
phi ~ dunif(0,1)          # proportion of suitable sites
theta <- 1-phi           # zero-inflation (proportion unsuitable)
ltheta <- logit(theta)

# abundance
beta0 ~ dnorm(0, 0.1)    # log(lambda) intercept
for(k in 1:7){          # Regression params in lambda
  beta[k] ~ dnorm(0, 1)
}
tau.lam <- pow(sd.lam, -2)
sd.lam ~ dunif(0, 2)    # site heterogeneity in lambda

# detection
for(j in 1:3){
  alpha0[j] <- logit(mean.p[j])
  mean.p[j] ~ dunif(0, 1) # p intercept for occasions 1-3
for(k in 1:13){        # Regression params in p
  alpha[k] ~ dnorm(0, 1)
}
tau.p.site <- pow(sd.p.site, -2)
sd.p.site ~ dunif(0, 2) # site heterogeneity in p
tau.p.survey <- pow(sd.p.survey, -2)
sd.p.survey ~ dunif(0, 2) # site-survey heterogeneity in p

# ZIP model for abundance
for (i in 1:nsite){
  a[i] ~ dbern(phi)
  eps.lam[i] ~ dnorm(0, tau.lam) # Random site effects in log(abundance)
  loglam[i] <- beta0 + inprod(beta[], lamDM[i,]) + eps.lam[i] * hlam.on
  loglam.lim[i] <- min(250, max(-250, loglam[i])) # 'Stabilize' log
  lam[i] <- exp(loglam.lim[i])
  mu.poisson[i] <- a[i] * lam[i]
  N[i] ~ dpois(mu.poisson[i])
}

# Measurement error model
for (i in 1:nsite){
  eps.p.site[i] ~ dnorm(0, tau.p.site) # Random site effects in logit(p)
  for (j in 1:nrep){
    y[i,j] ~ dbin(p[i,j], N[i])
    p[i,j] <- 1 / (1 + exp(-lp.lim[i,j]))
    lp.lim[i,j] <- min(250, max(-250, lp[i,j])) # 'Stabilize' logit
    lp[i,j] <- alpha0[j] + alpha[1] * elev[i] + alpha[2] * elev2[i] +
      alpha[3] * date[i,j] + alpha[4] * date2[i,j] +
      alpha[5] * dur[i,j] + alpha[6] * dur2[i,j] +
      alpha[7] * elev[i] * date[i,j] + alpha[8] * elev2[i] * date[i,j] +
      alpha[9] * elev[i] * dur[i,j] + alpha[10] * elev[i] * dur2[i,j] +

```

```

alpha[11] * elev2[i] * dur[i,j] + alpha[12] * date[i,j] * dur[i,j] +
alpha[13] * date[i,j] * dur2[i,j] +
eps.p.site[i] * hp.site.on + eps.p.survey[i,j] * hp.survey.on
eps.p.survey[i,j] ~ dnorm(0, tau.p.survey) # Random site-survey effects
}
}
# Posterior predictive distributions of Chi2 discrepancy
for (i in 1:nsite) {
  for (j in 1:nrep) {
    y.sim[i,j] ~ dbin(p[i,j], N[i]) # Create new data set under model
    e.count[i,j] <- N[i] * p[i,j] # Expected datum
    # Chi-square discrepancy for the actual data
    chi2.actual[i,j] <- pow((y[i,j]-e.count[i,j]),2) / (e.count[i,j]+e)
    # Chi-square discrepancy for the simulated ('perfect') data
    chi2.sim[i,j] <- pow((y.sim[i,j]-e.count[i,j]),2) / (e.count[i,j]+e)
    # Add small value e to denominator to avoid division by zero
  }
}
# Add up individual Chi2 values for overall fit statistic
fit.actual <- sum(chi2.actual[,]) # Fit statistic for actual data set
fit.sim <- sum(chi2.sim[,]) # Fit statistic for a fitting model
bpv <- step(fit.sim-fit.actual) # Bayesian p-value
c.hat <- fit.actual/fit.sim # c-hat estimate

# Derived parameters: Total abundance at 263 sampled sites
Ntotal263 <- sum(N[])
}
", fill = TRUE)
sink()

```

Here are the remaining ingredients for the analysis.

```

# Initial values
Nst <- apply(y, 1, max, na.rm = T) + 1
Nst[is.na(Nst)] <- round(mean(y, na.rm = TRUE))
Nst[Nst == "-Inf"] <- round(mean(y, na.rm = TRUE))
inits <- function(){ list(N=Nst, beta0=0, mean.p=rep(0.5,3), beta=runif(7, 0,0), alpha
= runif(13, 0,0))}

# Parameters monitored
params <- c("theta", "ltheta", "phi", "beta0", "beta", "sd.lam", "alpha0", "mean.p",
"alpha", "sd.p.site", "sd.p.survey", "fit.actual", "fit.sim", "bpv", "c.hat",
"Ntotal263")

```

It is quite difficult to find initial values that satisfy JAGS' high standards, so we fit the model in good old WinBUGS. The final three elements in the data bundle select the type of ZIP model that we are fitting by turning on or off additional random effects. We start with exactly the ZIP N -mixture model that we fit with `unmarked` in the last [Section 6.9](#)—i.e., the base model without any OD in either λ or p —and call this model 1. It has all switches set to “off” (= 0).

```

# Bundle data and choose to fit simple ZIP model (model 1)
win.data1 <- list(y=y, nsite=nrow(y), nrep=ncol(y),
  lamDM=lamDM, elev=elev, date=date, dur=dur, elev2=elev2,
  date2=date2, dur2=dur2, e=1e-06, hlam.on=0, hp.site.on=0,
  hp.survey.on=0)

# MCMC settings
ni <- 50000 ; nt <- 4 ; nb <- 10000 ; nc <- 3

# Call WinBUGS from R (ART 93 min) and summarize posteriors
out1 <- bugs(win.data1, inits, params, "ZIPNmix.txt", n.chains=nc, n.thin=nt,
  n.iter=ni, n.burnin=nb, debug=TRUE, bugs.directory=bugs.dir,
  working.directory=getwd())
print(out1, dig=3)

```

We compare the MLEs from `unmarked` with the Bayesian posterior inference in a table and in a graph (Figure 6.19). Essentially, with a large enough data set we always find that the posterior means from the Bayesian analysis with vague priors numerically agree very well with the MLEs. Perhaps this may allay the fears of some about the perceived dangers of Bayesian as opposed to non-Bayesian statistical analyses (e.g., Dennis, 1996; Lele and Dennis, 2009; Lele, 2015)?

```

# Compare MLEs and Bayesian posterior means (order first): table and graph
tmp <- summary(fm5ZIP)
ord.MLE <- rbind(tmp$psi[,1:2], tmp$state[,1:2], tmp$det[c(7:9, 1:6, 10:16),1:2])
ord.Bayes <- out1$summary[-c(1,3,12,16:18,32:39), 1:2]
cbind(ord.MLE, ord.Bayes)
par(mar=c(5,5,3,2), cex.lab=1.5, cex.axis=1.5)

```

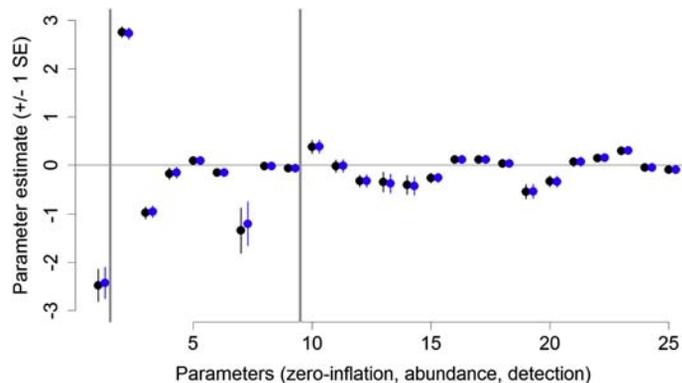


FIGURE 6.19

Comparison of MLEs (black; ± 1 SE) and Bayesian posterior means (blue; ± 1 posterior SD) of the parameters of the ZIP *N*-mixture model from Section 6.9 (model `fm5ZIP`). Gray vertical lines separate the parameters for the zero-inflation, abundance, and detection parts of the model (in this order).

```

plot(ord.MLE[,1], ylim=c(-3,3), pch=16, col="black", main="", frame=F,
xlab="Parameters (zero-inflation, abundance, detection)", ylab=
"Parameter estimate (+/- 1 SE)", cex=1.5)
segments(1:25, ord.MLE[,1]-ord.MLE[,2], 1:25, ord.MLE[,1]+ord.MLE[,2], lwd=2)
abline(h=0)
abline(v=c(1.5, 9.5), col="grey")
points((1:25)+0.3, ord.Bayes[,1], pch=16, col="blue", cex=1.5)
segments(1:25+0.3, ord.Bayes[,1]-ord.Bayes[,2], 1:25+0.3, ord.Bayes[,1]+ord.
Bayes[,2], col="blue", lwd=2)

```

Next, we want to make predictions—i.e., plot distribution maps and elevation gradients of population size—under the Bayesian model fit, and also compute a national population size estimate to compare with the non-Bayesian estimate in [Section 6.9](#). We could do the necessary computations for these derived quantities in BUGS directly, but this would be terribly slow. Here is an example of where it is more efficient to take the posterior MCMC samples from some parameters and then compute the derived quantities in R. To obtain the posteriors of the expected abundance (λ) that incorporate the zero-inflation part of the model, we have to do the following computation for every MCMC draw: $(1-\theta) * \exp(\beta_0 + \beta_1 * \text{covariate } 1 + \dots)$. We recycle some code from [Section 6.9.4](#).

```

library(unmarked)
data(Switzerland)      # Load Swiss landscape data in unmarked
CH <- Switzerland

```

We collect the covariates for the predictions into a design matrix and standardize all covariates using the same mean and sd that we used for the covariates in the analyzed data set.

```

ELEV <- (CH$elev-elev.mean)/elev.sd
ELEV2 <- ELEV^2
FOREST <- (CH$forest-forest.mean)/forest.sd
FOREST2 <- FOREST^2
CHdata <- cbind(elev = ELEV, elev2 = ELEV2, forest = FOREST, forest2 = FOREST^2, iRoute =
rep(0, length(CH$elev)), elev.forest = ELEV * FOREST, elev.forest2 = ELEV * FOREST2)
str(CHdata)           # This is a design matrix

```

Next, for every step in the MCMC output we compute the expected abundance (accounting for zero inflation). Before we do this, we define an array to hold the results and we subsample the MCMC output to prevent a weakling computer from crashing. We write the code such that we can input BUGS model fits from other models below, by substituting `out1` with `out7`, for instance.

```

MCMCout <- out1          # Choose results output from model 1
(nsamp <- length(MCMCout$sims.list$theta)) # how many MCMC samples do we have ?

# Subsample Markov chains
sub.sample.size <- 3000 # choose sample of 3000
selection <- sort(sample(1:nsamp, sub.sample.size))

# Array to hold predictions for every Swiss 1km2 quadrat
lamPred <- array(NA, dim=c(length(CH[,1]), sub.sample.size))

```

```

# Fill the array
for(i in 1:sub.sample.size){
  MCMCstep <- selection[i]
  lamPred[,i] <- (1-MCMCout$sims.list$theta[MCMCstep]) *
  exp(MCMCout$sims.list$beta0[MCMCstep] +
      CHdata %*% MCMCout$sims.list$beta[MCMCstep,1:7])
}

```

What have we done now? We have computed 3000 samples from the posterior distributions of the number of great tit territories in every single one of 42,275 1-km² quadrats in Switzerland. We can summarize these posterior distributions in suitable ways. For instance, we can map the posterior mean in every quadrat to obtain a map of abundance, exactly as we did in the last section (again using some of that code for [Figure 6.15](#)). We check for predictions of more than 100 pairs of great tits per 1 km² to censor them at 100, but we find that there are not any.

```

# Get posterior means for every quadrat and check if sensible
meanlam <- apply(lamPred, 1, mean) # Get posterior mean
max(meanlam) # Check maximum
sum(meanlam > 100) # Are any predictions >100 ?
plot(CH$elev, meanlam, ylim = c(0, max(meanlam))); abline(v=2250, col="red")
plot(CH$elev, meanlam, ylim = c(0,100)); abline(v = 2250, col = "red", lwd = 2)
meanlam[meanlam > 100] <- 100 # Censor all predictions
lamPred[lamPred > 100] <- 100

```

```

# Produce map of posterior mean of lambda
library(raster)
r <- rasterFromXYZ(data.frame(x = CH$x, y = CH$y, z = meanlam))
elevation <- rasterFromXYZ(cbind(CH$x, CH$y, CH$elevation))
elevation[elevation > 2250] <- NA
r <- mask(r, elevation)
mapPalette <- colorRampPalette(c("grey", "yellow", "orange", "red"))
par(mfrow = c(1,2), mar = c(5,5,1,5))
plot(r, col = mapPalette(100), axes = F, box = F, main = "")

```

Instead of summarizing the abundance distribution in two dimensions, we can summarize it in the third dimension—i.e., along the elevation gradient. We do this here and produce a histogram of the estimated number of great tit territories per 100-m elevation band in Switzerland.

```

elev.class <- 100*(CH$elev %/% 100 + 1) # Elevation class of each km2
tmp <- aggregate(lamPred, by = list(elev.class), FUN = sum)
N.elev <- as.matrix(tmp[, -1]) # Posterior sample of Ntotal per band
band <- tmp[, 1] # Elevation band (in m)
meanN <- apply(N.elev, 1, mean)
barplot(meanN, col = "grey", horiz = T, xlab = "Number of Great tit territories",
        ylab = "Elevation band (100m)", xlim = c(0, 200000))
axis(2, at = 1:length(band), labels = band)

```

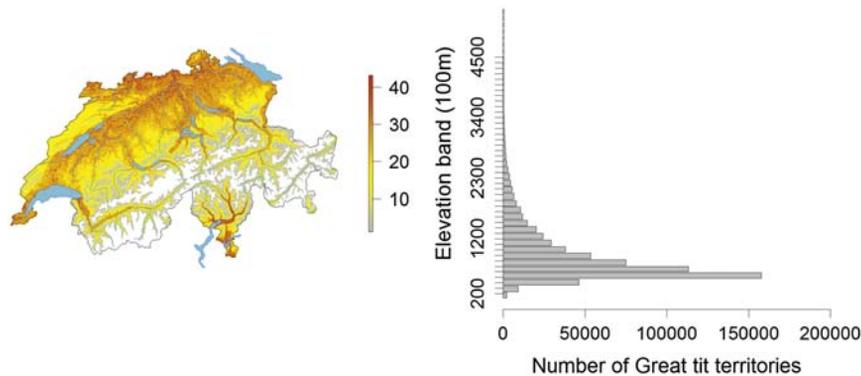


FIGURE 6.20

Summaries of the Bayesian posterior distributions of the expected abundance (λ , including zero-inflation) of great tits in Switzerland in 2013 in two dimensions, along the coordinate gradients (left), and in the third dimension along the elevation gradient (right, in number of pairs). Resolution of modeled data is 1 km². You can compare this map with its frequentist version in [Figure 6.15](#).

Not surprisingly, [Figure 6.20](#) (left) is essentially the same map as with the ML fit of the same model ([Figure 6.15](#), left). It would be trivial to also produce a map of the posterior SD in the Bayesian analysis. In the elevation histogram ([Figure 6.20](#), right), we see that although great tits live at highest densities in the lowlands, their largest numbers overall occur at medium elevations, because the area of these elevation bands in Switzerland is much greater than that of the lowest elevation bands.

Finally, we produce a national population size estimate again. To ensure comparability with the analyses in [Section 6.9](#), we again exclude quadrats with more than 50% water and those at heights >2250 m a.s.l.

```
# Posterior distribution of total number of great tit territories in 2013
keep <- which((CH$water < 50) & (CH$elev < 2251))
Ntot <- apply(lamPred[keep,], 2, sum)
hist(Ntot, breaks = 100, col = "grey", main = "Posterior of national population size")

# Point estimate and 95% CRI
mean(Ntot)
quantile(Ntot, prob = c(0.025, 0.975))

> mean(Ntot)
[1] 601510.4
> quantile(Ntot, prob = c(0.025, 0.975))
 2.5%    97.5%
494574.8 729662.7
```

These estimates are pretty similar to those obtained in the non-Bayesian analysis in [Section 6.9](#).

6.11.2 ADDING RANDOM EFFECTS IN BUGS

One of the great assets of Bayesian inference using MCMC is the ease with which you can add random effects to a model. There is a large number of reasons for why you may want to do that (Section 3.4), including the wish to accommodate overdispersion (OD), to investigate sources of variability (i.e., to partition variability in abundance or detection not explained by the covariates), or to accommodate grouping structures that induce dependencies in the data. We give two examples here. In the first, we allow for OD at multiple scales in our original model. In the second, we look at structure in the OD in abundance by fitting a linear model to a *variance* term of the model. This example underlines the frequently ignored fact that you may not only do covariate modeling for the mean structure of a response, but you may also explain patterns in the variance by adopting a linear or other covariate model for a variance term.

6.11.2.1 Accounting for Overdispersion (OD) at Multiple Scales

We start our illustration of random effects in BUGS by adding up to three sets of random effects into our N -mixture model 1 (corresponding to `fm5ZIP`): we add site random effects in abundance, and site- or site-by-survey random effects in detection. We wrote the BUGS code such that there are switches to turn on or off these additional random effects. These switches are set in the data bundle: when a switch is set to “on” (= 1), these sources of additional variability in λ and p are estimated from the data, whereas when it is “off” (= 0), the associated random effects are zeroed out and not part of the fitted model—i.e., not “connected to the data”—and therefore are not influencing the parameters that are connected to the data. Note that you will not get a zero estimate for the heterogeneity terms that are switched off, but will have to remember which nonzero estimate of the additional random effects is a data-free estimate based solely on the prior.

We will fit six variants of the basic model 1 that all accommodate some form of extra-Poisson or extrabinomial dispersion. With additional random effects, we typically need to run the chains for (much) longer to achieve convergence and it is not a typical to fail to obtain convergence at all. The following, “heavy” MCMC settings were sufficient to achieve convergence ($Rhat < 1.1$) for the main structural parameters of the model in all except three instances (when $Rhat$ was up to 1.2). This may be felt to be worrisome and some may wonder whether these models are estimable at all with our MHB sample size of 267 sites and three replicates. However, our own unpublished simulations and results reported in Tanadini (2010) suggest estimability of these models even with two replicates. You could fairly easily run your own simulation study: simply use function `simNmix` repeatedly to simulate data with certain random effects and then see whether the distribution of the estimates obtained with BUGS is centered on the data-generating value.

```
# MCMC settings
ni <- 10^6 ; nt <- 80 ; nb <- 200000 ; nc <- 3
```

As our second model, we fit a binomial mixture model with a zero-inflated Poisson-lognormal (PLN) mixture for abundance; i.e., we allow for random site effects in the abundance model and call this model 2.

```
# Bundle data and select model 2
win.data2 <- list(y = y, nsite = nrow(y), nrep = ncol(y), lamDM = lamDM, elev = elev,
  date = date, dur = dur, elev2 = elev2, date2 = date2, dur2 = dur2, e = 1e-06, hlam.on = 1,
  hp.site.on = 0, hp.survey.on = 0)
```

```
# Call WinBUGS from R (ART 4050 min) and summarize posteriors
out2 <- bugs(win.data2, inits, params, "ZIPNmix.txt", n.chains = nc, n.thin = nt,
n.iter = ni, n.burnin = nb, debug = F, bugs.directory = bugs.dir)
print(out2, dig = 3)
```

Third, we fit a binomial mixture model with a ZIP mixture for abundance and random normal site effects in detection and call this model 3.

```
# Bundle data and select model 3
win.data3 <- list(y = y, nsite = nrow(y), nrep = ncol(y), lamDM = lamDM, elev = elev,
date = date, dur = dur, elev2 = elev2, date2 = date2, dur2 = dur2, e = 1e-06, hlam.on = 0,
hp.site.on = 1, hp.survey.on = 0)
```

```
# Call WinBUGS from R (ART 4200 min) and summarize posteriors
out3 <- bugs(win.data3, inits, params, "ZIPNmix.txt", n.chains = nc, n.thin = nt,
n.iter = ni, n.burnin = nb, debug = F, bugs.directory = bugs.dir)
print(out3, dig = 3)
```

Fourth, the model with random normal site-by-survey effects in detection (this is model 4).

```
# Bundle data and select model 4
win.data4 <- list(y = y, nsite = nrow(y), nrep = ncol(y), lamDM = lamDM, elev = elev,
date = date, dur = dur, elev2 = elev2, date2 = date2, dur2 = dur2, e = 1e-06,
hlam.on = 0, hp.site.on = 0, hp.survey.on = 1)
```

```
# Call WinBUGS from R (ART 4020 min) and summarize posteriors
out4 <- bugs(win.data4, inits, params, "ZIPNmix.txt", n.chains = nc, n.thin = nt,
n.iter = ni, n.burnin = nb, debug = F, bugs.directory = bugs.dir)
print(out4, dig = 3)
```

Fifth, a model with random normal site effects both in abundance and in detection (model 5).

```
# Bundle data and select model 5
win.data5 <- list(y = y, nsite = nrow(y), nrep = ncol(y), lamDM = lamDM, elev = elev,
date = date, dur = dur, elev2 = elev2, date2 = date2, dur2 = dur2, e = 1e-06, hlam.on = 1,
hp.site.on = 1, hp.survey.on = 0)
```

```
# Call WinBUGS from R (ART 4250 min) and summarize posteriors
out5 <- bugs(win.data5, inits, params, "ZIPNmix.txt", n.chains = nc, n.thin = nt,
n.iter = ni, n.burnin = nb, debug = F, bugs.directory = bugs.dir)
print(out5, dig = 3)
```

Sixth, the model with site random effects in abundance and site-by-survey random effects in detection (model 6).

```
# Bundle data and select model 6
win.data6 <- list(y = y, nsite = nrow(y), nrep = ncol(y), lamDM = lamDM, elev = elev,
date = date, dur = dur, elev2 = elev2, date2 = date2, dur2 = dur2, e = 1e-06, hlam.on = 1,
hp.site.on = 0, hp.survey.on = 1)
```

```
# Call WinBUGS from R (ART 4230 min) and summarize posteriors
out6 <- bugs(win.data6, inits, params, "ZIPmix.txt", n.chains = nc, n.thin = nt,
n.iter = ni, n.burnin = nb, debug = F, bugs.directory = bugs.dir)
print(out6, dig = 3)
```

And finally, we fit the model with all three types of over-dispersion (model 7).

```
# Bundle data and select model 7
win.data7 <- list(y = y, nsite = nrow(y), nrep = ncol(y), lamDM = lamDM, elev = elev,
date = date, dur = dur, elev2 = elev2, date2 = date2, dur2 = dur2, e = 1e-06, hlam.on = 1,
hp.site.on = 1, hp.survey.on = 1)
```

```
# Call WinBUGS from R (ART 4625 min) and summarize posteriors
out7 <- bugs(win.data7, inits, params, "ZIPmix.txt", n.chains = nc, n.thin = nt,
n.iter = ni, n.burnin = nb, debug = F, bugs.directory = bugs.dir)
print(out7, dig = 3)
```

```
# Look at posteriors for random effects
MCMCout <- out7 # Choose which model you want to plot random effects
par(mfrow = c(1,3))
hist(MCMCout$sims.list$sd.lam, breaks = 60, col = "grey")
hist(MCMCout$sims.list$sd.p.site, breaks = 60, col = "grey")
hist(MCMCout$sims.list$sd.p.survey, breaks = 60, col = "grey")
```

We provide an overview of the fit and the inference about abundance and the random effects terms under all six models in [Table 6.3\(a\)](#) and [\(b\)](#). We also extrapolate the inferences to the rest of Switzerland as in the last section, to obtain an estimate of the national population size of great tits under each model.

Table 6.3(a) Comparison of seven ZIP models for the abundance of Swiss great tits in 2013. The term \hat{c} is the magnitude of OD, b_{pv} the Bayesian p -value, θ the zero-inflation parameter (the expected proportion of sites with structural zero counts), and λ (intercept) is the intercept of λ (on the log scale). The final two columns give the estimates of the total number of Great tit territories in the 263 surveyed quadrats and in all of Switzerland (excluding quadrats with $>50\%$ water and those with elevation >2250 m).

Model (Type of Heterogeneity)	\hat{c} -hat	b_{pv}	θ	λ (Intercept)	Pop. Size (263 quads)	National Pop. Size (in 000s with 95% CRI)
(1) Basic ZIP	1.54	0.02	0.08	2.73	3,549	591 (491–706)
(2) $\lambda(\text{site})$	1.05	0.36	0.04	3.07	13,303	1824 (836–3713)
(3) $p(\text{site})$	1.05	0.43	0.06	4.00	11,294	1663 (1080–2486)
(4) $p(\text{site.survey})$	0.99	0.56	0.07	3.05	3,664	611 (478–791)
(5) $\lambda(\text{site}), p(\text{site})$	1.06	0.40	0.04	3.75	10,403	1537 (863–2753)
(6) $\lambda(\text{site}), p(\text{site.survey})$	1.04	0.41	0.04	2.98	10,102	1398 (536–3756)
(7) $\lambda(\text{site}), p(\text{site}), p(\text{site.survey})$	0.99	0.59	0.03	3.27	5,651	829 (527–1368)

Table 6.3(b) Comparison of ZIP models in terms of their extra variance components (Posterior means and 95% CRI of SDs are given).

Model (Type of Heterogeneity)	sd.lam	sd.p.site	sd.p.survey
(1) Basic ZIP	—	—	—
(2) $\lambda(\text{site})$	0.70 (0.60–0.82)	—	—
(3) $p(\text{site})$	—	0.87 (0.75–1.02)	—
(4) $p(\text{site.survey})$	—	—	0.95 (0.81–1.10)
(5) $\lambda(\text{site}), p(\text{site})$	0.30 (0.00–0.71)	0.78 (0.13–1.05)	—
(6) $\lambda(\text{site}), p(\text{site.survey})$	0.69 (0.59–0.81)	—	0.12 (0.01–0.31)
(7) $\lambda(\text{site}), p(\text{site}), p(\text{site.survey})$	0.38 (0.18–0.55)	0.95 (0.70–1.19)	0.31 (0.17–0.46)

We see that the introduction of any of the three random effects brings down the OD coefficient to about 1 and results in a fitting model according to a Bayesian p -value. However, the inferences about abundance in terms of the intercept of the abundance model and the estimated population sizes for the 263 surveyed quadrats as well as that extrapolated to the whole of the country vary considerably (the latter two about fourfold). The random-effects SD estimates are also sensitive to model structure—i.e., to other random effects terms in the model. In some instances, some unexplained variance seems to be “soaked up” by one term when another was not in the model. Finally, there is some “competition” between zero-inflation and site random effects in lambda; with site random effects in lambda present, the estimate of the proportion of structural zero counts (theta) was clearly lower.

As is so often the case with Bayesian inference, we are thus confronted with a sort of embarrassment of riches: with BUGS it is usually easy to fit even very sophisticated models but then we typically lack easy and unequivocal ways of doing model selection. (Although the ability to use AIC for model selection in the analysis in `unmarked` did not help us much either, since the AIC pointed to the NB model with unrealistic predictions of lambda.) Although there is perhaps a danger of circularity, we think that few would dispute that common sense and subject matter knowledge must play important parts in model selection. The Swiss population is unlikely to number much more than about one million pairs of great tits, so from this perspective, only models 1, 4, 6, and 7 are potentially reasonable. However, they predict rather different elevation profiles for the expected abundance across Switzerland (Figure 6.21, code not shown). The models with additional random effects (4, 6, and 7) have a “hook” for very high elevations beyond the tree line around 2250 m where no great tits can live—we are not so much bothered by this, because it represents an extrapolation of the model with quadratic terms beyond observed covariate values. Models 4 and 7 in particular have more variable values of predicted λ at any given elevation: this makes sense given the additional random effects. But model 4 and especially model 7 make unrealistically high predictions around the tree line (red vertical line). Under model 7 λ is even predicted to *increase* again in the elevation range from about 1900–2250 m; this is not a realistic pattern. In our opinion, this rules out models 4 and 7 as a reasonable basis for inference, since they do not seem to perform well for one central goal of our analysis. The elevation profile of abundance predicted by model 6 looks broadly reasonable; however, the predicted density at low elevations is certainly too high. Perhaps the quadratic function of elevation is too rigid and we ought to try a more flexible semiparametric (spline) model; see Section 10.14.

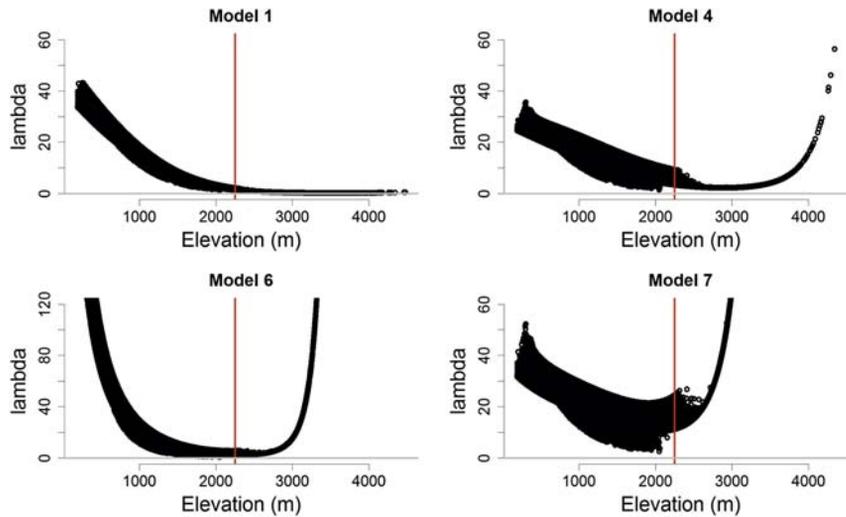


FIGURE 6.21

Comparison between the estimated elevation profiles of the expected abundance of great tits across Switzerland among models 1, 4, 6, and 7. The red vertical line represents the tree line at around 2250 m.

This leaves us with the base model 1, which does not formally fit but seems to produce sensible predictions of abundance overall. Hence, in this case adding random effects into the model to accommodate unexplained variability in abundance or detection did not help us so much. Nevertheless, in many cases this may be a fruitful avenue when looking for a fitting model. Remember, that all estimates of national total population sizes suffer from the issues of space discussed in [Section 6.10](#) and that accounting for an effective sample area greater than 1 km² reduces these crude estimates. Assuming an average home range size of 2 ha for great tits, we get an effective sample area of 1.344 km² associated with each 1-km² MHB sample quadrat and the Swiss national population size estimate of great tits under model 6 in [Table 6.3 \(a\)](#) would have to be reduced by a factor of 1.344.

6.11.2.2 Linear Modeling of a Variance in the *N*-mixture Model

We end this section on random effects with an example where we take the best model from the previous section (model 6) and investigate possible patterns in the OD in abundance—i.e., in the parameter sd.lam . Specifically, we look at the elevation profile of this OD in abundance, by fitting a log-linear model to the extra-Poisson variance:

$$\log(\sigma_{\lambda,i}^2) = \alpha_{\text{var.lambda}} + \beta_{\text{var.lambda}} * \text{elev}_i$$

Thus, we adopt a linear model for the variance on a log-transformed scale, since a variance is positive-valued like a Poisson mean, in a model that accounts for heteroskedasticity of a variance component by modeling it as a function of a covariate. As always, the first step when we want to model a parameter (i.e., explain it by covariates) is that we have to allow it to vary in the model. This is done by indexing it in algebra, denoting the dimension along which we want to explain its variability. We want to model pattern among sites, and hence we must index the variance by i . We do this in a stripped-down

version of the original ZIP model: we drop code for the GoF, the switches, and also the zero-inflation part, since with random effects in lambda, the estimated proportion of structural zero sites (i.e., unsuitable sites) is very close to 1. The following code is the result of preliminary exploratory analyses in which we identified priors for the linear model parameters for the variance that were just wide enough to count as vague, but not so wide as to cause trouble for the model to converge.

```
# Bundle and summarize data set
str( win.data8 <- list(y=y, nsite = nrow(y), nrep = ncol(y), lamDM = lamDM, elev = elev,
  date = date, dur = dur, elev2 = elev2, date2 = date2, dur2 = dur2) )

# Specify model in BUGS language
sink("Nmix.special.txt")
cat("
model {

# Specify priors
# abundance
beta0 ~ dnorm(0, 0.1)   # log(lambda) intercept
for(k in 1:7){         # Regression params in lambda
  beta[k] ~ dnorm(0, 1)
}

# Model for unexplained variance in lambda among sites
for(i in 1:nsite){
  tau.lam[i] <- 1/var.lam[i]
  log(var.lam[i]) <- alpha.var.lam + beta.var.lam * elev[i]
}

# Priors for intercept and slope of linear model for variance
alpha.var.lam ~ dunif(-1, 1)
beta.var.lam ~ dunif(0, 3)

# detection
for(j in 1:3){
  alpha0[j] <- logit(mean.p[j])
  mean.p[j] ~ dunif(0, 1)   # p intercept for occasions 1-3
}
for(k in 1:13){           # Regression params in p
  alpha[k] ~ dnorm(0, 1)
}
tau.p.survey <- pow(sd.p.survey, -2)
sd.p.survey ~ dunif(0, 1)   # site-survey heterogeneity in p

# Poisson-lognormal model for abundance
for(i in 1:nsite){
  eps.lam[i] ~ dnorm(0, tau.lam[i])   # Random site effects in log(abundance)
  loglam[i] <- beta0 + inprod(beta[], lamDM[i,]) + eps.lam[i]
  loglam.lim[i] <- min(250, max(-250, loglam[i]))   # 'Stabilize' log
  mu.poisson[i] <- exp(loglam.lim[i])
  N[i] ~ dpois(mu.poisson[i])
}
}
```

```

# Binomial measurement error model with extra-binomial dispersion
for (i in 1:nsite){
  for (j in 1:nrep){
    y[i,j] ~ dbin(p[i,j], N[i])
    p[i,j] <- 1 / (1 + exp(-lp.lim[i,j]))
    lp.lim[i,j] <- min(250, max(-250, lp[i,j])) # 'Stabilize' logit
    lp[i,j] <- alpha0[j] + alpha[1] * elev[i] + alpha[2] * elev2[i] +
      alpha[3] * date[i,j] + alpha[4] * date2[i,j] +
      alpha[5] * dur[i,j] + alpha[6] * dur2[i,j] +
      alpha[7] * elev[i] * date[i,j] + alpha[8] * elev2[i] * date[i,j] +
      alpha[9] * elev[i] * dur[i,j] + alpha[10] * elev[i] * dur2[i,j] +
      alpha[11] * elev2[i] * dur[i,j] + alpha[12] * date[i,j] * dur[i,j] +
      alpha[13] * date[i,j] * dur2[i,j] + eps.p.survey[i,j]
    eps.p.survey[i,j] ~ dnorm(0, tau.p.survey) # Random site-survey effects
  }
}
", fill = TRUE)
sink()

```

Here are the remaining ingredients for the analysis. For the parameters associated with the variance components, we use solutions from earlier fits of a similar model as initial values.

```

# Initial values
Nst <- apply(y, 1, max, na.rm = T) + 1
Nst[is.na(Nst)] <- round(mean(y, na.rm = TRUE))
Nst[Nst == "-Inf"] <- round(mean(y, na.rm = TRUE))
inits <- function(){ list(N=Nst, beta0=0, mean.p=rep(0.5,3), beta=runif(7, 0,0), alpha
=runif(13, 0,0), alpha.var.lam=0, beta.var.lam=1.5, sd.p.survey=0.3)}

# Parameters monitored
params <- c("beta0", "beta", "alpha.var.lam", "beta.var.lam", "alpha0", "mean.p",
"alpha", "sd.p.survey")

# MCMC settings
ni <- 180000 ; nt <- 100 ; nb <- 10000 ; nc <- 3

# Call WinBUGS from R (ART 374 min) and summarize posteriors
out8 <- bugs(win.data8, inits, params, "Nmix.special.txt", n.chains = nc, n.thin = nt,
n.iter = ni, n.burnin = nb, debug = TRUE, bugs.directory = bugs.dir,
working.directory = getwd())
print(out8, dig = 3)

```

As an informal check of whether the model gives reasonable estimates we compare its main estimates with those under the related model 6 and do indeed find fairly similar estimates, with the exception of the coefficients for `elev` and `elev2`.

```

print(cbind(out6$summary[c(4:11,13:31,33),1:2],
out8$summary[c(1:8,11:30),1:2]),2)

```

The estimate of the slope of the site-specific extra-Poisson variance (or SD) on elevation is clearly positive (posterior mean 1.48, CRI 1.21–1.82). Hence, at higher elevations of Switzerland, we have more unexplained among-site variability in the expected abundance of great tits than we do at lower elevations. To better understand this interesting relationship, we form predictions of the lambda OD against elevation and plot them.

```
# Predict site variance as a function of elevation
# Get posterior distribution of predictions first
orig.elev.pred <- seq(200, 2250, 50)
elev.pred <- (orig.elev.pred - mean(tits$elev)) / sd(tits$elev)
(n.mcmc <- length(out8$sims.list$alpha.var.lam)) # how many MCMC samples ?
post.sd.lam <- array(NA, dim = c(length(elev.pred), n.mcmc))
for(i in 1:length(elev.pred)){
  post.sd.lam[i,] <- sqrt(exp(out8$sims.list$alpha.var.lam +
    out8$sims.list$beta.var.lam * elev.pred[i]))
}

# Plot posterior mean and a sample of 500 regression lines from posterior
show <- sample(1:n.mcmc, 500)
matplot(orig.elev.pred, post.sd.lam[,show], xlab = "Elevation (m)", ylab = "sd.lam",
  type = "l", lty = 1, lwd = 1, col = "grey", frame = F, ylim = c(0, 6))
lines(orig.elev.pred, apply(post.sd.lam, 1, mean), lwd = 3, col = "blue")
```

We see a considerable increase in the extra-Poisson dispersion in lambda with increasing elevation (Figure 6.22). At low elevations up to about 500 m, the distribution of N is fairly close to a Poisson because the amount of OD is small, but at higher elevations the Poisson model with the specified covariates becomes increasingly poor to explain all the site-specific variability in latent abundance N .

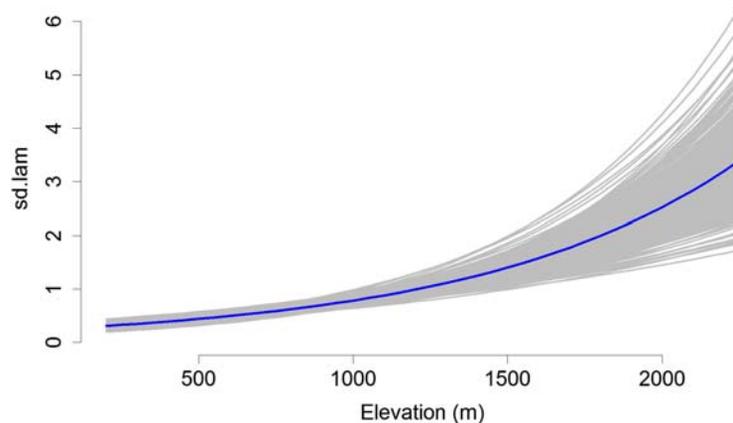


FIGURE 6.22

Relationship between unexplained site-specific heterogeneity in expected abundance ($sd.lam$) of Swiss great tits in 2013 and elevation. The blue line shows the posterior mean and the gray lines give a random sample of size 500 from the posterior distribution of the regression lines of the overdispersion standard deviation on (scaled) elevation.

Thus, the power of BUGS allowed us to uncover, in a rigorous parametric model, a quite fascinating pattern in the spatial variation of abundance of Swiss great tits.

This example concludes our illustration of the Bayesian treatment of the N -mixture model. A Bayesian treatment for these models becomes essential whenever we consider any of a number of extensions of the model.

6.12 TIME-FOR-SPACE SUBSTITUTION

Sometimes we have very sparse spatial replication or even none: all we have is a time series of counts from a single site. We can still jointly estimate abundance and detection if we have the necessary short-term replication within a period of closure. We simply treat the (“large-scale”) temporal replication as a substitute for the usual spatial replication. Yamaura et al. (2011) did this in the context of multi-species N -mixture models (see Chapter 11). We illustrate with a small simulation in which we imagine that we had counted a snake species at a single site for 12 summers, with four counts conducted at each. Assuming closure for a single summer, we simply fit the standard model as if we had surveyed 12 sites in a single year with four temporal replicates. We use our AHM function `simpleNmix` to generate a data set with the following default arguments:

```
simpleNmix(nyear = 12, nrep = 4, beta0 = 2, beta1 = 0.1, alpha0 = 0.5, alpha1 = -0.1,
alpha2 = 1)
```

This generates data for 12 years, with four replicate surveys in each, where there is a log-linear trend in abundance with $\log(\lambda_i) = \beta_0 + \beta_1 * Time_i$, and where detection probability is logit-linearly affected by year and the temperature during a survey according to $\log(p_{ij}) = \alpha_0 + \alpha_1 * Time_i + \alpha_2 * temp_{ij}$. We generate the data with opposing trends over time in abundance and detection to make the estimation problem harder.

We generate 2500 data sets and analyze them both with a simple Poisson GLM (with covariates time and temperature) and with the data-generating N -mixture model. These simulation settings represent averages of abundance, detection, and counts of around 15, 0.47, and 6.8.

```
library(unmarked)
simrep <- 2500 # Number of simreps
results <- array(NA, dim = c(simrep, 8)) # Array for results
for(i in 1:simrep){
  cat("Simrep", i, "\n")
  data <- simpleNmix(nyear = 12, nrep = 4) # Simulate a data set
  umf <- unmarkedFramePCount(y = data$C, siteCovs = data.frame(Time = data$Time),
  obsCov = list(temp = data$temp))
  fm1 <- pcount(~Time+temp~Time, data = umf)
  fm2 <- glm(c(data$C)~rep(data$Time,data$nrep)+c(data$temp),family='poisson')
  results[i, 1:5] <- coef(fm1)
  results[i, 6:8] <- coef(fm2)
}
colnames(results) <- c(names(coef(fm1)), names(coef(fm2)))
```

We compare the intercept (abundance) and the slope on time (population trend) for expected abundance (λ) in [Figure 6.23](#) (code not shown). We notice apparently unbiased estimates for both

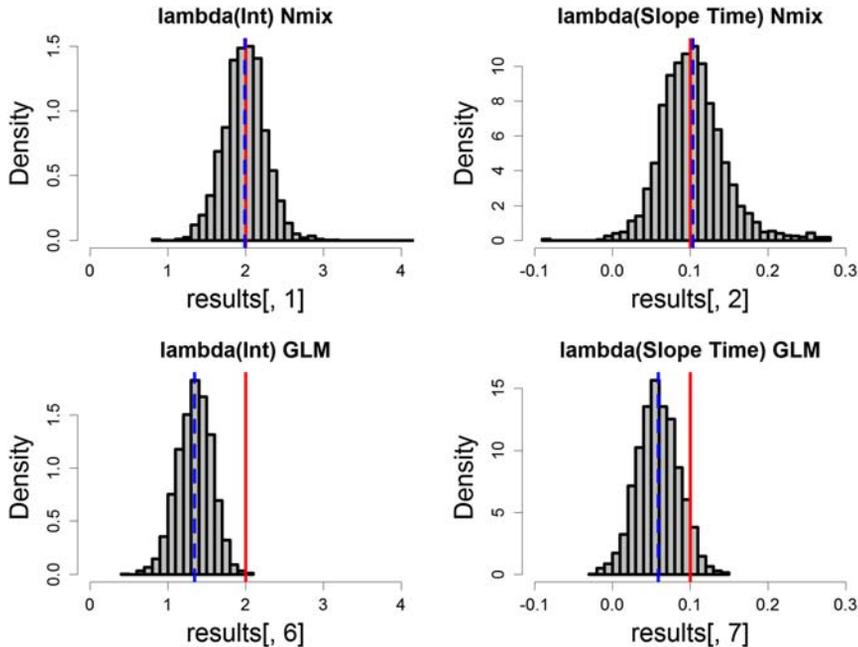


FIGURE 6.23

Summary of simulation exercise for a time-for-space substitution of the N -mixture model for the abundance intercept (left) and the population trend (right) estimated from count data with four replicates in each of 12 years. Top: N -mixture model; bottom: simple Poisson GLM. Both data generation and analysis also contained an effect of temperature on detection. Red line: truth in data generation; blue line: mean of the 2500 simulations.

intercept and population trend when using the N -mixture model, and substantial bias in a simple Poisson GLM. In the GLM we corrected for the effects of temperature on detection, but in this nonhierarchical analysis, the separate effects of time on abundance and detection cannot be teased apart, hence the bias in the trend estimate in the GLM.

The ability to fit the N -mixture models even in such extreme situations is interesting. However, in practice you should perhaps accompany the use of the model for real data with such borderline sample sizes with simulations to get a better feel for how good your estimates are likely to be.

6.13 THE ROYLE-NICHOLS MODEL AND OTHER NONSTANDARD N -MIXTURE MODELS

N -mixture models are HMs for inference about abundance that adjust explicitly for some kind of measurement error. Typically, they adopt a Poisson or similar distribution for spatial, temporal, or spatiotemporal variation in the latent abundance states N . However, depending on the protocol applied

for measuring abundance, the observation model may vary quite a bit. In most of this chapter, we cover the protocol that accommodates false-negative detection error, leading to a conditional binomial distribution for the observation process. In Chapters 7–9, we cover various protocols leading to the adoption of a multinomial distribution for the observation process. Here we cover two further designs leading to two further variants of N -mixture models. In the first (Section 6.13.1), instead of observing counts, we only have information on whether the count was zero or greater than zero—i.e., detection/nondetection (or “presence/absence”) data—leading to a Bernoulli/Poisson mixture model. In the second variant (Section 6.13.2), we may observe a member of N multiple times, effectively representing a kind of false-positive error in addition to the usual false-negatives. This leads to the adoption of a Poisson/Poisson mixture model.

6.13.1 THE ROYLE-NICHOLS OR BERNOULLI/POISSON N -MIXTURE MODEL

In Section 3.3.6 we saw that when suitable parametric assumptions are met, we can estimate abundance from mere detection/nondetection (“presence/absence”) data. The Royle-Nichols model (or RN model for short) is another such example (Royle and Nichols, 2003). The basic N -mixture model in this chapter is a binomial/Poisson mixture for the observed counts, whereas the RN model is a Bernoulli/Poisson mixture for observed detection/nondetection data. It is an important HM in the family tree of models in this book, because it provides a conceptual link between the hierarchical N -mixture models for abundance and the HM for occurrence (i.e., the classical occupancy model in Chapter 10). The RN model may be useful to estimate abundance from replicated measurements of presence/absence, to accommodate detection heterogeneity when focusing on occupancy (Dorazio, 2007) or to link occupancy data with abundance data in an integrated model (Conroy et al., 2008) and looks like this:

1. Model for quadrat population size (state process model):

$$N_i \sim \text{Poisson}(\lambda_i)$$

$$\log(\lambda_i) = \beta_0 + \text{covariate effects}$$

2. Measurement error model (observation model):

$$y_{ij}|N_i \sim \text{Bernoulli}(P_{ij}^*)$$

$$P_{ij}^* = 1 - (1 - p_{ij})^{N_i}$$

$$\text{logit}(p_{ij}) = \alpha_0 + \text{covariate effects}$$

The observations y_{ij} are binary, indicating that your species was detected or not during survey j at site i . The probability to detect the species (P_{ij}^* ; this is the “occupancy” or “per-quadrat detection probability”) is expressed as a function of the number of individuals at the site, N_i , and the per-individual detection probability p_{ij} (which in the literature is typically denoted r ; Royle and Nichols, 2003; Dorazio, 2007). This relationship is based on a simple binomial argument

that assumes independence and identical detection probability p_{ij} for all individuals N_i at site i during occasion j . The RN model is often described as an occupancy model because the modeled data are identical to those for an occupancy model, or as a heterogeneity occupancy model, because the relationship between abundance and per-individual detection probability adjusts for site-specific heterogeneity in per-quadrat detection probability P_{ij}^* . However, we prefer to describe the RN model as an N -mixture model with a modified observation process for detection/nondetection data.

We illustrate the RN model first with a simulation and then we fit it to Swiss tit data. We use function `occuRN` in `unmarked`, but the model can be fit in `BUGS` too (Yamaura et al., 2011). We use our AHM function `playRN` to illustrate the RN model in the experimental setting of a simulation. The function internally uses function `simNmix` to generate replicated count data under the standard N -mixture model of Royle (2004b) and then “degrades” these data to detection/nondetection and fits the RN model using `unmarked`. It also computes the BUPs for site-specific abundance N and compares them with the known true local abundances in a graph and with an informal linear regression (informal because it does not account for nonindependence of the N estimates). For a perfect RN model, and indeed for any HM, this regression of predicted vs. true latent variables should have a slope somewhat less than 1 because of shrinkage in the BUPs. As additional output you get the parameter estimates of the RN model. Use of `playRN` with varying values of sample size (number of sites M , number of repeated surveys J) and of `mean.abundance` and `mean.detection` will train your intuition about the RN model. (If you want to change the effects of three covariates then you have to change the definition of `playRN`.)

```
# Execute the function using various settings
playRN(M = 100, J = 3, mean.abundance = 0.1) # Increasing abundance
playRN(M = 100, J = 3, mean.abundance = 1)
playRN(M = 100, J = 3, mean.abundance = 5)
playRN(M = 100, J = 3, mean.detection = 0.3) # Increasing detection
playRN(M = 100, J = 3, mean.detection = 0.5)
playRN(M = 100, J = 3, mean.detection = 0.7)
playRN(M = 100, J = 20) # More visits
playRN(M = 1000, J = 3) # More sites
```

We generate 100 MHB-type data sets (with 267 sites and three visits) for a range of values of mean abundance between 0.1 and 10 and with the default mean detection of 0.3.

```
# Run simulation
lam <- c(0.1, 0.5, 1, 2.5, 5, 10) # 6 levels of mean abundance
simrep <- 100
results <- array(NA, dim = c(length(lam), simrep, 6))
for(i in 1:6){
  for(j in 1:simrep){
    cat(paste("\n *** lambda level", lam[i], ", simrep", j, "***\n"))
    tmp <- playRN(mean.abundance = lam[i])
    results[i,j,1:5] <- tmp$coef # Coefficients of RN model
    results[i,j,6] <- tmp$slope # Slope of regression of Nest on Ntrue
  }
}
```

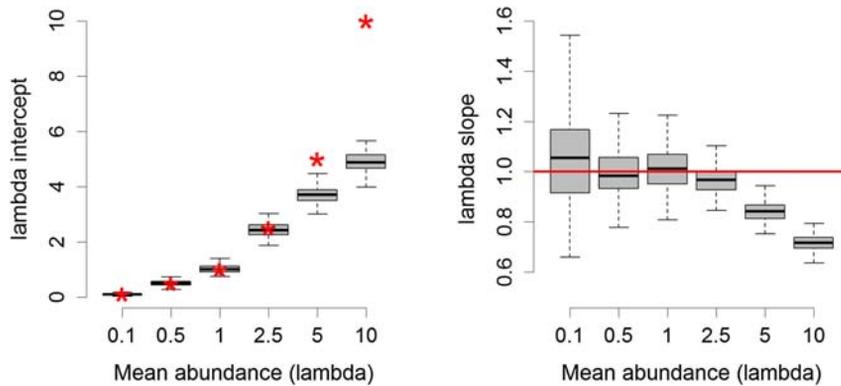


FIGURE 6.24

Summary of simulation for the RN model when mean abundance (λ) is varied (see text for details). Each boxplot summarizes estimates from 100 simulated data sets. Red asterisks and the line show the true values used in the data generation.

Summary of results for abundance (Figure 6.24)

```
par(mfrow = c(1, 2), mar = c(5, 5, 3, 2), cex.lab = 1.5, cex.axis = 1.5)
boxplot(t(exp(results[, , 1])), names = as.character(lam), outline = F, frame = F, col =
"grey", xlab = "Mean abundance (lambda)", ylab = "lambda intercept", ylim = c(0, 10))
points(1:6, lam, pch = "*", col = "red", cex = 3)
boxplot(t(results[, , 2]), names = as.character(lam), outline = F, frame = F, col = "grey",
xlab = "Mean abundance (lambda)", ylab = "lambda slope", ylim = c(0.5, 1.6))
abline(h = 1, col = "red", lwd = 3)
```

We summarize the sampling distributions of the intercept and the slope in the abundance model (Figure 6.24) and find that the model recovers unbiased and reasonably precise estimates of the abundance parameters up to a certain mean abundance (λ). This makes sense since as λ increases there is less and less heterogeneity in P_{ij}^* and so we lose information about model parameters. It is interesting to note that λ is to some extent controllable *by design*—i.e., by changing the size of the sample unit. These simulation results suggest that there is an optimal size of a quadrat for any species—the size should produce around one individual per sample unit. This concept may appear quite strange but the direct connection between plot size and statistical efficiency is an interesting use of these models.

Next we take the 2013 counts of Swiss tits and fit both the binomial/Poisson model to the counts directly, and the Bernoulli/Poisson (= RN) model to the counts turned into detection/non-detection data. We fit the initial model from Section 6.9 with a Poisson mixture since `occuRN` does not support ZIP or NB mixtures. We first organize the tit counts into a 3-D array `y3D`, where slices 1–6 represent great, blue, coal, crested, marsh, and willow tits, in that order. Function `occuRN` does not allow sites with all observations missing, so we only keep the 263 sites surveyed in 2013.

```

# Load data on Swiss tits
tits <- read.table("SwissTits_mhb_2004_2013.csv", header = T, sep = ";")
str(tits)                # Overview of data file
table(tits$latname)     # Available spec (Latin short) (not in order !)
table(tits$name)       # Same in English

# Select 2013 counts (all species) and put into 3D array
y <- as.matrix(tits[,c("count131", "count132", "count133")])
# Create same NA pattern in counts y as in survey date
y[is.na(cbind(tits$date131, tits$date132, tits$date133))] <- NA
# List of sites that were surveyed in 2013
keep <- which(apply(is.na(y[1:267,]), 1, sum) != 3) # surveyed sites

# Get covariate data (site and observational) and drop unsurveyed sites
elev <- tits[keep,14]
route <- tits[keep,15]
forest <- tits[keep,17]
date <- cbind(tits$date131, tits$date132, tits$date133)[keep,] # Survey date
dur <- cbind(tits$dur131, tits$dur132, tits$dur133)[keep,] # Survey duration

# Put counts (all species) into 3D array
y3D <- array(NA, dim = c(267, 3, 6)) # Define 3D array
for(i in 1:6){                       # Fill in slices
  y3D[, , i] <- y[((i-1)*267+1):(i*267), ]
}
y3D <- y3D[keep, , ]                 # only keep sites surveyed in 2013

# 'Degrade' counts to mere detection/nondetection data
y3DRN <- y3D                         # Copy counts
y3DRN[y3DRN > 1] <- 1                 # Overwrite any count >1 with 1 (for RN model)

```

Next, we write code to loop over all six species (you have to continue by pressing the Enter key after each species), plot the data, fit the standard N -mixture model (with function `pcount`) and the RN model (with `occuRN`), and compare the two sets of estimates.

```

library(unmarked)
spec.names <- c("Great tits", "Blue tits", "Coal tits", "Crested tits", "Marsh tits",
"Willow tits")

# Loop over 6 species of tits
par(mfrow = c(2,2), mar = c(5,4,3,1))
for(k in 1:6){
  cat("\n*** Analysis for ", spec.names[k], "***\n")
  # Plot observed data: counts vs survey date
  matplot(t(date), t(y3D[, , k]), type = "l", lwd = 3, lty = 1, frame = F, xlab =
"Survey date (1 = April 1)", ylab = "Observed counts", main = paste("Counts of",
spec.names[k], "as a function of survey date"))

  # Fit standard Nmix model (Nmix1)
  time <- matrix(rep(as.character(1:3), 263), ncol = 3, byrow = T)

```

```

summary(umf1 <- unmarkedFramePCount(y = y3D[, ,k],
siteCovs=data.frame(elev=scale(elev), forest=scale(forest), iLength=1/route),
obsCovs=list(time = time, date = scale(date), dur = scale(dur))) )
Nmix1 <- pcount(~(elev+I(elev^2)) * (date+I(date^2)) * (dur+I(dur^2)) + time - 1
~ (elev+I(elev^2)) * (forest+I(forest^2))+ iLength,
umf1, control=list(trace=TRUE, REPORT=5, maxit = 250))
(tmp1 <- summary(Nmix1))

# Fit RN model (Nmix2)
summary(umf2 <- unmarkedFrameOccu(y = y3DRN[, ,k],
siteCovs=data.frame(elev=scale(elev), forest=scale(forest), iLength=1/route),
obsCovs=list(time = time, date = scale(date), dur = scale(dur))) )
# Use solutions from Nmix1 as inits for Nmix2
Nmix2 <- occuRN(~(elev+I(elev^2)) * (date+I(date^2)) * (dur+I(dur^2)) + time - 1
~ (elev+I(elev^2)) * (forest+I(forest^2))+ iLength,
umf2, control=list(trace=TRUE, REPORT=5), starts = coef(Nmix1))
(tmp2 <- summary(Nmix2))

# Compare estimates under both models
# Table with MLEs and SEs
print(cbind(rbind(tmp1$state[,1:2], tmp1$det[,1:2]), rbind(tmp2$state[,1:2],
tmp2$det[,1:2])))

# Plot of all RN estimates versus all Nmix estimates
plot(coef(Nmix1), coef(Nmix2), xlab = "Coefficients Nmix", ylab = "Coefficients RN",
main = spec.names[k])
abline(0,1, lwd = 2)
abline(h = 0, lwd = 1, col = "grey")
abline(v = 0, lwd = 1, col = "grey")
abline(lm(coef(Nmix2) ~ coef(Nmix1)), lwd = 2, col = "blue")
browser()

# Overall discrepancy measure (for state model only): slope of regression and r2
print(slope <- coef(lm(coef(Nmix2)[1:10] ~ coef(Nmix1)[1:10]))[2]) # Slope
print(r <- cor(coef(Nmix2)[1:10], coef(Nmix1)[1:10])) # Correlation
}

```

When you execute this code, you will see that the RN quite often produces reasonable estimates (judged by their similarity to those under the binomial/Poisson model). [Table 6.4](#) shows that the slope of the RN abundance estimates on the *N*-mixture model-based abundance estimates is close to 1 in three out of six species and that their correlation is high in five out of six. Perhaps not surprisingly, the correspondence between the two sets of estimates was by far the worst for the most common species, the coal tit, and best for the rarest of them, the marsh tit. On the other hand, there was also a good agreement for the second most common species, the great tit, so rarity does not seem to be the only factor ensuring success of abundance estimation based on the RN model.

In practice, the RN model has not been extensively used to actually estimate abundance. Arguably, it is more sensitive to parametric assumptions and it will fail when abundance and/or detection are high. Moreover, adopting mixture distributions other than the Poisson, such as the NB, leads to unstable estimates and often also to biologically unreasonably high estimates for abundance

Table 6.4 Comparison of estimates for abundance models for six species of Swiss tits under binomial/Poisson (= traditional N -mixture) and Bernoulli/Poisson (= RN) models. Tits are ordered from most to least abundant, based on the exponentiated intercept of the abundance model under the binomial/Poisson model for counts. The second and third columns give the slope of the RN estimates of the abundance model on the corresponding estimates of the traditional N -mixture model, and the Pearson correlation coefficient of these two sets of 10 estimates each in the linear predictor for abundance.

Species	lambda (Intercept)	Slope RN Estimates on Nmix Estimates	Correlation Between RN Estimates and Nmix Estimates
Coal tit	19.5	0.24	0.35
Great tit	14.3	1.01	0.92
Willow tit	5.6	0.49	0.86
Blue tit	4.7	0.72	0.96
Crested tit	3.3	0.93	0.82
Marsh tit	2.6	0.99	0.96

(Royle and Nichols, 2003). Hence, the RN model may be most useful as an occupancy model that accounts for part of the site-specific heterogeneity in detection (Dorazio, 2007) or in integrated models to link occupancy data with data that are directly informative about abundance (Conroy et al., 2008). Note also that Yamaura et al. (2011) have used it as the basis for their community models (Chapter 11).

6.13.2 THE POISSON/POISSON N -MIXTURE MODEL

In this model for latent abundance based on counts of individuals, we allow not only false-negatives (we may fail to detect an individual), but also false-positives in the sense that an individual may be counted more than once during a single occasion. Typical examples for studies producing such data are camera traps without individual recognition, when an individual may produce multiple pictures, or snow track surveys where an individual may cross a transect multiple times. One natural model for count y_{ij} at site i at occasion j is this (Stanley and Royle, 2005; Guillera-Arroita et al., 2011):

1. Process model:

$$N_i \sim \text{Poisson}(\lambda_i)$$

$$\log(\lambda_i) = \beta_0 + \text{covariate effects}$$

2. Measurement error model:

$$y_{ij}|N_i \sim \text{Poisson}(N_i\phi_{ij})$$

$$\text{logit}(\phi_{ij}) = \alpha_0 + \text{covariate effects}$$

The first part of the model is the same as in any N -mixture model, but the second part expresses the counts as the product of the number of individuals N_i and a rate parameter ϕ_{ij} , which is the detection rate—i.e., the expected number of times that a member of N_i appears in count y_{ij} . We believe that this is

a very sensible model conceptually, and it can be easily fit in BUGS. Moreover, its parameters can be estimated with a single visit to each site—i.e., no repeated measurements are required. However, there may be problems with serial correlation in the detection rate, and in several of our unpublished applications, the model has not always seemed to produce sensible estimates of abundance. We suggest that you apply it with caution only or try out more advanced variants of such Poisson/Poisson models that accommodate serial correlation (Guillera-Aroita et al., 2011, 2012).

6.14 MULTISCALE *N*-MIXTURE MODELS

As we will discuss in some more detail in Section 10.10 for the occupancy case, various forms of temporal or spatial subsampling are common protocols in studies of occurrence and abundance. This means that sampling in time or in space occurs at two or possibly even more scales. For instance, we may do two repeat point counts at the same site at each of multiple times within a breeding season (temporal subsampling) or we may count at multiple sites within each of a series of several larger areas (spatial subsampling; see Figure 10.13). In both cases we can imagine an intrinsically nested structure of subunits within units. There may also be a combination of the two, when we have both spatial and temporal subsamples. This raises two potential issues: first, there may be a dependency between subunits in the same unit. For the temporal case, we would expect both abundance and detection for multiple, repeated counts at the same site to be more similar than multiple repeated counts at different sites, because the population may simply not turn over so quickly. Similarly, for the spatial case we might expect both parameters to be more similar for two sites that lie within the same area than for two sites that are located in two different areas, because we would expect the habitat to be more similar within the same area. And second, the additional information provided by two-scale sampling may allow us to fit more complex models. In the temporal case, we may adopt a model that allows for temporary emigration (the complement of availability), a common form of violation of the closure assumption. Adoption of such a model naturally accommodates the increased similarity of subunits within the same unit.

Multiple scales in models for abundance have received even less attention so far than multiple scales in occupancy models. Chandler et al. (2011) have developed a three-level abundance model for estimation of temporary emigration based on a multinomial mixture model. This model can be fit in `unmarked` using function `gmultmix` (see Section 7.5.3). The same model structure has been extended to multinomial mixture models for distance sampling protocols (function `gdistsamp`; see Section 9.5.3) and for binomial mixture models for repeated counts with function `gpcount`. All three functions may be useful for temporal subsampling by adopting a simple model of random temporary emigration that assumes a superpopulation of size M_i that is available during some larger time period at site i . At any given point in time j , only a fraction ϕ_{ij} is available, leading to a population size of N_{ij} . This is then repeatedly sampled with detection probability p_{ijk} during a short period of closure. When $\phi_{ij} = 1$, there is no temporary emigration and we are back to the two-level model for a fully closed (meta)population. For more information on these models, see Chandler et al. (2011), the help text for functions `gpcount`, `gmultmix` and `gdistsamp` and Sections 7.5.3 and 9.5.3. These models would be easy to fit in BUGS. Hence, for the temporal case of subsampling, the adoption of a structurally fully different model, with an additional layer in the HM representing a somewhat meaningful biological process (temporary emigration), is fairly straightforward. Johnson et al. (2014) used the observed maximum distances at each of a series of point counts to model

spatial variability in availability probability separately from ‘real’ detection probability (or ‘perceptibility’; Marsh and Sinclair, 1989).

In contrast, for the spatial case of subsampling a more phenomenological approach inspired by nested ANOVA, with random unit effects, may appear more straightforward. Imagine point count stations (subunits) nested in each of a number of reserves or national parks, or other spatial “blocks” or “units.” To account for the dependency among points within the same park and avoid “pseudoreplication” (Hurlbert, 1984) you can simply specify normal random effects for the “units” (i.e., reserve, park) in the linear predictors for abundance or detection (see Section 10.10). Adding such additional random effects into the N -mixture model cannot be done in `unmarked`, but it is trivially easy in `BUGS` and works fully analogous to the random effects in 6.11.2. For example, imagine that the MHB sample quadrats in Switzerland had been selected in one of 10 distinct regions of the country and we wanted to accommodate in our analysis this nested (or blocking) structure of the sample quadrats. We could then simply have provided a covariate `region`, which for each site codes for the region the site belongs to, and modified the linear model for abundance to include a region random effect `eps.region`.

```
loglam[i] <- beta0 + inprod(beta[], lamDM[i,]) + eps.lam[i] * hlam.on +
  eps.region[region[i]]
```

In the priors we would then add the following lines:

```
for(r in 1:10){
  eps.region[r] ~ dnorm(0, tau.region)
}
tau.region <- pow(sd.region, -2)
sd.region ~ dunif(0, U)
```

with the upper bound (U) of the uniform prior for the heterogeneity among regions chosen to be suitably large.

People have often wondered whether small-scale spatial replicate counts in each of a set of larger sites could provide information about detection probability, similar to the space-for-time substitution in the related occupancy model (see Section 10.11). We don’t think that one could directly treat small-scale replicates akin to the usual temporal replicates in the traditional N -mixture model. However, it seems likely that we could separately estimate abundance and detection in a model that specifies spatial correlation in abundance (provided there is some at the scale of the study). This would seem like a similar problem to that of estimating abundance and detection over multiple years, without replicate counts within years, in the model of Dail and Madsen (2011): in their case, temporal correlation in abundance is accommodated in the Markovian dynamics model and allows both abundance and detection to be estimated even with a single count per site and year. One way of parameterizing spatial correlation is by explicitly modeling the movement process as in the latent spatial point process models of Chandler and Royle (2013) and Ramsey et al. (2015).

6.15 SUMMARY AND OUTLOOK

We have covered the binomial N -mixture model of Royle (2004b) for closed populations. This is simply a Poisson or related model for abundance, but with a binomial measurement error model attached. It can be fit to counts of individuals that are replicated in space and in time, where the time

span is short so that the abundance at each site can be assumed constant. This is our canonical HM for inference about abundance from replicated counts. If all goes well—i.e., if the model assumptions are not violated too strongly—the binomial mixture model permits unbiased inferences about that central quantity in ecology and its applications: abundance. This sets this HM apart from a host of other HMs for abundance that only model some index of abundance or “relative abundance” (ver Hoef and Frost, 2003; ver Hoef and Jansen, 2007; Cressie et al., 2009; Zuur et al., 2012). In its most basic form, the model is a mixture between a Poisson distribution for abundance and a conditional binomial distribution for false-negative measurement error.

As always with HMs, we can readily switch one model component for another if this is dictated by the data or the goals of our analysis. For instance, to model excess variability in the latent abundance relative to a Poisson, we may change the Poisson for a negative-binomial (NB), zero-inflated Poisson (ZIP) (Wenger and Freeman, 2008), or a Poisson-lognormal (PLN) (Kéry et al., 2009) distribution and we have given examples for all of these. We have even shown an example of where some sites have little and others have substantial OD (Section 6.11.2.2). In that model, we expressed the site-specific extra-Poisson variance in lambda as a linear function of a covariate (elevation). Other possibilities for the abundance part of the model include a hurdle model (see Section 3.3.4; Ghosh et al., 2012; Dorazio et al., 2013), which unlike a ZIP permits only one type of zero abundance, that coming from the zero-inflation part, a Conway–Maxwell–Poisson distribution (Wu et al., 2013), which unlike NB and PLN allows both over- and underdispersion, or a Dirichlet process prior for abundance (Dorazio et al., 2008); the latter being a form of Bayesian nonparametrics for the abundance part of the model (Chapter 23 in Gelman et al., 2014).

Similarly, depending on the data collection protocol, you may choose any of a number of descriptions for the measurement error process. We have given examples with a binomial distribution (resulting in the classical binomial N -mixture model), a Bernoulli distribution (resulting in the RN model), and a Poisson distribution, which represents a measurement error model that combines false-negative and false-positive errors. In addition, individuals may not be detected independently, for instance, because they occur in groups or when there is temporal autocorrelation in individual detection probability in counts along a transect. You may then look up an N -mixture model with beta-binomial observation model (Martin et al., 2011; Dorazio et al., 2013) or else move to Markov-modulated point process models in the case of serial correlation (Guillera-Arroita et al., 2012). Finally, there is a host of protocols for the measurement of abundance that all lead to a multinomial distribution for the observation process. They include hierarchical capture–recapture and hierarchical distance sampling and are covered in great detail over the next three chapters.

The combination of two or more statistical distributions in the form of a mixture model determines the basic structure of our HM, and at each level of the model hierarchy we can recognize a sort of GLM (Chapter 3). This makes it clear that in principal we can apply all the usual GLM extensions to both the abundance and the detection parts of the model, such as inclusion of covariates, including the “wiggly” form of a GAM (see Section 10.14), or the addition of random effects to account for additional variability or hidden correlation structures, including spatial or temporal autocorrelation (Chapters 21 and 22).

We like to emphasize the modularity of these HMs. For instance, if you drop the measurement error part in an N -mixture model, then you are back to a traditional “flat” or (if your N -mixture model contains extra random effects) back to a conventional hierarchical Poisson or related GLM. Such

variants of Poisson and related GLMs form the backbone of inference methods about unbounded count data in the vast majority of examples in ecology (e.g., Chapter 6 in McCullagh and Nelder, 1989; ver Hoef and Frost, 2003; ver Hoef and Jansen, 2007; Cressie et al., 2009; Zuur et al., 2012; and also see Chapter 12 in volume 2). Often you may lack the necessary replicate measurements or other forms of extra information such as distance measurements, that permit the joint modeling of abundance and measurement error process. Or perhaps you do not like our emphasis on an explicit description of the measurement error process underlying your count data? Perhaps you find the resulting models too difficult to understand or you are worried about their robustness... or you work in the tropics where some have recently claimed that things are all different anyway and that such models are too hard to apply (Banks-Leite et al., 2014). But even then you can still use all of our models for abundance by simply dropping the measurement error part—i.e., by eliminating the observation model. Of course, you ought to be honest then and qualify your analysis as dealing with an *index* of abundance or with “*relative abundance*” (Johnson, 2008) Any direct statement about *abundance* is then out of reach for you. Speaking about *abundance*, when in reality your inference is about the unknown product of abundance and measurement error (i.e., on relative abundance), would be dishonest and is scientifically indefensible.

Two further topics that we have emphasized in this chapter are the power of simulation, as we do throughout the book, and the sensitivity of model inferences to distributional assumptions, especially about the latent abundance state. First, we have given several examples that show how simulation can give you extremely rich insights into the model, indeed, we set out to explain the model by simulation code in the R language. Further, we used simulation to study the effects of assumption violations and for study design. We hope that the code we provide will serve as a template for your own investigations for your specific needs.

Second, in practical applications of the *N*-mixture model there is the frequent dilemma that a standard Poisson model does not formally fit our data according to an omnibus test such as Chi-square, but the NB does, or at least fits substantially better, and moreover is much better supported by AIC, but then predicts unrealistically high levels of abundance. This is not a new observation (Kéry et al., 2005b; ver Hoef and Boveng, 2007; Joseph et al., 2009). Looking at residual diagnostics and empirical variance/mean relationships, we found that the NB was not adequate for our great tit data, although both GoF and the AIC model selection criterion selected it way ahead of the other two mixture distributions available in `unmarked` (Poisson, ZIP). In situations where the NB predicts very high abundance or (if you do not have any *a priori* knowledge about likely abundance levels) if the NB predicts substantially higher than the Poisson or ZIP, we would tentatively prefer to use one of the latter with a somewhat *ad hoc* correction for OD, provided that the lack of fit subsumed into such “overdispersion” is not extreme. Since use of the NB virtually always results in predicted abundance at least as high as that under the standard Poisson model, you will therefore err on the side of caution. We gave examples of how to propagate this added uncertainty into predictions of abundance and functions thereof, such as national population size estimates. Part of this material is tentative; it makes sense to us, but is not based on formal theory, nor has it been rigorously tested. Therefore, we repeat our call for more research on model diagnostics, GoF, and robustification in HMs such as the *N*-mixture model.

We have also covered the frequently forgotten fact that we almost never know the exact size and configuration of our study areas. There may be unsurveyed “holes” inside our nominal study area

where detection probability for an individual is essentially zero, leading to negative coverage bias (effective sample area is smaller than nominal sample area). Conversely, we may erroneously add in our count individuals that have activity ranges on the edge of our nominal study area (the ‘sunflower effect’), leading to positive coverage bias. We presented a method where we use a covariate (the length of a transect route) to adjust for negative coverage bias, but thereby we almost certainly exacerbated the problem of positive coverage bias; i.e., we estimated the population size in an area that is *larger* (to an unknown extent) than the nominal sample area. We then presented another *ad hoc* method to account for this positive bias based on ideas that have been used in closed population estimation for a long time (Dice, 1938; Karanth and Nichols, 1998). Again, our procedure makes sense to us and seems to be a way forward, but we make no claims that it is optimal or that it will work in all circumstances. The spatial reference of counts is another area where more research is needed, perhaps along the lines of the seminal paper by Chandler and Royle (2013), in which they introduce a spatially explicit N -mixture model. Their current model is challenged by real-world sample sizes and moreover needs adjacent sample sites, but perhaps some sort of “integrated analysis” (where different types of data sets are combined in a model) or else spatial subsampling might be a way forward.

Two further areas where more research would be fruitful are in the modeling of false-positives and density-dependent detection. The Poisson/Poisson model (Section 6.13.2) allows for the combination of false-negative and false-positive error rates, because a member of N may be counted more than once (the detection model is Poisson, and moreover the rate ϕ may be greater than 1). However, this model has had mixed success in our attempts to fit it to real data. Perhaps it is possible to formulate false-positive abundance models similar to those for occupancy (Royle and Link, 2006; Miller et al., 2011; Sutherland et al., 2013)—i.e., with an observation process for a count C that separates out the two processes:

$$C = C^- + C^+,$$

where $C^- \sim \text{Binomial}(N, p)$ and $C^+ \sim \text{Poisson}(N\lambda)$.

Here, C^- is the usual false-negative detection error part of the observation process, while C^+ describes false-positives that are expressed as a rate relative to the true abundance N . We doubt whether such a model would be identifiable from the data to which the standard N -mixture model is fit, but perhaps with some extra information it might be: as in the occupancy model of Miller et al. (2011), it might be possible to identify subsets of the data that are devoid of one of the error types, and a combined analysis might then be able to estimate all parameters.

Density-dependent detection is quite likely on biological grounds: for instance, it makes sense to assume that birds sing—i.e., advertise and defend their territory—more when they live at higher densities (Warren et al., 2013) and this has been shown experimentally in the field (Penteriani, 2003). Although there seems to be some form of circularity involved, you can actually specify in BUGS a model where the latent abundance N_i at a site i , perhaps log-transformed, is treated as an explanatory variable in the linear predictor for detection. Surprisingly to us, when we experimented with such a model it seemed to be estimable with simulated data and the effect of ignoring density-dependent detection was always a negative bias in abundance. This makes sense when we realize that such abundance effects on detection will, when not modeled, cause unmodeled site-specific detection heterogeneity that will bias low the estimates of abundance (see Section 6.7). However, when we fit the model to the Swiss tits, we failed to obtain reasonable estimates. It would be interesting to follow up this line of research.

In the following three Chapters 7–9, we retain the basic structure of the model for abundance and simply vary the observation model to reflect a change in the data collection protocol—i.e., the manner in which we *measure* abundance. We will collect some extra information that enables us to specify a different model of the false-negative detection process. This extra information will be individual identity across occasions for capture–recapture designs (Chapter 7). (Note that we also require individual identity for the binomial N -mixture model, but only within any occasion, to rule out multiple counts of the same individual.) Capture-recapture designs do not help us with our problem of defining the effective sampling area. In contrast, for the powerful distance sampling protocol (Chapters 8–9) the extra information comes in the form of measured distances, and this manifestation of space enables us to define the effective sampling area unambiguously. In Chapter 10, you will encounter an analogous HM where the latent state is presence/absence instead of abundance (i.e., the site-occupancy model). Finally, in Chapter 11, we cover the community versions of both site-occupancy and N -mixture models. In Chapters 12–14 (in volume 2) we will generalize the closed-population N -mixture models to open populations by modeling the population dynamics at each site as a function of gains and losses (Dail and Madsen, 2011; Chandler and King, 2011; Zipkin et al., 2014a,b; Hostetler and Chandler, 2015; Sollmann et al., 2015; Bellier et al., in review) or with reduced-parameter versions of such explicit population dynamics models.

EXERCISES

1. Take a count data set of your choice (ideally real data) and use `unmarked` to fit some binomial N -mixture models.
2. Based on code given in 6.3, devise a simulation that investigates the relationship between detection probability (p), the number of sites (M), the number of replicate surveys (J) and the bias of the maximum count at a site i as an estimator of N_i . In other words, how many surveys are required, on average, for the maximum count to amount to at least 95% of N_i on average.
3. Based on 6.4, devise a simulation that investigates the relationship between M , J , p , and the likelihood of estimability issues in the N -mixture model. You can diagnose the latter by a sensitivity of the numerical MLEs to the choice of K (the upper summation limit in the likelihood evaluation in `unmarked`).
4. In the example at the end of [Section 6.4](#), imagine that the theoretical ecologist’s theory predicts that the meta-population goes extinct when the (spatial) variance in population size becomes greater than 3.84. What is the probability of extinction of that meta-population? (Use JAGS for this exercise.)
5. Play around with different settings of function `simNmix` to get a feel for how count data arise in the presence of imperfect detection. Perhaps it is a good idea to write your own R code to visualize and summarize the simulated data.
6. Repeat the simulation study ([Section 6.6](#)) in BUGS, using reasonably vague priors for the parameters, and compare the incidence of freak high estimates of lambda with that when using MLEs.
7. Along the lines of [Section 6.6](#), conduct a simulation study of your own that investigates some design question about the N -mixture model that might be relevant to your own work.

8. Conduct another simulation to investigate the effects of density-dependent detection probability on the estimators of the N -mixture model (similar to [Section 6.7](#)); see also Warren et al. (2013). Is there a difference between positive and negative density dependence in the direction of bias? Can you account for this in a model fit in BUGS? (If you can it might be worth a paper!)
9. In [Section 6.8](#), see whether you can detect diagnostic patterns in the residuals of the models for specific assumption violations. (Again, this might be the start of a useful paper.)
10. In the modeling of Swiss great tits, determine the best day of the season to go out and survey for the birds. Do this for different elevation classes.

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APPLIED HIERARCHICAL MODELING IN ECOLOGY

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Marc Kéry is a population ecologist with the Swiss Ornithological Institute. He is the author of about 80 peer-reviewed journal articles and two books on a wide range of topics, including the analysis of large-scale monitoring programs, demographic population analyses, experimental design for animal and plant surveys, and the population ecology of rare species.

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