

Marc Kéry
J. Andrew Royle



APPLIED HIERARCHICAL MODELING IN ECOLOGY

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

Volume 2
Dynamic and Advanced Models



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

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MODELING INTERACTIONS AMONG SPECIES

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8.1 INTRODUCTION

This chapter is about the modeling of interactions between two or more species in terms of observed patterns in occurrence or abundance. Interactions among species lie at the heart of ecology, because they may result from such important ecological mechanisms as competition, predation, parasitism, or mutualism, collectively termed *biotic interactions* (Dormann et al., 2018a). In a strict sense, only manipulative experiments or direct behavioral observations of individuals enable you to decide whether an observed statistical association can be ascribed to actual biotic interactions, environmental effects, or both mechanisms together. For instance, a negative spatial correlation in the occurrence or

abundance of two species may be due to an antagonistic interaction, such as competition, parasitism, or predation. Alternatively, it may simply be the result of different habitat preferences of the two species, i.e., habitat filtering. Or it may be the result of a combination of both mechanisms. This is perhaps the major caveat for most applications of the models in this chapter: that a correlation does not necessarily imply causation.

When we say “species interactions” in this chapter, we mean an association or non-independence in the parameters of multiple species in an occurrence or abundance model. That is, we use the term “interaction” in a purely descriptive, statistical, or correlative sense. We will cover multispecies models for abundance and occurrence, which have specific parameters to account for the possible non-independence between pairs of species. In addition, these models will enable us, to different degrees, to test hypotheses about possible biological mechanisms underlying such non-independence among multiple species. Some of these models have a distinctly mechanistic feel, but even they will not enable you to make strong inferences about actual interactions between individuals of multiple species, unless you have the right kind of data (experimental or behavioral observations).

However, the models in this chapter can be powerful pattern discovery tools: they may *point* to some species pairs as candidates for direct biotic interactions. Discovery of strong positive or negative associations in abundance or occurrence (or possibly in another parameter) may then be followed up with more focused investigations about possible mechanistic underpinnings of such patterns. In addition, if we fit these models to data collected in the context of a manipulative experiment designed to isolate some biological mechanism, *then* they will enable us to make strong inferences about the effects of these mechanisms. And as always, if our models show a positive or negative association which was predicted based on *a priori* knowledge about possible biotic interactions between these species, then this provides stronger inference about the existence of these biotic interactions than the mere description of a pattern that was not hypothesized *a priori* (Platt, 1964; Burnham and Andersen, 2002; Nichols and Williams, 2006).

In Chapters 11 (in AHM1) and 3 and 5 in this volume, we have already encountered models for multiple species for occupancy and for survival. These models did not account for species interactions, in the sense that the prior distribution of the latent state variables assumed that all latent states were independent of one another. But it is nonetheless possible to observe associations among species in some of their parameters. For instance, in a community occupancy model, we will quite certainly observe positive or negative associations in the presence and absence of certain species pairs. We could investigate non-independence in the occurrence of species pairs based on the estimated presence/absence matrix. But none of the models in these chapters contained any *parameters* to measure the magnitude of an association. In contrast, the models in this chapter do contain such parameters; hence, we can formally test for associations, estimate their strength, and possibly model the statistical interaction strength by covariates, to test hypotheses about factors that may affect the species interactions. Thus, the models in this chapter are direct extensions of the static community models for occurrence and abundance in Chapter 11 in AHM1 and the dynamic community models in Chapter 5 in this volume. The extension is represented by the formal accommodation of non-independence of occurrence or abundance among different species by one or more parameter(s).

In this chapter, we focus on models of interactions for abundance and occurrence, which account for the effects of imperfect detection and allow inclusion of covariates. Both features are important in the investigation of possible causes of observed patterns in abundance and occurrence: differential detection probability of species by habitat, or depending on the presence or absence of another species, may lead to the spurious identification of species associations when detection probability is not

accounted for in an interaction model (Bailey et al., 2009; Yackulic et al., 2014). And when testing for potential biotic interactions in an observational study, we always need to be able to rule out, in a statistical sense, the null hypothesis of habitat filtering: that an observed association can be explained by environmental variation alone, i.e., without having to invoke biotic interactions. Hence the requirement for interaction models to be able to accommodate environmental covariates so that an observed species association can be “adjusted” for habitat differences. In addition, the magnitude or even the sign of an interaction between two species may change along spatial or temporal gradients (LaManna et al., 2015, Rota et al., 2016a,b, Tikhonov et al., 2017, Fidino et al., 2019). In some models, we may modulate the interaction strength as a function of environmental covariates.

We organize this chapter by the following dichotomies:

- occurrence versus abundance
- few species versus many species
- static versus dynamic (or open) models
- symmetric versus directed (asymmetric) interactions (Fig. 8.1)

Multispecies models of occurrence or abundance with interactions have been developed coming from three directions: (1) occupancy modeling (MacKenzie et al., 2002, 2004, 2006) on the one hand, and (2) what we may perhaps call (for want of a better term) mainstream community modeling on the other (e.g., Ovaskainen et al., 2010b; Clark et al., 2014; Pollock et al., 2014; Hui et al., 2015; Warton et al., 2015; Clark et al., 2017), with (3) the community occupancy (or D & R) models of Dorazio and Royle (2005) and Gelfand et al. (2005, 2006) as an important conceptual intermediate (see Chapter 11 in AHM1). The typical occupancy interaction models are for few species, but they accommodate interactions and imperfect detection, while the typical “mainstream community models” ignore imperfect detection, but do accommodate interactions, and many of them can be fit to more than just a handful of species. Finally, the conventional D & R community occupancy models work well for “many” species and they do correct for imperfect detection, but they do not accommodate non-independence of species occurrence, beyond what is induced by shared habitat and captured by the covariates in the model. Recently, Tobler et al. (2019) have unified developmental branches 2 (“mainstream”) and 3 (“D & R”) and developed multispecies occupancy models with species correlations that can deal with “many” species. In this chapter, we cover models in branch 1 (“classical occupancy”) and 3 (“D & R”), but make frequent reference to important developments in branch 2 (“mainstream”).



FIGURE 8.1

Schematic of symmetric (left) and asymmetric, or directional, interactions (right) between two species A and B. In models with symmetric interactions, we describe the non-independence of occurrence or abundance (here denoted z) between two species using a parameter θ that affects both species in a similar way, often by a correlation coefficient. In contrast, in models with directional interactions, occurrence or abundance of a dominant species (A) is assumed to affect the occurrence or abundance of a subordinate species (B), but not vice versa. That is, in a directional interaction, z^A is independent of z^B , but z^B is dependent on z^A . In models with directional dependence, we use the abundance or occurrence of one species as a predictor for abundance or occurrence of another.

Most models with interactions developed so far (and which accommodate observation error) are for occurrence rather than abundance. For occupancy, the concept of a statistical interaction, as opposed to independent occurrence, is particularly easy to understand. For instance, for two species A and B with marginal occupancy probabilities of ψ^A and ψ^B , the statistical definition of independence implies a probability of $\psi^A\psi^B$ for sites occupied by both species. Hence, if for instance $\psi^A = 0.6$ and $\psi^B = 0.2$, then we expect a probability of 0.12 for a site to hold both species. If in a large sample of surveyed sites both species co-occur at 20% of the sites, then this would suggest a positive association, while 5% of sites with co-occurrence would suggest a negative association between these two species. And in either case we could start wondering whether these patterns could be explained by biotic interactions, by habitat filtering, or by both mechanisms.

The first multispecies model with interaction and imperfect detection was the model of MacKenzie et al. (2004), which conceptualized species co-occurrence as a multi-state occupancy model (Chapter 6), where sites are classified by the presence or absence of each species. Hence, for $S = 2$ species, we have $2^S = 4$ different states: 11, 10, 01, and 00. Here, the first digit indicates presence or absence of the first species, and the second digit presence/absence of the second species. In this model, there is no notion of directionality in the interactions between pairs of species; so, this is a model of symmetric interactions. Non-independence in the occurrence of two species can be tested by comparison of the proportion of sites occupied by both species (ψ^{AB}) and the marginal proportions of occurrence for each species individually (i.e., ignoring presence or absence of the other species), ψ^A and ψ^B . MacKenzie et al. (2004) use this reasoning to define a “species interaction factor” $SIF = \psi^{AB}/\psi^A\psi^B$. Under independent occurrence of species A and B $SIF \approx 1$. In contrast, when $SIF > 1$ and $SIF < 1$, these species occur, respectively, more or less frequently together than expected by chance.

The model of MacKenzie et al. (2004) was a major conceptual advance, but owing to constraints for sets of probabilities from multiple species, adding in covariates makes it numerically unstable (MacKenzie et al., 2004, 2006, 2018; Richmond et al., 2010; Waddle et al., 2010). Hence, the model is of limited use in practice, because in most models for interactions, we would want to add environmental and possibly other covariates, too.

However, this model has spawned several waves of new developments, which can all be seen as reparameterizations of the basic multi-state model from 2004 (Darryl MacKenzie, pers. comm.). The first wave was the conditional occupancy models of Richmond et al. (2010) and Waddle et al. (2010), which assumed *asymmetric* interactions, where one or more species is assumed to occur independently, but occurrence and possibly detection of some other species is affected by the presence or absence of another occurring species. Thus, these authors expressed the occurrence of one species *conditional* upon the presence of another. In this model, adding covariates for the occupancy probability of each species is straightforward and no longer leads to numerical instability. The first models published in 2010 were static, but they were extended to the dynamic case at about the same time by Jim Hines in his powerful PRESENCE software, although dynamic, conditional multispecies occupancy models seem to have been formally described only later, first by Cayuela et al. (2013), and subsequently also by Jones and Kroll (2016), Michel et al. (2016) and Gallo et al. (2019).

The second wave was the multivariate Bernoulli model of Rota et al. (2016a), which also makes covariate modeling more straightforward, but which is basically a model for symmetric interactions. Rota et al. (2016a) implement their model in Stan, but a maximum likelihood implementation has since been incorporated in MARK and, thanks to Ken Kellner, unmarked. Fidino et al. (2019) developed a reparameterization of that model in terms of a Categorical distribution, extended the model to dynamics, and gave an implementation in JAGS. Other interesting applications or further

developments of dynamic occupancy models with interactions include Miller et al. (2012), Péron et al. (2016), Green et al. (2018) and Hepler and Erhardt (2020). We also refer you to Chapter 14 in MacKenzie et al. (2018) for a recent review and synthesis of occupancy models with interactions.

Another line of development has dealt with the modeling of interactions in static communities comprising “many” species (e.g., 20 or more) and is represented by two variants of an occupancy models in Tobler et al. (2019), which both account for imperfect detection, and by a completely separate line of development of multispecies or joint species distribution models (JSDMs), including Latimer et al. (2009), Ovaskainen et al. (2010b), Clark et al. (2014), Pollock et al. (2014), Hui et al. (2015), Letten et al. (2015), Warton et al. (2015), Ovaskainen et al. (2016a, 2017), Clark et al. (2017), and Tikhonov et al. (2017). With the exception of the models by Tobler et al., all these occupancy-type of models have so far ignored imperfect detection and none of them has yet been extended to the dynamic, or open, case as in the models in Chapter 5 (but see Thorsen et al., 2016).

In contrast to the relatively active development of occupancy models with interactions, the development of abundance models with interactions, which incorporate imperfect detection, has lagged behind. Published studies include Dorazio et al. (2015), Clare et al. (2016), Roth et al. (2016), and Brodie et al. (2018); see also Johnson and Sinclair (2017) for an interesting, albeit *p*-ignorant multispecies abundance model. It would be interesting to develop and apply more abundance models with interactions, since counts carry more information about associations among species than do binary presence/absence data. Hence, abundance models will probably have more power to detect dependencies among species.

In this chapter, we first focus on occupancy models and start with models for few species and assuming symmetric interactions ([Section 8.2](#)). We do not cover the first such model by MacKenzie et al. (2004) because of the practical problems mentioned above, but instead present the multi-state parameterization by Rota et al. (2016a), which can be fit in unmarked, and we also show an implementation in JAGS. Then, in [Section 8.3](#) we cover the model of Waddle/Richmond in which we must define a dominance hierarchy among a handful of species. In this model, we estimate the “effects” (always in the statistical sense of a correlation) of a dominant species on one or more subordinate species by simply using the estimated presence or absence, or abundance (Clare et al., 2016; Roth et al., 2016), of the dominant species in the model for the subordinate species. The assumption of unidirectional interactions and the practical restriction of this type of model to a mere handful of species may somewhat limit its scope. Nevertheless, it offers a very simple and yet very powerful framework for investigating in more depth patterns that may be caused by such dominance relationships among species. We first cover static versions of this model ([Section 8.3.1](#)) and then the same modeling principle of pairwise interactions within a dynamic occupancy model ([Section 8.3.2](#)). In [Section 8.4](#), we cover the latent-variable multispecies occupancy model of Tobler et al. (2019). This is a model for symmetric interactions among “many” species, which in practice usually means up to a couple dozen. Such models can quickly become very parameter-rich and, for data sets with, say, more than 100 species, may be impossible to fit with JAGS.

Finally, in [Section 8.5](#) we cover some abundance versions of these models. So far, very few multispecies abundance models have been developed that accommodate imperfect detection. This is somewhat surprising, since you will see that they can be built in a fairly straightforward fashion by using a multivariate Normal (MVN) distribution to describe correlations in a model assuming symmetric interactions. In addition, we illustrate multispecies abundance models with the Waddle/Richmond-type of directional interaction and the latent-variable approximation to an MVN as in the model of Tobler et al. (2019). We illustrate all three interaction models for abundance in the context of a multispecies Binomial N-mixture model.

8.2 JOINT OCCUPANCY MODELS FOR FEW SPECIES WITH SYMMETRIC INTERACTIONS

A common approach in statistics to model correlations among parameters is the use of a MVN distribution for sets of parameters which are treated as random effects (Cam et al., 2002; Link and Barker, 2005). For instance, Section 7.6.2 in Kéry and Schaub (2012) and Schaub et al. (2013) show the use of MVN “annual residuals” to capture a temporal correlation in apparent survival among “groups” (e.g., first-year and older individuals) in the context of a CJS model fit in JAGS. Now, it might appear straightforward to model pairwise correlations among species in a static, multispecies occupancy model in an analogous way, but this would be wrong; you would get “estimates” for the correlations, but these will be determined by the priors only. That is, the parameters of the MVN are not identifiable in a standard, multispecies occupancy model as covered in Chapter 11 in AHM1. The reason for this is that in a Bernoulli model for unreplicated binary data, we cannot estimate any kind of overdispersion, and adoption of an MVN for residuals would be exactly that: trying to estimate additional dispersion parameters (Mick McCarthy, pers. comm.). At the level of presence/absence of a species at a site, a static occupancy model is binary, and hence, no random-effects modeling is possible at the level of the actual site.

For static occupancy of multiple species, but ignoring detection, Pollock et al. (2014) developed a symmetric interaction model based on a probit link for occupancy, which they implemented using the auxiliary variable approach of Chib and Greenberg (1998). Their model then became the basis for one of the two models developed by Tobler et al. (2019) which also accommodate imperfect detection. In practice, it seems that multivariate probit models work best when you have not more than, say, 10 species. We don’t cover these models here, but you can look up BUGS code for the *p*-ignorant and the *p*-savvy variant of the model in Pollock et al. (2014) and Tobler et al. (2019), respectively.

Instead, we cover the model of Rota et al. (2016a) as a powerful framework for modeling correlated occupancy for a smallish number of species, while accounting for imperfect detection. This model has been incorporated into `unmarked` recently, and we give an example using the new `occuMulti` function in [Section 8.2.2](#). There is no hard limit on the number of species that could be analyzed with this model, but it seems that with maximum likelihood, as in the `unmarked` implementation, attempts at fitting the model and obtaining SEs usually fail when there are more than 10 or so species (Chris Rota, pers. comm.), and the same may happen if we attempt to add more than a handful of covariates. In addition, it seems that fairly large data sets may be required, e.g., with 500–1000 sites or more in a static model (although in a dynamic model sample size may be built up over multiple years, Mason Fidino, pers. comm.). Rota et al. (2016a) fit their model in Stan, for which they also provide code, and Fidino et al. (2019) give JAGS code for a variant of that same model extended to dynamics. In such Bayesian implementations, the use of weakly informative priors may sometimes permit you to successfully model larger numbers of species or smaller numbers of sites. In [Section 8.2.3](#), we implement the model in JAGS.

8.2.1 THE STATIC MODEL WITH SYMMETRIC INTERACTIONS OF ROTA et al. (2016)

The model of Rota et al. (2016a) is a generalization of the single-species occupancy model of MacKenzie et al. (2002) and Tyre et al. (2003): where the latter use a univariate Bernoulli distribution for the partially latent presence/absence state of a site by a single species, Rota et al. use a multivariate Bernoulli (MVB) distribution for the partially latent state of a site in terms of the presence/absence of multiple species. To aid your understanding of the MVB model for the general case with S species, it is helpful to first consider the case where $S = 1$, i.e., the single-species model of MacKenzie et al. (2002)

and Tyre et al. (2003), but to describe the model in a way that emphasizes the connections with the model when $S > 1$. In this section, we closely follow the paper by Rota et al. (2016a).

In the classical, single-species model, we make the following assumption about presence or absence z at a particular site:

$$z \sim \text{Bernoulli}(\psi)$$

The parameter ψ is the probability that a site is occupied. For covariate modeling, we typically use a logit link and hence model a covariate X at the scale of the log odds of the occupancy probability ψ :

$$\log\left(\frac{\psi}{1-\psi}\right) = \beta_0 + \beta_1 \times X$$

Dai et al. (2013) call the log odds of occupancy the “*natural parameter*” of the model and denote it f . We can then write $f = \log(\frac{\psi}{1-\psi}) = \log(\frac{\psi_1}{\psi_0})$, i.e., express the natural parameter as the log of the ratios of the probabilities that a site is occupied (ψ_1) and that it is not occupied (ψ_0).

To introduce the multispecies occupancy model of Rota et al. (2016a), we assume for clarity of exposition that we only have two species ($S = 2$). While in the $S = 1$ case, the possible states of a site are simply 1 (presence) and 0 (absence), in the $S = 2$ case, we have four possible states for each site: 11, 10, 01, and 00. In general, S species define 2^S possible states of a site. Rota et al. use the multivariate Bernoulli distribution to describe the state of a site in terms of the presence/absence of each species, e.g., $\{0, 1, 0, 0\}$ denotes a site in state 10 (only the first species is present), while $\{0, 0, 0, 1\}$ denotes a site where both species are absent. Hence, to describe the realized state of a particular site in terms of an underlying stochastic process we write

$$\mathbf{Z} \sim \text{MVB}(\psi_{11}, \psi_{10}, \psi_{01}, \psi_{00}),$$

where \mathbf{Z} is the state vector of length 4 which has a single 1, and $\{\psi_{11}, \psi_{10}, \psi_{01}, \psi_{00}\}$ are the four probabilities corresponding to the four possible states of the site: 11, 10, 01, and 00. Since these probabilities must sum to one, not all of them are parameters that must be estimated when fitting the model. Rather, we can express one of the four as one minus the sum of the other three. This is exactly analogous to the $S = 1$ case, where we can express ψ_0 as $1 - \psi_1$ and only estimate ψ_1 .

With $S = 2$, there are three natural parameters f rather than just the single one for $S = 1$, when we want to use covariates to model structure in the probability parameters of the MVB distribution:

$$f_1 = \log(\psi_{10} / \psi_{00})$$

$$f_2 = \log(\psi_{01} / \psi_{00})$$

$$f_{12} = \log\left(\frac{\psi_{11}\psi_{00}}{\psi_{10}\psi_{01}}\right)$$

These are, respectively, the log odds of the probabilities that only the first species occurs, that only the second species occurs, and that both species occur together. In general, S species need $2^S - 1$ such natural parameters: there are S main effects, $S(S-1)/2$ two-way interactions, and the remainder are higher-order interactions.

The description of the model in terms of the natural parameters may not be easy to grasp, and the following analogy may be helpful. You can think of the linear-model structure of this model as being analogous to that of an S -way analysis of variance (ANOVA). Think of each species A, B, C, ... as being akin to a factor with two levels (presence, absence) and then, as in an ANOVA, we can expand a

linear model in a factorial fashion and express the expected response as the sum of main effects (A, B, C,...), second-order interactions (A:B, A:C,...), third-order interactions (A:B:C,...), and so forth. There are also strong analogies of the Rota et al. model to log-linear modeling of contingency tables, which involves specification of main effects (or table margins) and increasingly higher-order interactions, which represent the non-independence or effects of different combinations of the table margins (Darryl MacKenzie, pers. comm.).

One peculiarity of the occupancy model of Rota, which we don't usually have in the linear model for an ANOVA, is that we model through covariates not only the natural parameters which stand for the main effects, but also the interaction terms. As in the $S = 1$ case, we can model a natural parameter as a linear or possibly more complex function of some covariates, e.g.,

$$f_1 = \log(\psi_{10} / \psi_{00}) = \mathbf{X}'_\alpha \boldsymbol{\alpha}$$

$$f_2 = \log(\psi_{01} / \psi_{00}) = \mathbf{X}'_\beta \boldsymbol{\beta}$$

$$f_{12} = \log\left(\frac{\psi_{11}\psi_{00}}{\psi_{10}\psi_{01}}\right) = \mathbf{X}'_\gamma \boldsymbol{\gamma},$$

where \mathbf{X}_α , \mathbf{X}_β , and \mathbf{X}_γ are vectors of covariates (which may be identical or not and may or may not have the same dimensions) and $\boldsymbol{\alpha}$, $\boldsymbol{\beta}$, and $\boldsymbol{\gamma}$ are vectors containing an intercept and slope parameters. Hence, f_1 describes the conditional occupancy probability of species 1 when the other species is absent, f_2 describes the conditional occupancy probability of species 2 when species 1 is absent, and f_{12} describes the pairwise non-independence in the occurrence probability of the two species. Thus, when $f_{12} = 0$, the two species occur independently of one another.

We use the multinomial logit link to reconstitute the four probabilities in the state probability vector of the MVB distribution, $\{\psi_{11}, \psi_{10}, \psi_{01}, \psi_{00}\}$, from the three natural functions f in the model for $S = 2$.

$$\begin{aligned}\psi_{11} &= \frac{\exp(f_1 + f_2 + f_{12})}{1 + \exp(f_1) + \exp(f_2) + \exp(f_1 + f_2 + f_{12})} \\ \psi_{10} &= \frac{\exp(f_1)}{1 + \exp(f_1) + \exp(f_2) + \exp(f_1 + f_2 + f_{12})} \\ \psi_{01} &= \frac{\exp(f_2)}{1 + \exp(f_1) + \exp(f_2) + \exp(f_1 + f_2 + f_{12})} \\ \psi_{00} &= \frac{1}{1 + \exp(f_1) + \exp(f_2) + \exp(f_1 + f_2 + f_{12})}\end{aligned}$$

Other quantities of interest, such as the marginal probability of occurrence of species s or the conditional probability of occurrence of a species, given the presence or absence of another species, can be easily obtained using basic probability. For our example with $S = 2$, the marginal probability of occurrence of species 1, i.e., ignoring whether species 2 is present or not, is

$$P(z_1 = 1) = \psi_{11} + \psi_{10}.$$

Hence, we can add the two probabilities ψ_{11} and ψ_{10} because they refer to two mutually exclusive events: a site is either in state 11 or in state 10, but cannot be in both.

As another example, the conditional probability that species 1 is present, given that species 2 is present or absent, is

$$P(z_1 = 1|z_2) = \frac{\psi_{1z_2}}{\psi_{1z_2} + \psi_{0z_2}}.$$

This is simply an application of the definition of a conditional probability for two events A and B : $P(A|B) = P(A \cap B)/P(B)$.

Finally, you must understand that how covariate effects are expressed in this model is directly in terms of conditional occupancy probabilities. Hence, assuming for illustration just a single covariate X for every natural parameter in the $S = 2$ case, we get

$$f_1 = \log(\psi_{10} / \psi_{00}) = \alpha_0 + \alpha_1 X,$$

$$f_2 = \log(\psi_{01} / \psi_{00}) = \beta_0 + \beta_1 X, \text{ and}$$

$$f_{12} = \log\left(\frac{\psi_{11}\psi_{00}}{\psi_{10}\psi_{01}}\right) = \gamma_0 + \gamma_1 X.$$

We can obtain the probabilities of all four states in the presence of covariates for the natural parameters using the above expression for the conditional occupancy probabilities. Rota et al. (2016a) show that after some algebraic rearrangement we get

$$P(z_1 = 1|z_2 = 0) = \frac{\psi_{10}}{\psi_{10} + \psi_{00}} = \text{logit}^{-1}(\alpha_0 + \alpha_1 X)$$

$$P(z_1 = 1|z_2 = 1) = \frac{\psi_{11}}{\psi_{11} + \psi_{01}} = \text{logit}^{-1}((\alpha_0 + \gamma_0) + (\alpha_1 + \gamma_1)X)$$

$$P(z_2 = 1|z_1 = 0) = \frac{\psi_{01}}{\psi_{01} + \psi_{00}} = \text{logit}^{-1}(\beta_0 + \beta_1 X)$$

$$P(z_2 = 1|z_1 = 1) = \frac{\psi_{11}}{\psi_{11} + \psi_{10}} = \text{logit}^{-1}((\beta_0 + \gamma_0) + (\beta_1 + \gamma_1)X)$$

These relations are crucial for you to understand the model output when you add covariates. The interpretation of the slope parameters associated with the main effects natural parameters f_1 and f_2 is directly in terms of a change in the log odds ratio for a unit change in the value of covariate X . In contrast, the interpretation of the slope parameters associated with the single interaction effects natural parameter in the $S = 2$ case, f_{12} , is in terms of the *difference* in the log odds ratio of occupancy probability of one species from a unit change of X when the other species is present and absent. See the main paper as well as Appendix S1 of Rota et al. (2016a) for more on the interpretation and parametric structure of this model.

We think this is a powerful model, but it may not be easy to understand at first sight. Don't be surprised if you must read the model description several times until the penny drops and you feel comfortable fitting it to your data set and interpreting its output. Understanding of a model is often helped by actually fitting it and looking at the model output. Hence, it may still be useful for you to continue now even if you haven't fully understood the model at this stage. But later you may have to go back and re-read its technical description, as often as you need to fully understand the model.

8.2.2 IMPLEMENTATION OF THE ROTA ET AL. MODEL IN unmarked

Here we implement the model in unmarked, using the new `occuMulti` function, and gratefully acknowledge the R code provided by Ken Kellner (note that we wrote this section with R 3.6.2 and unmarked version > 0.13.1.). For illustration we use a variant of the mesocarnivore data set used by Rota et al. (2016a,b), which is incorporated in the `AHMbook` package under the name `MesoCarnivores`. It contains detection/nondetection data from 1,437 camera-trapping sites in six mid-Atlantic states in the United States for three medium-sized carnivore species: bobcat (`Lynx rufus`), coyote (`Canis latrans`), and red fox (`Vulpes vulpes`). We use this data set to illustrate the $S = 3$ case of the model with symmetric interactions. Detection data are pooled into weeks instead of days, so overall detection probabilities will differ from those reported in the paper. This greatly speeds up the model and, moreover, avoids having to deal with the exceptionally low daily detection probabilities that are typical for camera trap data.

```

# Load libraries and check out help texts of two main functions
library(AHMbook)
library(unmarked)
?occuMulti           # Check out help text for two main functions
?unmarkedFrameOccuMulti

# Read in data set and bundle up detection/nondetection data
data(MesoCarnivores)
?MesoCarnivores
str(data <- MesoCarnivores)
str(ylist <- list(bobcat = data$bobcat, coyote = data$coyote,
  redfox = data$redfox))

List of 3
 $ bobcat: int [1:1437, 1:3] 0 0 0 0 0 0 0 0 0 0 ...
 $ coyote: int [1:1437, 1:3] 0 0 0 0 0 0 0 0 0 0 ...
 $ redfox: int [1:1437, 1:3] 0 0 0 0 0 1 0 0 0 0 ...

# Get sample sizes
nsites <- 1437          # row dimension of above data
nssurveys <- 3           # column dimension ...
nspcpecies <- 3

```

We have six site covariates but use only three of them here, which are all related to the intensity of human land use: the proportion of disturbed land in the surrounding 5 km (`Dist`), housing density in the surrounding 5 km (`HDens`), and whether the camera trap was located on or off a trail (`Trail`).

```
# Prepare site covariates and look at them
Dist <- scale(data$sitecovs[, 'Dist_5km'])
HDens <- scale(data$sitecovs[, 'HDens_5km'])
table(Trail <- data$sitecovs[, 'Trail'])
head(sitecovs <- data.frame(Dist = Dist, HDens = HDens, Trail = Trail))
```

We don't have any real observational covariates, so for illustration we just invent one which we call date and fill with random numbers. You could think of it as survey date, which is a covariate that often has an effect on detection probability.

```

# Invent some random observation covariate data for illustration
date <- matrix(rnorm(n = nsites * nsurveys), ncol = nsurveys)

# Create obsCovs
str(obsCovs <- list(date = date))

# Build unmarked frame and summarize it
summary(umf <- unmarkedFrameOccuMulti(y = ylist, siteCovs = sitecovs,
  obsCovs = obsCovs))

```

```

unmarkedFrame Object

1437 sites
3 species: bobcat coyote redfox
Maximum number of observations per site: 3
Mean number of observations per site:
bobcat: 3 coyote: 3 redfox: 3
Sites with at least one detection:
bobcat: 196 coyote: 401 redfox: 161
Tabulation of y observations:
bobcat:
  0   1
4057 254
coyote:
  0   1
3685 626
redfox:
  0   1
4054 257

... [ rest of output truncated ] ....

```

This raw data summary suggests that coyotes are the most widespread species, with detections at $401/1437 = 28\%$ of sites, followed by bobcats (14%) and then foxes (11%).

Internally, when building the unmarked data frame, we generate a full factorial design, i.e., construct the model design in terms of *all* the natural parameters f . This is stored in slot `fDesign`, and it is very important for you to understand this structure of the model when you set up formulas for covariates. We look at the design matrix.

```

umf@fDesign
  f1[bobcat] f2[coyote] f3[redfox] f4[bobcat:coyote]
psi[111]      1       1       1       1
psi[110]      1       1       0       1
psi[101]      1       0       1       0
psi[100]      1       0       0       0
psi[011]      0       1       1       0
psi[010]      0       1       0       0
psi[001]      0       0       1       0
psi[000]      0       0       0       0
  f5[bobcat:redfox] f6[coyote:redfox] f7[bobcat:coyote:redfox]
psi[111]      1       1       1
psi[110]      0       0       0
psi[101]      1       0       0
psi[100]      0       0       0
psi[011]      0       1       0
psi[010]      0       0       0
psi[001]      0       0       0
psi[000]      0       0       0

```

Thus, we see how each possible state of a site can be described in terms of the three main effects, three second-order interactions and one third-order interaction. Be aware of the list of the names of the natural parameters and their order, because we need this to set up linear model formulas for them.

```

# View order of params, helpful for setting up formulas
colnames(umf@fDesign)
[1] "f1[bobcat]"           "f2[coyote]"
[3] "f3[redfox]"           "f4[bobcat:coyote]"
[5] "f5[bobcat:redfox]"    "f6[coyote:redfox]"
[7] "f7[bobcat:coyote:redfox]"

```

We illustrate the model by fitting five variants here:

- Model 1: a Null model which is represented by three independent occupancy models, one for each species, with intercepts-only formulas for both occupancy and detection
- Model 2: we add one covariate (proportion of disturbed land within 5 km; `Dist`) in the main effects of occupancy plus one covariate in detection (whether a camera is on or off a trail; `Trail`)
- Model 3: the simplest possible JSDM with intercepts for all natural parameters, including second-order interactions (though dropping the third-order interaction by fixing it at zero)
- Model 4: a more complex JSDM with the same covariates on the main effects as model 2, but now also allowing for the simplest possible structure of correlated occurrence, i.e., with intercepts for the natural parameters that represent interaction species effects (and hence, with the interaction structure of model 3)
- Model 5: mostly the same as model 3, but this time with a covariate also on the two-way interaction parameters (housing density within 5 km; `HDens`)

We note that models with interactions must obey the rules of marginality (McCullagh & Nelder 1989). That is, a model with two-way interactions between species must also contain the species main effects. Similarly, in a model with three-way interactions you should specify species main effects and their two-way interactions as well.

To fit a model in `unmarked`, we first define two objects containing the model formulas for occupancy and detection, and then we plug them into the call to `occuMulti`, along with the unmarked data frame. We start with model 1, which is equivalent to fitting three separate intercepts-only occupancy models to the three species.

```
# Specify models for occupancy in terms of natural parameters f
occ_formulael <- c(
  # bobcat, coyote, red fox occupancy, respectively
  # Modeled as constant
  ' ~ 1', ' ~ 1', ' ~ 1',
  # Two-way interactions are fixed at 0
  # bobcat:coyote, bobcat:redfox, coyote:redfox
  rep(0,3),
  # Fix 3-way interaction at 0
  0
)
# Constant detection by species
det_formulael <- rep(' ~ 1', 3)

# Fit model 1
(fml <- occuMulti(det_formulael, occ_formulael, umf))

Occupancy:
            Estimate      SE       z   P(>|z|)
[bobcat] (Intercept) -1.171 0.1328 -8.82 1.13e-18
[coyote] (Intercept) -0.629 0.0744 -8.46 2.79e-17
[redfox] (Intercept) -1.846 0.0944 -19.56 3.58e-85

Detection:
            Estimate      SE       z   P(>|z|)
[bobcat] (Intercept) -1.104 0.1396 -7.91 2.59e-15
[coyote] (Intercept) -0.333 0.0764 -4.36 1.30e-05
[redfox] (Intercept) -0.252 0.1182 -2.13 3.29e-02

AIC: 6710.658
```

This is just the simplest occupancy model $\psi(\cdot)p(\cdot)$ (where the dot denotes constant parameters) fit to all three species simultaneously, but independently. You should obtain exactly the same estimates when using `occu` for each species separately.

We continue with model 2, where we add covariates in occupancy and detection, but still keep the models for the three species independent. Hence, this model is still just a shortcut to what you would get when running function `occu` three times. As soon as you put some structure on the natural parameters in this model (i.e., add covariates), the model runs start to take longer. It is then useful to get some information about the fitting process. Hence, we ask for the current value of the negative log-likelihood to be printed out at every iteration of the algorithm.

```
# Specify models for occupancy in terms of natural parameters f
occ_formulae2 <- c(
  # bobcat, coyote, red fox occupancy, respectively
  # Modeled as a linear function of Dist
  rep(' ~ Dist', 3),
  # same: ' ~ Dist',' ~ Dist',' ~ Dist',
  # Two-way interactions are fixed at 0
  # bobcat:coyote, bobcat:redfox, coyote:redfox
  rep(0, 3),
  # Fix 3-way interaction also at 0
  0
)
# Detection by species
det_formulae2 <- rep(~as.factor(Trail)', 3)
# det_formulae2 <- rep(~as.factor(Trail) + date', 3)

# Fit model 2
(fm2 <- occuMulti(det_formulae2, occ_formulae2, umf,
  control = list(maxit = 500, trace = TRUE, REPORT = 1)))

Occupancy:
            Estimate      SE      z  P(>|z|)
[bobcat] (Intercept) -0.5542 0.1587 -3.4930 4.78e-04
[bobcat] Dist        -0.5224 0.1293 -4.0413 5.32e-05
[coyote] (Intercept)  0.1917 0.1058  1.8116 7.01e-02
[coyote] Dist        -0.0069 0.0845 -0.0817 9.35e-01
[redfox] (Intercept) -1.5358 0.1195 -12.8554 8.02e-38
[redfox] Dist        -0.2912 0.1123 -2.5926 9.53e-03

Detection:
            Estimate      SE      z  P(>|z|)
[bobcat] (Intercept) -2.58 0.1619 -15.91 5.54e-57
[bobcat] as.factor(Trail)1 1.89 0.1714 11.02 3.01e-28
[coyote] (Intercept) -1.96 0.0998 -19.65 5.63e-86
[coyote] as.factor(Trail)1 2.17 0.1227 17.68 5.52e-70
[redfox] (Intercept) -1.40 0.1836 -7.61 2.80e-14
[redfox] as.factor(Trail)1 1.63 0.2186  7.44 1.00e-13

AIC: 6257.525
```

We see some clear effects of humanity on the occupancy of all three species. In the detection models, it becomes clear that all three species are much more easily detected on than off trails, something found often in camera-trap studies for carnivores. (You could also try the fake date covariate in detection and would find that random noise does not explain a significant amount of variation in detection probability of these species.)

Model 3 is the simplest possible JSDM with correlated species occurrence. It has intercepts for all natural parameters except for f_{123} (the three-way interaction in occupancy), which we keep fixed at 0.

Hence, in this model we now allow for possible non-independence in the occurrence of the three species by adding parameters that represent the two-way (i.e., pairwise) interactions in occupancy. We estimate these interaction parameters as constants for now, i.e., do not model them with covariates.

```
# Specify models for occupancy in terms of natural parameters f
occ_formulae3 <- c(
  # bobcat, coyote, red fox occupancy, respectively
  # Modeled as constant
  rep(' ~ 1', 3),
  # same: ' ~ 1', ' ~ 1', ' ~ 1',
  # Two-way interactions are intercept-only
  # bobcat:coyote, bobcat:redfox, coyote:redfox
  rep('~1', 3),
  # same: '~1', '~1', '~1',
  # Still fix 3-way interaction at 0 (for an intercept model would write: '1')
  0
)
# Detection by species
det_formulae3 <- rep('~1', 3)

# Fit model 3
(fm3 <- occMulti(det_formulae3, occ_formulae3, umf,
  control = list(maxit = 500, trace = TRUE, REPORT = 1)))

Occupancy:
            Estimate      SE      z  P(>|z|)
[bobcat] (Intercept) -1.76 0.179 -9.81 1.03e-22
[coyote]  (Intercept) -1.30 0.137 -9.54 1.37e-21
[redfox]  (Intercept) -2.20 0.152 -14.44 2.81e-47
[bobcat:coyote] (Intercept) 1.72 0.262  6.56 5.48e-11
[bobcat:redfox] (Intercept) -1.38 0.377 -3.66 2.57e-04
[coyote:redfox] (Intercept)  1.41 0.248  5.69 1.31e-08

Detection:
            Estimate      SE      z  P(>|z|)
[bobcat] (Intercept) -1.106 0.1398 -7.91 2.59e-15
[coyote]  (Intercept) -0.331 0.0761 -4.35 1.38e-05
[redfox]  (Intercept) -0.253 0.1183 -2.13 3.28e-02

AIC: 6626.111
```

All two-way interactions in occupancy are significant, and we can confirm this conclusion by forming 95% CIs for the occupancy parameters. We see that 0 does not fall within the CIs of any of the occupancy parameters.

```
confint(fm3, type = 'state') # CIs for occupancy parameters
                                0.025      0.975
psi([bobcat] (Intercept))     -2.1100157 -1.4072536
psi([coyote] (Intercept))     -1.5717770 -1.0362043
psi([redfox] (Intercept))     -2.4983062 -1.9012367
psi([bobcat:coyote] (Intercept)) 1.2042902  2.2311451
psi([bobcat:redfox] (Intercept)) -2.1154563 -0.6387872
psi([coyote:redfox] (Intercept))  0.9254514  1.8992954
```

We continue with model 4, for which we take model 3 with the nonzero pairwise interactions in occupancy, and add back the two covariates from model 2, Dist in the main effect of occupancy and Trail in detection.

```

# Specify models for occupancy in terms of natural parameters f
occ_formulae4 <- c(
  # bobcat, coyote, red fox occupancy, respectively
  # Main species effect modeled with a covariate
  rep(' ~ Dist', 3),
  # Two-way interactions are still intercept-only
  # bobcat:coyote, bobcat:redfox, coyote:redfox
  rep('`~1', 3),
  # Still fix 3-way interaction at 0
  0
)
# Detection by species
det_formulae4 <- rep(~as.factor(Trail)', 3)

# Fit model 4
(fm4 <- occMulti(det_formulae4, occ_formulae4, umf,
  control = list(maxit = 500, trace = TRUE, REPORT = 1)))

Occupancy:
              Estimate      SE      z  P(>|z|)
[bobcat] (Intercept) -1.010 0.2393 -4.22 2.42e-05
[bobcat] Dist        -0.637 0.1438 -4.43 9.51e-06
[coyote] (Intercept) -0.529 0.1919 -2.75 5.89e-03
[coyote] Dist        0.160 0.0986  1.62 1.05e-01
[redfox] (Intercept) -1.762 0.2311 -7.62 2.47e-14
[redfox] Dist        -0.463 0.1271 -3.65 2.67e-04
[bobcat:coyote] (Intercept) 1.304 0.3223  4.05 5.20e-05
[bobcat:redfox] (Intercept) -1.881 0.3996 -4.71 2.52e-06
[coyote:redfox] (Intercept) 1.224 0.3179  3.85 1.18e-04

Detection:
              Estimate      SE      z  P(>|z|)
[bobcat] (Intercept) -2.59 0.162 -15.97 2.11e-57
[bobcat] as.factor(Trail) 1.89 0.171  11.08 1.60e-28
[coyote] (Intercept) -1.94 0.100 -19.31 4.48e-83
[coyote] as.factor(Trail) 1 2.15 0.123  17.43 4.63e-68
[redfox] (Intercept) -1.38 0.184  -7.50 6.46e-14
[redfox] as.factor(Trail) 1 1.61 0.219   7.34 2.10e-13

AIC: 6213.46

# Can look at 95% CIs
confint(fm4, type = 'state') # For occupancy
confint(fm4, type = 'det')   # For detection

```

Finally, in model 5, we take model 4 and add a covariate (HDens) in the three natural parameters that represent the pairwise interactions in occupancy.

```

# Specify models for occupancy in terms of natural parameters f
occ_formulae5 <- c(
  # bobcat, coyote, red fox occupancy, respectively
  # Main species effects all modeled with two covariates
  rep(' ~ Dist', 3),
  # Two-way interactions are a function of housing density
  # bobcat:coyote, bobcat:redfox, coyote:redfox
  rep('`~HDens', 3),
  # Still fix 3-way interaction at 0
  0
)

```

```

# Detection by species
det_formulae5 <- rep(~as.factor(Trail), 3)

# Fit model 5
(fm5 <- occuMulti(det_formulae5, occ_formulae5, umf,
control = list(maxit = 500, trace = TRUE, REPORT = 1)))

Occupancy:
            Estimate      SE      z P(>|z|)
[bobcat] (Intercept) -1.154 0.261 -4.42 9.81e-06
[bobcat] Dist        -0.648 0.146 -4.43 9.28e-06
[coyote] (Intercept) -0.569 0.207 -2.75 5.94e-03
[coyote] Dist         0.203 0.106  1.91 5.64e-02
[redfox] (Intercept) -1.844 0.246 -7.50 6.57e-14
[redfox] Dist        -0.335 0.128 -2.62 8.91e-03
[bobcat:coyote] (Intercept) 1.046 0.374  2.80 5.17e-03
[bobcat:coyote] HDens   -2.239 0.654 -3.43 6.14e-04
[bobcat:redfox] (Intercept) -1.545 0.427 -3.62 2.95e-04
[bobcat:redfox] HDens    1.284 0.432  2.98 2.93e-03
[coyote:redfox] (Intercept) 1.421 0.366  3.89 1.01e-04
[coyote:redfox] HDens    1.277 0.386  3.31 9.42e-04

Detection:
            Estimate      SE      z P(>|z|)
[bobcat] (Intercept) -2.54 0.1632 -15.57 1.22e-54
[bobcat] as.factor(Trail)1 1.83 0.1707  10.72 7.99e-27
[coyote] (Intercept) -2.00 0.0993 -20.13 4.41e-90
[coyote] as.factor(Trail)1 2.16 0.1211  17.86 2.47e-71
[redfox] (Intercept) -1.56 0.1621  -9.64 5.51e-22
[redfox] as.factor(Trail)1 1.82 0.2044   8.92 4.63e-19

```

AIC: 6123.852

We use AIC to rank the models. We find that the most complex model gets all the AIC weight.

```
modSel(f1 <- fitList(fm1, fm2, fm3, fm4, fm5))
```

	nPars	AIC	delta	AICwt	cumltvWt
fm5	18	6123.85	0.00	1.0e+00	1.00
fm4	15	6213.46	89.61	3.5e-20	1.00
fm2	15	6257.57	133.72	9.2e-30	1.00
fm3	9	6626.11	502.26	8.6e-110	1.00
fm1	6	6710.66	586.81	3.8e-128	1.00

So the most complex model offers the best description of the data (in an AIC sense). But it is difficult to understand what a complex model is telling us about the modeled system from just staring at the parameter estimates. Therefore, we form predictions to better understand what model 5 is telling us about the co-occurrence and the detection of the three mesocarnivore species.

We start by plotting the marginal occupancy of each species as a function of disturbance. The `predict` function for `occuMulti` has additional arguments, and here we use argument `species` to specify the species for which we want occupancy to be predicted. For these predictions, a parametric bootstrap is used to compute standard errors and 95% prediction intervals. We set the number of bootstrap replicates by argument `nsims`. For smooth CI bounds, you will want a large number, but you will see that this doesn't take very long.

```
# Create prediction covariate for Dist and form predictions
r <- range(data$sitecovs$Dist)
x <- seq(r[1], r[2], length.out = 100)
x_scaled <- (x - mean(data$sitecovs$Dist)) / sd(data$sitecovs$Dist)
nd <- data.frame(Dist = x_scaled, HDens = 0)
pred.bobcat <- predict(fm5, type = 'state', species = 'bobcat', newdata = nd,
  se.fit = TRUE, nsims = 10^5)
pred.coyote <- predict(fm5, type = 'state', species = 'coyote', newdata = nd,
  se.fit = TRUE, nsims = 10^5)
pred.redfox <- predict(fm5, type = 'state', species = 'redfox', newdata = nd,
  se.fit = TRUE, nsims = 10^5)
```

We plot the predictions of the response of each species to the proportion of disturbed land out to 5 km around each site (Fig. 8.2).

Next, we produce a plot of the predicted occupancy of one species conditional on combinations of presence and absence of the other two species. For this, the `predict` function in `unmarked` has yet an additional argument: `cond`. For instance, if we set `cond = 'redfox'`, then `predict` returns occupancy of the target species conditional on red fox presence. In contrast, if we set `cond = '-redfox'`, then `predict` returns occupancy of the target species conditional on red fox absence. We can also combine multiple species in a conditional argument. For instance, `cond = c('redfox', 'coyote')` yields the prediction of occupancy of the target species at a site where red fox are absent and coyotes are present. We illustrate with the bobcat and form predictions of occupancy conditional on all combinations of presence and absence of the other two species. Note that as always, we need to provide for `newdata` values for all covariates that are in the state or the detection models. We find that bobcat occupancy is highest at sites where coyotes are also present and lowest where red fox are present.

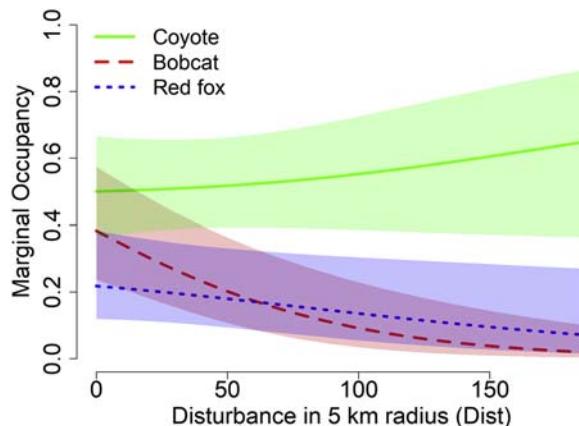


FIGURE 8.2

Predictions of marginal occupancy probability for each species, i.e., regardless of whether one of the other species is present or not. Thick lines show point predictions, and shaded area show the bounds of a 95% prediction interval obtained by a parametric bootstrap.

```
# Predict conditional occupancy and present in a table
nd <- data.frame(Dist = 0, HDens = 0)
bob_none <- predict(fm5, type = 'state', species = 'bobcat',
  cond = c('~-coyote', '-redfox'), newdata = nd, nsims = 10^5)
bob_coyote <- predict(fm5, type = 'state', species = 'bobcat',
  cond = c('coyote', '-redfox'), newdata = nd, nsims = 10^5)
bob_redfox <- predict(fm5, type = 'state', species = 'bobcat',
  cond = c('~-coyote', 'redfox'), newdata = nd, nsims = 10^5)
bob_both <- predict(fm5, type = 'state', species = 'bobcat',
  cond = c('coyote', 'redfox'), newdata = nd, nsims = 10^5)
round(occtab <- rbind('Neither' = bob_none, 'Coyote' = bob_coyote,
  'Red fox' = bob_redfox, 'Both' = bob_both), 3)
```

	Predicted	SE	lower	upper
Neither	0.240	0.047	0.159	0.345
Coyote	0.473	0.109	0.268	0.688
Red fox	0.063	0.033	0.025	0.152
Both	0.161	0.089	0.054	0.397

Finally, we form predictions that illustrate how an environmental covariate (housing density, HDens, in our case) affects the pairwise interactions among the modeled species. We first want to plot bobcat conditional occupancy as a function of HDens with and without the presence of coyote (Fig. 8.3). We see that with coyote presence there is a much higher bobcat occupancy at low housing densities, but when coyote are absent, we find the opposite pattern (as determined by a positive intercept and a negative coefficient of HDens for the natural parameter bobcat:coyote). It would be straightforward to produce a similar plot of conditional bobcat occupancy as a function of red fox presence and absence and HDens.

```
# Predict interaction parameter (Fig. 8.3, plotting code not shown)
r <- range(data$sitecovs$HDens)
x <- seq(r[1], r[2], length.out = 100)
x_scaled <- (x - mean(data$sitecovs$HDens)) / sd(data$sitecovs$HDens)
nd <- data.frame(Dist = 0, HDens = x_scaled)
pr_nocoyote <- predict(fm5, type = 'state', species = 'bobcat',
  cond = '~-coyote', newdata = nd, se.fit = TRUE, nsims = 10^6)
pr_coyote <- predict(fm5, type = 'state', species = 'bobcat',
  cond = 'coyote', newdata = nd, se.fit = TRUE, nsims = 10^6)
```

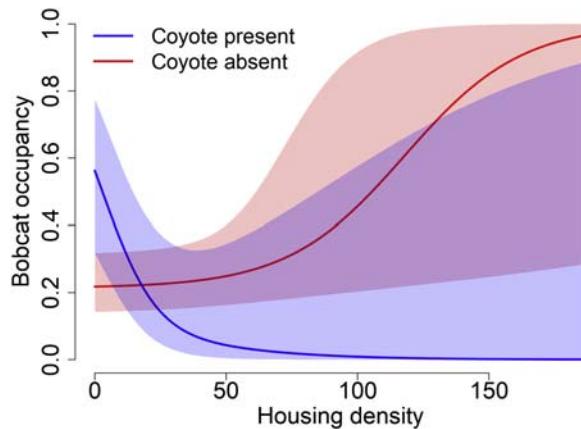


FIGURE 8.3

Predictions of conditional occupancy probability of the Bobcat as a function of a continuous covariate (Housing density, HDens), given presence/absence of Coyote and averaged over the presence/absence of the remaining species (Red fox).

As always, using a canned program like `unmarked` is convenient, but sometimes you may need a model that is different from the specific one implemented in such a package. In that case, JAGS may help. Therefore, we next illustrate a Bayesian implementation of the model in JAGS.

8.2.3 IMPLEMENTATION IN JAGS

Fidino et al. (2019) developed a dynamic version of the model of Rota et al. (2016a) and implemented it in JAGS (see also Hepler and Erhardt, 2020, for another recent development of a dynocc model with species interactions). They write the model with a Categorical distribution instead of the multivariate Bernoulli. Here we show a simpler, static version of their model and acknowledge code generously provided by Mason Fidino. We illustrate the same model as we just fit in `unmarked`. Hence, we fit an effect of `Dist` on the species main effects in occupancy, an effect of `HDens` on the two-way interactions in occupancy, and an effect of `Trail` on the detection probability of each species. At the end of the section, we briefly sketch out a more complex variant that allows for intercept effects in the two-way interactions of the detection model, i.e., where detection of one species may differ depending on who else is present at a site. Such a model can currently not be fit in `unmarked`, but may sometimes be important, when the presence of one species affects the behavior of another (think of the predator-ungulate example below).

```
# Get data set and put into right format
library(AHMbook)
library(abind)
data(MesoCarnivores)
str(data <- MesoCarnivores)
str(ylist <- list(bobcat = data$bobcat, coyote = data$coyote, redfox = data$redfox))

# Put species detections in an array (site x rep x species)
y <- abind(ylist, along = 3)

# Get sample sizes
nsites <- dim(y)[1] # 1437 sites
nsurveys <- dim(y)[2] # 3 surveys
nspc <- dim(y)[3] # 3 species
ncat <- 2^nspc # 8 possible community states

# Prepare site covariates for occupancy and look at them
Dist <- scale(data$sitecovs[, 'Dist_5km'])
HDens <- scale(data$sitecovs[, 'HDens_5km'])
summary(data$sitecovs[, 1]) ; summary(data$sitecovs[, 2])

# Prepare one site covariate to serve as an observational covariate for detection
table(Trail <- data$sitecovs[, 'Trail']) # summarize
Trail <- matrix(cbind(Trail, Trail, Trail), ncol = 3)

# Condense multi-species detection array to be site x survey
ycat <- apply(y, c(1,2), paste, collapse = "")
ycat[ycat == "000"] <- 1 # Unoccupied (abbreviated 'U')
ycat[ycat == "100"] <- 2 # Only bobcat ('B') detected
ycat[ycat == "010"] <- 3 # Only coyote ('C') detected
ycat[ycat == "001"] <- 4 # Only red fox ('F') detected
ycat[ycat == "110"] <- 5 # Bobcat and coyote ('BC')
ycat[ycat == "011"] <- 6 # Coyote and fox ('CF')
ycat[ycat == "101"] <- 7 # Bobcat and fox ('BF')
ycat[ycat == "111"] <- 8 # All three species ('BCF')

# Convert each column to a numeric: this is our response variable
ycat <- apply(ycat, 2, as.numeric)
```

One major step is to prepare the response for the analyses, which is a categorical description of the observed state of a site at each visit, where states are defined in terms of the detection/nondetection of all three species. We do this next. Note that these binary strings are not detection histories across occasions, but multispecies detections for each site and occasion. We first convert the original data into the multispecies detections for each site and then code them by the numbers 1–8.

```
# Condense multi-species detection array to be site x survey
ycat <- apply(y, c(1,2), paste, collapse = "")
ycat[ycat == "000"] <- 1 # Unoccupied (abbreviated 'U')
ycat[ycat == "100"] <- 2 # Only bobcat ('B') detected
ycat[ycat == "010"] <- 3 # Only coyote ('C') detected
ycat[ycat == "001"] <- 4 # Only red fox ('F') detected
ycat[ycat == "110"] <- 5 # Bobcat and coyote ('BC')
ycat[ycat == "011"] <- 6 # Coyote and fox ('CF')
ycat[ycat == "101"] <- 7 # Bobcat and fox ('BF')
ycat[ycat == "111"] <- 8 # All three species ('BCF')

# Convert each column to a numeric: this is our response variable
ycat <- apply(ycat, 2, as.numeric)
```

Then, we prepare the model matrices for four parts of the model: occupancy main effects, occupancy two-way interactions, detection main effects, and detection interactions. The code here is written in a fairly general manner and also allows to fit models with interactions in detection; see our comments at the end of this section.

```

# Model matrix for first order occupancy (psi): main effects
psi_cov <- matrix(NA, ncol = 2, nrow = nsites)
psi_cov[,1] <- 1                                # Intercept
psi_cov[,2] <- Dist                             # Slope of Dist

# Model matrix for second order occupancy (psi): 2-way interactions
psi_inxs_cov <- matrix(NA, ncol = 2, nrow = nsites)
psi_inxs_cov[,1] <- 1                            # Intercept
psi_inxs_cov[,2] <- HDens                         # Slope of HDens

# Model matrix for first order detection (rho): main effects
rho_cov <- array(NA, dim = c(nsites, nsurveys, 2))
rho_cov[,,1] <- 1                                # Intercept
rho_cov[,,2] <- Trail                           # Site off/on trail

# Model matrix for second order detection (rho): 2-way interactions
rho_inxs_cov <- rep(1, nsites)                   # Intercept

# Bundle and summarize data set
str(bdata <- list(y = ycat, psi_cov = psi_cov, psi_inxs_cov = psi_inxs_cov,
  rho_cov = rho_cov, rho_inxs_cov = rho_inxs_cov, nsites = nsites,
  nsurveys = nsurveys, nfist_order_psi = ncol(psi_cov),
  nsecond_order_psi = ncol(psi_inxs_cov), nfist_order_rho = dim(rho_cov)[3],
  nsecond_order_rho = 1, ncat = ncat) )

List of 12
$ y                  : num [1:1437, 1:3] 1 1 1 1 1 4 1 1 1 1 ...
$ psi_cov            : num [1:1437, 1:2] 1 1 1 1 1 1 1 1 1 1 ...
$ psi_inxs_cov       : num [1:1437, 1:2] 1 1 1 1 1 1 1 1 1 1 ...
$ rho_cov            : num [1:1437, 1:3, 1:2] 1 1 1 1 1 1 1 1 1 1 ...
$ rho_inxs_cov       : num [1:1437] 1 1 1 1 1 1 1 1 1 1 ...
$ nsites              : int 1437
$ nsurveys            : int 3
$ nfist_order_psi    : int 2
$ nsecond_order_psi  : int 2
$ nfist_order_rho    : int 2
$ nsecond_order_rho  : num 1
$ ncat                : num 8

```

This model is structurally fairly complex and therefore we provide ample comments. We denote quantities related to the occupancy state of a site by species according to the first letter of the species' name: B for bobcat, C for coyote, and F for the fox, while U stands for unoccupied (i.e., none of the three species occur). When reading through the BUGS code trying to understand which part does what, remember that this is a multi-state model (see Chapter 6) and we build up its definition in three steps: (1) the basic hierarchical model separating latent and observed quantities, with a Categorical distribution for each, (2) the arrays containing the cell probabilities for these distributions, and (3) the linear models specified for the fundamental parameters that govern the cell probabilities.

```

# Specify model in BUGS language
cat(file = 'static_categorical.txt', "
model{

# --- Priors ---
# First order psi
betaB[1] <- logit(mean.psib)           # fo occupancy intercepts
betaC[1] <- logit(mean.psic)
betaF[1] <- logit(mean.psif)
mean.psib[1] ~ dunif(0, 1)
mean.psic[1] ~ dunif(0, 1)
mean.psif[1] ~ dunif(0, 1)
for(fo_psi in 2:nfirst_order_psi){ # fo occupancy slopes
  betaB[fo_psi] ~ dnorm(0, 0.1)
  betaC[fo_psi] ~ dnorm(0, 0.1)
  betaF[fo_psi] ~ dnorm(0, 0.1)
}
# Second order psi priors
for(so_psi in 1:nsecond_order_psi){
  betaBC[so_psi] ~ dnorm(0, 0.1)
  betaBF[so_psi] ~ dnorm(0, 0.1)
  betaCF[so_psi] ~ dnorm(0, 0.1)
}
# First order detection priors (rho)
alphaB[1] <- logit(mean.pB)           # fo detection intercepts
alphaC[1] <- logit(mean.pC)
alphaF[1] <- logit(mean.pF)
mean.pB ~ dunif(0, 1)
mean.pC ~ dunif(0, 1)
mean.pF ~ dunif(0, 1)
for(fo_rho in 2:nfirst_order_rho){ # fo detection slopes
  alphaB[fo_rho] ~ dnorm(0, 0.1)
  alphaC[fo_rho] ~ dnorm(0, 0.1)
  alphaF[fo_rho] ~ dnorm(0, 0.1)
}
# Second order detection priors (rho)
# none in this model

# --- 'Likelihood' ---
# (1) Basic hierarchical model: states and observations
# Latent state model
for(i in 1:nsites) {
  z[i] ~ dcat(lsv[i, ( 1:ncat )] )
}
# Detection model
for(i in 1:nsites) {
  for(j in 1:nsurveys) {
    y[i, j] ~ dcat(rdm[i, j, ( 1:ncat ), z[i] ] )
  }
}

# (2) Define the latent state vector and the observation matrices
for( i in 1:nsites ) {
  # Latent state probabilities in latent state vector (lsv)
  # Probabilities for each state
  lsv[i, 1] <- 1 #-----| U
  lsv[i, 2] <- exp( psib[i] ) #-----| B
  lsv[i, 3] <- exp( psic[i] ) #-----| C
  lsv[i, 4] <- exp( psif[i] ) #-----| F
  lsv[i, 5] <- exp( psibc[i] ) #-----| BC
  lsv[i, 6] <- exp( psicf[i] ) #-----| CF
  lsv[i, 7] <- exp( psibf[i] ) #-----| BF
  lsv[i, 8] <- exp( psibcf[i] ) #-----| BCF
}

```

```

for(j in 1:nsurveys){
  # Detection matrix (OS = observed state, TS = true state)
  # rdm = rho detection matrix. Each row sums to 1
  # OS along rows, TS along columns
  # True state = U
  rdm[i, j, 1, 1] <- 1 #-----| OS = U
  rdm[i, j, 2, 1] <- 0 #-----| OS = B
  rdm[i, j, 3, 1] <- 0 #-----| OS = C
  rdm[i, j, 4, 1] <- 0 #-----| OS = F
  rdm[i, j, 5, 1] <- 0 #-----| OS = BC
  rdm[i, j, 6, 1] <- 0 #-----| OS = CF
  rdm[i, j, 7, 1] <- 0 #-----| OS = BF
  rdm[i, j, 8, 1] <- 0 #-----| OS = BCF
  # True state = B
  rdm[i, j, 1, 2] <- 1 #-----| OS = U
  rdm[i, j, 2, 2] <- exp( rhoB[i, j] ) #-----| OS = B
  rdm[i, j, 3, 2] <- 0 #-----| OS = C
  rdm[i, j, 4, 2] <- 0 #-----| OS = F
  rdm[i, j, 5, 2] <- 0 #-----| OS = BC
  rdm[i, j, 6, 2] <- 0 #-----| OS = CF
  rdm[i, j, 7, 2] <- 0 #-----| OS = BF
  rdm[i, j, 8, 2] <- 0 #-----| OS = BCF
  # True state = C
  rdm[i, j, 1, 3] <- 1 #-----| OS = U
  rdm[i, j, 2, 3] <- 0 #-----| OS = B
  rdm[i, j, 3, 3] <- exp( rhoC[i, j] ) #-----| OS = C
  rdm[i, j, 4, 3] <- 0 #-----| OS = F
  rdm[i, j, 5, 3] <- 0 #-----| OS = BC
  rdm[i, j, 6, 3] <- 0 #-----| OS = CF
  rdm[i, j, 7, 3] <- 0 #-----| OS = BF
  rdm[i, j, 8, 3] <- 0 #-----| OS = BCF
  # True state = F
  rdm[i, j, 1, 4] <- 1 #-----| OS = U
  rdm[i, j, 2, 4] <- 0 #-----| OS = B
  rdm[i, j, 3, 4] <- 0 #-----| OS = C
  rdm[i, j, 4, 4] <- exp( rhoF[i, j] ) #-----| OS = F
  rdm[i, j, 5, 4] <- 0 #-----| OS = BC
  rdm[i, j, 6, 4] <- 0 #-----| OS = CF
  rdm[i, j, 7, 4] <- 0 #-----| OS = BF
  rdm[i, j, 8, 4] <- 0 #-----| OS = BCF
  # True state = BC
  rdm[i, j, 1, 5] <- 1 #-----| OS = U
  rdm[i, j, 2, 5] <- exp( rhoBC[i, j] ) #-----| OS = B
  rdm[i, j, 3, 5] <- exp( rhoCB[i, j] ) #-----| OS = C
  rdm[i, j, 4, 5] <- 0 #-----| OS = F
  rdm[i, j, 5, 5] <- exp( rhoBC[i, j] + rhoCB[i, j] ) #---| OS = BC
  rdm[i, j, 6, 5] <- 0 #-----| OS = CF
  rdm[i, j, 7, 5] <- 0 #-----| OS = BF
  rdm[i, j, 8, 5] <- 0 #-----| OS = BCF
  # True state = CF
  rdm[i, j, 1, 6] <- 1 #-----| OS = U
  rdm[i, j, 2, 6] <- 0 #-----| OS = B
  rdm[i, j, 3, 6] <- exp( rhoCF[i, j] ) #-----| OS = C
  rdm[i, j, 4, 6] <- exp( rhoFC[i, j] ) #-----| OS = F
  rdm[i, j, 5, 6] <- 0 #-----| OS = BC
  rdm[i, j, 6, 6] <- exp( rhoCF[i, j] + rhoFC[i, j] ) #---| OS = CF
  rdm[i, j, 7, 6] <- 0 #-----| OS = BF
  rdm[i, j, 8, 6] <- 0 #-----| OS = BCF
}

```

```

# True state = BF
rdm[i, j, 1, 7] <- 1 #-----| OS = U
rdm[i, j, 2, 7] <- exp( rhoBF[i, j] ) #-----| OS = B
rdm[i, j, 3, 7] <- 0 #-----| OS = C
rdm[i, j, 4, 7] <- exp( rhoFB[i, j] ) #-----| OS = F
rdm[i, j, 5, 7] <- 0 #-----| OS = BC
rdm[i, j, 6, 7] <- 0 #-----| OS = CF
rdm[i, j, 7, 7] <- exp( rhoBF[i, j] + rhoFB[i, j] ) #---| OS = BF
rdm[i, j, 8, 7] <- 0 #-----| OS = BCF
# True state = BCF
rdm[i, j, 1, 8] <- 1 #-----| OS = U
rdm[i, j, 2, 8] <- exp( rhoBCF[i, j] ) #-----| OS = B
rdm[i, j, 3, 8] <- exp( rhoCBF[i, j] ) #-----| OS = C
rdm[i, j, 4, 8] <- exp( rhoFBC[i, j] ) #-----| OS = F
rdm[i, j, 5, 8] <- exp( rhoBCF[i, j] + rhoCBF[i, j] ) #-| OS = BC
rdm[i, j, 6, 8] <- exp( rhoCBF[i, j] + rhoFBC[i, j] ) #-| OS = CF
rdm[i, j, 7, 8] <- exp( rhoBCF[i, j] + rhoFBC[i, j] ) #-| OS = BF
rdm[i, j, 8, 8] <- exp( rhoBCF[i, j] + rhoCBF[i, j] +
    rhoFBC[i, j] ) #-----| OS = BCF
}

# (3) Specify linear models for the parameters in lsv and rdm
# Linear models for the occupancy parameters
# ...for states B, C, and F
psiB[i] <- inprod( betaB, psi_cov[i, ] )
psiC[i] <- inprod( betaC, psi_cov[i, ] )
psiF[i] <- inprod( betaF, psi_cov[i, ] )
# ...for states BC, CF, and BF (in that order)
psiBC[i] <- psiB[i] + psiC[i] + inprod( betaBC, psi_inxs_cov[i, ] )
psiCF[i] <- psiC[i] + psiF[i] + inprod( betaCF, psi_inxs_cov[i, ] )
psiBF[i] <- psiB[i] + psiF[i] + inprod( betaBF, psi_inxs_cov[i, ] )
# ...for state BCF
psiBCF[i] <- psiB[i] + psiC[i] + psiF[i] + inprod( betaBC, psi_inxs_cov[i, ] ) +
    inprod( betaCF, psi_inxs_cov[i, ] ) + inprod( betaBF, psi_inxs_cov[i, ] )

# Linear models for the detection parameters
# => Here we could specify detection interactions as well
for(j in 1:nsurveys){
    # Baseline detection linear predictors
    # do not incorporate interactions.
    rhoB[i, j] <- inprod( alphaB, rho_cov[i, j, ] )
    rhoC[i, j] <- inprod( alphaC, rho_cov[i, j, ] )
    rhoF[i, j] <- inprod( alphaF, rho_cov[i, j, ] )
    # Asymmetric interactions between all 3 species
    rhoBC[i, j] <- rhoB[i, j]
    rhoBF[i, j] <- rhoB[i, j]
    rhoCB[i, j] <- rhoC[i, j]
    rhoCF[i, j] <- rhoC[i, j]
    rhoFB[i, j] <- rhoF[i, j]
    rhoFC[i, j] <- rhoF[i, j]
    # Asymmetric interactions when all 3 species are present
    rhoBCF[i, j] <- rhoB[i, j]
    rhoCBF[i, j] <- rhoC[i, j]
    rhoFBC[i, j] <- rhoF[i, j]
}
}
")

```

As often with multi-state models, finding initial values that satisfy JAGS can be tricky. We need to initialize all chains such that any contradiction between data, model, and those inits is avoided. As is typical with occupancy models, we do this by initializing the state of each site at the highest observed state. An alternative that should often work is to just set the initial state to the maximum community state. This would be 8—“occupied by all three species”—across all sites for a model with three species.

```

# get the maximum possible state across all 3 potential surveys at a site
# returns a site x species matrix
zinit <- apply(y, c(1,3), sum, na.rm = TRUE)
zinit[zinit>1] <- 1 # make binary

# convert to a category
zcat <- apply(zinit, 1, paste, collapse = ")
zcat[zcat == "000"] <- 1 # nobody there
zcat[zcat == "100"] <- 2 # only bobcat
zcat[zcat == "010"] <- 3 # only coyote
zcat[zcat == "001"] <- 4 # only fox
zcat[zcat == "110"] <- 5 # bobcat and coyote
zcat[zcat == "011"] <- 6 # coyote and fox
zcat[zcat == "101"] <- 7 # bobcat and fox
zcat[zcat == "111"] <- 8 # all three

# make numeric again
zcat <- as.numeric(zcat)

# Inits function
inits <- function() list(z = zcat)

# Parameters monitored
params <- c('betaB', 'betaC', 'betaF', 'betaBC', 'betaBF', 'betaCF',
  'alphaB', 'alphaC', 'alphaF', 'mean.psiB', 'mean.psiC', 'mean.psiF',
  'mean.pB', 'mean.pC', 'mean.pF', 'z')

# MCMC settings
na <- 10000 ; nc <- 3 ; ni <- 50000 ; nb <- 30000 ; nt <- 20

# Call JAGS (ART 335 min), check convergence and summarize posteriors
library(jagsUI)
out1 <- jags(bdata, inits, params, 'static_categorical.txt', n.chains = nc,
  n.adapt = na, n.burnin = nb, n.iter = ni, n.thin = nt, parallel = TRUE)
par(mfrow = c(3,3)) ; traceplot(out1)
which(out1$summary[,8] > 1.1)
print(out1$summary[1:24, -c(4:6)], 3)

      mean      sd    2.5%   97.5% Rhat n.eff overlap0      f
betaB[1] -1.1412 0.2712 -1.69251 -0.6280 1.01    339      0 1.000
betaB[2] -0.6594 0.1482 -0.96154 -0.3856 1.01    406      0 1.000
betaC[1] -0.5343 0.2144 -0.98863 -0.1479 1.03     74      0 0.998
betaC[2]  0.2107 0.1129  0.00607  0.4518 1.01    315      0 0.979
betaF[1] -1.8587 0.2668 -2.39865 -1.3824 1.00   1296      0 1.000
betaF[2] -0.3743 0.1399 -0.66442 -0.1159 1.00   1084      0 0.999
betaBC[1]  0.8798 0.4150  0.05126  1.6751 1.06     40      0 0.984
betaBC[2] -2.8701 0.9379 -4.96531 -1.3914 1.03     81      0 1.000
betaBF[1] -1.5007 0.4597 -2.42223 -0.6409 1.01    171      0 1.000
betaBF[2]  1.7285 0.9461  0.46911  4.0528 1.03     68      0 0.997
betaCF[1]  1.5942 0.4749  0.80321  2.6352 1.01    395      0 1.000
betaCF[2]  1.9149 0.9643  0.82842  4.3680 1.04     70      0 1.000
alphaB[1] -2.5295 0.1645 -2.85495 -2.2177 1.00   2034      0 1.000
alphaB[2]  1.8092 0.1685  1.48266  2.1413 1.00   1414      0 1.000
alphaC[1] -2.0232 0.1043 -2.22755 -1.8163 1.01    349      0 1.000
alphaC[2]  2.1582 0.1195  1.92025  2.3862 1.00   3000      0 1.000
alphaF[1] -1.6145 0.1739 -1.94695 -1.2800 1.01    275      0 1.000
alphaF[2]  1.8453 0.2080  1.42525  2.2442 1.00   1203      0 1.000
mean.psiB  0.2455 0.0495  0.15545  0.3480 1.01    373      0 1.000
mean.psiC  0.3709 0.0490  0.27118  0.4631 1.03     75      0 1.000
mean.psiF  0.1378 0.0306  0.08328  0.2006 1.00   1235      0 1.000
mean.pB   0.0746 0.0113  0.05443  0.0982 1.00   2056      0 1.000
mean.pC   0.1172 0.0108  0.09730  0.1399 1.01    356      0 1.000
mean.pF   0.1674 0.0242  0.12489  0.2176 1.01    281      0 1.000

```

We can compare the MLEs from unmarked (in the last section) and the posterior means from JAGS and will notice similar estimates, as we expect when using vague priors. We don't show this here, but if you do it, then you will notice that there are slight differences for parameters 8 and 10–12, which have skewed posterior distributions and for which the posterior median or mode yield a better agreement with the MLEs.

We make graphs to understand what the model is telling us about the processes that we think produced our data set and plot predictions of marginal and conditional occupancy. Our recipe for forming these predictions is:

- Predict the eight latent state probabilities as a function of the parameter estimates from our model and those covariates for which we want to predict occupancy.
- Use basic probability to compute marginal or conditional probabilities as needed by simple addition of cells (for marginal probabilities) or by addition followed by suitable scaling (for conditional probabilities).

First, we illustrate with predictions of occupancy for covariate `Dist`, while keeping `HDens` at its observed mean. We work with the posterior means only; if you want prediction SEs and CRIs, you must work with the full list of posterior draws instead, and most quantities in the code that follows here will need one added dimension.

```
# Grab posterior means of parameters
(tmp <- out1$mean[1:6])

# Create prediction covariates for occupancy as a function of Disturbance
# (at average Housing density)
(r <- range(data$sitecovs[, 'Dist_5km']))
(mnx <- mean(data$sitecovs[, 'Dist_5km']))
(sdx <- sd(data$sitecovs[, 'Dist_5km']))
Dist.pred.orig <- seq(r[1], r[2], length.out = 1000) # Create new data
Dist.pred <- (Dist.pred.orig-mnx) / sdx # ... and scale as the real data
HDens.pred <- rep(0, 1000)

# Create model matrices for the prediction covariates
head(psi_cov1 <- cbind(1, Dist.pred)) # We vary this covariate ...
head(psi_cov2 <- cbind(1, HDens.pred)) # .. while this stays constant

# Assemble the linear predictors
# ...for states B, C, and F
psiB <- as.numeric( psi_cov1 %*% tmp$betaB )
psiC <- as.numeric( psi_cov1 %*% tmp$betaC )
psiF <- as.numeric( psi_cov1 %*% tmp$betaF )
# ...for states BC, CF, and BF (in that order)
psiBC <- psiB + psiC + as.numeric( psi_cov2 %*% tmp$betaBC )
psiCF <- psiC + psiF + as.numeric( psi_cov2 %*% tmp$betaCF )
psiBF <- psiB + psiF + as.numeric( psi_cov2 %*% tmp$betaBF )
# ...for state ABC
psiBCF <- psiB + psiC + psiF + psiBC + psiCF + psiBF

# Assemble the state probability vector for every DIST covariate value
lsv <- lsp <- matrix(NA, ncol = ncat, nrow = 1000 )
colnames(lsv) <- colnames(lsp) <- c('U', 'B', 'C', 'F', 'BC', 'CF', 'BF', 'BCF')
```

```

# Compute latent state vector (lsv) and latent state probabilities (lsp)
lsv[, 1] <- 1                                # none of the three species
lsv[, 2] <- exp( psiB )                        # only B
lsv[, 3] <- exp( psiC )                        # only C
lsv[, 4] <- exp( psiF )                        # only F
lsv[, 5] <- exp( psIBC)                         # both B and C
lsv[, 6] <- exp( psiCF)                         # both C and F
lsv[, 7] <- exp( psiBF)                         # both B and F
lsv[, 8] <- exp( psiBCF)                        # all three species

# Probability of each state
for(i in 1:nrow(lsv)){
  lsp[i, ] <- lsv[i, ( 1:ncat )] / sum(lsv[i, ( 1:ncat )])
}

# Plot the lsp as a function of covariate Dist (Fig. 8.4)
matplot(Dist.pred.orig, lsp, type = 'l', lty = 1, lwd = 5, col = 1:8,
frame = FALSE, xlab = 'Disturbance', ylab = 'Probability of state',
ylim = c(0, 0.65), las = 1)
legend('topleft', lwd = 3, lty = 1, col = 1:8, colnames(lsp), bty = 'n',
cex = 1.2, ncol = 2)

```

[Fig. 8.4](#) shows the predicted change of the latent state probabilities as a function of covariate *Dist* and at the average of covariate *HDens*. The main pattern seems to be that sites occupied by coyotes only increase greatly in frequency with increasing values of *Dist*, while the probability of most other community states declines.

Since the probability of all eight states must sum to 1, we can now add different components of the latent state probability vector to obtain marginal or conditional probabilities as a function of *Dist*. For instance, the probability of bobcat presence at a site regardless of the presence/absence of the other species (i.e., its marginal occupancy probability) is the sum $P(B) + P(BC) + P(BF) + P(BCF)$. To illustrate, we first compute the marginal occupancy probability in relation to *Dist* for all three species, which yields a plot analogous to [Fig. 8.2](#). (though with different colors, sorry...).

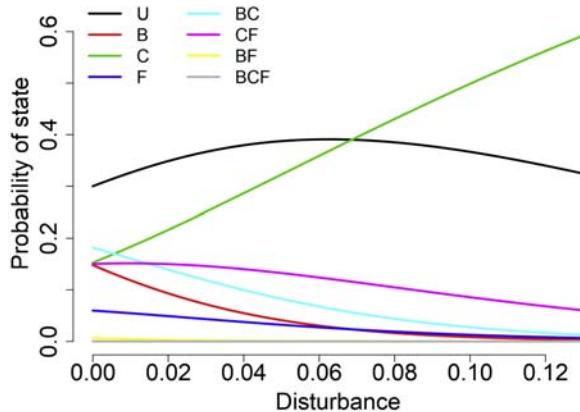


FIGURE 8.4

Predictions of all eight latent state probabilities (*lsp*) as a function of covariate *Dist*, while keeping covariate *HDens* at its observed average. The unoccupied state is denoted “U” and the other states are denoted B (bobcat), C (coyote), and F (red fox), either alone or as a combination when two or more species co-occur.

```
# Compute and plot marginal occupancy for all three species (not shown)
bobcat.marginal <- rowSums(lsp[,c(2,5,7,8)])
coyote.marginal <- rowSums(lsp[,c(3,5,6,8)])
fox.marginal <- rowSums(lsp[,c(4,6,7,8)])
matplot(Dist.pred.orig, cbind(bobcat.marginal, coyote.marginal, fox.marginal),
        type = 'l', lty = 1:3, lwd = 3, col = 1:3, frame = FALSE, xlab = 'Disturbance',
        ylab = 'Marginal occupancy probability', ylim = c(0, 0.7))
legend('top', c('Bobcat', 'Coyote', 'Red Fox'), lwd = 3, lty = 1:3, col = 1:3,
       horiz = TRUE, bty = 'n')
```

Next, we compute some conditional occupancy probabilities. To understand how to compute them by combining cells of the latent state vector, consider first the simple case of two events A and B, where $P(A|B) = P(A \cap B)/P(B)$. That is, the probability of event A given that B holds is equal to the joint probability of A and B (i.e., that both hold, happen or are true), divided by the marginal probability of event B. Importantly, for the three-species occupancy model, both the marginal and the joint probability of an event will typically be composed of the sum of two or more probabilities in the latent state vector. For instance, the conditional occupancy for bobcat given presence of coyote is $(P(BC) + P(BCF))/(P(C) + P(BC) + P(CF) + P(BCF))$, while the conditional occupancy probability for bobcat given coyote absence is $(P(B) + P(BF))/(P(U) + P(B) + P(F) + P(BF))$. We now compute the conditional occupancy probabilities for all three species, given that they occur either alone or with exactly one of the other two species and plot them (Fig. 8.5).

```
# Compute conditional occupancy for all species
B.alone <- lsp[, 'B'] / rowSums(lsp[, c('U', 'B')])
B.given.coyote <- rowSums(lsp[, c('BC', 'BCF')]) / rowSums(lsp[, c('C', 'BC', 'CF', 'BCF')])
B.given.fox <- rowSums(lsp[, c('BF', 'BCF')]) / rowSums(lsp[, c('F', 'CF', 'BF', 'BCF')])
C.alone <- lsp[, 'C'] / rowSums(lsp[, c('U', 'C')])
C.given.bobcat <- rowSums(lsp[, c('BC', 'BCF')]) / rowSums(lsp[, c('B', 'BC', 'BF', 'BCF')])
C.given.fox <- rowSums(lsp[, c('CF', 'BCF')]) / rowSums(lsp[, c('F', 'CF', 'BF', 'BCF')])
F.alone <- lsp[, 'F'] / rowSums(lsp[, c('U', 'F')])
F.given.bobcat <- rowSums(lsp[, c('BF', 'BCF')]) / rowSums(lsp[, c('B', 'BC', 'BF', 'BCF')])
F.given.coyote <- rowSums(lsp[, c('CF', 'BCF')]) / rowSums(lsp[, c('C', 'BC', 'CF', 'BCF'))
```

```
# Plot them (Fig. 8.5) -> see website
```

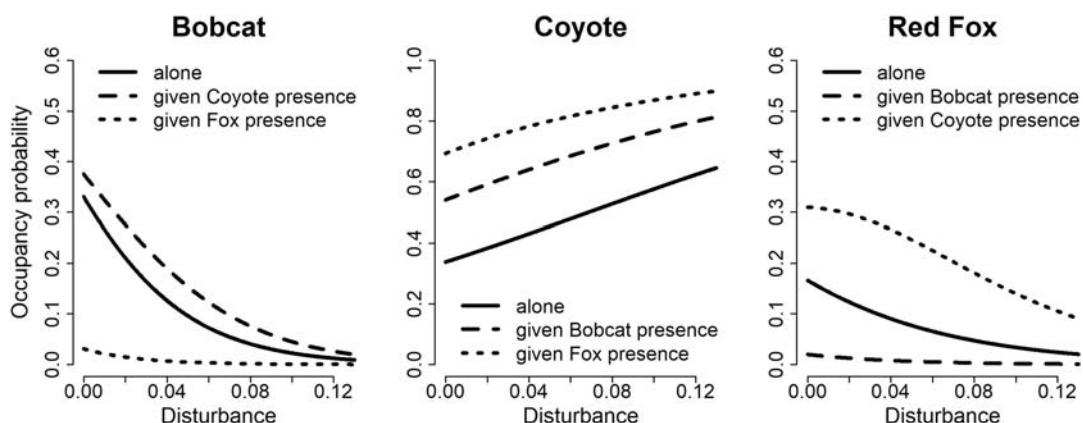
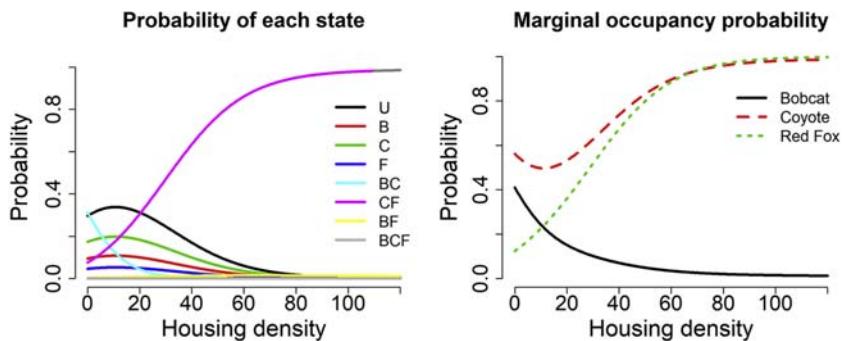


FIGURE 8.5

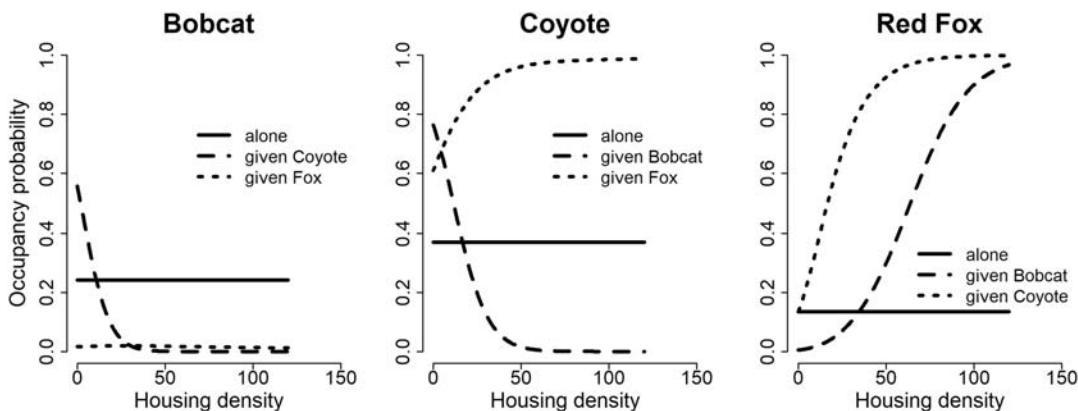
Predictions of conditional occupancy probability as a function of covariate `Dist` for all three species either alone, i.e., conditional on the absence of both of the other two, or conditional on the presence of exactly one of them.

**FIGURE 8.6**

Predictions of occupancy as a function of covariate HDens, keeping covariate Dist at its observed average. Left: all eight latent state probabilities (lsp), right: marginal occupancy probability of all three species.

Next, we plot predictions for HDens, while keeping disturbance constant (see website for code). Fig. 8.6 shows the predicted change of the latent state probabilities as a function of covariate HDens (and at the average of covariate Dist) and then combines these to the marginal occupancy probability for each species.

Then, we plot again the conditional occupancy probabilities as before, but now in response to Housing density (Fig. 8.7). Don't be surprised by the constant predictions for each species alone: in our model, first-order occupancy is not a function of HDens, but only of Dist. Hence, when keeping Dist constant in the current set of predictions, we get a horizontal line.

**FIGURE 8.7**

Predictions of conditional occupancy probability as a function of covariate HDens for all three species either alone, i.e., conditional on the absence of both of the other two, or on the presence of exactly one of them.

We also form predictions of detection probability as a function of whether a camera trap is placed on or off a trail (see code on webpage). We see that all species are dramatically easier to detect on than off trails.

```
# Posterior means of p
      off trail on trail
Bobcat      0.07     0.86
Coyote      0.12     0.90
Red Fox     0.17     0.86

# 95% CRIs
, , off trail

      Bobcat Coyote Red Fox
2.5%    0.05   0.10    0.12
97.5%   0.10   0.14    0.22

, , on trail

      Bobcat Coyote Red Fox
2.5%    0.81   0.87    0.81
97.5%   0.89   0.92    0.90
```

Finally, we compute the state probability and the most likely state for each site and plot the latter, where state is defined by the presence/absence of the three study species, based on the estimates of the latent state z (Fig. 8.8, which shows this for just 500 sites). We discover that a majority of sites are unoccupied and extremely few hold all three species. Some apparent groups of sites with identical most likely state, as one goes from left to right, are probably due to “study site effects,” i.e., many camera trap sites within the same study site will tend to have the same set of species occurring.

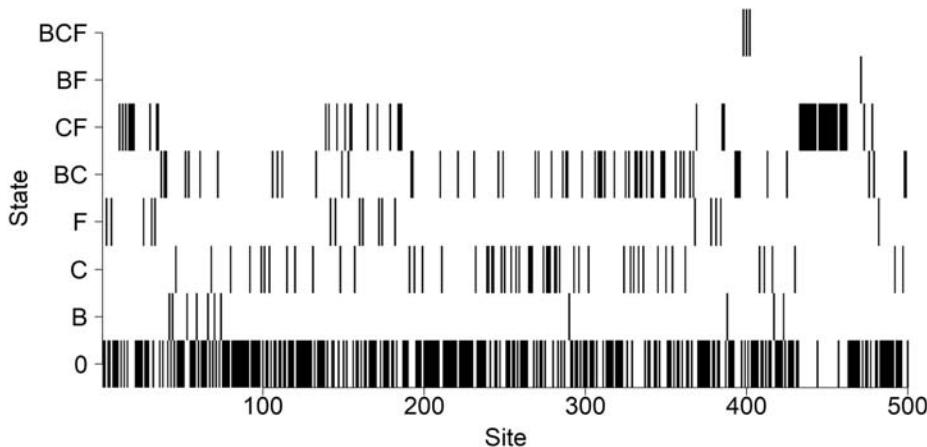


FIGURE 8.8

Estimates of the most likely state for a sample of 500 sites, as a summary of the MCMC samples of the latent state variable z .

```

# Compute and plot most likely states for a sample of the sites
nsims <- out1$mcmc.info$n.samples
state.prob <- most.likely <- array(NA, dim = c(1437, 8))
colnames(state.prob) <- colnames(most.likely) <- c("U", "B", "C", "F",
  "BC", "CF", "BF", "BCF") # label
for(i in 1:1437){
  state.prob[i,] <- tabulate(out1$sims.list$z[,i], nbins = 8)/nsims
  tmp <- tabulate(out1$sims.list$z[,i], nbins = 8)
  most.likely[i,] <- floor(tmp / max(tmp))
}
head(state.prob)      # Gives probability that a site is in a certain state
head(most.likely)     # Just picks the most likely state

par(mar = c(5,5,6,2), cex.main = 2) # Plot 8.8
image(x = 1:500, y = 1:8, z = most.likely[1:500,], col = c('white', 'black'),
  xlab = 'Sites 1-500', ylab = 'State', axes = FALSE)
axis(1)
axis(2, at = 1:8, labels = c("U", "B", "C", "F", "BC", "CF", "BF", "BCF"), las = 1)

```

To finish off this section, we briefly sketch out the model if you want to fit an interaction effect in detection just with an intercept. That is, have a different intercept in the detection model for each species, depending on which other species is present. Since we wrote the model in BUGS in a fairly general way and we have already provided the necessary data in the data bundle, the only required changes are in the bottom part of the BUGS model, which becomes this:

```

# Linear models for the detection parameters
for(j in 1:nsurveys){
  # Baseline detection linear predictors
  # do not incorporate interactions.
  rhoB[i, j] <- inprod(alphaB, rho_cov[i, j, ] )
  rhoC[i, j] <- inprod(alphaC, rho_cov[i, j, ] )
  rhoF[i, j] <- inprod(alphaF, rho_cov[i, j, ] )
  # Asymmetric interactions between all species pairs
  rhoBC[i, j] <- rhoB[i, j] + inprod(alphaBC, rho_inxs_cov[i] )
  rhoBF[i, j] <- rhoB[i, j] + inprod(alphaBF, rho_inxs_cov[i] )
  rhoCB[i, j] <- rhoC[i, j] + inprod(alphaCB, rho_inxs_cov[i] )
  rhoCF[i, j] <- rhoC[i, j] + inprod(alphaCF, rho_inxs_cov[i] )
  rhoFB[i, j] <- rhoF[i, j] + inprod(alphaFB, rho_inxs_cov[i] )
  rhoFC[i, j] <- rhoF[i, j] + inprod(alphaFC, rho_inxs_cov[i] )
  # Asymmetric interactions when all 3 species are present
  rhoBCF[i, j] <- rhoB[i, j] + inprod(alphaBC, rho_inxs_cov[i]) +
    inprod(alphaBF, rho_inxs_cov[i])
  rhoCBF[i, j] <- rhoC[i, j] + inprod(alphaCB, rho_inxs_cov[i]) +
    inprod(alphaCF, rho_inxs_cov[i])
  rhoFBC[i, j] <- rhoF[i, j] + inprod(alphaFB, rho_inxs_cov[i]) +
    inprod(alphaFC, rho_inxs_cov[i])
}

```

The main novelty is in the middle part of this section, where we specify a constant two-way interaction in detection (remember that the detection interaction covariate matrix, `rho_inxs_cov`, contains just a single vector of 1's, corresponding to an intercept for this part of the model). Therefore, for the bobcat for instance, we estimate a different detection probability when it occurs alone than when coyote or red fox are also present at a site. Thus, this model contains six additional parameters for these interaction terms, and so we need to add the following section to the priors:

```

# for second order rho priors
for(so_rho in 1:nsecond_order_rho){
  alphaBC[so_rho] ~ dnorm(0, 0.1)
  alphaCB[so_rho] ~ dnorm(0, 0.1)
  alphaBF[so_rho] ~ dnorm(0, 0.1)
  alphaFB[so_rho] ~ dnorm(0, 0.1)
  alphaCF[so_rho] ~ dnorm(0, 0.1)
  alphaFC[so_rho] ~ dnorm(0, 0.1)
}

```

We did in fact experiment with this model for the mesocarnivore data set, but did not have much success: the model yielded some predictions that we deemed doubtful and therefore we did not pursue it any further. Rota et al. (2016a) also considered a similar model, albeit with a partial interaction only, where detection of a species was specified conditional on presence only of the largest species, the coyote. This model did not receive much weight in their model selection and was not used for inference. We note that Rota et al. (2016a) and Hepler and Erhardt (2020) use the Watanabe Akaike information criterion (WAIC) and Fidino et al. (2019) the conditional predictive ordinate (CPO; Hooten & Hobbs, 2015) for model selection.

8.2.4 BRIEF COMMENTS ON THE MULTI-STATE MULTISPECIES OCCUPANCY MODEL OF ROTA ET AL.

This concludes our illustration of the new interaction parameterization of a multispecies, multi-state occupancy model by Rota et al. (2016a). This is a powerful model because it is a JDSM that allows incorporation of covariates and accommodation of imperfect detection. In contrast to the original multi-state model of MacKenzie et al. (2004), it provides numerically stable estimates when covariates are added into the model. In contrast to the models by Waddle and Richmond (in the next section), it is a model for symmetric interactions, i.e., it does not require us to define an *a priori* direction for each pairwise interaction, because it does not need this additional assumption.

However, this model is conceptually more complex, and we think that most people will need to do some mental exercise before they will really grasp the meaning and the function of all parameters and therefore, how to interpret and manipulate the output, e.g., to produce predictions of marginal and conditional occupancy probabilities. But if your research question or management problem requires fitting multi-species models with interactions, then we think that this will be an effort that is spent well.

Nevertheless, you will have to be aware that the model may be challenging in practice to fit, especially with maximum likelihood. You will typically not be able to entertain very complex covariate models and in addition need large sample sizes. For instance, when developing the material with unmarked presented in Section 8.2.2, we had experimented with a just slightly more complex model that had an additional effect of HDens in the main effects of species-specific occupancy. However, in the most complex model (analogous to fm5), we obtained several boundary estimates. And when we experimented with a more real-world sample size by randomly subsampling 10% of the 1,400 sites, we again encountered numerical problems in the form of boundary estimates or SEs that were NaN's for models 3–5.

It is likely that not only the sample size (in terms of the number of sites) will determine whether you can successfully fit such occupancy models to your data set, but also specific features of the data set. As always, low values of detection probability may cause problems to estimate features of the state model. One main feature of the model is the estimation of statistical interactions; hence, you need observed data to estimate these interaction terms. So, for instance, when two species are never observed to co-occur at a site, then you will not be able to estimate the interaction term associated with this combination of co-occurrence. Tabulation of the observed occurrences of all pairwise combinations of the modeled species may be helpful to diagnose problems in the implementation of the model for a particular data set. You could then set to zero the two-way natural parameters for species never observed together and still estimate the others.

8.3 JOINT OCCUPANCY MODELS FOR FEW SPECIES WITH DIRECTIONAL INTERACTIONS

Models for symmetric interactions are perhaps best thought of as “screening tools” for a larger number of potentially interacting species, where interactions may be suggested by the non-independence of

parameters for certain species pairs. The models of Richmond et al. (2010) and Waddle et al. (2010) are more suitable for in-depth investigations of interspecific patterns of co-occurrence and abundance of a small number of species. These authors independently developed essentially the same occupancy model for interacting species, and similar principles for modeling directional interactions can be adopted for models of abundance (see Fig. 8.1 right and Sections 8.5.2 and 8.5.3). In their conditional models, parameters of one (or more) subordinate species B are expressed conditional on the presence or absence (or abundance, or even detection) of another, dominant species A. The dependent parameters may include intercepts, in which case the presence of species A may affect the mean occupancy, abundance, or detection of species B. In addition, the dependent parameters may also be coefficients, e.g., for environmental covariates, in which case we can test whether the presence/absence or abundance of species A “affects” (as always in a correlative sense) the habitat use of the other species. Thus, in this framework, we can also test whether a species correlation (expressed as a dominance relationship A → B) changes along spatial or temporal dimensions described by some covariate.

In these models, we always assume that some species is dominant and some other(s) subordinate, with an entirely unidirectional relationship between the two. Such completely one-sided relationships include cases of predator/prey, host/parasite, native/invasive, and small-/large-bodied species pairs. In addition, we think that this type of model for interactions can also be used in an explorative manner when the directionality of any possible relationship between two species is not so clear. Thus, we think that statistically, application of these models for species pairs might be justified even if all interactions were symmetric, but we just have to remember that our inferences are purely correlation-based when we interpret the results.

Conceptually, these models are very simple: we merely use the presence/absence (z) or the abundance (N) of one species as a covariate for any of the parameters in the model for another species. This principle of modeling interactions is certainly not new and has been adopted many times prior to the publications of Richmond et al. (2010) and Waddle et al. (2010), e.g., by Leathwick and Austin (2001), Leathwick (2002), Meier et al. (2010), and Pellissier et al. (2010). However, none of these earlier studies adopted models that accommodated detection error. The detection probability of a subordinate species may well depend on whether a dominant species is present or not. As an example, think of an ungulate species which may behave in a more or less conspicuous manner when its main predator is present than when it is absent. Hence, it may often be important to correct for imperfect detection in such interaction models. Direct behavioral mechanisms may not be the only ones where presence/absence of the dominant species may affect detection probability of the subordinate in an occupancy model: the same pattern may also be due to differential abundance of a subordinate species when the dominant is present or absent (and hence may be relevant in plant studies as well). As always, all things equal, differences in abundance in an occupancy model will produce a signal in detection probability.

The choice of where to add a dependence of the dominant species in the model for the subordinate species is up to your biological intuition and your questions. For instance, you may believe that there might be an effect on the overall level in occupancy only, in which case you would estimate two occupancy intercepts, one when the dominant species is absent and the other when it is present. Or you might think that the overall level of detection probability is also affected by the presence/absence of the dominant species and then you would do the same also for the detection intercept (Bailey et al., 2009; Yackulic et al., 2014). More exciting still might be the possibility that the response of the subordinate species to covariates might be affected by the occurrence or the abundance of the dominant species, i.e., that the type of interaction changes along an environmental gradient (LaManna et al., 2012, Rota et al., 2016a,b, Tikhonov et al., 2017, Fidino et al., 2019) or over time. In this case, you would also stratify covariate coefficients in the model for the subordinate species by presence or absence of the dominant species or, in the case of an abundance model (see Section 8.5), specify a statistical interaction between the abundance of the dominant species and a coefficient in the model for the subordinate.

Michel et al. (2016) provide a neat example of where Tawny Owl (*Strix aluco*) occurrence affected habitat choice of the Little Owl (*Athene noctua*), which may fall prey to the Tawny. Of course, you can make this choice data-based by inspecting the posterior distribution of the difference of the two parameters estimated for the subordinate in the presence or the absence of the dominant species. If the two posterior distributions are similar, and the posterior distribution of the difference is centered near zero, then you might consider simplifying the model by dropping the effect of the dominant species for that parameter. Alternatively, you might use some model selection criterion (Hooten and Hobbs, 2015).

8.3.1 THE HUBBARD BROOK DATA SET

For illustration, we will use a point-count data set on 13 Neotropical, leaf-gleaning passerines (warblers *Parulidae* and vireos *Vireonidae*) from the Hubbard Brook Experimental Forest in New Hampshire (Doran and Holmes, 2005; Betts et al., 2008; Holmes, 2011; Van Tatenhove et al., 2019, courtesy of our good old friend T. Scott Sillett). The Hubbard Brook study area measures 31.6 km² and ranges from 200–1000 m in elevation. Three replicated point counts of 10 min each, out to a maximum distance of 100 m, were conducted in each spring between 1999 and 2018 at a total of 373 locations. Data set *HubbardBrook* contains a subset of the data for the following species: American Redstart (AMRE), Black-and-white Warbler (BAWW), Blue-headed Vireo (BHVI), the magnificent Blackburnian Warbler (BLBW; see Fig. 8.9), Blackpoll Warbler (BLPW), the famous Black-throated Blue Warbler (BTBW; see Fig. 8.10), Black-throated Green Warbler (BTNW), Canada Warbler (CAWA), Magnolia Warbler (MAWA), Myrtle Warbler (MYWA), Nashville Warbler (NAWA), Ovenbird (OVEN), and Red-eyed Vireo (REVI). The data set includes a number of site covariates such as elevation and aspect, and two observational covariates: survey date and hour of survey. To characterize spring advancement, we use the date of full canopy leaf expansion (Lany et al., 2016).



FIGURE 8.9

A glorious male Blackburnian Warbler (*Setophaga fusca*), the most handsome species in the Hubbard Brook data set (photo by Robert Royse).

**FIGURE 8.10**

The runner-up: a male Black-throated Blue Warbler (*Setophaga caerulescens*) (photo by Robert Royse).

```

# Load Hubbard Brook data set
library(AHMbook)
data(HubbardBrook)
str(HubbardBrook)

# Get four-letter codes for the 13 species
speclist <- dimnames(HubbardBrook$counts)[[4]]

# Restrict all data to last 10 years: 2009-2018
year <- 2009:2018
str(counts <- HubbardBrook$counts[,11:20,]) # Counts
str(dates <- HubbardBrook$dates[,11:20])      # Survey dates
str(hours <- HubbardBrook$times[,11:20])       # Survey hour (in hours)

# Date of full canopy leaf expansion as a phenological measure
budburst <- c(138.4, 133.8, 143.6, 133.9, 137.3, 146.6, 142.0, 148.3, 143.3, 141.0)
plot(year, budburst, xlab = 'Year', ylab = 'Day of budburst', ylim = c(130, 150),
     type = 'b', pch = 16, cex = 2)                # not shown

```

We here restrict our analyses to the six most common and widespread species: Blue-headed Vireo (BHWI), Blackburnian Warbler (BLBW), Black-throated Blue Warbler (BTBW), Black-throated Green Warbler (BTNW), Ovenbird (OVEN), and Red-eyed Vireo (REVI).

```

# Get subset of six of the more common species
old.speclist <- speclist                                # Make copy of original
sel.species <- c(3:4, 6:7, 12:13)                      # Select those 6 species
speclist[sel.species]                                    # Check them out
speclist <- speclist[sel.species]                       # Update species list

# Restrict count data to the selected six species
str(counts <- counts[,,,sel.species])

# Scale and mean-impute both survey dates and survey hour (times)
DATES <- standardize(dates)
DATES[is.na(DATES)] <- 0
HOURS <- standardize(hours)
HOURS[is.na(HOURS)] <- 0

```

We express site aspect by northerliness (“north”) in radians, so that 0 means a site is facing due South and 3.14, i.e., π , means due North.

```

# Grab and scale elevation and aspect covariates
hist(elev <- HubbardBrook$sitecov$Elev, col = 'gold')
hist(aspect <- HubbardBrook$sitecov$Aspect, col = 'gold')
elev <- (elev - 500) / 100                            # center on 500 and scale by 100
north <- abs(HubbardBrook$sitecov$Aspect-180)/180 * pi

```

So we now have data from 6 species over 10 years, at 373 sites, and with 3 repeat counts in each year.

```

# Get sample sizes
nsites <- dim(counts)[1]
nreps <- dim(counts)[2]
nyears <- dim(counts)[3]
nspec <- dim(counts)[4]

# Look at relative abundance and occurrence patterns of those species
maxC <- apply(counts, c(1,3,4), max, na.rm = TRUE)
maxC[maxC == '-Inf'] <- NA
obsz <- maxC
obsz[obsz > 1] <- 1                                  # Observed p/a array for site, year and species

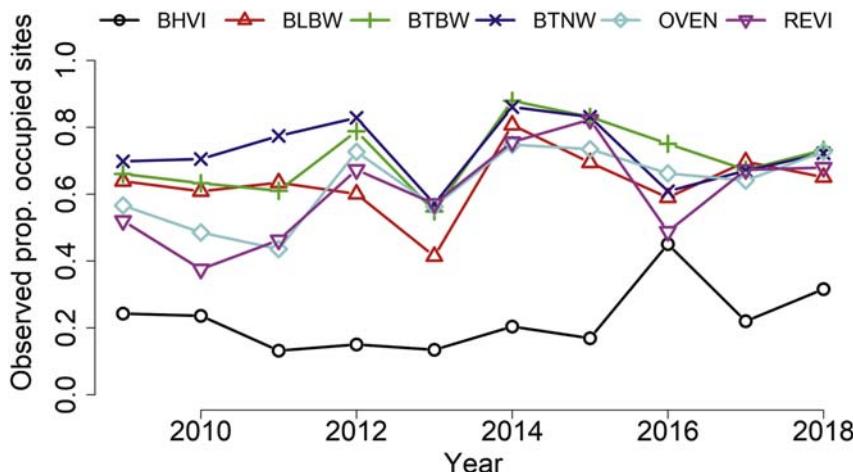
# Number of surveyed plots per year (for last 10 years)
tmp <- maxC[,1]
tmp[!is.na(tmp)] <- 1
(nplots.per.year <- apply(tmp, 2, sum, na.rm = TRUE))

# Observed proportion of occupied sites per year
noocc.obs <- apply(obsz, c(2,3), sum, na.rm = TRUE)
psi.obs <- noocc.obs / nplots.per.year

# Plot observed proportion of occupied sites (points) (Fig. 8.11)
par(cex.lab = 1.5, cex.axis = 1.5)
matplot(year, psi.obs, type = 'b', lty = 1,
       main = 'Observed occupancy per year and species', pch = 1:6, col = 1:6,
       xlab = 'Year', ylab = 'Observed occupancy', frame = FALSE, las = 1,
       ylim = c(0, 1.15), cex = 1.5, lwd = 3)
legend('topleft', legend = speclist, pch = 1:6, lwd = 2, col = 1:6,
       bty = 'n', horiz = TRUE, cex = 1.5)

```

We now use the Hubbard Brook data set to illustrate occupancy models with directional interactions and in [Section 8.5](#) for some interaction models for abundance.

**FIGURE 8.11**

Annual variation in the apparent distribution of six passerine species in the Hubbard Brook Experimental Forest between 2009 and 2018. We here express apparent distribution by the proportion of surveyed sites at which a species was detected in a year.

8.3.2 DIRECTIONAL DEPENDENCE IN A STATIC OCCUPANCY MODEL

We start by illustrating the model of Waddle et al. (2010) by choosing two Hubbard Brook species and modeling the parameters of the “subordinate” species as a function of the estimated presence (z) of the “dominant” species. Red-eyed Vireo (REVI) and Black-throated Green Warbler (BTNW) nest and forage in the same deciduous habitat, but the vireo is much larger (Scott Sillett, pers. comm.). Hence, we here assume that the vireo is the dominant and the warbler is the subordinate species. We start by selecting the data for these two species from one year (2016); in the next section we will fit an analogous dynamic model to their data for all 10 years.

```
# Quantize counts to become detection/nondetection data
y <- counts ; y[y > 1] <- 1

# Pull out REVI and BTNW data from 2016
str(yR <- y[, , '2016', 'REVI'])
str(yB <- y[, , '2016', 'BTNW'])

# Bundle and summarize data set
str(bdata <- list(yR = yR, yB = yB, nsites = nsites, nreps = nreps,
  elev = elev, north = north, DATES = DATES[,'2016'], HOURS = HOURS[,'2016']))

List of 8
$ yR   : num [1:373, 1:3] 0 1 1 1 1 1 1 1 1 0 ...
$ yB   : num [1:373, 1:3] 0 0 0 1 0 0 0 1 0 0 ...
$ nsites: num 373
$ nrep  : num 3
$ elev  : num [1:373] -0.26 -0.08 0.46 0.72 0.88 0.78 0.74 0.74 0.85 ...
$ north : num [1:373] 0.1107 0.3218 0.0907 0.0588 1.9757 ...
$ DATES: num [1:373, 1:3] -1.45 -1.45 -1.45 -1.45 -1.45 ...
$ HOURS: num [1:373, 1:3] -1.969 -1.778 -1.464 -1.218 -0.958 ...
```

Here's a recipe for writing a Waddle-type of occupancy model for two species:

- We stack two occupancy models.
- We use the latent presence/absence indicator (z) of the dominant species as a covariate in the occupancy model for the subordinate. Thus, z of the dominant species links the two occupancy models via an effect on the occupancy and/or detection of the subordinate species.
- There are certain bookkeeping challenges to keep track of the multitude of parameters. Here, we give parameters for the two species the same names, but we add an “R” for the dominant Red-eyed Vireo and a “B” for the subordinate Black-throated Green Warbler.

We fit effects of four of our favorite Hubbard Brook covariates: elevation and aspect (north) for occupancy and survey date and hour for detection probability. We allow for possible “effects” of the presence of vireos on all the parameters in the occupancy model for the warbler. That is, we stratify every parameter in the warbler model by $zR + 1$. (We need to add 1 because $zR = \{0, 1\}$, but we want parameter `theta[1]` to refer to vireo absence and `theta[2]` to vireo presence.)

As always, the clearest and most concise manner to describe the model, other than in the BUGS language, is algebra. We specify a single, or joint, model for both species, with the following two parts:

- (1) For the dominant species (Red-eyed Vireo), we have a simple static occupancy model:

$$\begin{aligned} z_i^R &\sim \text{Bernoulli}(\psi_i^R) && \# \text{ State model} \\ y_{i,j}^R &\sim \text{Bernoulli}(z_i^R p_{i,j}^R) && \# \text{ Observation model} \\ \text{logit}(\psi_i^R) &= \beta_0^R + \beta_1^R * \text{elev}_i + \beta_2^R * \text{north}_i && \# \text{ Linear model for occupancy of R} \\ \text{logit}(p_{i,j}^R) &= \alpha_0^R + \alpha_1^R * \text{date}_{i,j} + \alpha_2^R * \text{date}_{i,j}^2 + \alpha_3^R * \text{hour}_{i,j} && \# \text{ Linear model for detection of R} \end{aligned}$$

- (2) For the subordinate species (Black-throated Green Warbler), we have another static occupancy model, and we let the presence of the dominant species interact with some or all parameters. We fit the following model:

$$\begin{aligned} z_i^B &\sim \text{Bernoulli}(\psi_i^B) && \# \text{ State model} \\ y_{i,j}^B &\sim \text{Bernoulli}(z_i^B p_{i,j}^B) && \# \text{ Observation model} \\ \text{logit}(\psi_i^B) &= (1 - z_i^R)(\beta_{0,1}^B + \beta_{1,1}^B * \text{elev}_i + \beta_{2,1}^B * \text{north}_i) + z_i^R (\beta_{0,2}^B + \beta_{1,2}^B * \text{elev}_i + \beta_{2,2}^B * \text{north}_i) \\ \text{logit}(p_{i,j}^B) &= (1 - z_i^R)(\alpha_{0,1}^B + \alpha_{1,1}^B * \text{date}_{i,j} + \alpha_{2,1}^B * \text{date}_{i,j}^2 + \alpha_{3,1}^B * \text{hour}_{i,j}) + \\ & z_i^R (\alpha_{0,2}^B + \alpha_{1,2}^B * \text{date}_{i,j} + \alpha_{2,2}^B * \text{date}_{i,j}^2 + \alpha_{3,2}^B * \text{hour}_{i,j}) \end{aligned}$$

We here specify the interactions of BTNW parameters with REVI occurrence as an “if-else” statement, or “switch,” in the linear predictors for occupancy and detection. So when the dominant REVI is absent at a site, $z_i^R = 0$ and $(1 - z_i^R) = 1$, and the first part in the two sums gets switched on. We will then estimate the two sets of parameters $\{\beta_{0,1}^B, \beta_{1,1}^B, \beta_{2,1}^B\}$ and $\{\alpha_{0,1}^B, \alpha_{1,1}^B, \alpha_{2,1}^B, \alpha_{3,1}^B\}$. Alternatively, when REVI is present at a site, $z_i^R = 1$ and $(1 - z_i^R) = 0$. This will switch on the second part in the two sums, and we will estimate the two sets of parameters $\{\beta_{0,2}^B, \beta_{1,2}^B, \beta_{2,2}^B\}$ and $\{\alpha_{0,2}^B, \alpha_{1,2}^B\}$.

$\alpha_{2,2}^B, \alpha_{3,2}^B$. In the BUGS code, we specify these switches by nested indexing, e.g., we write `beta0B[zR[i] + 1]` for the intercept of B (remember that we add 1 to the binary `zR` because we need an index with the values 1 and 2). See also Fig. 8.15 for a graphical representation of this model.

In the Waddle/Richmond-type of interaction model, the presence of a dominant species is used as a covariate in the model for a subordinate species. More accurately, its presence is treated as a factor, i.e., a categorical explanatory variable with two levels: presence and absence. As always with linear models with factors, there are different parameterizations for the same model, and then (some of) the parameters may have a different interpretation; see Section 3.2.1 in AHM1. So, in our model, rather than using the presence of the dominant species as a “switch,” we could also use it directly in the model as an indicator variable. For the occupancy model of the subordinate warbler, we could write the linear predictor as follows:

$$\text{logit}(\psi_i^B) = \beta_0^B + \beta_1^B * z_i^R + \beta_2^B * \text{elev}_i + \beta_3^B * \text{north}_i + \beta_4^B * z_i^R * \text{elev}_i + \beta_5^B * z_i^R * \text{north}_i$$

In R linear model notation, we would write this linear model as `logit(psiB) ~ elev * zR + north * zR`, or as `logit(psiB) ~ zR + elev + north + zR:elev + zR:north`. This might then lead you to think more naturally about a reduced model, where the effects of elevation and aspect are unaffected by the presence of the dominant species, i.e., this linear model: `logit(psiB) ~ zR + elev + north` (thanks to Darryl MacKenzie for pointing this out).

As always with occupancy models, we can have fun with the estimates of the z matrix. For instance, we can classify the 373 sites by presence or absence of the two species, which yields four possible occupancy states. We calculate the number of sites in each occupancy state defined by the presence/absence of the two species as a derived quantity. As another set of derived quantities, we compute the difference in all parameters in the occupancy model for the warbler between sites where the vireo is present as compared to where the vireo is absent. The estimates of these differences can guide our choice about how much model complexity is needed, i.e., whether we need effects of vireo presence (`zR`) in all parameters of the warbler model.

```
# Specify model in BUGS language
cat(file = "staticWaddle.txt", "
model {

  # Model for Red-eyed vireo (REVI): the 'dominant' species
  # Priors for intercepts and coefficients
  mean.psiR <- ilogit(beta0R)
  beta0R ~ dnorm(0, 0.1)
  alpha0R ~ dnorm(0, 0.1)
  mean.pR <- ilogit(alpha0R)
  beta1R ~ dnorm(0, 0.1)
  beta2R ~ dnorm(0, 0.1)
  alpha1R ~ dnorm(0, 0.1)
  alpha2R ~ dnorm(0, 0.1)
  alpha3R ~ dnorm(0, 0.1)

  # Likelihood for REVI ('dominant')
  # Ecological model
  for (i in 1:nsites){
    zR[i] ~ dbern(psiR[i])
    logit(psiR[i]) <- beta0R + beta1R * elev[i] + beta2R * north[i]
    # Observation model
    for (j in 1:nreps){
      yR[i,j] ~ dbern(pR[i,j] * zR[i])
      logit(pR[i,j]) <- alpha0R + alpha1R * DATES[i,j] + alpha2R *
        pow(DATES[i,j],2) + alpha3R * HOURS[i,j]
    }
  }
}
```

```

# Model for Black-throated Green Warbler (BTNW) : the 'subordinate' sp.
# Priors for intercepts and coefficients
for(k in 1:2){ # Note all are stratified by presence/absence of REVI !
  mean.psiB[k] <- ilogit(beta0B[k])
  beta0B[k] ~ dnorm(0, 0.1)
  beta1B[k] ~ dnorm(0, 0.1)
  beta2B[k] ~ dnorm(0, 0.1)
  alpha0B[k] ~ dnorm(0, 0.1)
  mean.pB[k] <- ilogit(alpha0B[k])
  alpha1B[k] ~ dnorm(0, 0.1)
  alpha2B[k] ~ dnorm(0, 0.1)
  alpha3B[k] ~ dnorm(0, 0.1)
}

# Likelihood for BTNW ('subordinate')
# Ecological model
for (i in 1:nsites){
  zB[i] ~ dbern(psiB[i])
  logit(psiB[i]) <- beta0B[zR[i]+1] + beta1B[zR[i]+1] * elev[i] +
    beta2B[zR[i]+1] * north[i]      # note nested indexing as a 'switch' !
  # Observation model
  for (j in 1:nreps){
    yB[i,j] ~ dbern(pB[i,j] * zB[i])
    logit(pB[i,j]) <- alpha0B[zR[i]+1] + alpha1B[zR[i]+1] * DATES[i,j] +
      alpha2B[zR[i]+1] * pow(DATES[i,j],2) + alpha3B[zR[i]+1] * HOURS[i,j]
  }
}

# Derived quantities
# Differences in BTNW parameters between REVI presence and absence
diffbeta0B <- beta0B[2] - beta0B[1] # 'presence of R minus absence ...'
diffbeta1B <- beta1B[2] - beta1B[1]
diffbeta2B <- beta2B[2] - beta2B[1]
diffalpha0B <- alpha0B[2] - alpha0B[1]
diffalpha1B <- alpha1B[2] - alpha1B[1]
diffalpha2B <- alpha2B[2] - alpha2B[1]
diffalpha3B <- alpha3B[2] - alpha3B[1]
# Tally up number of sites in each of 4 states
for(i in 1:nsites){
  tmpRB[i] <- zR[i] * zB[i]
  tmpRb[i] <- zR[i] * (1-zB[i])
  tmprB[i] <- (1-zR[i]) * zB[i]
  tmprb[i] <- (1-zR[i]) * (1-zB[i])
}
nRB <- sum(tmpRB[])           # Number of sites with both species present
nRb <- sum(tmpRb[])           # Number of sites with only the vireo present
nrB <- sum(tmprB[])           # Number of sites with only the warbler present
nrb <- sum(tmprb[])           # Number of sites with both species absent
}

# Initial values
zst <- rep(1, nsites)
inits <- function() list(zR = zst, zB = zst)

# Parameters monitored
params <- c('mean.psiR', 'beta1R', 'beta2R', 'mean.pR', 'alpha1R', 'alpha2R', 'alpha3R',
  'mean.psiB', 'beta1B', 'beta2B', 'mean.pB', 'alpha1B', 'alpha2B', 'alpha3B', 'diffbeta0B',
  'diffbeta1B', 'diffbeta2B', 'diffalpha0B', 'diffalpha1B', 'diffalpha2B', 'diffalpha3B',
  'nRB', 'nRb', 'nrB', 'nrb')

# MCMC settings
na <- 5000 ; nc <- 3 ; ni <- 30000 ; nb <- 10000 ; nt <- 20

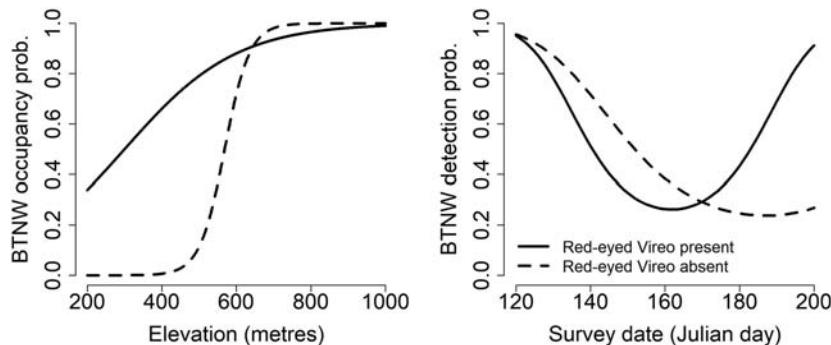
```

```
# Call JAGS (ART 39 min), assess convergence and summarize posteriors
out1 <- jags(bdata, inits, params, "staticWaddle.txt", n.adapt = na,
n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb, parallel = TRUE)
par(mfrow = c(3,3)) ; traceplot(out1)
which(out1$summary[,8] > 1.1)
print(out1, 2)

      mean    sd   2.5%   50%  97.5% overlap0     f Rhat n.eff
mean.psiR  0.95  0.04   0.86   0.96   1.00 FALSE 1.00 1.00 1769
beta1R    -1.64  0.35  -2.44  -1.61  -1.04 FALSE 1.00 1.00 3000
beta2R     0.20  0.21  -0.26   0.20   0.60 TRUE  0.83 1.00 3000
... output truncated ...
diffbeta0B  5.74  3.53  -2.15   5.76  12.77 TRUE  0.94 1.01  684
diffbeta1B -2.33  1.52  -5.82  -2.20   0.40 TRUE  0.96 1.01  313
diffbeta2B  1.74  2.44  -2.94  1.53   7.12 TRUE  0.78 1.03  86
diffalpha0B -0.15  0.34  -0.79  -0.15   0.55 TRUE  0.68 1.00 3000
diffalpha1B  0.67  0.24   0.22   0.66   1.15 FALSE 1.00 1.00 3000
diffalpha2B  0.15  0.29  -0.44  0.16   0.69 TRUE  0.71 1.00  977
diffalpha3B  0.33  0.20  -0.05  0.33   0.71 TRUE  0.96 1.00  533
nRB       247.96 15.25 215.00 250.00 275.00 FALSE 1.00 1.05  52
nRb       17.02 14.34  0.00 14.00  52.00 TRUE  1.00 1.05  51
nrB       90.19  8.71  75.00 90.00 109.00 FALSE 1.00 1.00 603
nrb      17.82  8.93  0.00 19.00  34.00 TRUE  1.00 1.00 1993
```

First, note that we estimate that 248 sites were occupied by both species, 17 by vireos only, 90 by warblers only, and 18 were unoccupied. Next, under our model any “effect” of Red-eyed Vireo presence on the presence/absence of the warbler will be reflected by a difference between the two elements in the warbler’s parameters. We test for such a difference in the derived quantities with names starting with “diff”: only for one of these differences does the CRI not overlap 0 (diffalpha1B). Interestingly, at sites where the vireo is present, there is a positive linear effect of date on detection probability of the warbler, while at sites where the vireo is absent, there is a negative effect. In addition, we note fairly large differences for the occupancy intercepts (diffbeta0B) and the effect of elevation (diffbeta1B) when vireos are present as opposed to when they are absent. Clearly, we need plots to understand the functional form of these estimated relationships (see website for code).

We see that contrary to any vague hypothesis that we might have had about the competitive exclusion of the smaller BTNW by the larger REVI, Fig. 8.12 (left) actually suggests that vireo presence is “beneficial” to the warbler: at lower elevations, the warbler is essentially absent unless the vireo is present. We don’t really believe that this pattern is the result of a direct interaction between the two species. Rather, we think that vireo presence is a proxy for some habitat covariate that is not in our model and which affects the occupancy probability of both species similarly. Fig. 8.12 (right) shows a striking difference in seasonal patterns of detection probability of the warbler depending on whether vireos are present or not. As always, we cannot formally “prove” the hypothesis of a direct interaction between the two species in our observational study, but we think that this is rather unlikely. Instead, we think again that these patterns are the result of hidden habitat variation and due to the effects of habitat quality for the warbler, for which the presence of the vireo is a mere proxy. The concave shape of the detection profile of the warbler at sites where vireos are present is characteristic for birds that nest, and where the two detection peaks may be either due to males singing before nesting and then an increase in detection probability later due to the presence of noisy young or alarming parents. Alternatively, the second peak could be due to a recrudescence of singing prior to a second brood (both species double-brood in good habitat: Scott Sillett, pers. comm.). In contrast, the warbler detection profile at sites where vireos are absent may mean either that no broods take place there at all or that there are no second broods.

**FIGURE 8.12**

Left: Estimated relationship between occupancy and elevation for Black-throated Green Warblers when Red-eyed Vireos are present (*solid line*) as compared to when they are absent (*dashed line*). Right: The analogous figure for the estimated relationship between detection probability and survey date.

8.3.3 DIRECTIONAL DEPENDENCE IN A DYNAMIC OCCUPANCY MODEL

Generalization of the Waddle formulation of an occupancy model with species interactions to a multi-season model is straightforward (Cayuela et al., 2013; Jones and Kroll, 2016; Michel et al., 2016; Green et al., 2018; Gallo et al., 2019). Such dynamic models with directional dependencies among pairs of species may be more powerful to detect species interaction patterns than static models (Mutshinda et al., 2011; Kissling et al., 2012), in part because they build up larger sample sizes over the years (Mason Fidino, pers. comm.). We illustrate with an open model, using the same two species (REVI and BTNW) over all 10 years, in the context of a dynamic occupancy model (see Chapter 4). As before, one of the main challenges is to not get confused by the profusion of parameters. We again label REVI parameters with an “R” and BTNW parameters with a “B.”

```
# Grab REVI and BTNW data for all 10 years
str(yR <- y[,,, 'REVI'])
str(yB <- y[,,, 'BTNW'])

# Bundle and summarize data set
bbcov <- as.numeric(scale(budburst))
str(bdata <- list(yR = yR, yB = yB, nsites = nsites, nyears = nyears,
  nreps = nreps, elev = elev, north = north, DATES = DATES, HOURS = HOURS,
  bbcov = bbcov) )

List of 10
$ yR    : num [1:373, 1:3, 1:10] 1 1 0 1 1 0 1 0 0 1 ...
$ yB    : num [1:373, 1:3, 1:10] 1 0 1 0 0 0 0 1 1 0 ...
$ nsites: int 373
$ nyears: int 10
$ nreps : int 3
$ elev   : num [1:373] -0.26 -0.08 0.46 0.72 0.88 0.78 0.74 0.74 ...
$ north  : num [1:373] 0.1107 0.3218 0.0907 0.0588 1.9757 ...
$ DATES : num [1:373, 1:3, 1:10] -1.36 -1.36 -1.36 -1.36 -1.36 ...
$ HOURS : num [1:373, 1:3, 1:10] -1.58 -1.378 -1.039 -0.798 -0.572 ...
$ bbcov : num [1:10] -0.489 -1.42 0.562 -1.399 -0.712 ...
```

For illustration of the interaction model, we focus on persistence and colonization which we make dependent on elevation, aspect (north), and on the budburst phenology covariate. We let these models for the warbler interact with vireo presence/absence (zR). These statistical interactions represent our

formulation of the potential biological interactions between the two species. Finally, we specify our favorite Hubbard Brook detection covariates (survey date and hour), but leave initial occupancy constant.

```

# Specify model in BUGS language
cat(file = "dynamicWaddle.txt", "
model {

# Dynocc model for Red-eyed Vireo (REVI; 'dominant')
# Priors for initial occupancy
mean.psiR ~ dunif(0, 1)
alpha.lpsiR <- logit(mean.psiR)
# Linear models and priors for phi and gamma
for (i in 1:nsites){
  for(t in 1:(nyears-1)){
    alpha.lphiR[i,t] <- alpha0.lphiR + beta.lphiR[1] * elev[i] +
      beta.lphiR[2] * north[i] + beta.lphiR[3] * bbcov[t]
    alpha.lgammaR[i, t] <- alpha0.lgammaR + beta.lgammaR[1] * elev[i] +
      beta.lgammaR[2] * north[i] + beta.lgammaR[3] * bbcov[t]
  }
}
for(v in 1:3){
  beta.lphiR[v] ~ dnorm(0, 0.1)
  beta.lgammaR[v] ~ dnorm(0, 0.1)
}
mean.phiR ~ dunif(0,1)
alpha0.lphiR <- logit(mean.phiR)
mean.gammaR ~ dunif(0,1)
alpha0.lgammaR <- logit(mean.gammaR)
# Priors for p
for(t in 1:nyears){
  alpha.lpR[t] <- mean.pR[t]
  mean.pR[t] ~ dunif(0, 1)
}
alpha1R ~ dnorm(0, 0.1)
alpha2R ~ dnorm(0, 0.1)
alpha3R ~ dnorm(0, 0.1)

# Likelihood for 'REVI'
# Ecological submodel
for (i in 1:nsites){
  # Initial conditions of system
  zR[i,1] ~ dbern(psi1R[i])
  logit(psi1R[i]) <- alpha.lpsiR
  # State transitions
  for (t in 2:nyears){
    zR[i,t] ~ dbern(zR[i,t-1]*phiR[i,t-1] + (1-zR[i,t-1])*gammaR[i,t-1])
    logit(phiR[i,t-1]) <- alpha.lphiR[i, t-1]
    logit(gammaR[i,t-1]) <- alpha.lgammaR[i, t-1]
  }
}

# Observation model
for (i in 1:nsites){
  for (j in 1:nreps){
    for (t in 1:nyears){
      yR[i,j,t] ~ dbern(zR[i,t] * pR[i,j,t])
      logit(pR[i,j,t]) <- alpha.lpR[t] + alpha1R * DATES[i,j,t] +
        alpha2R * pow(DATES[i,j,t],2) + alpha3R * HOURS[i,j,t]
    }
  }
}

# Dynocc model for Black-throated Green Warbler (BTNW; 'subordinate')
# Priors for initial occupancy
mean.psiB ~ dunif(0, 1)
alpha.lpsiB <- logit(mean.psiB)
```

```

# Linear models and priors for phi and gamma
for (i in 1:nsites){
  for(t in 1:(nyears-1)){
    alpha.lphiB[i,t] <- alpha0.lphiB[zR[i,t]+1] + beta.lphiB1[zR[i,t]+1] * elev[i] +
      beta.lphiB2[zR[i,t]+1] * north[i] + beta.lphiB3[zR[i,t]+1] * bbcov[t]
    alpha.lgammaB[i,t] <- alpha0.lgammaB[zR[i,t]+1] +
      beta.lgammaB1[zR[i,t]+1] * elev[i] + beta.lgammaB2[zR[i,t]+1] * north[i] +
      beta.lgammaB3[zR[i,t]+1] * bbcov[t]
  }
}
for(k in 1:2){  # Note here stratification by vireo presence/absence
  mean.phiB[k] ~ dunif(0,1)
  alpha0.lphiB[k] <- logit(mean.phiB[k])
  mean.gammaB[k] ~ dunif(0,1)
  alpha0.lgammaB[k] <- logit(mean.gammaB[k])
  beta.lphiB1[k] ~ dnorm(0, 0.1)
  beta.lphiB2[k] ~ dnorm(0, 0.1)
  beta.lphiB3[k] ~ dnorm(0, 0.1)
  beta.lgammaB1[k] ~ dnorm(0, 0.1)
  beta.lgammaB2[k] ~ dnorm(0, 0.1)
  beta.lgammaB3[k] ~ dnorm(0, 0.1)
}
}

# Priors for model of p
for(t in 1:nyears){
  alpha.lpB[t] <- mean.pB[t]
  mean.pB[t] ~ dunif(0, 1)
}
alpha1B ~ dnorm(0, 0.1)
alpha2B ~ dnorm(0, 0.1)
alpha3B ~ dnorm(0, 0.1)

# Likelihood for 'BTNW'
# Ecological submodel
for (i in 1:nsites){
  # Initial conditions of system
  zB[i,1] ~ dbern(psi1B[i])
  logit(psi1B[i]) <- alpha.lpsiB
  # State transitions
  for (t in 2:nyears){
    zB[i,t] ~ dbern(zB[i,t-1]*phiB[i,t-1] + (1-zB[i,t-1])*gammaB[i,t-1])
    logit(phiB[i,t-1]) <- alpha.lphiB[i,t-1]
    logit(gammaB[i,t-1]) <- alpha.lgammaB[i,t-1]
  }
}

# Observation model
for (i in 1:nsites){
  for (j in 1:nreps){
    for (t in 1:nyears){
      yB[i,j,t] ~ dbern(zB[i,t] * pB[i,j,t])
      logit(pB[i,j,t]) <- alpha.lpB[t] + alpha1B * DATES[i,j,t] +
        alpha2B * pow(DATES[i,j,t],2) + alpha3B * HOURS[i,j,t]
    }
  }
}

# Derived quantities
# Differences in BTNW parameters between REVI presence and absence
diffalpha0.lphiB <- alpha0.lphiB[2] - alpha0.lphiB[1]
diffalpha0.lgammaB <- alpha0.lgammaB[2] - alpha0.lgammaB[1]
diffbeta.lphiB1 <- beta.lphiB1[2] - beta.lphiB1[1]
diffbeta.lphiB2 <- beta.lphiB2[2] - beta.lphiB2[1]
diffbeta.lphiB3 <- beta.lphiB3[2] - beta.lphiB3[1]
diffbeta.lgammaB1 <- beta.lgammaB1[2] - beta.lgammaB1[1]
diffbeta.lgammaB2 <- beta.lgammaB2[2] - beta.lgammaB2[1]
diffbeta.lgammaB3 <- beta.lgammaB3[2] - beta.lgammaB3[1]

```

```

# Tally up number of sites in each of 4 states
for (t in 1:nyears){
  for(i in 1:nsites){
    tmpRB[i,t] <- zR[i,t] * zB[i,t]
    tmpRb[i,t] <- zR[i,t] * (1-zB[i,t])
    tmprB[i,t] <- (1-zR[i,t]) * zB[i,t]
    tmprb[i,t] <- (1-zR[i,t]) * (1-zB[i,t])
  }
  nRB[t] <- sum(tmpRB[,t]) # Number of sites with both species
  nRb[t] <- sum(tmpRb[,t]) # Number of sites with only the vireo
  nrB[t] <- sum(tmprB[,t]) # Number of sites with only the warbler
  nrb[t] <- sum(tmprb[,t]) # Number of sites with neither species
}
}
")

# Initial values
zst <- array(1, dim = c(nsites, nyears))
inits <- function() { list(zR = zst, zB = zst) }

# Parameters monitored
params <- c('mean.psiR', 'mean.phiR', 'mean.gammaR', 'mean.pR',
  'alpha.lpsiR', 'alpha0.lphiR', 'alpha0.lgammaR', 'beta.lphiR',
  'beta.lgammaR', 'alpha.lpR', 'alpha1R', 'alpha2R', 'alpha3R',
  'mean.psib', 'mean.phiB', 'mean.gammab', 'mean.pB', 'alpha.lpsiB',
  'alpha0.lphiB', 'alpha0.lgammab', 'beta.lphiB1', 'beta.lphiB2',
  'beta.lphiB3', 'beta.lgammab1', 'beta.lgammab2', 'beta.lgammab3',
  'alpha.lpB', 'alpha1B', 'alpha2B', 'alpha3B', 'diffalpha0.lphiB',
  'diffalpha0.lgammab', 'diffbeta.lphiB1', 'diffbeta.lphiB2',
  'diffbeta.lphiB3', 'diffbeta.lgammab1', 'diffbeta.lgammab2',
  'diffbeta.lgammab3', 'nRB', 'nRb', 'nrB', 'nrb')

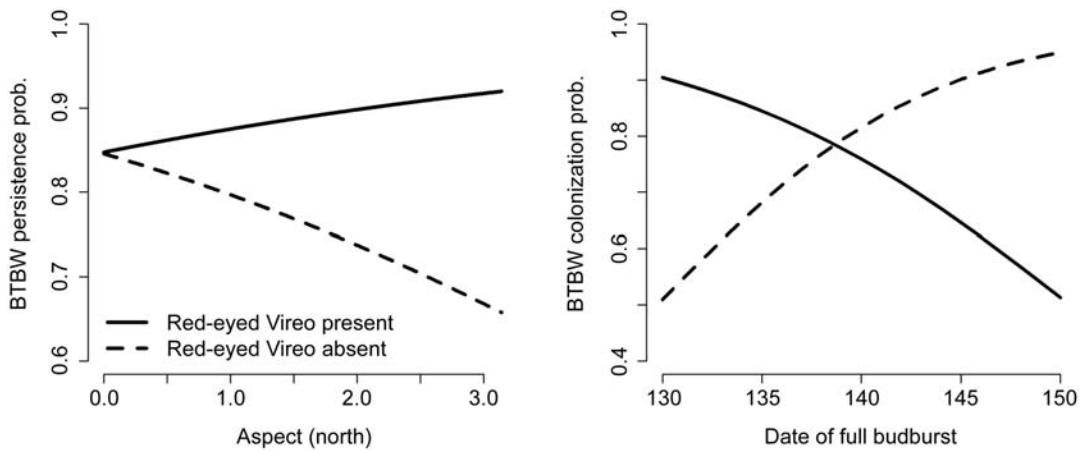
# MCMC settings
na <- 5000 ; ni <- 10000 ; nt <- 5 ; nb <- 5000 ; nc <- 3

# Call JAGS (ART 323 min), check convergence and summarize posteriors
out2 <- jags(bdata, inits, params, "dynamicWaddle.txt", n.adapt = na,
  n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb, parallel = TRUE)
par(mfrow = c(3,3)) ; traceplot(out2) ; par(mfrow = c(1,1))
which(out2$summary[,8] > 1.1)
print(out2$summary[, -c(4:6, 10:11)], 2)

      mean        sd       2.5%     97.5%   Rhat n.eff
mean.psiR  0.58788  0.03053  0.527482  0.64761 1.00 3000
mean.phiR  0.97604  0.00893  0.954922  0.98890 1.03   84
mean.gammaR 0.62962  0.05668  0.517656  0.73867 1.00 831
... output truncated ...
diffalpha0.lphiB  0.01327  0.67091 -1.454793  1.20533 1.03   72
diffalpha0.lgammaB -0.84677  1.37805 -3.826917  1.41830 1.05   56
diffbeta.lphiB1 -0.03145  0.22120 -0.480559  0.39371 1.00 514
diffbeta.lphiB2  0.56479  0.24648  0.121004  1.08160 1.02 131
diffbeta.lphiB3 -0.14117  0.30585 -0.706631  0.48144 1.00 3000
diffbeta.lgammab1 0.49208  0.39742 -0.236849  1.32898 1.03   79
diffbeta.lgammab2 -0.43980  0.37352 -1.189054  0.29883 1.01 240
diffbeta.lgammab3 -1.19232  0.50848 -2.292762 -0.30256 1.00 684
... output truncated ...

```

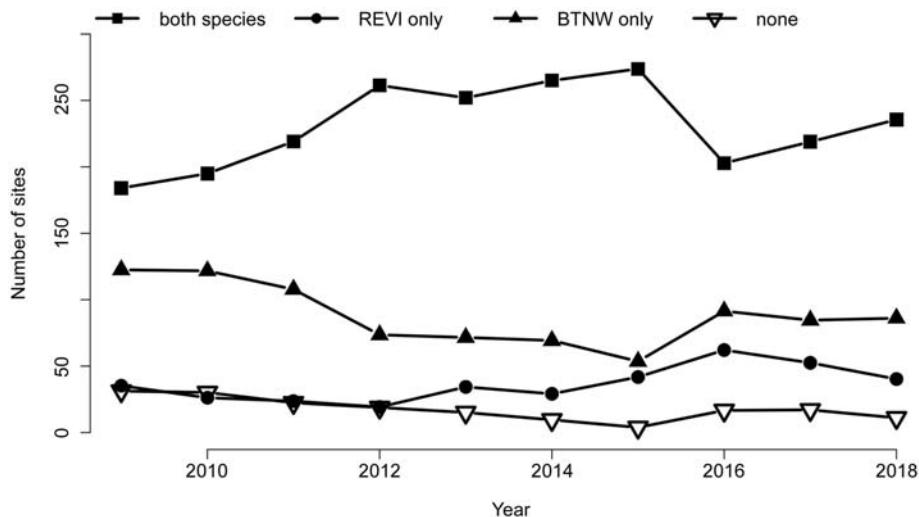
The “contrast derived quantities” (those starting with “diff”) suggest differences in lphiB2 (the coefficient of aspect in the model for persistence, CRI = 0.12/1.08) and lgammaB3 (the coefficient of budburst in colonization, CRI = -2.29/-0.20) for the warbler, depending on whether the vireo is present or not. In the hope of understanding the influence of these parameters on warbler persistence and colonization, we form predictions with these covariates and plot them ([Fig. 8.13](#)). We learn that between 2009 and 2018, Black-throated Green Warbler persistence in Hubbard Brook slightly increased at sites with more north-facing aspect when Red-eyed Vireos were present (left), but decreased sharply with more northern aspects when vireos were absent.

**FIGURE 8.13**

Estimated relationships between persistence and aspect (left) and between colonization and the date of full budburst (right) for Black-throated Green Warblers when Red-eyed Vireos are present at a site (solid line) as compared to when they are absent (dashed line).

Colonization probability was greater in "early" years at sites with vireos, but greater in "late" years at sites where vireos were absent (right).

As always in an occupancy model, we could use the estimates of the z matrix in clever ways to learn something about the analyzed population. Fig. 8.14 shows the result of tallying up the number of sites in Hubbard Brook for the four occupancy states defined by presence and absence of Red-eyed Vireo and Black-throated Green Warbler.

**FIGURE 8.14**

Estimates of the number of sites in each of the four occupancy states defined by the presence and absence of the Red-eyed Vireo (REVI) and the Black-throated Green Warbler (BTNW) in Hubbard Brook between 2009 and 2018 under the dynamic occupancy model with directional mode of interactions. CRIs are omitted to avoid clutter.

8.3.4 STRUCTURAL EQUATION MODELING OF SPECIES INTERACTION NETWORKS

[Fig. 8.15](#) shows a graphical representation of the static two-species occupancy model with directional interactions from [Section 8.3.2](#). Although strictly a linear model in the GLM sense, we see that it actually represents a fairly complex, reticular system of hypothesized causal relationships. We could envision situations where we might even increase the complexity of a modeled system of interactions among species. One way of increasing complexity further might be by adding directional dependencies among covariates: for instance, elevation and aspect could first affect vegetation cover, and this in turn could affect bird occurrence. Alternatively, we might add complexity on the side of the modeled bird species: for instance, we might add a predator which may perhaps prefer as prey one of the two species over the other. In this way, we could generate a more complex species interaction network. In such a network, it might be interesting to estimate “interaction strengths” and to distinguish direct from indirect “causes” in the occurrence or the abundance of a species, as a function of both the environment and the other species in the network with which the focal species putatively interacts.

Structural equation models (SEMs) are a class of models for describing such net-like relationships among hypothesized causes and effects (Shipley, 2000; Grace, 2006; Grace et al., 2012). In the usual applications, SEMs are framed fully within a correlative mode of inference. Hence, they cannot really identify causes and effects; for this we would still need data from manipulative experiments or direct observations of the behavior of individuals of these species. Nevertheless, SEMs offer an interesting framework for representing, in a statistical model, hypothesized cause-effect relationships in an interaction network. SEMs can be fit in BUGS and we are aware of three published studies so far, all involving CJS models (Cubaynes et al., 2012; Gimenez et al., 2012; Souchay et al., 2018). In addition, Joseph et al. (2016) fit a static occupancy model with SEM components in Stan. None of them focused on the modeling of interactions among their target species (birds and amphibians). But it seems obvious that SEMs could be a natural framework for specifying and testing hypotheses about interactions in species networks and that the models of Waddle et al. (2010) and Richmond et al. (2010) might be a useful starting point for doing this in the context of an occupancy model. The hierarchy of latent structure and observed data in an occupancy or related model lends itself very naturally to be extended with additional latent structure, to become an SEM (Joseph et al., 2016).

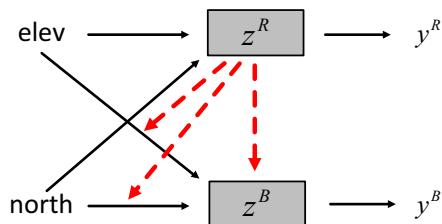


FIGURE 8.15

A graphical representation of a two-species static occupancy model with directional interactions (as in [Section 8.3.2](#)): z^R and z^B (in the gray boxes) and y^R and y^B represent, respectively, the latent presence/absence and the observed detection/nondetection of the Red-eyed Vireo and the Black-throated Green Warbler. Solid arrows represent the covariate effects on the occurrence of these two species on the left and the observation process on the right. Dashed arrows represent the statistical interactions between the presence/absence of the species supposed to be dominant (R) and the parameters in the occupancy model of the species supposed to be the subordinate (B). (To prevent graphical clutter, effects of survey date and hour in the observation process are omitted.)

8.4 JOINT OCCUPANCY MODELS FOR “MANY” SPECIES: JOINT SPECIES DISTRIBUTION MODELS (JSDMS)

8.4.1 A BRIEF INTRODUCTION TO JSDMS

The models for species interactions considered so far were for just a small handful of species. In principle, it would be possible to extend both frameworks that we have encountered so far to many species: for symmetric interactions, a multivariate Bernoulli (MVB) distribution (or the multivariate probit model of Pollock et al., 2014), and for directional interactions the use of the occurrence or abundance of one species as a covariate in the model of another species. However, in practice, modeling directional interactions among many species becomes impossible, because it is just too cumbersome to describe all the interactions, we don’t know all possible interactions, or it may simply not be sensible to assume purely unidirectional interactions for every species pair in a modeled community. Hence, in practice, we model symmetric interactions as soon as we have more than just a small handful of species.

However, one problem with such models is that they quickly become very data-hungry on the one hand, but also very computationally expensive on the other. Large numbers of parameters will be required to describe just the two-way interactions and more still for higher-order interactions. For instance, we need $n * (n - 1)/2$ parameters when modeling all pairwise interactions among n species. As an example, this represents 435 covariances alone for a smallish community of 30 species. In addition, for rare species we will hardly have any data to estimate such covariances. Hence, a lot of effort in ecological statistics has been spent to make the fitting of multispecies models with interactions computationally easier via more efficient algorithms (Dorazio and Rodriguez, 2012; Hepler et al. 2018; Hepler and Erhardt, 2020), approximations (or dimension-reduction techniques; Hui et al., 2015; Warton et al., 2015) or specialized software (Ovaskainen et al., 2017; Tikhonov et al., 2017).

Historically, the first occupancy-based community models with species interactions were all developed ignoring detection probability (e.g., Latimer et al., 2009; Ovaskainen et al., 2010b; Clark et al., 2014; Pollock et al., 2014). Such models have lately become called *joint species distribution models* (JSDMs), because they describe the joint distribution of multiple species, including their possible non-independence via parameters for pairwise statistical interactions. These models have increasingly used probit rather than the logit link for binary presence/absence data, because a probit leads to more efficient MCMC algorithms (Chib and Greenberg, 1998; Dorazio and Rodriguez, 2012; Scharf et al., 2021). In more recent years, latent variables (LV) were recognized to be a powerful dimension-reduction technique also for JSDMs, and most recent JDSM developments are based on LVs (e.g., Hui et al., 2015; Letten et al., 2015; Warton et al., 2015; Hui, 2016; Ovaskainen et al., 2016a,b; Thorson et al., 2016; Tikhonov et al., 2017). In an SDM with LVs, instead of estimating a full, unstructured variance-covariance (VC) matrix of some parameter for all pairs of species in a community, we only estimate the site-specific values of a small number of unobserved, or latent, explanatory variables, along with their associated coefficients for each species. Doing this for a fairly small number of LVs usually allows one to obtain an adequate approximation of the full VC matrix (Warton et al., 2015, but see Tobler et al., 2019). One interesting side effect of these models is that the latent variables and their coefficients can be used for model-based ordination, i.e., to order sites based on species composition or to order species based on their response to the environment (Hui et al., 2015; Warton et al., 2015). Hui (2016) has developed the R package `boreal`, which is a wrapper for JAGS, and which permits fitting correlated-response GLMs using LV techniques. Thus, it can fit almost exactly the model in this section and also that in [Section 8.5.4](#), just without any component for detection probability.

Most recent JSMD developments for “many” species have ignored imperfect detection (Beissinger et al., 2016), except for Tobler et al. (2019), who develop two joint occupancy models for many species and which do account for imperfect detection. In the next section, we present one of these models, a community occupancy model with latent variables. In Section 8.5.4, we translate that model into abundance to become a joint N-mixture community model.

JAGS may not be the best software to fit complex community models with interactions to data sets from moderate to large communities. Nevertheless, we continue to use this software here, because it is such a flexible and user-friendly, general-purpose statistical modeling software and because the BUGS language makes it so wonderfully transparent what kind of model we actually fit (Crainiceanu et al., 2005; Kéry, 2010). In the future it is to be hoped that more powerful, customized software for JSMDs will be developed, which will allow full accommodation of imperfect detection for data sets that have the required replicated detection/nondetection or count data (Beissinger et al., 2016; Tobler et al., 2019).

For a general overview of recent community, or joint, community models of the kind showcased in this chapter we refer you to Warton et al. (2015, 2016), Beissinger et al. (2016), Dormann et al. (2018a) and Tobler et al. (2019). Also see Wilkinson et al. (2019) for a useful conceptual and practical comparison of several recently developed JSMDs and their associated software.

8.4.2 THE LATENT-VARIABLE OCCUPANCY MODEL OF TOBLER et al. (2019)

Tobler et al. (2019) develop two community models with species interactions and imperfect detection. The first is based on the multivariate probit model of Pollock et al. (2014) and the second on the latent-variable models in Hui et al. (2015), Letten et al. (2015), and Hui (2016). These new models could be described as a variant of the community occupancy models in Chapter 11 in AHM1, but with a multivariate Normal (MVN) distribution for site random effects tacked on to allow for non-independence of species occurrences (see Section 8.5.1). Alternatively they could be called JSMDs like the models by Pollock et al. (2014), Hui et al. (2015), and others, but with a submodel for imperfect detection added. Thus, the Tobler et al. models unify two important developmental lines in ecological statistics: those of multispecies occupancy models of the type pioneered by Dorazio and Royle (2005) and those of the multispecies GLM-type of interaction models for which Latimer et al. (2009) and Ovaskainen et al. (2010b) provide some of the earliest examples. Here, we illustrate the latent-variable models of Tobler et al. (2019), which proved to be computationally more efficient than the extension to imperfect detection of the model by Pollock et al. (2014). This section draws heavily on Tobler et al. (2019).

The starting point of this model is a multispecies occupancy model with a probit link function that we specify via the use of an auxiliary variable. To model non-independence among species pairs, instead of estimating an MVN distribution with unstructured VC matrix, we specify L latent site variables, the values of which we are able to estimate along with their coefficients for each species. Thus, we express the occurrence z of species k at site i through the values of a standard Normally distributed random variable w with mean μ and variance (or standard deviation) equal to 1.

$$w_{i,k} \sim \text{Normal}(\mu_{i,k}, 1), \text{ and } z_{i,k} = I(w_{i,k} > 0)$$

Hence, $z = 1$ if $w > 0$ and $z = 0$ if $w \leq 0$, and this is simply a way of specifying a probit link for occupancy probability ψ via the auxiliary variable w (Dorazio and Rodriguez, 2012; Scharf et al., 2021). Our detection submodel in the LV model of Tobler et al. (2019) is the usual Bernoulli distribution with a logit link for covariate effects in detection probability p . Alternatively, we might also use another probit link for detection as did for instance Dorazio and Rodriguez (2012). Covariates for occupancy probability can be specified as a linear regression model for μ , e.g., we might write

$$\mu_{i,k} = \beta_{0,k} + \beta_{1,k} * elev_i + \beta_{2,k} * north_i,$$

where $\beta_{0,k}$, $\beta_{1,k}$ and $\beta_{2,k}$ are the probit-scale intercepts and the linear effects of site elevation and aspect, respectively, for species k . We will typically model these species-level parameters hierarchically, as in the community occupancy models in Chapter 11 in AHM1, by drawing each from a Normal distribution with estimated hyperparameters that describe the mean and the variability of all the species in the sampled community.

To account for correlations among species, we introduce a set of L latent variables $\mathbf{l}_{i,l} = (l_{i,1}, \dots, l_{i,L})$ (note this is a lower-case L, not an upper-case I as we use for the indicator function) and a vector of L associated, species-specific latent variable coefficients $\boldsymbol{\theta}_i = (\theta_{i,1}, \dots, \theta_{i,L})$. These latent variables can be thought of as unknown site-specific covariates, or unobserved predictors, which are specified as standard Normal random variables, i.e., as draws from a Normal distribution with zero mean and unit variance. Somewhat miraculously, their values for each site can be estimated, along with the coefficients associated with each latent variable, for every species!

To make things more explicit, we could express the above model with two latent variables added as follows, still employing the probit link via the auxiliary variable construction, but now writing explicitly the residuals associated with the auxiliary variables, as do Tobler et al. (2019):

$$\begin{aligned} z_{i,k} &= I(w_{i,k} > 0) \\ w_{i,k} &= \beta_{0,k} + \beta_{1,k} * elev_i + \beta_{2,k} * north_i + \theta_{1,k} * l_{i,1} + \theta_{2,k} * l_{i,2} + \varepsilon_{i,k}, \end{aligned}$$

with $l_{i,1} \sim \text{Normal}(0, 1)$ and $l_{i,2} \sim \text{Normal}(0, 1)$ and

$$\varepsilon_{i,k} \sim \text{Normal}(0, \sigma_k^2) \text{ and } \sigma_k^2 = 1 - \sum_{l=1}^L \theta_{k,l}^2$$

Note that this model has an intercept β_0 and four slope parameters ($\beta_1, \beta_2, \theta_1, \theta_2$). All are indexed by k , which means that they differ for every species. Two of the coefficients (β_1, β_2) relate $w_{i,k}$ to the two known site covariates `elev` and `north`, while the two other coefficients (θ_1, θ_2) relate it to the two unknown site covariates, the values of which are also estimated. The “residual” ε causes w to have a Normal distribution with unit variance, as required for a probit regression.

As a requirement for identifiability when modeling binary responses, the latent variable coefficients θ must be constrained to lie between -1 and 1 using a Uniform prior distribution. Furthermore (citing directly from Tobler et al. (2019), but adjusting to our notation), “... with more than a single variable (i.e., when $L > 1$), we need to impose constraints on θ additional to those given above (Hui et al. 2015) to ensure parameter identifiability. In particular, if θ is an $n \times L$ matrix of coefficients for L latent variables and n species, the diagonal elements are constrained to lie between 0 and 1, and the upper diagonal elements are set to 0. To account for the variance absorbed by the latent variables, the variance of the residuals $\varepsilon_{i,k}$ needs to be adjusted to ensure that the total variance is equal to one. We therefore calculate an adjusted variance σ_k^2 for each species k . Specifically, the formula for the variance of $\varepsilon_{i,k}$ used above ensures that the overall variance of $w_{i,k}$ remains at one... After fitting the latent variable model, the full species correlation matrix R can be derived from the correlation in the latent variables as $R = \theta\theta^T + \text{diag}(\sigma_1^2, \sigma_2^2, \dots, \sigma_n^2)$.”

We find it quite remarkable that we should be able to estimate both the values of such latent variables $l_{i,l}$ for every site i as well as the values of the latent variable coefficients $\theta_{k,l}$ for every species k and every latent variable l . And not just for two latent variables, but in principle also for 10, 20, or more. One practical question then clearly is “how many latent variables are required for an adequate representation of the correlation matrix?”. Conventional wisdom seems to suggest that as few as 2–5 may be

sufficient (Warton et al., 2015), but simulation results reported in Tobler et al. (2019) suggest that as many as $n/2$ may be required for a model with n species, regardless of whether the model accommodates imperfect detection or not. In practice, we may either make an educated guess of how many are required and then fit a model with that many latent variables, or we fit the same model with different numbers of latent variables and then plot the sum of the residual correlation against the number of LVs (Tobler et al., 2019). As a more sophisticated solution, one could also estimate the optimal number of LVs in a Bayesian analysis (Warton et al., 2015; Ovaskainen et al., 2017; Tikhonov et al., 2017).

Here, we simply give a brief illustration of Tobler et al.’s community occupancy model, or JDSM, using 2 latent variables. We use data set `SwissAtlasHa` which contains replicated count data of 78 Swiss passerine species that Tobler et al. (2019) used as a case study. The original data set contains 79 taxa, but we lumped together two subspecies of the Carrion Crow. For a description of that data set, we cite again from Tobler et al. (2019): “*We applied the LV model to the community of 79 passerine bird species detected in Switzerland during the surveys for the most recent Swiss breeding bird atlas (Knaus et al. 2018), where 2–3 surveys were conducted along irregular transects of typically 4–6 km length during one breeding season (15 April–1 July) between 2012–2016 in a total of 2,318 randomly selected 1-km² quadrats. We expected species interactions to take place at the local scale of a territory, which for most passersines is on the order of one to a few hectares (see Kéry and Royle, 2016, p. 279–282, for one group of passersines, the Paridae family). The comparatively large sampling area of 1 km² per site in the Swiss atlas might mask the consequences of species interactions on presence-absence patterns at the biologically relevant (local) scale. We therefore randomly picked one 1-ha quadrat within each 1-km² quadrat, provided it was covered by the survey transect.*” The data set contains seven site covariates: x- and y-coordinate (in our usual funny transformed scale to protect the locations of the MHB quadrats), mean quadrat elevation (in meters), slope (in degrees), aspect (“north,” calculated as the cosine of aspect, which is equal to 1 if the aspect is north and -1 if the aspect is south), and forest cover (as a proportion within a 1-ha Queens neighborhood, i.e., for all 8 neighboring cells). The number of replicate surveys (2 or 3) conducted is also provided as a site covariate. For an observational covariate, the data set contains the Julian date of every survey. In our model, we will fit linear and quadratic effects of elevation, slope, north, and forest cover in occupancy and linear and quadratic effects of survey date in detection.

Next, we load that data set, threshold the counts to become binary detection/nondetection data, make a restriction to 1200 sites and approx. 30 species (to avoid having to wait for weeks for the models to run), and fit a community occupancy model with 2 LVs for illustration. In [Section 8.5.4](#), we fit the N-mixture version of this model to the actual counts.

```
# Load data set from Tobler et al. (2019)
library(AHMbook)
data(SwissAtlasHa)
str(dat <- SwissAtlasHa)

# Grab counts and threshold them to become detection/nondetection data
str(counts <- dat$counts)           # Array of counts (2318 x 3 x 78)
y <- counts
y[y > 1] <- 1                      # Array of detection/nondetection data
str(y)

# Subset sites to a random sample of 1200 (about half)
set.seed(1, sample.kind = "Rounding")
sel.sites <- sort(sample(1:2318, 1200, replace = FALSE))
str(cc <- counts[sel.sites,,])
str(yy <- y[sel.sites,,])
```

```

# Calculate sum of max counts across sites and obs. number of occ. sites
tmp <- apply(cc, c(1,3), max, na.rm = TRUE)
summax <- apply(tmp, 2, sum) # p-ignorant estimate of Ntotal
tmp <- apply(yy, c(1,3), max, na.rm = TRUE)
nobs <- apply(tmp, 2, sum) # p-ignorant estimate of sum(z)
sort(nobs) # Look at species ordered by nobs

# Restrict data set according to number of observed occurrences
sel.species <- which(nobs > 39) # yields about 30 species left
cc <- cc[, sel.species]
yy <- yy[, sel.species]
str(cc) ; str(yy) # Counts and det/nondet. for 1200 sites and approx. 30 spec.

# Determine sample sizes
(nsites <- dim(yy)[1])
(nspec <- dim(yy)[3])
table(nreps <- dat$sitecova[sel.sites,'nsurveys']) # 2 or 3 surveys per site

# Grab, restrict, scale and mean-impute covariates
library(abind)
str(xocc <- as.matrix(dat$sitecova[sel.sites,3:6])) # Occ. covariates
str(xocc <- cbind(xocc, xocc^2)) # Add squares of covariates
xocc <- scale(xocc) # Scale column-wise
str(xdet <- dat$dates[sel.sites,]) # Detection covariates
xdettmp <- standardize(xdet) # Scale matrix-wide
xdettmp[is.na(xdettmp)] <- 0 # Mean-impute dates of 3rd survey
str(xdet <- abind(xdettmp, xdettmp^2, along = 3) )

# Provide for different numbers of LVs: could try 2, 5, 10, 15
NLV <- c(2, 5, 10, 15) # Here we will just take 2

# Bundle data (incl. choice of number of LVs)
str(bdata <- list(y = aperm(yy, c(1,3,2)), Xocc = xocc, Xdet = xdet,
  ncov.occ = ncol(xocc), ncov.det = 2, nlv = NLV[1], nsites = nsites,
  nspec = nspec, nreps = nreps))

List of 9
$ y : num [1:1200, 1:30, 1:3] 0 0 0 1 0 0 0 0 0 0 ...
$ Xocc : num [1:1200, 1:8] -1.033 -0.724 -0.413 -1.055 -0.726 ...
$ Xdet : num [1:1200, 1:3, 1:2] -1.34 -1.38 -1.42 -1.68 -1.34 ...
$ ncov.occ: int 8
$ ncov.det: num 2
$ nlv : num 2
$ nsites : int 1200
$ nspec : int 30
$ nreps : num [1:1200] 3 3 3 3 3 3 3 3 3 3 ...

# Specify model in BUGS language
cat(file = "JSDMocc.txt", "
model{
# Community priors for occupancy
mu.beta0 <- logit(mean.psi0) # Intercept
mean.psi0 ~ dunif(0, 1)
tau.beta0 <- pow(sd.beta0, -2)
sd.beta0 ~ dunif(0, 2)
for(v in 1:ncov.occ) { # Coefficients
  mu.beta[v] ~ dnorm(0, 0.2)
  tau.beta[v] <- pow(sd.beta[v], -2)
  sd.beta[v] ~ dunif(0, 2)
}

```

```

# Community priors for detection
mu.alpha0 <- logit(mean.p)                                # Intercept
mean.p ~ dunif(0, 1)
tau.alpha0 <- pow(sd.alpha0, -2)
sd.alpha0 ~ dunif(0, 1)
for(v in 1:ncov.det) {                                       # Coefficients
  mu.alpha[v] ~ dnorm(0, 0.1)
  tau.alpha[v] <- pow(sd.alpha[v], -2)
  sd.alpha[v] ~ dunif(0, 1)
}

# Define species random effects for all coefficients
for (k in 1:nspc) {
  # Random species effects in the occupancy model
  beta0[k] ~ dnorm(mu.beta0, tau.beta0)      # Intercepts
  for(v in 1:ncov.occ) {                      # Coefficients
    beta[k, v] ~ dnorm(mu.beta[v], tau.beta[v])
  }
  # Random effects for detection
  alpha0[k] ~ dnorm(mu.alpha0, tau.alpha0) # Intercepts
  for(v in 1:ncov.det) {                  # Coefficients
    alpha[k, v] ~ dnorm(mu.alpha[v], tau.alpha[v])
  }
}

# Priors for latent variables: standard Normal rv
for(i in 1:nsites) {
  for(l in 1:nlv){
    LV[i,l] ~ dnorm(0, 1)
  }
}

# Latent variable coefficients with constraints
# Diagonal elements positive, upper diagonal equal to 0
for(l in 1:(nlv-1)){
  for(l2 in (l+1):nlv){
    lv.coef[l,l2] <- 0
  }
}
## Sign constraints on diagonal elements
for(l in 1:nlv) {
  lv.coef[l,l] ~ dunif(0, 1)
}
# Lower diagonal free
for(l in 2:nlv){
  for(l2 in 1:(l-1)){
    lv.coef[l,l2] ~ dunif(-1, 1)
  }
}
# Other elements free
for(l in (nlv+1):nspc) {
  for(l2 in 1:nlv){
    lv.coef[l,l2] ~ dunif(-1, 1)
  }
}

```

```

# Define the multi-species occupancy model
for (i in 1:nsites) {                                     # Loop over sites
  for (k in 1:nspc) {                                    # Loop over species
    # Probit link GLM for occupancy via auxiliary variable approach
    eta[i,k] <- beta0[k] + inprod(beta[, k], Xocc[i, ]) +
      inprod(lv.coef[, k], LV[i, ])
    # Draw Gaussian auxiliary variable, with variance constrained to 1
    mu.psi[i,k] ~ dnorm(eta[i,k], 1/(1-sum(lv.coef[, 1:nlv]^2)))
    z[i,k] <- step(mu.psi[i,k])
    # Bernoulli GLM for detection
    for (j in 1:nreps[i]) {                               # Loop over 2 or 3 surveys
      logit(p[i,k,j]) <- alpha0[k] + alpha[k, 1] *
        Xdet[i,j,1] + alpha[k, 2] * Xdet[i,j,2]
      y[i,k,j] ~ dbern(p[i,k,j]*z[i,k])
    }
  }
}
")

```

We found this model to be *very* hard to fit in JAGS, and even with just 2 latent variables, runs lasted for several days (which would become weeks for 5 or more latent variables). In addition, chains especially for the latent variable coefficients (θ above, or “`lv.coef`” in the BUGS code) were mixing very badly. We fit the model in multiple steps, first with somewhat “blind” initial values, but later using the posterior means of earlier model runs as starting values for many parameters. Note that the initialization for `mu.psi` in a latent probit model is functionally analogous to the usual initialization of the `z` variables in a traditional occupancy model. We also note that the constraints on the LV coefficients in the model must be replicated in the initial values.

```

# 'Blind' initial values
inits <- function() {
  lv.coef <- matrix(0, nspec, bdata$nlv)
  lv.coef[1:bdata$nlv, 1:bdata$nlv] <- 0
  for(l in 1:bdata$nlv-1){ lv.coef[l, (l+1):bdata$nlv] <- NA}
  LV <- matrix(rnorm(bdata$nlv * nsites), nsites, bdata$nlv)
  lv.coef <- matrix(runif(bdata$nlv * nspec, -sqrt(1/(bdata$nlv+1)),
    sqrt(1/(bdata$nlv+1))), nspec, bdata$nlv) * lv.coef
  mu.psi <- array(1, dim = c(nsites, nspec))          # yields psi = 0.84
  list(LV = LV, lv.coef = lv.coef , mu.psi = mu.psi)
}

# Parameters to be monitored
params <- c('mean.psi0', 'mu.beta0', 'sd.beta0', 'mu.beta', 'sd.beta',
  'mean.p', 'mu.alpha0', 'sd.alpha0', 'mu.alpha', 'sd.alpha', 'beta0',
  'beta', 'alpha0', 'alpha', 'LV', 'lv.coef')           # could add 'z'

# MCMC settings
na <- 10000 ; ni <- 250000 ; nt <- 100 ; nb <- 150000 ; nc <- 3

# Call JAGS (ART is long !), check convergence and summarize posteriors
out1 <- jags(bdata, inits, params, "JSDMocc.txt", n.adapt = na,
  n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb, parallel = TRUE)
summary(out1)
par(mfrow = c(3,3)) ; traceplot(out1)                 # All estimands
par(mfrow = c(3,3)) ; traceplot(out1, 'lv.coef')       # Only lv coefficients
which(out1$summary[,8] > 1.1)
out1X <- update(out1, n.iter = 50000)                # Can update additional 50k

```

Very long runs are necessary to accumulate a post-convergence sample of decent size. So what can we do once we have our MCMC samples? Remember that this model is basically just a fancy variant of a community occupancy model as in Chapter 11 in AHM1. Hence, you can do all the output analyses that we have seen in Chapter 11, e.g., summarize the community means or draw spaghetti plots of the species-level responses of occupancy and detection probability to the modeled covariates. Similarly, we can analyze the estimated presence/absence matrix z , e.g., by computing species similarity measures to compare sites or compare species in terms of the sites at which they co-occur.

The main novelty of this model over the models in Chapter 11 is the accommodation of non-independence in occupancy via the estimated latent variables along with their coefficients for all species. We can use those (1) to recover the matrix of pairwise residual correlations in the occurrence of the species (Warton et al., 2015; Tobler et al., 2019) and (2) for ordination (Hui et al., 2015). We illustrate the former very briefly and refer you to other papers on JSMDs for more information about output analyses from such models, e.g., how to compute correlations in species occurrence due to the modeled covariates as opposed to the residual covariance (Pollock et al., 2014; Hui, 2016) and about the use of LV models for ordination (Hui et al., 2015; Warton et al., 2015; Hui, 2016). We use function `getLVcorrMat` to obtain an estimate of the correlation matrix in our occupancy model as $R = \theta\theta^T + diag(\sigma_1^2, \sigma_2^2, \dots, \sigma_n^2)$; note this will be different in the Nmix variant of this model in Section 8.5.4.

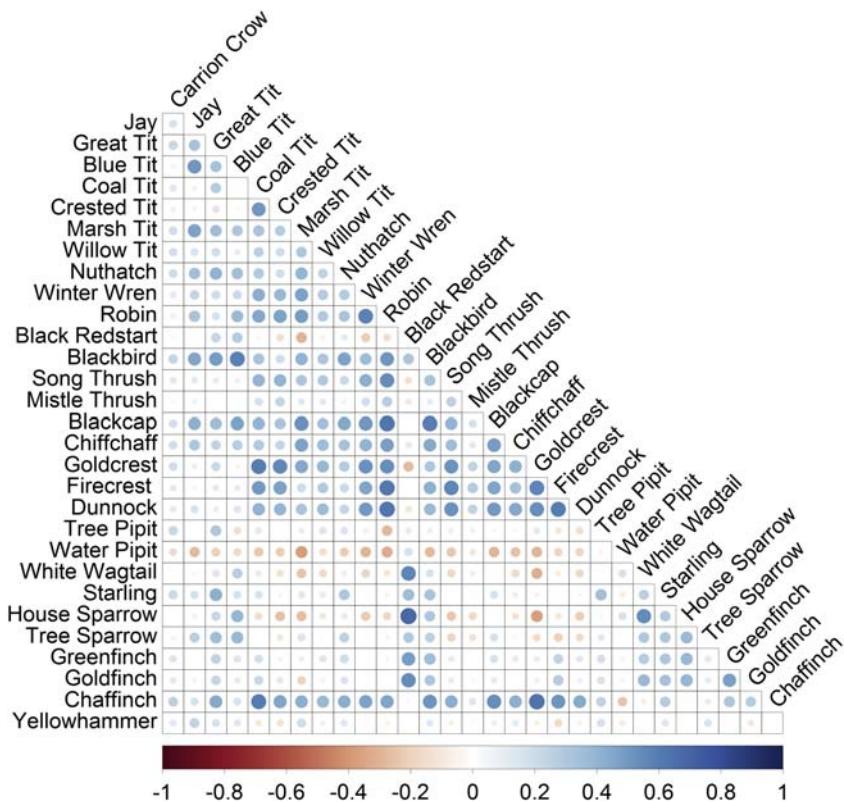
```
# Compute the posterior mean of the correlation matrix
R <- getLVcorrMat(lv.coef = out1$sims.list$lv.coef) # From AHMbook
colnames(R) <- rownames(R) <- names(sel.species)
R # unwieldy

# Plot the correlation matrix (Fig. 8.16)
library(corrplot)
corrplot(R, type = "lower", diag = FALSE, mar = c(1,0.5,5,1), tl.col = 'black',
tl.pos = 'ld', tl.srt = 45, xpd = TRUE, main = 'Residual correlations')
```

We see predominantly positive residual correlations (Fig. 8.16), with only a handful of negative correlations, including the Water Pipit and the Black Redstart. While most of the 30 analyzed species are either pure or partial forest-dwellers, these two species avoid the forest entirely, with the redstart occurring often in urban and also in craggy areas and the pipit in alpine areas above the tree line.

8.5 JOINT MODELS FOR ABUNDANCE

So far, most published models for interactions that accommodate imperfect detection have been for occupancy rather than for abundance. Some of the rare exceptions include Dorazio et al. (2015), Chambert et al. (2016), Clare et al. (2016), Roth et al. (2016), and Brodie et al. (2018), while Hui (2016) and Johnson and Sinclair (2017) develop interesting abundance models with interactions, but which lack a submodel for detection. In spite of this, it is conceptually fairly straightforward to extend to abundance some of the types of interaction modeling that we have covered in the previous sections. Here, we illustrate some abundance versions of interaction models that accommodate imperfect detection. It would be valuable to explore and develop more abundance models with interactions because arguably interactions are more easily detected in the more information-rich counts than in binary detection/nondetection data.

**FIGURE 8.16**

Estimated pairwise residual correlations in the occupancy probability of 30 Swiss passerine species at a random sample of 1,200 1-ha quadrats (Tobler et al., 2019). You can compare this with the matrix from the abundance variant of the model in Fig. 8.18.

8.5.1 STATIC BINOMIAL N-MIXTURE MODEL WITH FEW SPECIES AND SYMMETRIC INTERACTIONS

A common approach in statistics to model correlations among parameters is the use of a multivariate Normal (MVN) distribution for sets of parameters which are treated as random effects. In Section 8.2., we have very briefly discussed why this was *not* possible in the usual Bernoulli/Bernoulli version of a static occupancy model for binary responses (see also Pollock et al., 2014). However, for non-binary response variables such as counts, adoption of an MVN is a viable strategy to model correlations. That is, we can take a static multispecies N-mixture model (as in Section 11.10 in AHM1), invoke separate sets of random site effects for each species, and place an MVN prior on them. The off-diagonal elements of the variance-covariance (VC) matrix of the MVN are the covariances, which can be scaled to become correlation coefficients. They measure the degree to which the abundance of each species pair tends to covary in space, after the effects of any environmental covariates have been accounted for. Hence, we can explain variation in the abundance of each species as usual by introducing covariates into the linear predictor for the expected abundance. But in addition, we can measure the degree of additional (positive or negative) association in the abundances of species pairs, beyond what is

explained by these covariates. By comparing the correlations between two models, one of which contains environmental covariates and the other which does not, we could investigate how residual correlations change when we “adjust” for the effects of the environment as expressed by these covariates. This is important when we attempt to distinguish between habitat filtering and actual biotic interactions as the potential causes for an observed association.

In this section, we start with a community N-mixture model (see Section 11.10 in AHM1) fit to six Hubbard Brook warblers, add site random effects in the linear predictor for abundance for every species and then place an MVN prior on these. We only illustrate a model with covariates, but you could also fit a model without covariates and investigate how adjustment for different covariates affects the estimated residual association in the abundance of pairs of species. We fit the following model where i denotes sites, j occasions and k species:

1. State process (abundance):

$$N_{i,k} \sim \text{Poisson}(\lambda_{i,k})$$

2. Observation process (detection):

$$C_{i,j,k} \sim \text{Binomial}(N_{i,k}, p_{i,j,k})$$

3. Model for species heterogeneity in expected abundance:

$$\log(\lambda_{i,k}) = \beta_{0,k} + \beta_{1,k} * X_i + \eta_{i,k}$$

Here, $\beta_{0,k}$ and $\beta_{1,k}$ are the intercept and the slope of a site-specific covariate X for species k , and η_i is a vector of species random effects, or “residuals,” on which we place an MVN prior with a zero-mean vector of length 6 and variance-covariance matrix Σ :

$$\eta_i \sim \text{MVN}(\mathbf{0}, \Sigma)$$

The species-by-species variance-covariance matrix Σ looks like this,

$$\Sigma = \begin{bmatrix} \sigma_1^2 & \sigma_{1,2} & \sigma_{1,3} & \sigma_{1,4} & \sigma_{1,5} & \sigma_{1,6} \\ \sigma_{2,1} & \sigma_2^2 & \sigma_{2,3} & \sigma_{2,4} & \sigma_{2,5} & \sigma_{2,6} \\ \sigma_{3,1} & \sigma_{3,2} & \sigma_3^2 & \sigma_{3,4} & \sigma_{3,5} & \sigma_{3,6} \\ \sigma_{4,1} & \sigma_{4,2} & \sigma_{4,3} & \sigma_4^2 & \sigma_{4,5} & \sigma_{4,6} \\ \sigma_{5,1} & \sigma_{5,2} & \sigma_{5,3} & \sigma_{5,4} & \sigma_5^2 & \sigma_{5,6} \\ \sigma_{6,1} & \sigma_{6,2} & \sigma_{6,3} & \sigma_{6,4} & \sigma_{6,5} & \sigma_6^2 \end{bmatrix},$$

where σ_k^2 is the variance of the random site residuals for species k and $\sigma_{u,v}$ is the covariance between the random site residuals for the species pair u and v (and hence, $\sigma_{u,v} = \sigma_{v,u}$). We need to estimate $n(n-1)/2$ separate covariance parameters for the pairwise correlations among n species. In our Bayesian analysis, as a vague prior for the variance-covariance matrix, we adopt an inverse Wishart distribution with an identity scale matrix R and degrees of freedom equal to the number of species plus 1. See Section 7.6.2 in Kéry and Schaub (2012) and Schaub et al. (2013) for more information on the modeling of a variance-covariance matrix in BUGS and Riecke et al. (2019) for more on the choice of vague priors for VC matrices.

We again work with the Hubbard Brook data set; you may need to reload and reprepare the data as we did in [Section 8.3.1](#). In the abundance model, we add linear effects of elevation and aspect (“north”), while in the detection model, we add effects of survey date (with linear and quadratic terms) and survey time (linear). We bundle up all the data along with the scale matrix R and the df for the inverse Wishart prior.

```
Rmat <- diag(nspec)           # Identity matrix
df <- nspec + 1

# Bundle and summarize data set
str(bdata <- list(C = counts[,'2016'], nsites = nsites, nspec = nspec,
  nreps = nreps, elev = elev, north = north, DATES = DATES[,'2016'],
  HOURS = HOURS[,'2016'], R = Rmat, df = df) )

List of 10
 $ C      : num [1:373, 1:3, 1:6] 0 0 0 0 0 0 0 0 0 0 ...
 $ nsites: num 373
 $ nspec  : num 6
 $ nreps  : num 3
 $ elev   : num [1:373] -0.26 -0.08 0.46 0.72 0.88 0.78 0.74 0.74 ...
 $ north   : num [1:373] 0.1107 0.3218 0.0907 0.0588 1.9757 ...
 $ DATES   : num [1:373, 1:3] -1.45 -1.45 -1.45 -1.45 -1.45 ...
 $ HOURS   : num [1:373, 1:3] -1.969 -1.778 -1.464 -1.218 -0.958 ...
 $ R       : num [1:6, 1:6] 1 0 0 0 0 0 1 0 0 ...
 $ df      : num 7

# Specify model in BUGS language
cat(file = "Nmix1.txt", "
model {
# Priors
# Intercepts and coefficients all fixed effects
for(k in 1:nspec){
  mean.lambda[k] <- exp(beta0[k])
  beta0[k] ~ dnorm(0, 0.1)
  alpha0[k] <- logit(mean.p[k])
  mean.p[k] ~ dunif(0,1)
  beta1[k] ~ dnorm(0, 0.1)
  beta2[k] ~ dnorm(0, 0.1)
  alpha1[k] ~ dnorm(0, 0.1)
  alpha2[k] ~ dnorm(0, 0.1)
  alpha3[k] ~ dnorm(0, 0.1)
}

# Specify MVN prior for random site effects in lambda for each species
for (i in 1:nsites){
  eta.lam[i,1:nspec] ~ dmnorm(mu.eta[], Omega[,])
}
for (k in 1:nspec){
  mu.eta[k] <- 0
}

# Vague inverse Wishart prior for variance-covariance matrix
Omega[1:nspec,1:nspec] ~ dwish(R[,], df)
Sigma2[1:nspec,1:nspec] <- inverse(Omega[,])

# Scale var/covar matrix to become the correlation matrix
for (i in 1:nspec){
  for (k in 1:nspec){
    rho[i,k] <- Sigma2[i,k] / (sqrt(Sigma2[i,i]) * sqrt(Sigma2[k,k]))
  }
}
```

```

# Likelihood
# Ecological model for true abundance
for (i in 1:n/sites){
  for(k in 1:nspec){
    N[i,k] ~ dpois(lambda[i,k])
    log(lambda[i,k]) <- beta0[k] + beta1[k] * elev[i] +
      beta2[k] * north[i] + eta.lam[i,k]

    # Observation model for replicated counts
    for (j in 1:nreps){
      C[i,j,k] ~ dbin(p[i,j,k], N[i,k])
      logit(p[i,j,k]) <- alpha0[k] + alpha1[k] * DATES[i,j] +
        alpha2[k] * pow(DATES[i,j],2) + alpha3[k] * HOURS[i,j]
    }
  }
}

# Derived quantities
for(k in 1:nspec){
  Ntot[k] <- sum(N[,k])  # Total abundance per species
}
)

# Initial values
Nst <- maxC[, '2016', ] + 1
Nst[is.na(Nst)] <- 1
inits <- function() list(N = Nst, mean.p = rep(0.2, 6), Omega = diag(6))

# Parameters monitored
params <- c('mean.lambda', 'beta1', 'beta2', 'mean.p', 'alpha1', 'alpha2', 'alpha3', 'Sigma2',
  'rho', 'Ntot')

# MCMC settings
na <- 5000 ; nc <- 3 ; ni <- 300000 ; nb <- 100000 ; nt <- 200

# Call JAGS (ART 400 min), assess convergence and summarize posteriors
out1 <- jags(bdata, inits, params, "Nmix1.txt", n.adapt = na,
  n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb, parallel = TRUE)
par(mfrow = c(3,3)) ; traceplot(out1)
which(out1$summary[,8] > 1.1)
print(out1, 2)

```

Using an MVN distribution to model pairwise interactions for 6 species yields 15 correlation parameters. We inspect these residual correlations in expected abundance in a table (for code see below) and in a plot (Fig. 8.17). We see that all correlation coefficients except for one (OVEN-REVI) are not distinguishable from zero, and their 95% CRIs overlap zero. There is a weak indication of a negative residual correlation for the BTBW-OVEN and the BLBW-REVI species pairs. In addition, for the last six species pairings in the plot, estimates suggest positive correlations, but only for the Ovenbird (OVEN) and the Red-eyed Vireo (REVI), does the 95% CRI not include 0.

```

# Get residual correlations
tmp2 <- round(out1$mean$rho, 2)
dimnames(tmp2) <- list(speclist, speclist)
tmp2                                # This is with adjustment for two environmental covariates

```

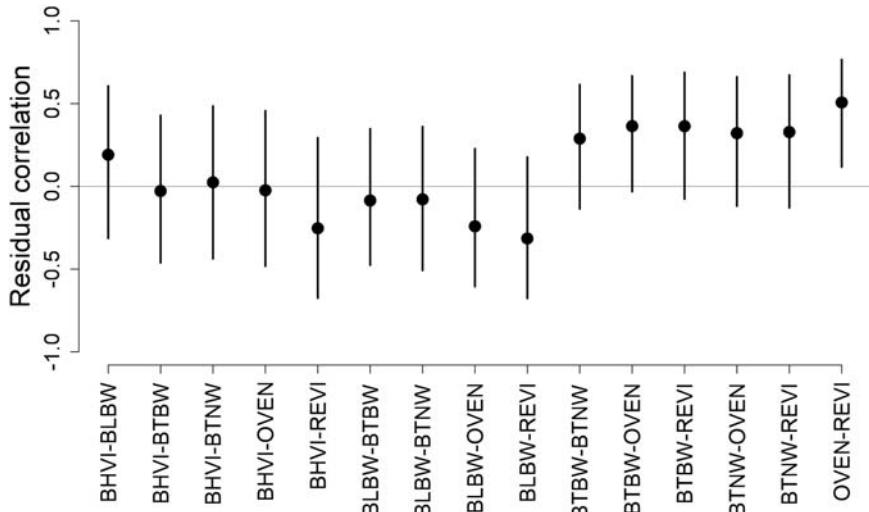


FIGURE 8.17

Estimates of pairwise correlations in residual abundance of the six most common Hubbard Brook passersines in the data set under an N-mixture model with two covariates in the expected abundance lambda (with 95% CRLs).

8.5.2 STATIC BINOMIAL N-MIXTURE MODEL WITH TWO SPECIES AND DIRECTIONAL INTERACTIONS

In Section 8.3.2, we fit an occupancy model with the interaction formulation from Waddle et al. (2010) which uses the estimated presence/absence (z) of one species as a covariate in the occupancy model of another species. We can extend that formulation to an abundance model, but then the “dominant species covariate” is no longer binary as for z , but can take on potentially any non-negative integer number. We could consider a model where the occurrence z^A of species A affects the expected abundance $E(N^B)$ of species B or vice versa, i.e., that abundance of A (N^A) affects the expected occurrence of B ($E(z^B) = \psi^B$), but it is perhaps more natural to develop a model with an abundance/abundance link between two species (N^A is assumed to affect $E(N^B)$).

We illustrate with counts of the Red-eyed Vireo (REVI) and Black-throated Green Warbler (BTNW) and fit the following two-species Binomial N-mixture model, which is a variant of the models of Clare et al. (2016), Roth et al. (2016), and Brodie et al. (2018).

(1) For the potentially dominant Red-eyed Vireo, we specify a static Binomial N-mixture model:

$$N_i^R \sim \text{Poisson}(\lambda_i^R) \quad \# \text{ State model}$$

$$C_{i,j}^R \sim \text{Binomial}\left(N_i^R, p_{i,j}^R\right) \quad \# \text{ Observation model}$$

$$\log(\lambda_i^R) = \beta_0^R + \beta_1^R * elev_i + \beta_2^R * north_i$$

$$\text{logit}(p_{i,j}^R) = \alpha_0^R + \alpha_1^R * date_{i,j} + \alpha_2^R * date_{i,j}^2 + \alpha_3^R * hour_{i,j}$$

(2) For the potentially subordinate Black-throated Green Warbler, we specify another Binomial N-mixture model, where the parameters in the state model of species B interact with the realized abundance at a site of the Red-eyed Vireo (N_i^R). For this illustration, we do not let the parameters in the detection model of B interact with abundance of R, although we could do this in principle.

$$N_i^B \sim \text{Poisson}(\lambda_i^B) \quad \# \text{ State model}$$

$$C_{i,j}^B \sim \text{Binomial}\left(N_i^B, p_{i,j}^B\right) \quad \# \text{ Observation model}$$

$$\log(\lambda_i^B) = \beta_0^B + \beta_1^B * \text{elev}_i + \beta_2^B * \text{north}_i + \gamma_0 * N_i^R + \gamma_1 * N_i^R * \text{elev}_i + \gamma_2 * N_i^R * \text{north}_i$$

In this formulation of the directional interaction $R \rightarrow B$, the γ terms will tell us how much evidence there is for such an association in the abundance between the two species. This formulation allows us to distinguish between an overall effect of the abundance of R (γ_0), an effect of the abundance of R on the elevation-abundance relationship of B (γ_1), and likewise for the aspect-abundance relationship of B (γ_2).

```
# Select REVI and BTNW data from 2016
str(CR <- counts[, , '2016', 'REVI'])
str(CB <- counts[, , '2016', 'BTNW'])

# Bundle and summarize data set
str(bdata <- list(CR = CR, CB = CB, nsites = nsites, nreps = nreps, elev = elev,
                  north = north, DATES = DATES[,, '2016'], HOURS = HOURS[,, '2016']) )

List of 8
$ CR      : num [1:373, 1:3] 0 1 1 2 1 1 1 1 0 0 ...
$ CB      : num [1:373, 1:3] 0 0 0 1 0 0 0 1 0 0 ...
$ nsites: num 373
$ nreps  : num 3
$ elev   : num [1:373] -0.26 -0.08 0.46 0.72 0.88 0.78 0.74 0.74 ...
$ north   : num [1:373] 0.1107 0.3218 0.0907 0.0588 1.9757 ...
$ DATES  : num [1:373, 1:3] -1.45 -1.45 -1.45 -1.45 -1.45 ...
$ HOURS  : num [1:373, 1:3] -1.969 -1.778 -1.464 -1.218 -0.958 ...

# Specify model in BUGS language
cat(file = "Nmix2.txt", "
model {

# Model for Red-eyed Vireo (REVI): the 'dominant' species
# Priors for intercepts and coefficients
mean.lambdaR ~ dunif(0, 5)
beta0R <- log(mean.lambdaR)
alpha0R <- logit(mean.pR)
mean.pR ~ dunif(0,1)
beta1R ~ dnorm(0, 0.1)
beta2R ~ dnorm(0, 0.1)
alpha1R ~ dnorm(0, 0.1)
alpha2R ~ dnorm(0, 0.1)
alpha3R ~ dnorm(0, 0.1)

# Likelihood for REVI ('dominant')
# Ecological model
for (i in 1:nsites){
  NR[i] ~ dpois(lambdaR[i])
  log(lambdaR[i]) <- beta0R + beta1R * elev[i] + beta2R * north[i]
  # Observation model
  for (j in 1:nreps){
    CR[i,j] ~ dbin(pR[i,j], NR[i])
    logit(pR[i,j]) <- alpha0R + alpha1R * DATES[i,j] +
      alpha2R * pow(DATES[i,j],2) + alpha3R * HOURS[i,j]
  }
}
```

```

# Model for Black-throated Green Warbler (BTNW): the 'subordinate' sp.
# Priors for intercepts and coefficients
mean.lambdaB ~ dunif(0, 5)
beta0B <- log(mean.lambdaB)
beta1B ~ dnorm(0, 0.1)
beta2B ~ dnorm(0, 0.1)
alpha0B <- logit(mean.pB)
mean.pB ~ dunif(0,1)
alpha1B ~ dnorm(0, 0.1)
alpha2B ~ dnorm(0, 0.1)
alpha3B ~ dnorm(0, 0.1)
gamma0 ~ dnorm(0, 0.1) # These are the 'interaction coefficients' !
gamma1 ~ dnorm(0, 0.1)
gamma2 ~ dnorm(0, 0.1)

# Likelihood for BTNW ('subordinate')
# Ecological model
for (i in 1:nsites){
  NB[i] ~ dpois(lambdaB[i])
  lambdaB[i] <- exp(beta0B + beta1B * elev[i] + beta2B * north[i] +
    gamma0 * NR[i] + gamma1 * elev[i] * NR[i] + gamma2 * north[i] * NR[i])
  # Observation model
  for (j in 1:nreps){
    CB[i,j] ~ dbin(pB[i,j], NB[i])
    logit(pB[i,j]) <- alpha0B + alpha1B * DATES[i,j] +
      alpha2B * pow(DATES[i,j],2) + alpha3B * HOURS[i,j]
  }
}
}

# Initial values
Nst <- rep(10, nsites)
inits <- function() list(NR = Nst, NB = Nst)

# Parameters monitored
params <- c('mean.lambdaR', 'beta1R', 'beta2R', 'mean.pR', 'alpha1R',
  'alpha2R', 'alpha3R', 'mean.lambdaB', 'beta1B', 'beta2B', 'mean.pB',
  'alpha1B', 'alpha2B', 'alpha3B', 'gamma0', 'gamma1', 'gamma2')

# MCMC settings
na <- 5000 ; nc <- 3 ; ni <- 100000 ; nb <- 50000 ; nt <- 50

# Call JAGS (ART 40 min), assess convergence and summarize posteriors
out2 <- jags(bdata, inits, params, "Nmix2.txt", n.adapt = na,
  n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb, parallel = TRUE)
par(mfrow = c(3,3)) ; traceplot(out2)
which(out2$summary[,8] > 1.1)
print(out2, 2)

      mean     sd   2.5%    50%   97.5% overlap0      f Rhat n.eff
mean.lambdaR  2.45  0.62   1.53   2.36    3.94    FALSE 1.00 1.00  1314
... output truncated ...
gamma0        0.09  0.10  -0.12   0.10    0.27    TRUE  0.85 1.02   110
gamma1       -0.01  0.03  -0.07  -0.01    0.04    TRUE  0.70 1.00   528
gamma2        0.03  0.04  -0.05   0.03    0.12    TRUE  0.76 1.00   702

```

Based on this model and the three gamma estimates, we cannot claim that there was an association between Red-eyed Vireo abundance in Hubbard Brook in 2016 and abundance of Black-throated Green Warbler.

8.5.3 AN OPEN BINOMIAL N-MIXTURE MODEL FOR TWO SPECIES WITH DIRECTIONAL INTERACTIONS

Presumably, open models with interactions can provide stronger evidence for biotic interactions. Variance is reduced because more things are kept constant in such temporal comparisons than in mere spatial comparisons at a snapshot in time. In addition, we build up larger sample sizes over time. Both may increase the power to detect statistical interactions.

It would be conceptually straightforward to specify an open binomial N-mixture model (including a Dail-Madsen model) with symmetric interactions by placing an MVN prior on species-specific parameters that vary in space or time. For simplicity, we here illustrate an open static model with directional interactions. We develop a model that tests for an association between the number of Red-eyed Vireos (R) at a site in year $t - 1$ and the expected number of Black-throated Green Warblers (B) at site i in year t . This lag in the modeled effect of R means that we cannot specify an interaction between the two species in the first year. But from the second to the last year t , we will express the expected abundance lambda of the warbler as follows:

$$\lambda_{i,t}^B = \exp\left(\beta_0^B + \dots + \gamma * N_{i,t-1}^R\right),$$

where γ is the effect at site i of one Red-eyed Vireo last year on the expected abundance of the Black-throated Green Warbler in this year. We could also experiment with different formulations of an effect, e.g., by taking the log (though then we would have to add a small number to avoid problems when $N_{i,t-1}^R = 0$) or by taking the square root of $N_{i,t-1}^R$. Both formulations would mean that the effect of one additional vireo diminishes with increasing N^R . For this illustration, we only fit an effect of the Red-eyed Vireo on the average expected abundance of the Black-throated Green Warbler, but not on the warbler's response to site elevation and aspect.

```
# Select all REV1 and BTNW data
str(CR <- counts[,, 'REV1'])
str(CB <- counts[,, 'BTNW'])
table(CR) ; table(CB)      # Descriptifs of these counts

# Bundle and summarize data set
str(bdata <- list(CR = CR, CB = CB, nsites = nsites, nyears = nyyears,
nreps = nreps, elev = elev, north = north, DATES = DATES, HOURS = HOURS) )

List of 9
$ CR     : num [1:373, 1:3, 1:10] 2 1 0 1 1 0 1 0 0 1 ...
$ CB     : num [1:373, 1:3, 1:10] 1 0 1 0 0 0 0 1 1 0 ...
$ nsites: num 373
$ nyears: num 10
$ nreps : num 3
$ elev   : num [1:373] -0.26 -0.08 0.46 0.72 0.88 0.78 0.74 0.74 ...
$ north  : num [1:373] 0.1107 0.3218 0.0907 0.0588 1.9757 ...
$ DATES  : num [1:373, 1:3, 1:10] -1.36 -1.36 -1.36 -1.36 -1.36 ...
$ HOURS  : num [1:373, 1:3, 1:20] -1.655 -1.45 -1.109 -0.753 -1.204 ...

# Specify model in BUGS language
cat(file = "Nmix3.txt", "
model {

# Model for Red-eyed Vireo (REV1): the 'dominant' species
# Priors for intercepts and coefficients
for(t in 1:nyears){
  mean.lambdaR[t] ~ dunif(0, 10)
  beta0R[t] <- log(mean.lambdaR[t])
  alpha0R[t] <- logit(mean.pR[t])
  mean.pR[t] ~ dunif(0,1)
}
```

```

beta1R ~ dnorm(0, 0.1)
beta2R ~ dnorm(0, 0.1)
alpha1R ~ dnorm(0, 0.1)
alpha2R ~ dnorm(0, 0.1)
alpha3R ~ dnorm(0, 0.1)

# Likelihood for REVI ('dominant')
# Ecological model
for(t in 1:nyears){
  for (i in 1:nsites){
    NR[i,t] ~ dpois(lambdaR[i,t])
    lambdaR[i,t] <- exp(beta0R[t] + beta1R * elev[i] + beta2R * north[i])
    # Observation model
    for (j in 1:nreps){
      CR[i,j,t] ~ dbin(pR[i,j,t], NR[i,t])
      logit(pR[i,j,t]) <- alpha0R[t] + alpha1R * DATES[i,j,t] +
        alpha2R * pow(DATES[i,j,t],2) + alpha3R * HOURS[i,j,t]
    }
  }
}

# Model for Black-throated Green Warbler (BTNW): the 'subordinate' sp.
# Priors for intercepts and coefficients
for(t in 1:nyears){
  mean.lambdaB[t] ~ dunif(0, 10)
  beta0B[t] <- log(mean.lambdaB[t])
  alpha0B[t] <- logit(mean.pB[t])
  mean.pB[t] ~ dunif(0,1)
}
beta1B ~ dnorm(0, 0.1)
beta2B ~ dnorm(0, 0.1)
alpha1B ~ dnorm(0, 0.1)
alpha2B ~ dnorm(0, 0.1)
alpha3B ~ dnorm(0, 0.1)
gamma ~ dnorm(0, 0.1) # This is the 'interaction coefficient'

# Likelihood for BTNW ('subordinate')
# For year 1 = 2009: no lagged effect of NR
for (i in 1:nsites){
  NB[i,1] ~ dpois(lambdaB[i,1])
  lambdaB[i,1] <- exp(beta0B[1] + beta1B * elev[i] + beta2B * north[i])
  for (j in 1:nreps){
    CB[i,j,1] ~ dbin(pB[i,j,1], NB[i,1])
    logit(pB[i,j,1]) <- alpha0B[1] + alpha1B * DATES[i,j,1] +
      alpha2B * pow(DATES[i,j,1],2) + alpha3B * HOURS[i,j,1]
  }
}
# For years 2010-2018: including a lagged effect of NR
for(t in 2:nyears){
  NB[i,t] ~ dpois(lambdaB[i,t])
  lambdaB[i,t] <- exp(beta0B[t] + beta1B * elev[i] +
    beta2B * north[i] + gamma * NR[i,t-1])
  for (j in 1:nreps){
    CB[i,j,t] ~ dbin(pB[i,j,t], NB[i,t])
    logit(pB[i,j,t]) <- alpha0B[t] + alpha1B * DATES[i,j,t] +
      alpha2B * pow(DATES[i,j,t],2) + alpha3B * HOURS[i,j,t]
  }
}
}
")

```

```

# Cheap initial values: make sure N is initialized high enough
Nst <- array(10, dim = c(nsites, nyears))
inits <- function() list(NR = Nst, NB = Nst)

# Parameters monitored
params <- c('mean.lambdaR', 'beta1R', 'beta2R', 'mean.pR', 'alpha1R', 'alpha2R', 'alpha3R',
           'mean.lambdaB', 'beta1B', 'beta2B', 'mean.pB', 'alpha1B', 'alpha2B', 'alpha3B', 'gamma')

# MCMC settings
na <- 5000 ; nc <- 3 ; ni <- 100000 ; nb <- 50000 ; nt <- 50

# Call JAGS (ART 509 min), assess convergence and summarize posteriors
out3 <- jags(bdata, inits, params, "Nmix3.txt", n.adapt = na,
              n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb, parallel = TRUE)
par(mfrow = c(3,3)) ; traceplot(out3)
which(out3$summary[,8] > 1.1)
print(out3$summary[,-(4:6)], 3)

      mean      sd    2.5%   97.5%   Rhat  n.eff  overlap0      f
mean.lambdaR[1] 2.29138 0.4938 1.55938 3.4651 1.00  3000       0 1.000
... output heavily truncated ...
gamma          0.02872 0.0153 -0.00229 0.0588 1.00  2586       1 0.964

```

The point estimate (posterior mean) of the “species interaction coefficient” gamma is 0.029, and although the 95% CRI overlaps zero somewhat, there is a high probability (0.96) that the parameter is positive. Hence, we may feel somewhat justified to say that more Red-eyed Vireos in Hubbard Brook last year are associated with more Black-throated Green Warblers in this year. Given this estimate, we would expect (on average) the number of warblers to change at a site by a rate of $\exp(0.02872 * \text{number of vireos at } t - 1)$. For example, 4 vireos at time $t - 1$ would result in roughly a 12% increase of warblers at time t . Of course, always remember that this is a description of a pattern only and not a proof of causation.

We have emphasized repeatedly that the use of the abundance of one species as a covariate in the model for another species is a natural approach to testing for interactions between species and indeed this has been done repeatedly in *p*-ignorant models (e.g., Leathwick and Austin, 2001; Pellissier et al., 2010). Doing this inside of an estimation framework that corrects for imperfect detection, such as an N-mixture model, presumably makes our inferences more robust. We have illustrated with the estimated abundance with a lag of one year, but you could use as a covariate the abundance of a species presumed dominant at the same time or at a larger lag still, and at the same site or rather within some neighborhood, by taking the average out to some distance of the focal site. Hierarchical models provide full flexibility to tailor your model to your ecological questions, as well as to the possibilities of your data set.

8.5.4 THE N-MIXTURE MODEL VARIANT OF THE LATENT-VARIABLE MODEL OF TOBLER et al. (2019)

In Section 8.4.2, we have presented the latent-variable multispecies, or community, occupancy model from Tobler et al. (2019) to the thresholded counts of the 30 more widespread Swiss passerine species surveyed in 1 hectare squares randomly chosen within 1,200 1-km² survey quadrats from the latest Swiss breeding bird atlas (Knaus et al., 2018). Here, we fit the analogous Binomial N-mixture model to the actual counts in this data set. This model is a direct extension of a Poisson-GLM-based model implemented in the R package *boral* (Hui, 2016), although there the model lacks the detection component which we include here. Hence, we fit a community Binomial N-mixture model as in Chapter 11 in AHM1, but in the linear predictor for abundance add site- and species-specific residuals that are correlated across species. For illustration, we again fit the model with just two latent variables.

You will have to first repeat the data preparation steps from [Section 8.4.2](#). here, because we use objects from there.

```

# Determine sample sizes
(nsites <- dim(cc)[1]) ; (nspec <- dim(cc)[3]) ; (nreps <- dim(cc)[2])
table(nreps <- dat$sitecova[sel.sites,'nsurveys']) # 2/3 surveys per site

# Prepare occupancy and detection covariates and choose # latent vars
library(abind)
str(xocc <- as.matrix(dat$sitecova[sel.sites,3:6]))# Occ. covariates
str(xocc <- cbind(xocc, xocc^2)) # Add squares of covariates
xocc <- scale(xocc) # Scale column-wise
str(xdet <- dat$dates[sel.sites,]) # Detection covariates
xdettmp <- standardize(xdet) # Scale matrix-wide
xdettmp[is.na(xdettmp)] <- 0 # Mean-impute dates of 3rd survey
str(xdet <- abind(xdettmp, xdettmp^2, along = 3) )

# Bundle data
nlv <- 2 # Choose number of latent variables
str(bdata <- list(C = aperm(cc, c(1,3,2)), Xocc = xocc, Xdet = xdet,
  ncov.occ = ncol(xocc), ncov.det = 2, nlv = nlv, nsites = nsites,
  nspec = nspec, nreps = nreps))

List of 9
$ C : num [1:1200, 1:30, 1:3] 0 0 0 1 0 0 0 0 0 0 ...
$ Xocc : num [1:1200, 1:8] -1.033 -0.724 -0.413 -1.055 -0.726 ...
$ Xdet : num [1:1200, 1:3, 1:2] -1.34 -1.38 -1.42 -1.68 -1.34 ...
$ ncov.occ: int 8
$ ncov.det: num 2
$ nlv : num 2
$ nsites : int 1200
$ nspec : int 30
$ nreps : num [1:1200] 3 3 3 3 3 3 3 3 3 3 ...

# Specify model in BUGS language
cat(file = "JSDMnmix.txt", "
model{
# Community priors for abundance
mu.beta0 <- log(mean.lambda) # Intercepts
mean.lambda ~ dunif(0, 1)
tau.beta0 <- pow(sd.beta0, -2)
sd.beta0 ~ dunif(0, 3)
for(v in 1:ncov.occ) { # Coefficients
  mu.beta[v] ~ dnorm(0, 0.1)
  tau.beta[v] <- pow(sd.beta[v], -2)
  sd.beta[v] ~ dunif(0, 3)
}

# Community priors for detection
mu.alpha0 <- logit(mean.p) # Intercept
mean.p ~ dunif(0, 1)
tau.alpha0 <- pow(sd.alpha0, -2)
sd.alpha0 ~ dunif(0, 2)
for(v in 1:ncov.det) { # Coefficients
  mu.alpha[v] ~ dnorm(0, 1)
  tau.alpha[v] <- pow(sd.alpha[v], -2)
  sd.alpha[v] ~ dunif(0, 1)
}

```

```

# Define species random effects for all coefficients
for (k in 1:nspec) {
  # Random species effects in the abundance model
  beta0[k] ~ dnorm(mu.beta0, tau.beta0)      # Intercepts
  for(v in 1:ncov.occ) {                      # Coefficients
    beta[k, v] ~ dnorm(mu.beta[v], tau.beta[v])
  }
  # Random effects for detection
  alpha0[k] ~ dnorm(mu.alpha0, tau.alpha0) # Intercepts
  for(v in 1:ncov.det) {                  # Coefficients
    alpha[k, v] ~ dnorm(mu.alpha[v], tau.alpha[v])
  }
}

# Priors for latent variables: standard Normal rv #
for(i in 1:nsites) {
  for(l in 1:nlv){
    LV[i,l] ~ dnorm(0, 1)
  }
}

# Latent variable coefficients with constraints
# (slightly different from occupancy version of the model)
# Upper diagonal equal to 0
for(l in 1:(nlv-1)){
  for(l2 in (l+1):nlv){
    lv.coef[l,l2] <- 0
  }
}
# Sign constraints on diagonal elements (positive)
for(l in 1:nlv) {
  lv.coef[l,l] ~ dnorm(0, 0.1)I(0, )
}

# Lower diagonal free
for(l in 2:nlv){
  for(l2 in 1:(l-1)){
    lv.coef[l,l2] ~ dnorm(0, 0.1)
  }
}

# Other elements also free
for(l in (nlv+1):nspec) {
  for(l2 in 1:nlv){
    lv.coef[l,l2] ~ dnorm(0, 0.1)
  }
}

# Define the multi-species binomial N-mixture model
for (i in 1:nsites) {                                # Loop over sites
  for (k in 1:nspec) {                                # Loop over species
    # State model
    N[i,k] ~ dpois(exp(loglam[i,k]))
    loglam[i,k] <- beta0[k] + inprod(beta[k, ], Xocc[i, ]) +
      inprod(lv.coef[k, ], LV[i, ])
    # Observation model
    for (j in 1:nreps[i]) {                          # Loop over 2 or 3 surveys
      logit(p[i,k,j]) <- alpha0[k] + alpha[k, 1] * Xdet[i,j,1] +
        alpha[k, 2] * Xdet[i,j,2]
      C[i,k,j] ~ dbinom(p[i,k,j], N[i,k])
    }
  }
}
")

```

As for the occupancy variant of this model, we found this model very hard to converge. We accumulated a posterior sample in several steps, first with one set of initial values, and subsequently with the posterior means of a previous model run as the initial values for some of the estimated quantities.

```

# (Original) Initial values
init <- function() {
  tmp <- apply(bdata$C, c(1,2), max)
  tmp[is.na(tmp)] <- 0
  Nst <- tmp + 5
  lv.coef <- matrix(0, nspec, bdata$nlv)
  lv.coef[1:bdata$nlv, 1:bdata$nlv] <- 0
  for(l in 1:bdata$nlv-1){ lv.coef[l, (l+1):bdata$nlv] <- NA}
  LV <- matrix(rnorm(bdata$nlv * nsites), nsites, bdata$nlv)
  lv.coef <- matrix(runif(bdata$nlv * nspec, -sqrt(1/(bdata$nlv+1)),
    sqrt(1/(bdata$nlv+1))), nspec, bdata$nlv) * lv.coef
  beta0 <- rep(0, nspec)                                # yields lambda = 1
  list(N = Nst, LV = LV, lv.coef = lv.coef , beta0 = beta0)
}

# Parameters to be monitored
params <- c('mean.lambda', 'mu.beta0', 'sd.beta0', 'mu.beta', 'sd.beta',
  'mean.p', 'mu.alpha0', 'sd.alpha0', 'mu.alpha', 'sd.alpha', 'beta0',
  'beta', 'alpha0', 'alpha', 'LV', 'lv.coef')           # could add 'N'

# MCMC settings
na <- 10000 ; ni <- 150000 ; nt <- 50 ; nb <- 100000 ; nc <- 2

# Call JAGS (ART 36 h), check convergence and summarize posteriors
out2X <- jags(bdata, init, params, "JSDMnmix.txt", n.adapt = na,
  n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb, parallel = TRUE)
par(mfrow = c(4,4)) ; traceplot(out2X)                 # All params
par(mfrow = c(4,4)) ; traceplot(out2X,'lv.coef')       # Only LV coefficients
par(mfrow = c(1,1)) ; traceplot(out2X, 'deviance')     # Only the deviance
which(out2X$summary[,8] > 1.1)

```

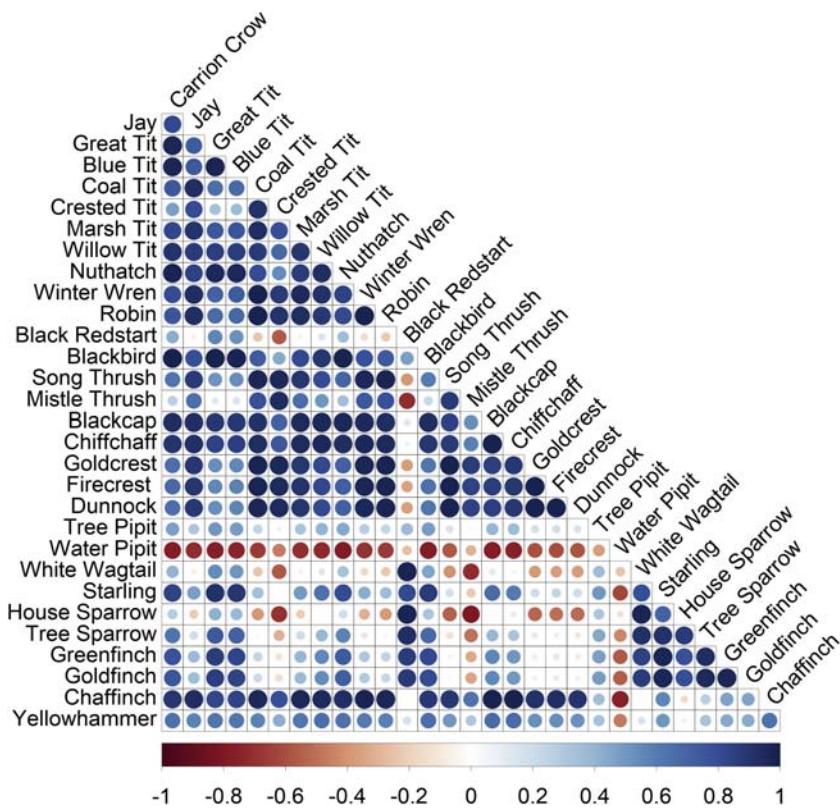
As for the occupancy variant of the model, remember that this is basically the same model as the one we covered in Section 11.10 in AHM1 and we could summarize community-level (hyper-) parameters or look in more detail at species-level responses to the environment using spaghetti plots. We are not going to do this here but just focus on the main novelty of this model: the (residual) correlation in the abundance among pairs of species. Since this is captured by the estimated latent variables and the species-level response to them, we must first compute the pairwise residual correlation matrix. For an Nmix model, the residual correlation matrix is computed slightly differently from the occupancy model as $R = \theta\theta^T$ (Hui et al. 2015; Hui 2016). Fig. 8.18 shows a plot of the correlation matrix. Comparing this figure with Fig. 8.16, we see a much stronger signal of (statistical) interactions in the analysis of abundance (i.e., with the Nmix model) than in the analysis of occupancy. This is hardly surprising, since counts carry so much more information about species associations than do binary presence/absence data.

```

# Compute the posterior mean of the correlation matrix
R <- getLVCcorrMat(lv.coef = out2X$sims.list$lv.coef, type= "Nmix")
colnames(R) <- rownames(R) <- names(sel.species)
R                      # unwieldy

# Plot the correlation matrix (Fig. 8.18) and dendrogram (Fig. 8.19)
library(corrplot)
corrplot(R, type = "lower", diag = FALSE, mar = c(1,0.5,5,1),
  tl.col = 'black', tl.pos = 'ld', tl.srt = 45, xpd = TRUE,
  main = 'Residual correlations')
dist <- as.dist(1 - R) # so R = 1 -> dist = 0
plot(hclust(dist), xlab = "", sub = "", ylab = "Correlation coefficient",
  yaxt = 'n')             # Fig. 8.19
axis(2, at = c(0, 0.5, 1, 1.5, 2), labels = c(1, 0.5, 0, -0.5, -1), las = 1)

```

**FIGURE 8.18**

Estimated pairwise residual correlations in the expected abundance of 30 Swiss passerine species at a random sample of 1,200 1 ha quadrats. You can compare these residual correlations with those computed from the otherwise identical occupancy variant of the model in [Fig. 8.16](#).

We can also express these correlations using a hierarchical cluster dendrogram ([Fig. 8.19](#)). The resulting figure may again tell you something about the organization of the community of these 30 Swiss passernes. Indeed, if you know Swiss birds then you will be amazed to recognize groups of species that you will also expect to find together in the field. But we don't think that these patterns represent mutualistic relationships for the most part. Rather, we assume that a majority of them will represent species associations that arise by shared choice of the habitat in terms of habitat predictors that are not in our model.

This was just a quick demonstration of the abundance version of the latent-variable JSDM with imperfect detection that was developed by Tobler et al. (2019) based on the work of Pollock et al. (2014) and various papers of Francis Hui and his colleagues. We see that modeling abundance rather than detection/nondetection is much more powerful to detect species interactions, and we are fascinated to recognize species groupings that “make sense” in the light of our knowledge about these species. Both the occupancy version of the model ([Section 8.4.2](#)) and the abundance version in this section are interesting and powerful models for detecting structure in communities of species, before

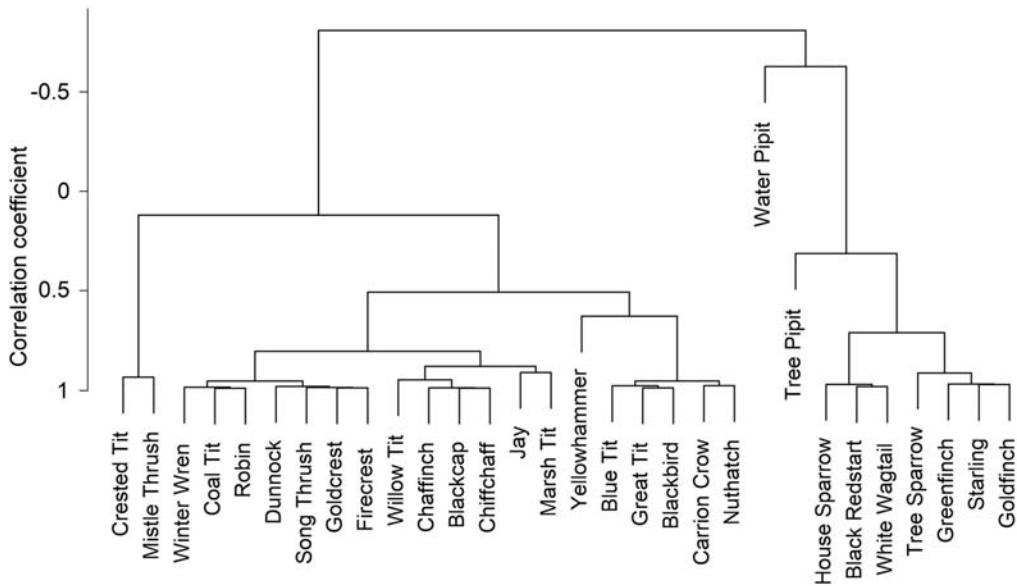


FIGURE 8.19

Hierarchical cluster dendrogram based on the estimated residual correlations from the multispecies N-mixture model with two latent variables fit to the counts of 30 Swiss passerine species at a random sample of 1,200 1-ha quadrats.

and after we have corrected for specific environmental covariates. But we found both models to be hard to fit in JAGS in practice, even though we simplified the estimation task considerably by only analyzing a subset of sites and species and by only fitting a minimum of two latent variables. Hence, be prepared for some practical challenges when you want to use these models to learn about underlying structure in your data and also be prepared to explore alternative computational solutions.

8.6 SUMMARY AND OUTLOOK

Biotic interactions include such key ecological mechanisms as competition, predation, parasitism, and disease (all negative), or facilitation and mutualism (positive). They represent some of the major mechanisms that structure communities and therefore contribute to observed spatial and temporal patterns in the distribution and abundance of a species. In this chapter, we have covered a series of models for occupancy and abundance that allow you to investigate the possible results of such biotic interactions in terms of the non-independence in occurrence or abundance among species. All else equal, with a negative biotic interaction between two species we would expect a negative correlation in occupancy or abundance. That is, one species would tend to be absent where the other is present and vice versa, and one species would tend to be more abundant when the other is less abundant and vice versa.

However, and this is the major caveat for all the models in this chapter, without data from controlled experiments or direct behavioral observations, i.e., based solely on observational data, we can't make strong inferences about actual biotic interactions. Even with the best such models, we describe patterns only. Hence, a positive association in the occurrence of two species may be due to positive biotic interactions, habitat filtering, or both. Therefore, to narrow down the potential that an observed association is indeed due to a biotic interaction, any interaction model must allow flexible incorporation of covariates. In this way, we may test whether any associations remain after we have "adjusted" for the effects of the habitat.

We have seen two main construction principles for interaction models, corresponding to what we have termed symmetric and asymmetric, or directional, interactions. With symmetric interactions, we typically estimate some sort of correlation coefficient for a feature such as occupancy or abundance. With directional interactions, we simply use the occurrence or abundance of one species as a covariate in the model for another species. As a variation of this second principle of modeling species interactions, we have briefly discussed structural equation models (SEM, Grace et al., 2012), which we think offer some potential to explore hypotheses about species interactions in more complex interaction networks.

All the models in this chapter can be powerful pattern discovery tools, although perhaps more so the models for symmetric interactions, because they are simpler, we don't need to specify directionality, and hence we can usually fit these more unspecific models to a larger number of species all at once. This allows for a more efficient screening for "striking" pairwise patterns in a community. But models for symmetric interactions and models for directional interactions could also be employed in combination: we could use the former to screen a larger number of species and then follow up with more detailed analyses of the association patterns for striking species pairs using models for directional interactions or SEMs for interaction networks.

Though powerful in principle, there are several practical challenges in fitting these models, and they are in conflict with each other: on the one hand, these models can be extremely data-hungry, but on the other, they often require extremely long run times. However, this latter problem is exacerbated by bigger sample sizes. In the three case studies of this chapter, we had approximate sample sizes (in terms of the number of sites) of 1,400 in the *MesoCarnivores* data set, 400 in the *HubbardBrook* data, and 1,200 in the *SwissAtlasHa* data. In some ways, we were at a limit with these data sets and our software. For instance, none of the models with species interactions in [Section 8.3](#) could be successfully fit to a subsampled variant of the *MesoCarnivores* data set with only 140 sites in unmarked. And working with the full 1,400 sites and an interaction model with just one additional covariate in the main effects of occupancy produced boundary estimates and NaN's for some SEs in unmarked. As another example, some experimentation with the model of Rota et al. (2016a) fit to the *HubbardBrook* data set again produced boundary estimates. Finally, the latent variable models for the Swiss atlas data revealed badly mixing chains especially for the coefficients of the latent variables and required run times of several days with JAGS, even though we only fit the minimum of 2 latent variables. Hence, both unmarked and JAGS may quickly reach their limits for these types of models. Different, more powerful or custom-built software may then be required. Avoiding any unnecessary model complexity is particularly important in interaction models.

We have presented both static and dynamic models and models of occupancy and of abundance. A benefit of dynamic, or generally multi-season, models is that in them the information about species interactions is combined over time and hence, a larger sample size is accumulated over the years; this is helpful for the detection of interactions (Mason Fidino, pers. comm.). A benefit of abundance models is that abundance data carry more information about species associations than do presence/absence data. Hence, identification of interactions will be easier when modeling abundance than when modeling

occurrence. As a result, all else equal, the power to detect interactions will arguably be greatest in multiyear abundance models. Ironically though, these are perhaps the least well-developed types of interaction models, at least in the arena of hierarchical models that accommodate imperfect detection. This should provide the motivation to develop and apply more open abundance models with interactions.

In the future, for the modeling of symmetric interactions, we expect to see more applications of the models of Rota et al. (2016a), Fidino et al. (2019) and Hepler and Erhardt (2020). Recognizing more clearly the relationships between this type of model and classical log-linear modeling for contingency tables may be beneficial (Darryl MacKenzie, pers. comm.). For the modeling of “many” species, the type of models developed by Pollock et al. (2014) and the latent variable models of Hui et al. (2014) were both “translated” into an occupancy-type of model (i.e., with imperfect detection) by Tobler et al. (2019); see [Section 8.4.2](#). In a sense, this was a trivial extension, and yet it was an important step forwards. We would expect more developments along these lines as well as applications of these models. Some of the most sophisticated JSMDs, and computational implementations of such models, allow both “many” species and the modeling of species interactions by covariates and have been implemented in powerful special-purpose software (Ovaskainen et al., 2017; Tikhonov et al., 2017). This software does not yet accommodate imperfect detection, but it is to be hoped that this important extension will be achieved in the near future.

Models of directional interactions are simple conceptually and easy to understand. They are also easier to fit in practice both with maximum likelihood (though not yet with unmarked) and certainly with BUGS. Their extension to, and relationships with, structural equation model types should be investigated more.

It is possible, and has been done multiple times, to make detection probability dependent on the presence/absence, or the abundance, of another species. Likewise, it would appear interesting to consider the effects of the presence/absence of one species on the false-positive probability of another. Chambert et al. (2016) describe such a model in the context of abundance. We know of no such occupancy model, but we think it would make sense to assume that false-positives in one species may depend in this way on another species, perhaps one that it resembles a lot or one that is far more common than the target species. In community applications with many species, false-positives appear to be a very real challenge, and it is likely that their frequency and type will depend on the particular sets of species that occur at a site. Incorporation of such dependencies between the state process of some species and the observation process of others looks like an interesting, but challenging problem (see Wright et al. 2020 for a recent paper on the topic).

Bringing space into interaction modeling may be worthwhile. That is, combining the modeling and estimation of spatial structure that cannot be explained by available covariates and the modeling of species interactions. Thorson et al. (2016) provide one interesting example and apply it to communities of 10–20 species, though unfortunately their model ignores imperfect detection. Ovaskainen et al. (2016b) apply a spatially explicit JSMD to 55 butterfly species again ignoring bias incurred by imperfect detection. In contrast, Rota et al. (2016b) develop a multispecies, spatial occupancy model with a component for detection, but they only have two species. See also the recent model by Hepler and Erhardt (2020).

In this chapter, we have only shown standard occupancy and Binomial N-mixture sampling protocols. However, the extension of these methods to other sampling protocols would be fairly straightforward, e.g., to capture-recapture, double-observer, or distance sampling (Chapters 7–9 in AHM1) when modeling the abundance of multiple species, or to removal and time-to-detection designs (Chapter 10 in AHM1) when modeling occupancy. You would simply switch the type of observation model in your hierarchical model. This modularity is one of the beauties of hierarchical models.

Finally, the principles described in this chapter could be applied to species responses other than occurrence or abundance. For instance, the modeling of non-independence among a set of species could be applied to multispecies models of survival (Chapter 3) or of trends in abundance (Chapters 1 and 2) or occurrence (Chapter 4). The degree of non-independence among species in such responses could be due to shared descent (i.e., phylogeny; e.g., Frishkoff et al., 2017). Thus, it would be perfectly doable to extend the community CJS models in Chapter 3 such that they would account for similarity among species due to shared descent, by adding a latent-variable part. Ovaskainen et al. (2019) offer a neat example of this idea of transferability of a community modeling framework. They take their modeling framework originally developed for abundance or occurrence responses (Ovaskainen et al., 2017) and then adapt it to an entirely different response: measurements that characterize the movements of individuals from multiple species. We think that there are more opportunities for such “lateral transfers” of statistical methodology in ecology and related sciences.

Marc Kéry • J. Andrew Royle

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