Chapter 8

Basic Presence/Absence Situation

In the preceding chapters we have considered the problem of estimating the probability of occupancy (or proportion of units occupied) in a single season. The methods we have detailed may provide some indication of the current patterns in occupancy within that season; a snapshot of the population at a single point in time. However as discussed in Chapter 1, despite the popularity of doing so, it is not always appropriate to attempt to infer process from an observed pattern. Often there are many processes that could result in the same pattern being observed at any given time (e.g., Pirsig, 1974; Romesburg, 1981; Nichols, 1991; Williams et al., 2002).

A much more reliable approach to understanding the processes occurring within a system is to observe how the system behaves over a longer timeframe. This should not be at all surprising. As an analogy, suppose that you are given a randomly selected photograph from a stack of photographs taken throughout a football game. You are then asked to comment on the current state of the game, and how the game has progressed up to that point. It would be possible to tell something about the current state of play, such as which team has the ball and possibly the score; however, it would be impossible to make further comment on how the game has progressed. Not until you are able to go through the entire stack of photographs (in order) would you be able to get some idea of how the game progressed. It is the same situation in ecological studies where processes of population dynamics can only be fully understood by observing the population at systematic points in time, noting how the patterns change and modeling these changes in terms of relevant rate parameters. As emphasized in Chapter 1, strong inferences arise when system behavior (e.g., estimated changes in rate parameters) is compared against predictions of *a priori* hypotheses, especially when system dynamics are generated by experimental manipulations within the context of experimental design. The models of this chapter were developed to provide the estimates needed for such investigations.

In this chapter we turn our attention to the problem of estimating occupancy over multiple seasons and, in particular, understanding the underlying population dynamics that may cause changes in the occupancy state of a unit. These dynamic parameters are of interest in many areas of ecology, including

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metapopulation studies where the processes of local extinction and colonization (often hypothesized to be functions of patch size and isolation from neighboring patches, respectively) produce an *incidence* function (e.g., Diamond, 1975; Hanski, 1994a, 1994b). However most of the methods used to study these parameters do not explicitly account for detection probability. Moilanen (2002) found false absences to be the greatest contributor of bias to the estimation of the incidence function parameters. In monitoring programs, often the rate of change in occupancy may be of as much or greater interest than the absolute level of occupancy at any point in time. Changes in the use of different habitats over time will also be of interest in many species-habitat studies. For example, are the same habitats used by a species in summer and winter, or what effect has a change in the habitat had on the species patterns of use?

We consider two general approaches for modeling changes in occupancy over time: (1) a model where underlying dynamics are implied but not explicitly accounted for (effectively combining several single-season models); and (2) explicitly modeling potential changes in the occupancy state of a unit over time with colonization and local extinction probabilities.

8.1 BASIC SAMPLING SCHEME

We assume a situation where s units are selected from an area of interest with the intent of establishing the presence or absence of a species, as in single-season studies, although now the assessment is for multiple points in time. Units may constitute naturally occurring sampling units such as discrete ponds or patches of vegetation, investigator-defined monitoring stations, or quadrats chosen from a predefined area of interest.

The timeframe of the study can now be considered at two scales. Firstly, at the larger scale, the study is conducted over multiple (T) seasons (e.g., years or breeding seasons, denoted by t). Each season is common to all units, with the occupancy state of units able to change between seasons, but not within seasons. Within each season, the smaller time scale, appropriate sampling methods are used to survey units K_t times (Fig. 8.1). Such a design is similar to Pollock's robust design (Pollock, 1982) used in mark–recapture studies where seasons represent the primary sampling periods and surveys within seasons represent secondary sampling periods. Effectively, the general design considered here is a sequence of single-season studies conducted at (usually) the same units for multiple seasons.

At each survey of a unit, the target species is detected (1) or not detected (0) and is never falsely detected when absent. The resulting sequence of detections and nondetections for unit i, conducted during season t, is denoted as the detection history $\mathbf{h}_{t,i}$. The complete detection history for unit i is denoted as $\mathbf{h}_i$,

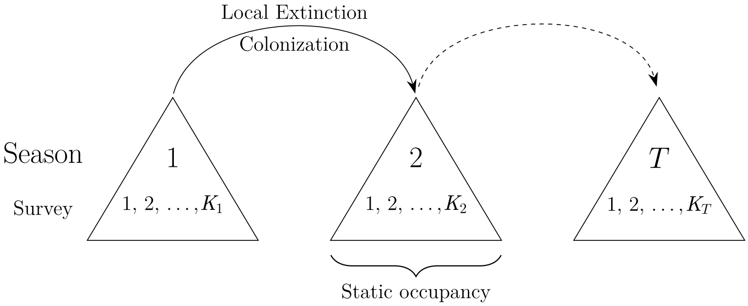

FIGURE 8.1 Graphical representation of the sampling situation for a multi-season occupancy study. Each triangle represents a season (t), with multiple (K_t) surveys within seasons. Occupancy status is static at units within seasons, but may change between seasons through the processes of colonization and local extinction.

and is the sequence of the T single season detection histories. For example the detection history $\mathbf{h}_i = 110\,000\,010$ represents a three-season study (with three surveys per season) where the target species was detected in the first and second surveys in season 1, was never detected in season 2, and detected only in the second survey in season 3. Similar to the single-season situation, due to imperfect detectability, we do not know whether the species was present but undetected in season 2 or was genuinely absent. That is, we do not know whether the species persisted at the unit for all three seasons (i.e., never went locally extinct), or went locally extinct and then (re)colonized the unit.

8.2 AN IMPLICIT DYNAMICS MODEL

One approach to modeling detection/nondetection data from multiple seasons is to effectively apply a single season model to the data collected in each of the T seasons. Under this approach, occupancy in one season is considered to be a random process in the sense that the occupancy status of a unit in the previous season has no effect on the probability of occupancy at the units in the current season. Regardless of the underlying processes of change in occupancy, only the resulting pattern or level of occupancy each season is modeled. Here, let ψ_t be the probability a unit is occupied in season t, and $p_{t,j}$ be the probability of detecting the species in the jth survey of a unit during season t (given the species was present at the unit in season t). Using the model-based approach of MacKenzie et al. (2002) (as detailed in Chapter 4), the observed data likelihood for season t would be

$$ODL_t\left(\psi_t, \mathbf{p}_t | \mathbf{h}_{t,1}, \mathbf{h}_{t,2}, \ldots, \mathbf{h}_{t,s}\right) = \prod_{i=1}^{s} Pr\left(\mathbf{h}_{t,i} | \psi_t, \mathbf{p}_t\right),$$

with the observed data likelihood evaluated for the full T seasons being the product of the seasonal likelihoods, i.e.,

$$ODL(\boldsymbol{\psi}, \mathbf{p}|\mathbf{h}_1, \mathbf{h}_2, \ldots, \mathbf{h}_s) = \prod_{t=1}^{T} ODL_t\left(\psi_t, \mathbf{p}_t|\mathbf{h}_{t,1}, \mathbf{h}_{t,2}, \ldots, \mathbf{h}_{t,s}\right).$$

This same model can also be developed directly from the detection histories using the same techniques as in the previous chapters: taking a verbal description of the detection histories and translating them into a mathematical equation. Consider again the detection history $\mathbf{h}_i = 110\,000\,010$. A verbal description of these data would be:

In season 1: the unit was occupied with the species being detected in the first and second surveys, but not in the third.

In season 2: the unit was either occupied with the species not being detected in any of the 3 surveys, or the unit was unoccupied.

In season 3: the unit was occupied with the species being detected in the second survey, but not in the first or third surveys.

Translating these statements into mathematical equations using the defined model parameters we have:

Season 1: $\psi_1 p_{1,1} p_{1,2}\left(1 - p_{1,3}\right)$,
Season 2: $\psi_2\left(1 - p_{2,1}\right)\left(1 - p_{2,2}\right)\left(1 - p_{2,3}\right) + (1 - \psi_2)$,
Season 3: $\psi_3\left(1 - p_{3,1}\right) p_{3,2}\left(1 - p_{3,3}\right)$.

Therefore the probability of observing the entire detection history would be:

$$\begin{aligned} Pr(\mathbf{h}_i = 110\,000\,010|\boldsymbol{\psi}, \mathbf{p}) = {} & \psi_1 p_{1,1} p_{1,2}\left(1 - p_{1,3}\right) \\ & \times\left[\psi_2\left(1 - p_{2,1}\right)\left(1 - p_{2,2}\right)\left(1 - p_{2,3}\right) + (1 - \psi_2)\right] \\ & \times \psi_3\left(1 - p_{3,1}\right) p_{3,2}\left(1 - p_{3,3}\right). \end{aligned} \tag{8.1}$$

This procedure can be used to obtain the probability statement for each of the s observed detection histories, and the observed data likelihood would be calculated as

$$ODL(\boldsymbol{\psi}, \mathbf{p}|\mathbf{h}_1, \mathbf{h}_2, \ldots, \mathbf{h}_s) = \prod_{i=1}^{s} Pr(\mathbf{h}_i|\boldsymbol{\psi}, \mathbf{p}).$$

Expressed in terms of the underlying random variables, the implicit dynamics model would be:

$$z_{t,i} \sim Bernoulli(\psi_t),$$

$$h_{t,ij}|z_{t,i} \sim Bernoulli\left(z_{t,i} p_{t,j}\right),$$

which could be used to construct the complete data likelihood.

As in Chapter 4, this model can be easily generalized so that the probabilities of occupancy and detection are functions of covariates, and to allow for missing observations. Models can also be considered where there is some structural relationship among probabilities in different seasons. For example, Field et al. (2005) modeled a systematic decline in occupancy over time by defining seasonal occupancy probabilities with a linear trend on the logit scale, i.e., $logit(\psi_t) = \beta_0 + \beta_1 t$.

Finally, we note that although the above modeling may appear to be relatively phenomenological, in the sense that vital rates (probabilities of local extinction and colonization) governing the dynamic process do not appear explicitly in this model, it actually makes fairly restrictive assumptions about these vital rates. In Section 10.4, we show that the implicit dynamics model is based on the assumption that the probability of the species not going locally extinct at a previously occupied unit is equal to the probability of colonization of a previously unoccupied unit. In the next section, we discuss a more general explicit model of occupancy dynamics, from which the above implicit dynamics model can be obtained as a special case.

8.3 MODELING DYNAMIC CHANGES EXPLICITLY

As noted in the previous section, the dynamic processes governing changes in the occupancy state variable are the colonization of an unoccupied unit by the species and the local extinction of the species at an occupied unit. In this section we consider models that directly incorporate these dynamic processes, as they are often of direct interest. They are somewhat analogous to the birth and death processes of the abundance state variable and as such supply information relevant to the long-term sustainability of a population. As the drivers of the system (with respect to occupancy), understanding how these dynamic processes are affected by changes of habitat or climatic conditions (for example) may be important for the successful management of ecological systems.

For the remainder of this chapter we consider the dynamic changes in occupancy as a first-order Markov process. That is, the probability of a unit being occupied in season t depends upon the occupancy state of the unit in the previous season, $t-1$. In some situations, higher order Markov processes (e.g., occupancy probability at t depends upon state of occupancy at both $t-1$ and $t-2$) may be biologically reasonable to represent long-term 'memory' about the occupancy state of a unit. For example from mark–resight data, Hestbeck et al. (1991) modeled transition probabilities between different wintering grounds for Canada Geese (*Branta canadensis*) as a second-order Markov process to represent long term fidelity of individual birds to each region. Such an extension could be applied using the multi-season, multi-state model (Chapter 9) where the state of a unit is defined in terms of occupancy status in both the current and previous season (compared to a first-order Markov process model where, as developed below, states are defined in terms of the current season only). This is very similar to the approach used in the mark–recapture multi-event models (Pradel, 2005), although as in the mark–recapture setting, we would expect such modeling to be quite data hungry (Cole et al., 2014). Green et al. (2011) considered a second-order Markov model to accommodate the maturation period for wood frogs (*Lithobates sylvatica*), but inference methods were not fully developed.

Modeling changes in occupancy as a Markov process also accounts for a form of temporal autocorrelation. When observations on the same sampling unit are positively correlated, values close in time are more similar than those separated by longer periods (i.e., the sampling variance for a short time series will tend to be less than that of a longer time series). In the occupancy context this equates to the expectation that a unit that is occupied now may be more likely to be occupied again in the near future than one that is currently unoccupied. A Markov process adequately models this autocorrelation process.

Markovian changes in occupancy can also be considered as inducing a form of heterogeneity in occupancy probabilities where the probability of a unit being occupied in season t will be different for units that were occupied in the previous season, compared to the units that were unoccupied.

Formally, we define colonization (γ_t) and local extinction (ϵ_t) probabilities to be:

$\gamma_t =$ the probability that an unoccupied unit in season t is occupied by the species in season $t+1$; and

$\epsilon_t =$ the probability that a unit occupied in season t is unoccupied by the species in season $t+1$.

These dynamic processes represent the probabilities of a unit transitioning between the occupied and unoccupied state between consecutive seasons (Fig. 8.2).

Below we detail three approaches to modeling multiple-season occupancy data that explicitly account for the processes of colonization and local extinction. First, we briefly discuss some historical approaches that were developed for situations where the species is (assumed to be) always detected when present at a unit (i.e., detection probability equals 1). We then focus on two methods that allow for the imperfect detection of the species; a 'conditional' and an 'unconditional' approach. The 'conditional' approach exploits the similarities between the type of data collected in the current context and capture–recapture data collected from individuals. This approach is 'conditional' in the sense that the detection history for a unit is only modeled from the season in which the

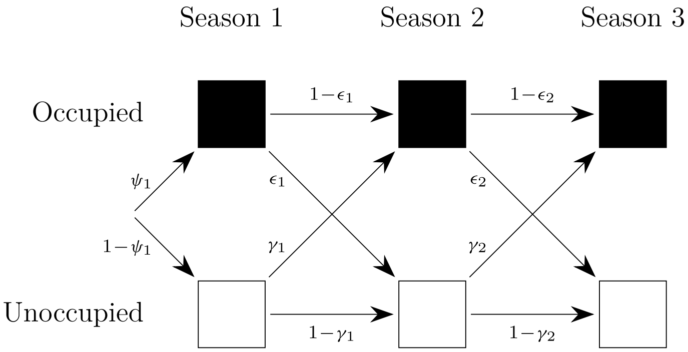

FIGURE 8.2 Representation of how the occupancy state of a unit may change between seasons in terms of the processes of first season occupancy (ψ_1), colonization (γ), and local extinction (ϵ). Filled boxes indicate the unit is occupied (species present) in that season while empty boxes indicate the unit is unoccupied (species absent).

species is first detected, i.e., the modeling conditions upon the first detection of the species. This is due to the fact that in capture–recapture, an individual is unknown to the researchers prior to the first time it is caught and marked. As a result, it is not generally possible to obtain seasonal estimates of occupancy, only estimates of the dynamic processes themselves. The second approach (upon which we largely focus) is an ‘unconditional’ approach, where the modeling makes full use of the detection histories. Here it is possible to estimate both occupancy and the dynamic parameters.

8.3.1 Modeling Dynamic Processes when Detection Probability is 1

In the late 1960s and throughout the 1970s, the ecological literature contained a number of studies of animals on islands in which the presence or absence of breeding populations (frequently of birds) was assessed over a number of different years (see Diamond and May, 1977, and papers cited therein). This work was motivated largely by the models of MacArthur and Wilson (1967), which suggested that species richness on islands reflected a dynamic equilibrium between rates of local extinction and colonization. Diamond and May (1977) recommended that such data be viewed as having resulted from a stationary Markov process defined by corresponding rates of extinction and colonization, a recommendation that had been anticipated by Simberloff (1969). Diamond and May (1977) focused on the implications of this model for (1) detection–nondetection data collected at varying time intervals and (2) computation of various turnover statistics.

Clark and Rosenzweig (1994) (also see Rosenzweig and Clark, 1994) considered the problem of estimating extinction and colonization rates for such a Markov model from detection–nondetection data. They provided maximum likelihood estimates assuming both a stationary process with rate parameters constant over time, and detection probabilities of 1. Erwin et al. (1998) expanded this general modeling approach, considering reduced-parameter non-Markovian models, as well as Markovian models permitting time-specific rates of local extinction and colonization. These models only provide reasonable estimates in the situation where presence and absence can be ascertained (Clark and Rosenzweig, 1994; Erwin et al., 1998) and are thus of limited usefulness.

8.3.2 Conditional Modeling of Dynamic Processes

Barbraud et al. (2003) considered models for colony unit dynamics, the same problem considered by Erwin et al. (1998), but wanted to relax the assumption of detection probabilities equal to 1. They considered the estimation problem by focusing on the analogy between occupancy dynamics of colony units and population dynamics of individual animals. The simplest form of colony detection history data for multiple seasons consists of 1's and 0's denoting detection or nondetection, respectively, at each study unit. These data are analogous to capture history data for individual animals in animal populations open to gains and losses. For example, the capture history 1 0 1 0 would indicate an animal caught in periods (analogous to 1 survey per season) 1 and 3, but not in periods 2 and 4. The usual approach to modeling such data uses parameters for survival from one sample period to the next and capture probability at each period (e.g., see Lebreton et al., 1992). Interior 0's (followed and preceded by one or more 1's; e.g., period 2) are usually viewed unambiguously as 'present but not captured' and thus modeled with the complement of capture probability. However, this analogy is not especially useful for occupancy studies in which an interior 0 can reflect either 'present but not detected' or 'absent, but followed by recolonization'.

Barbraud et al. (2003) recognized that there is a close analogy between occupancy studies and capture–recapture studies with temporary emigration (Kendall et al., 1997; Kendall, 1999; Williams et al., 2002). In the case of temporary emigration, an interior 0 can result from either 'presence without capture' or 'temporary emigration' of the animal. Unfortunately, the probability of being a temporary emigrant is confounded with capture probability in standard models for open populations (Burnham, 1993; Kendall et al., 1997). However, Kendall and Nichols (1995) and Kendall et al. (1997) recognized that the robust design (described above, also see Pollock, 1982) provides the information needed to estimate capture probability conditional on presence in the sampled area and thus allows separate estimates of this conditional capture probability and the probability of being a temporary emigrant.

Barbraud et al. (2003) viewed the Markovian temporary emigration model of Kendall et al. (1997) as potentially most useful for estimation in the context of occupancy dynamics. This temporary emigration model contains two parameters for the probability of being a temporary emigrant (i.e., the probability that an animal was not in the study population, but still part of the 'superpopulation') at any sampling period: (1) for animals that were not temporary emigrants the previous period, $t-1$; and (2) for animals that were temporary emigrants the previous period. The temporary emigration parameter for animals that were not temporary emigrants the previous period (i.e., within the study population at $t-1$, outside the study population at t) was viewed as local extinction probability in the context of occupancy studies (i.e., unit was occupied at $t-1$, unoccupied at t). The complement of the second temporary emigration parameter, i.e., $1 - Pr$(an animal outside the study population at $t-1$, was also outside the study population at t), was viewed as a probability of colonization in occupancy studies. Under this analogy, the usual survival probability of open capture–recapture models was set equal to 1, as it reflected the probability that a unit always 'survived' (i.e., units will never 'die' in the sense that the species could always recolonize the unit a later time). Note, one situation where this might not be a reasonable assumption is where a change in the habitat or local environment of a unit renders it uninhabitable for the species, in which case the joint modeling of habitat and occupancy may be useful (see Chapter 13). To complete the analogy between the temporary emigration problem and occupancy dynamics, we note that the random temporary emigration model of Kendall et al. (1997) is equivalent to the implicit dynamics model for occupancy (Section 8.2).

The advantage of recognizing this analogy between the modeling of temporary emigration and occupancy dynamics involved software and computations. Software had been developed by Kendall and Hines (1999) and White and Burnham (1999) to obtain parameter estimates under the temporary emigration models of Kendall et al. (1997) using robust design data. Barbraud et al. (2003) thus used these programs (MARK: White and Burnham, 1999; RDSURVIV: Kendall and Hines, 1999) with data from two survey flights per year over the Camargue delta in southern France to estimate local rates of extinction and colonization for purple heron (*Ardea purpurea*) and gray heron (*Ardea cinerea*) breeding colonies at reed bed sites. Of particular interest, biologically, was the modeling of time-specific local colonization in one area of the Camargue as a function of local extinction probability in a neighboring disturbed area. This ultrastructural modeling dealt explicitly with spatial dependencies in occupancy and provided indirect inference about animal movement without using marked individuals (Barbraud et al., 2003).

We do not present the actual temporary emigration model here, as it is best viewed as a special case of the model of MacKenzie et al. (2003) which is presented in detail below. Readers especially interested in the details of the temporary emigration modeling approach for occupancy studies are directed to Barbraud et al. (2003). The primary difference between the two approaches (Barbraud et al., 2003; MacKenzie et al., 2003) is the conditional nature of the temporary emigration modeling. In capture–recapture studies of animal populations, most models condition on the release of individual animals at their periods of first capture (exceptions include the temporal symmetry models of Nichols et al., 1986, 2000a; Pradel, 1996; Williams et al., 2002). Stated differently, the 0's occurring in a capture history before an animal's first capture are not typically modeled. However, in occupancy studies in which potential units are identified at the beginning of the study, such conditioning is not needed, and initial 0's can be modeled. We thus refer to the temporary emigration modeling of Barbraud et al. (2003) as 'conditional', and contrast this with the 'unconditional' approach of MacKenzie et al. (2003). Both approaches should provide approximately unbiased estimates of the dynamic processes, but the approach of MacKenzie et al. (2003) should be more efficient and leads more readily to estimates of occupancy for each season of the study.

8.3.3 Unconditional Modeling of Dynamic Processes

MacKenzie et al. (2003) used the colonization and local extinction probabilities defined above (γ_t and ϵ_t) to extend the single-season model of MacKenzie et al. (2002). Once occupancy state (the probability of occupancy) is established in the first season (ψ_1), potential changes in the occupancy state of a unit between seasons are simply incorporated using the dynamic parameters. To construct their model, MacKenzie et al. (2003) used the now familiar approach of taking a verbal description of a detection history and translating it into a mathematical equation, giving the probability of observing the detection history. For example, consider again the detection history $\mathbf{h}_i = 110\,000\,010$ where the occupancy status of the unit in the second season is unknown. A verbal description of these data that incorporates the concepts of colonization and local extinction would be:

In season 1: the unit was occupied with the species being detected in the first and second surveys, but not in the third.

From the end of season 1 to the start of season 3 (immediately before surveying commenced): either the species did not go locally extinct between seasons 1 and 2, was not detected in any of the 3 surveys within season 2 and did not go locally extinct between seasons 2 and 3, *or* the species went locally extinct between seasons 1 and 2, then recolonized the unit between seasons 2 and 3.

In season 3: the species was detected in the second survey, but not in the first or third survey.

Translating these statements into mathematical equations using the model parameters defined earlier we have:

Season 1:

$$\psi_1 p_{1,1} p_{1,2} \left(1 - p_{1,3}\right),$$

From the end of season 1 to the start of season 3:

$$(1 - \epsilon_1)\left(\prod_{j=1}^{3}\left(1 - p_{2,j}\right)\right)(1 - \epsilon_2) + \epsilon_1 \gamma_2,$$

Season 3:

$$\left(1 - p_{3,1}\right) p_{3,2} \left(1 - p_{3,3}\right).$$

The probability of observing the complete detection history would be,

$$\begin{aligned} Pr(\mathbf{h}_i = 110\,000\,010|\boldsymbol{\theta}) = \psi_1 p_{1,1} p_{1,2} \left(1 - p_{1,3}\right) & \\ \times \left[(1 - \epsilon_1)\left(\prod_{j=1}^{3}\left(1 - p_{2,j}\right)\right)(1 - \epsilon_2) + \epsilon_1 \gamma_2\right] & \\ \times \left(1 - p_{3,1}\right) p_{3,2} \left(1 - p_{3,3}\right), & \qquad (8.2) \end{aligned}$$

where $\boldsymbol{\theta}$ is the set of parameters in the model.

Note the differences between Eqs. (8.2) and (8.1), where the dynamic processes are not explicitly modeled. Here the model incorporates a mechanistic process for how the occupancy state of a unit may change between seasons, whereas in the former model only the state of occupancy each season is considered.

Formally, the explicit dynamics model could be defined in terms of the underlying latent and observed random variables as:

$$\begin{gathered} z_{1,i} \sim Bernoulli(\psi_1)\,, \\ \left(z_{t,i} | z_{t-1,i} = 0\right) \sim Bernoulli(\gamma_{t-1}) \text{ for } t = 2, \ldots, T, \\ \left(z_{t,i} | z_{t-1,i} = 1\right) \sim Bernoulli(1 - \epsilon_{t-1}) \text{ for } t = 2, \ldots, T, \\ h_{t,ij} | z_{t,i} \sim Bernoulli\left(z_{t,i} p_{t_j}\right). \end{gathered}$$

Note that unlike for the implicit dynamics model, the Bernoulli distribution associated with the occupancy random variables $z_{t,i}$ for $t = 2 \ldots, T$, is different dependent upon the presence or absence of the species at the unit in the previous season. If the species was absent from unit i in the previous season ($z_{t-1,i} = 0$), the species is present in season t with probability γ_t (i.e., probability of the unit being colonized by the species), whereas, if the species was present at unit i in the previous season ($z_{t-1,i} = 1$), the species is present in season t with probability $1 - \epsilon_t$ (i.e., probability the species did not go locally extinct at the unit). In the implicit dynamics model, the probability of unit i being occupied in season t is always ψ_t, irrespective of the occupancy status of the unit in season $t - 1$. The conditional nature of the explicit dynamics model is what characterizes a first-order Markov process.

Generally, there may be a number of different possible pathways that could result in an observed detection history. MacKenzie et al. (2003) therefore suggest it might be most convenient to describe the model using matrix notation (see Appendix for a brief introduction to matrices). Let $\boldsymbol{\phi}_t$ be the 2×2 matrix denoting the probability of a unit transitioning between occupancy states from season t to $t + 1$. Rows of $\boldsymbol{\phi}_t$ represent the occupancy state of the unit in season t (state 0 = unoccupied; state 1 = occupied), and columns represent the occupancy state at $t + 1$, that is:

$$\boldsymbol{\phi}_t = \begin{bmatrix} 1-\gamma_t & \gamma_t \\ \epsilon_t & 1-\epsilon_t \end{bmatrix}.$$

Further, let $\boldsymbol{\phi}_0$ be the row vector:

$$\boldsymbol{\phi}_0 = \begin{bmatrix} 1-\psi_1 & \psi_1 \end{bmatrix},$$

where ψ_1 is the probability the unit is occupied in the first season. This vector models whether a unit was occupied or unoccupied in the first season. Next, define $\mathbf{p}_{t,j}$ to be the detection probability matrix, defining the probability of each type of observation (or observed state) in survey j of season t, given the true occupancy state of a unit in season t (as used in Chapters 5 and 6). At this stage, there are only two possible outcomes of each survey, nondetection or detection of the species. Therefore:

$$\mathbf{p}_{t,j} = \begin{bmatrix} 1 & 0 \\ 1-p_{t,j} & p_{t,j} \end{bmatrix}$$

where rows represent the true occupancy state of a unit in season t, and columns the observed state in survey j of season t. As we described for the single-season multi-state model, the probability of observing the detection history $\mathbf{h}_{t,i}$ for unit i in season t, conditional upon occupancy state, can be represented as the column vector $\mathbf{p}_{\mathbf{h},t}$. This is found by element-wise multiplication of the respective columns of $\mathbf{p}_{t,j}$, column 1 for nondetections and column 2 for detections, associated with the observation made during each survey within the season (see

Chapter 5 for details). For instance, $\mathbf{p}_{\mathbf{h},t}$ for the within-season detection history $\mathbf{h}_{t,i} = 101$ would be:

$$\begin{aligned}\mathbf{p}_{101,t} &= \begin{bmatrix} 0 \\ p_{t,1} \end{bmatrix} \odot \begin{bmatrix} 1 \\ 1 - p_{t,2} \end{bmatrix} \odot \begin{bmatrix} 0 \\ p_{t,3} \end{bmatrix} \\ &= \begin{bmatrix} 0 \\ p_{t,1}\left(1 - p_{t,2}\right) p_{t,3} \end{bmatrix}.\end{aligned}$$

This expression indicates that the probability of observing this detection history is 0 if the unit was unoccupied (the first element; as the species could not be detected if it was absent from the unit), and $p_{t,1}\left(1 - p_{t,2}\right) p_{t,3}$ if the unit was occupied by the species (the second element). The first element of $\mathbf{p}_{\mathbf{h},t}$ will always be 0 whenever the species is detected at least once at the unit during season t. Using similar reasoning, if the species is never detected at a unit during season t ($\mathbf{h}_{t,i} = 000$), the first element will always be 1, as this is the only observable detection history for a unit that is unoccupied, that is:

$$\mathbf{p}_{000,t} = \begin{bmatrix} 1 \\ \prod_{j=1}^{3}\left(1 - p_{t,j}\right) \end{bmatrix}.$$

Using this matrix notation, the probability statement for an observed detection history, for all seasons, could be calculated as:

$$Pr(\mathbf{h}_i | \psi_1, \boldsymbol{\gamma}, \boldsymbol{\epsilon}, \mathbf{p}) = \boldsymbol{\phi}_0 \prod_{t=1}^{T-1}\left(D\left(\mathbf{p}_{\mathbf{h},t}\right) \boldsymbol{\phi}_t\right)\mathbf{p}_{\mathbf{h},T}, \tag{8.3}$$

where $D\left(\mathbf{p}_{\mathbf{h},t}\right)$ is a diagonal matrix with the elements of $\mathbf{p}_{\mathbf{h},t}$ along the main diagonal (top left to bottom right), zero otherwise. Diagonalizing the vector is required merely for the matrix algebra to work out correctly. Note that what Eq. (8.3) is doing is performing a series of matrix multiplications (see Appendix) that automatically sum together the various possible outcomes that could have resulted in the same observed detection history, rather than manually evaluating the different options as was done when developing Eq. (8.2).

Initially Eq. (8.3) may look somewhat confusing, but stepping through the various components, we see that it does have an intuitive interpretation. $\boldsymbol{\phi}_0$ establishes the probability that a unit is either unoccupied or occupied immediately prior to surveys commencing in season 1. The term $\left(D\left(\mathbf{p}_{\mathbf{h},t}\right) \boldsymbol{\phi}_t\right)$ calculates the probability of observing the particular sequence of detections and nondetections in season t (conditional upon occupancy state), and then the probability of the unit transitioning to the occupied or unoccupied state immediately before

TABLE 8.1 Examples of detection histories ($\mathbf{h}_i$) and the associated probabilities of observing them ($Pr(\mathbf{h}_i \mid \boldsymbol{\psi}_1, \boldsymbol{\gamma}, \boldsymbol{\epsilon}, \mathbf{p})$) using the unconditional explicit dynamics model

$\mathbf{h}_i$	$Pr(\mathbf{h}_i \mid \boldsymbol{\psi}_1, \boldsymbol{\gamma}, \boldsymbol{\epsilon}, \mathbf{p})$
11 10 01	$= \boldsymbol{\phi}_0 D(\mathbf{p}_{11,1})\, \boldsymbol{\phi}_1 D(\mathbf{p}_{10,2})\, \boldsymbol{\phi}_2 \mathbf{p}_{01,3}$ $= \begin{bmatrix} 1-\psi_1 & \psi_1 \end{bmatrix} \begin{bmatrix} 0 & 0 \\ 0 & p_{1,1}p_{1,2} \end{bmatrix} \begin{bmatrix} 1-\gamma_1 & \gamma_1 \\ \epsilon_1 & 1-\epsilon_1 \end{bmatrix} \begin{bmatrix} 0 & 0 \\ 0 & p_{2,1}(1-p_{2,2}) \end{bmatrix} \begin{bmatrix} 1-\gamma_2 & \gamma_2 \\ \epsilon_2 & 1-\epsilon_2 \end{bmatrix} \begin{bmatrix} 0 \\ (1-p_{3,1})\, p_{3,2} \end{bmatrix}$ $= \psi_1 p_{1,1} p_{1,2}(1-\epsilon_1)\, p_{2,1}(1-p_{2,2})(1-\epsilon_2)(1-p_{3,1})\, p_{3,2}$
00 10 00	$= \boldsymbol{\phi}_0 D(\mathbf{p}_{00,1})\, \boldsymbol{\phi}_1 D(\mathbf{p}_{10,2})\, \boldsymbol{\phi}_2 \mathbf{p}_{00,3}$ $= \begin{bmatrix} 1-\psi_1 & \psi_1 \end{bmatrix} \begin{bmatrix} 1 & 0 \\ 0 & \prod_{j=1}^{2}(1-p_{1,j}) \end{bmatrix} \begin{bmatrix} 1-\gamma_1 & \gamma_1 \\ \epsilon_1 & 1-\epsilon_1 \end{bmatrix} \begin{bmatrix} 0 & 0 \\ 0 & p_{2,1}(1-p_{2,2}) \end{bmatrix} \begin{bmatrix} 1-\gamma_2 & \gamma_2 \\ \epsilon_2 & 1-\epsilon_2 \end{bmatrix} \begin{bmatrix} 1 \\ \prod_{j=1}^{2}(1-p_{3,j}) \end{bmatrix}$ $= \left((1-\psi_1)\,\gamma_1 + \psi_1 \left(\prod_{j=1}^{2}(1-p_{1,j}) \right)(1-\epsilon_1) \right) p_{2,1}(1-p_{2,2}) \left(\epsilon_2 + (1-\epsilon_2) \prod_{j=1}^{2}(1-p_{3,j}) \right)$
00 00 00	$= \boldsymbol{\phi}_0 D(\mathbf{p}_{00,1})\, \boldsymbol{\phi}_1 D(\mathbf{p}_{00,2})\, \boldsymbol{\phi}_2 \mathbf{p}_{00,3}$ $= \begin{bmatrix} 1-\psi_1 & \psi_1 \end{bmatrix} \begin{bmatrix} 1 & 0 \\ 0 & \prod_{j=1}^{2}(1-p_{1,j}) \end{bmatrix} \begin{bmatrix} 1-\gamma_1 & \gamma_1 \\ \epsilon_1 & 1-\epsilon_1 \end{bmatrix} \begin{bmatrix} 1 & 0 \\ 0 & \prod_{j=1}^{2}(1-p_{2,j}) \end{bmatrix} \begin{bmatrix} 1-\gamma_2 & \gamma_2 \\ \epsilon_2 & 1-\epsilon_2 \end{bmatrix} \begin{bmatrix} 1 \\ \prod_{j=1}^{2}(1-p_{3,j}) \end{bmatrix}$ $= (1-\psi_1) \left(\begin{array}{l} (1-\gamma_1) \left((1-\gamma_2) + \gamma_2 \prod_{j=1}^{2}(1-p_{3,j}) \right) + \\ \gamma_1 \left(\prod_{j=1}^{2}(1-p_{2,j}) \right) \left(\epsilon_2 + (1-\epsilon_2) \prod_{j=1}^{2}(1-p_{3,j}) \right) \end{array} \right) + \psi_1 \left(\prod_{j=1}^{2}(1-p_{1,j}) \right) \left(\begin{array}{l} \epsilon_1 \left((1-\gamma_2) + \gamma_2 \prod_{j=1}^{2}(1-p_{3,j}) \right) + \\ (1-\epsilon_1) \left(\prod_{j=1}^{2}(1-p_{2,j}) \right) \left(\epsilon_2 + (1-\epsilon_2) \prod_{j=1}^{2}(1-p_{3,j}) \right) \end{array} \right)$

surveying begins in season $t+1$. This is done recursively from season 1 to immediately before the final season of surveying (season T), hence the product term $\prod_{t=1}^{T-1}\left(D\left(\mathbf{p}_{\mathbf{h},t}\right)\boldsymbol{\phi}_t\right)$. At this stage the equation has calculated the probability of observing the particular detection history up to the end of the second to last season of surveying, and the unit being in either the occupied or unoccupied state immediately prior to the surveying in season T. Therefore to complete the probability statement, the probability of observing the sequence of detections and nondetections in the final season (conditional upon occupancy state) is required, i.e., $\mathbf{p}_{\mathbf{h},T}$. This final term is not diagonalized (i.e., is just a 2×1 column vector) so the result of the series of matrix multiplications is just a single number, as the first term was a 1×2 row vector and all intervening matrices were of dimension 2×2 (see Appendix for more details on the aspect of matrix multiplication). Some examples of observed detection histories and their probability statements, according to the above model, are given in Table 8.1. We encourage readers to take the time to work through these examples to cement their understanding of the model. From the probability statements for each observed detection history, the model observed data likelihood can be calculated in the usual manner (assuming independence of detection histories), i.e.,

$$ODL(\psi_1,\boldsymbol{\gamma},\boldsymbol{\epsilon},\mathbf{p}|\mathbf{h}_1,\ldots,\mathbf{h}_s)=\prod_{i=1}^{s}Pr(\mathbf{h}_i|\psi_1,\boldsymbol{\gamma},\boldsymbol{\epsilon},\mathbf{p}).$$

Note that if $T=1$, that is the study is only conducted for a single season, then the above equation reduces to $Pr(\mathbf{h}_i|\psi_1,\mathbf{p})=\boldsymbol{\phi}_0\mathbf{p}_{\mathbf{h},1}$. This is an equivalent formulation for calculating the probability of observing a detection history for the single season model of MacKenzie et al. (2002) (and described in Chapter 4), and this matrix form is the same as that presented for the single-season multi-state model in Chapter 5.

The complete data likelihood (CDL) for the unconditional explicit dynamics model can also be determined by considering the underlying latent and observed random variables, similar to the approach outlined in Section 4.4.1, but with additional complexity to account for changes in occupancy over time. Briefly, the key is to again assume that the latent variable for the occupancy status of a unit is known in each season. If so, the joint probability of observing the detection history data and presence/absence of the species in each season for unit i could be expressed as:

$$Pr(\mathbf{h}_i,\mathbf{z}_i|\psi_1,\boldsymbol{\gamma},\boldsymbol{\epsilon},\mathbf{p})=\prod_{t=1}^{T}Pr\left(\mathbf{h}_{t,i}|\mathbf{p}_t,z_{t,i}\right)$$

$$\times \prod_{t \in \tau_0} Pr\left(z_{t,i} | \gamma_{t-1}, z_{t-1,i} = 0\right)$$
$$\times \prod_{t \in \tau_1} Pr\left(z_{t,i} | \epsilon_{t-1}, z_{t-1,i} = 1\right)$$
$$\times Pr\left(z_{1,i} | \psi_1\right),$$

where τ_0 is the set of seasons between 2 and T in which unit i was unoccupied by the species in the previous season, and τ_1 is the set of seasons between 2 and T in which unit i was occupied by the species in the previous season. Therefore, using a CDL approach, there are four independent components associated with the joint probability statement that determines the probability of:

1. first-season occupancy, $Pr\left(z_{1,i} | \psi_1\right)$;
2. extinctions, $\prod_{t \in \tau_1} Pr\left(z_{t,i} | \epsilon_{t-1}, z_{t-1,i} = 1\right)$;
3. colonizations, $\prod_{t \in \tau_0} Pr\left(z_{t,i} | \gamma_{t-1}, z_{t-1,i} = 0\right)$;
4. detection of the species in each survey given the species presence at the unit in each season, $\prod_{t=1}^{T} Pr\left(\mathbf{h}_{t,i} | \mathbf{p}_t, z_{t,i}\right)$.

Note that these terms are ordered 4–1 in the expression for the CDL above, following convention for the ordering of the conditional events. The relevant thing to note with the CDL approach is that unlike using the ODL, there is no summation of terms, as assuming the $z_{t,i}$ values are known removes the ambiguity associated with nondetection of the species during a season. However, a different set of estimation algorithms must be used to account for the fact that the $z_{t,i}$ values are actually unobserved (e.g., expectation-maximization algorithm or MCMC).

8.3.4 Missing Observations

Missing observations can be easily accounted for using this type of modeling approach, as in the single-season case. If the missing observations occur within season t, then the vector $\mathbf{p}_{\mathbf{h},t}$ is adjusted by removing the corresponding $p_{t,j}$ parameter(s). For example, if the history 11- is obtained at primary period t (where "-" indicates a missing observation), then:

$$\mathbf{p}_{11\text{-},t} = \begin{bmatrix} 0 \\ p_{t,1} p_{t,2} \end{bmatrix}.$$

This represents that fact that no information, on either detection or nondetection, has been collected about the parameter $p_{t,3}$ from the unit with this detection history.

Similarly, the model can be adjusted to allow for situations where a unit was not surveyed for an entire season. Consider the following detection history, where the unit was not surveyed at all in the second season, $\mathbf{h}_i = 10{-}{-}11$. Again, no information has been collected regarding either the detection or non-detection of the species, although here the occupancy state of the unit at season 2 is also unknown, hence all possibilities must be allowed for. This can be achieved by (effectively) omitting $\mathbf{p}_{\mathbf{h},2}$ entirely; i.e. the probability of this detection history is

$$Pr(\mathbf{h}_i = 10{-}{-}11 | \psi_1, \boldsymbol{\gamma}, \boldsymbol{\epsilon}, \mathbf{p}) = \boldsymbol{\phi}_0 D\left(\mathbf{p}_{10,1}\right) \boldsymbol{\phi}_1 \boldsymbol{\phi}_2 \mathbf{p}_{11,3}.$$

By having the ability to accommodate missing observations, the unconditional model of MacKenzie et al. (2003) provides a great deal of flexibility in the way the data can be collected in the field, and still be analyzed using this technique. Not only can there be unequal sampling effort across units within seasons, but potentially, not all units have to be surveyed each season (within reason). However, it is important to note that even though no data were collected from this unit during the second season, the associated colonization and local extinction probabilities still appear in the probabilistic statement (within $\boldsymbol{\phi}_2$). As such, it is assumed that these probabilities are either the same, or are functions of the same covariates, at units that are and are not surveyed within that season. This assumption of the model must be carefully considered if a study design is proposed that intentionally avoids surveying all units each season.

8.3.5 Including Covariate Information

Thus far in this chapter, an implicit assumption has been made that all model parameters are constant across all units. Failure of this assumption results in heterogeneity in model parameters, which could result in inferences that are inaccurate. As already discussed in Chapters 4 and 7, one approach to dealing with potential heterogeneity is the inclusion of information on variables that may affect the value of one or more parameters, or covariates. Indeed, the relationship between the covariates and certain parameters of interest may often be the primary motivation for conducting the study (e.g., habitat variables in habitat modeling, or measures of isolation and patch size in metapopulation studies). As noted in Chapters 3 and 4, covariate information can be included in the model by use of an appropriate link function, e.g., the logit link (Chapter 3). The mechanics for doing so are identical to those presented in Section 4.4.8, hence we do not cover this material again here.

Similar to the single season case, occupancy, colonization and local extinction probabilities could all be functions of variables that have a single, constant value for the duration of the season (season-specific covariates). These may be variables that characterize units during each sampling season (e.g., habitat type, average value of a weather-related variable measured during the season, elevation or patch size) or variables that characterize the change in a quantity between seasons (e.g., changes in habitat composition). Detection probabilities can be functions of season-specific covariates, but also functions of variables that may change with each survey of a unit (e.g., rainfall in preceding 24 hours, air temperature or observer).

There is one pertinent point about potential covariates whose values may change from one season to the next and missing observations. As noted above, these methods can allow for situations where units may not be surveyed in some seasons, however in doing so, the occupancy-related parameters associated with that season are still included in the probability statement and model likelihood. When those parameters are being modeled as functions of covariates, the value of the respective covariates for each unit, including the unsurveyed ones, must be known to calculate the parameter value. There will be some classes of covariates for which this is problematic; covariates whose values are dynamic over time and can only be determined during a survey of that unit. In such a case investigators will have to develop some reasonable means to determine what the covariate values may have been at the unsurveyed units, or else recognize that they can not use the set of affected covariates in an analysis of the full data set (but possibly on a subset of the data with no missing values). Covariates that are unchanging over time, or the value of which can be determined independently of the detection/nondetection surveys, could still be used.

Having the ability to incorporate covariate information of these types provides a great deal of flexibility in the models that could be considered as reasonable descriptions of the processes that give rise to the data. Moreover, different hypotheses about the system can often be expressed as models that involve different sets of covariates for each parameter type. The strength of evidence for each hypothesis can then be determined by fitting the suite of models with the different sets of covariates and making a formal comparison of the models (e.g., by using the AIC model selection criterion). For example, in metapopulation studies, local extinction probabilities are frequently assumed to be decreasing functions of patch area (e.g., Moilanen, 1999). That is, the species is more likely to go extinct from small patches than large patches. This may be reasonable for some species, but perhaps not in every case. Furthermore in some situations, variation in the areas of the sampled patches may be insufficient to discern such an effect on local extinction probabilities. Therefore, a second hypothesis would be that local extinction probabilities are constant with respect to patch area. These competing hypotheses could be formulated as two models with different sets of covariates for ϵ_t. To represent the area hypothesis, a model could be fit to the data where 'patch area' is included as a covariate for extinction probability, and a second model without the 'patch area' covariate for ϵ_t (but identical in all other respects) could be fit to represent the second hypothesis. The level of support for each of the two models would then reflect the degree of support of each hypothesis. Note that one could also use a similar approach to determine the functional form of such a relationship (e.g., linear or quadratic), or even compare link functions. However, we caution that such comparisons should only be done on the basis of sound biological reasoning, not in the pursuit of a 'best' model.

8.3.6 Alternative Parameterizations

MacKenzie et al. (2003) noted that in some situations quantities other than the probability of occupancy in the first season, seasonal colonization and local extinction probabilities may be of interest. They suggested that these quantities could be derived from the estimated parameters, or the model could be reparameterized so that the quantities are estimated directly.

One immediate option is to parameterize the explicit dynamics model in terms of the probabilities of first-season occupancy, seasonal colonization and seasonal persistence; where persistence is defined as the probability of the unit being occupied by the species in successive seasons. That is:

$$\begin{aligned}\phi_t &= Pr(\text{species present at unit in season } t+1 \mid \text{species present at unit in} \\ &\quad \text{season } t) \\ &= 1-\epsilon_t.\end{aligned}$$

As the above indicates, persistence is the complement of local extinction probability, and distinguishing between the two is similar to distinguishing between survival and mortality probabilities of individuals. One advantage of parameterizing the explicit dynamics model in terms of persistence rather than local extinction is that all occupancy-related parameters are in terms of the probability of the species being present at a unit, whereas local extinction is in terms of the probability of the species being absent from a unit. We would point out, however, that persistence probabilities can be easily derived from estimates obtained using the original parameterization by simply substituting $\hat{\epsilon}_t$ into the above equation. Because persistence is the complement of local extinction, the standard error of $\hat{\epsilon}_t$ is also the standard error for $\hat{\phi}_t$. Furthermore, if covariates have been included in the modeling of local extinction and the effect sizes estimated, to interpret the effect of those covariates in terms of persistence probability, one just changes the sign of the estimated effect size. Once again, no adjustment to the standard errors of the effect sizes is necessary.

Seasonal estimates of occupancy are another such quantity. In some applications (e.g., monitoring), the processes of colonization and local extinction may not be of direct interest with the main focus of the study being how occupancy changes over time. The three probabilities are simply related by the recursive equation:

$$\psi_{t+1} = \psi_t(1-\epsilon_t) + (1-\psi_t)\gamma_t, \tag{8.4}$$

i.e., units occupied next season are a combination of those units occupied this season where the species does not go locally extinct, $\psi_t(1-\epsilon_t)$, and the units that are currently unoccupied that are colonized by the species before next season, $(1-\psi_t)\gamma_t$. This is analogous to how the abundance of a species at a particular point in time is comprised of the survivors from the previous period, and new recruits. Eq. (8.4) can be rearranged to make either of the dynamic processes the subject, that is:

$$\gamma_t = \frac{\psi_{t+1} - \psi_t(1-\epsilon_t)}{(1-\psi_t)}$$

or

$$\epsilon_t = 1 - \frac{\psi_{t+1} - (1-\psi_t)\gamma_t}{\psi_t}.$$

The same model as described above would be used, except rather than estimate the γ_t and ϵ_t parameters directly, one would directly estimate, for example, the seasonal occupancy and local extinction probabilities. The value for γ_t could then be derived using the above formula and used in the model to evaluate the likelihood.

There may be a temptation to use the recursive occupancy equation above in association with the implicit dynamic modeling approach described in Section 8.2 as a means of incorporating colonization and local extinction probabilities into a multi-season occupancy model. However, doing so does not yield the explicit dynamics approach described above. For example, consider the simple detection history $\mathbf{h}_i = 10\,01$. Using the unconditional approach of MacKenzie et al. (2003), the probability of observing this history would be (where $\boldsymbol{\theta}$ denotes the set of parameters in the model):

$$Pr(\mathbf{h}_i = 10\,01|\boldsymbol{\theta}) = \psi_1 p_{1,1}\left(1-p_{1,2}\right)(1-\epsilon_1)\left(1-p_{2,1}\right)p_{2,2},$$

while using the implicit dynamics model from Section 8.2, the probability would be:

$$Pr(\mathbf{h}_i = 10\,01|\boldsymbol{\theta}) = \psi_1 p_{1,1}\left(1-p_{1,2}\right)\psi_2\left(1-p_{2,1}\right)p_{2,2}.$$

Substituting the expression for ψ_2 given by Eq. (8.4) into the implicit dynamics model, does not give the equivalent of the unconditional explicit dynamics model. That is:

$$\begin{aligned}
Pr(\mathbf{h}_i = 10\,01|\boldsymbol{\theta}) &= \psi_1 p_{1,1}\left(1 - p_{1,2}\right)\psi_2\left(1 - p_{2,1}\right)p_{2,2} \\
&= \psi_1 p_{1,1}\left(1 - p_{1,2}\right)\left[\psi_1(1 - \epsilon_1) + (1 - \psi_1)\gamma_1\right]\left(1 - p_{2,1}\right)p_{2,2} \\
&\neq \psi_1 p_{1,1}\left(1 - p_{1,2}\right)(1 - \epsilon_1)\left(1 - p_{2,1}\right)p_{2,2}.
\end{aligned}$$

Another quantity suggested by MacKenzie et al. (2003) is the rate of change in occupancy. By analogy with population size (where the comparable measure is known as the *finite rate of change* or *growth rate*), they suggest it could be defined as:

$$\lambda_t = \frac{\psi_{t+1}}{\psi_t}.$$

Using the recursive occupancy equation as an intermediate step, the unconditional model could be reparameterized so that λ_t is estimated directly. However there are some practical problems that limit the usefulness of this parameterization. First, there are bounds on the allowable values of λ_t that vary with ψ_t. For example, suppose that currently the probability of occupancy is 0.5 (i.e., $\psi_t = 0.5$), then the maximal rate of change in occupancy, as defined above, must be 2, otherwise the probability of occupancy in the next season will exceed 1.0. However, if currently $\psi_t = 0.2$, then the maximal rate of change in occupancy would be 5. Second, you cannot have a constant, long-term, rate of change greater than 1 as eventually it will result in an estimate of $\psi_{t+1} > 1$. For instance, suppose the probability of occupancy in season 1 is 0.2. A long-term rate of change of 1.2 (i.e., occupancy probability increases by 20% each season) would suggest that in season 10 occupancy is greater that 1.0 (0.20, 0.24, 0.29, ..., 0.72, 0.86, 1.03).

An alternative definition for the rate of change in occupancy is to use odds ratios, that is:

$$\lambda'_t = \frac{\psi_{t+1}/(1 - \psi_{t+1})}{\psi_t/(1 - \psi_t)}. \tag{8.5}$$

While it may seem more complicated to interpret, it has the advantage of not suffering from the restrictions of the above definition. Also, the general concept is similar to that of using a logit or log-odds link function (recall from Chapter 3 that the odds ratio is the amount by which the odds of occupancy in season t is multiplied to get the odds of occupancy in season $t + 1$). Further, if λ'_t is constant across time (i.e., $\lambda'_1 = \lambda'_2 = \cdots = \lambda'_{T-1}$), then $ln(\lambda')$ will correspond to the trend parameter when modeling occupancy as a linear function of time on the logit scale:

$$\begin{aligned} logit(\psi_t) &= \beta_0 + \beta_1 t \\ &= \beta_0 + ln\left(\lambda'\right) t. \end{aligned}$$

In some applications, researchers express an interest in ‘turnover’ of the species, which could be defined in multiple ways. One definition would be the probability that a unit that is occupied has just become occupied. That is:

$$\tau_t = \frac{(1-\psi_t)\,\gamma_t}{\psi_{t+1}}.$$

Another definition for ‘turnover’ would be the probability of a unit changing occupancy status between seasons:

$$\tau_t' = \psi_t \epsilon_t + (1-\psi_t)\,\gamma_t.$$

Using either of these definitions it would be possible to reparameterize the unconditional explicit dynamics model, through a series of calculations, such that these alternative quantities of interest can be estimated directly. As noted above, however, instead of attempting to estimate these other parameters of interest directly, they could be derived by substituting the estimated values from the original parameterization into the respective series of equations, with the associated standard error determined by application of the delta method (Chapter 3). The main advantage of reparameterizing the model in terms of these alternative quantities is when there is a desire to directly model such quantities (e.g., consistency over time or as functions of covariates). When covariates are being incorporated, for some quantities a link function other than the logit-link may have to be used.

The choice of which parameterization may be most appropriate in a given situation depends on the goals of the study and scientific questions being addressed. If the main focus is on the underlying dynamic processes and factors that may affect them, then the original parameterization should be used. In many management scenarios, it is natural to focus upon occupancy estimates and changes in occupancy over time (e.g., trends in occupancy), suggesting that one of the alternative parameterizations may be more appropriate. However, we point out that while identifying whether the level of occupancy is increasing or decreasing over time has some utility, oftentimes a deeper understanding of the underlying dynamics will lead to a better understanding about how management actions may influence occupancy dynamics, and therefore which actions will obtain management goals most efficiently.

The results from fitting different parameterizations of the model to the same data are comparable, including the comparison of model selection metrics such as AIC. There is nothing inherently wrong with the comparison of multiple parameterizations of the model, however we suggest that choice of parameterization should be generally governed by the study objective rather than fitting models with all possible parameterizations and using model selection criteria to differentiate among them. We have often found the original parameterization to be the most numerically stable, particularly when a model contains a large number of covariates. As colonization and local extinction probabilities must take values in the 0–1 interval, there are constraints on allowable values for the occupancy probability. Enforcing these constraints when using a reparameterized version of the unconditional model can make the computer algorithms unstable.

8.3.7 Example: House Finch Expansion in North America

House finches (*Carpodacus mexicanus*) are native to western, but not eastern, North America. However, they were released in 1942 on Long Island, New York, and have exhibited an impressive westward expansion since that time. The magnitude of this expansion is such that it is obvious in the raw data of the North American Breeding Bird Survey (BBS; Robbins et al., 1986). Here we subject the BBS data to the probabilistic modeling of this chapter in an effort to draw formal inferences about this expansion. The BBS has been conducted annually since the mid-1960s by volunteer observers. The counts are conducted during the peak of the breeding season, usually during June. Observers follow a route along roads for ~39.2 km, stopping every 0.8 km for 50 consecutive stops. At each stop, a point count is conducted for three minutes with observers counting all birds detected within a 400 m radius. There are now >4000 BBS routes throughout North America, so the geographic coverage is extensive.

The BBS protocol specifies that routes be run once each breeding season, so the data do not contain the temporal replication that we typically use for occupancy modeling. We thus take a different approach and view each of the 50 stops as a replicate count from the area covered by the route. This is far from ideal. For example, under the view that the area covered by each stop is a random selection from the area covered by all stops, we would ideally be sampling with replacement. Nevertheless, given the survey design and protocol of the BBS, we view our approach as not only reasonable, but better than most available approaches.

To investigate the westward expansion during the period 1976–2001, data from 694 BBS routes within 2600 km from the Long Island point of release were considered at 5-year intervals (i.e., 1976, 1981, 1986, . . .). We used a relatively phenomenological kind of modeling in which we focused on how these probabilities were related to distance from Long Island in each year. Thus, distance (d) and year ($year$) were covariates in our analysis. Distance was measured at

100 km increments, at the scale of 1000 km (i.e., $d = 0.1 = 100$ km). Year was included in the models as a categorical covariate, or factor, with the final year value for each parameter type treated as the standard or reference category (1996 for colonization and extinction as these are between period events, and 2001 for detection). The only other covariate used an *ad hoc* approach to dealing with relative abundance of birds that was possible because of the large number of stops per route. Specifically, we created a categorical variable for observed frequency of occurrence (f) indicating whether house finches were detected on >10 stops in the route in any previous year or not (i.e., were locally highly abundant). This covariate was used to model detection probability, along with an interaction between year and distance, and is similar in intent to defining a 'trap response' covariate to allow the detection probability to be different (higher) for routes after they reached this observed frequency threshold. The logit-link function was used for all parameter types.

These covariates were used for detection probability in all models that were fit to the data, denoted as $p(year \times d + f)$. Only distance and year were used to model local rates of extinction and colonization, and only distance was used to model the initial occupancy level, $\psi_{76}(d)$. We assumed house finch were initially more common closer to the release point, hence did not consider a model where occupancy probability in 1976 was the same at all distances, i.e., $\psi_{76}(\cdot)$, to be biologically reasonable. Our prediction was that there would be an increase in rate of colonization with distance as time progressed, i.e., the effect of distance on colonization would increase over time, suggesting an interaction between the year and distance covariates. We had no real expectation about rate of extinction probabilities, other than they would be generally low. Therefore, we did not consider models that included an interaction between the distance and year covariate to guard against obtaining a spurious result with such a small number of events. We expected occupancy to increase with distance as time progressed, in much the same manner as colonization (although note that occupancy probabilities were derived using Eq. (8.4) for 1981 onward).

Twenty models were fit to the data using the `R` package `RPresence` and the top eight ranked models appear in Table 8.2. The model with lowest AIC received a model weight of 0.77, indicating a good degree of support, with the second-ranked model having an AIC model weight of 0.23. No other models considered were supported in comparison. There is very strong evidence of an interaction between the year and distance covariates for colonization (as included for both top models), with the effect of distance on colonization being different in different years. There is also very strong evidence that extinction probability changes with distance (as appears as a covariate in both top models), with some evidence of an additive year effect (as included in second-ranked model).

TABLE 8.2 Summary of model selection results for the house finch example. Factors affecting occupancy, colonization, and local extinction probabilities include distance (d) and year ($year$). Occupancy and detection probabilities were modeled as functions of these same factors and a categorical variable for observed frequency of occurrence (f); specifically $\psi_{76}(d)$ and $p(year \times d + f)$, respectively. Models are notated in terms of the factors included for colonization (γ) and extinction probabilities. Given are the relative differences in AIC values compared to the top ranked model (ΔAIC), AIC model weights (w), the numbers of parameters in the models ($Npar$), and twice the negative log-likelihood ($-2l$). Results are only presented for the top eight ranked models

Model	ΔAIC	w	$Npar$	$-2l$
$\gamma(year \times d)\epsilon(d)$	0.00	0.77	27	44,414.09
$\gamma(year \times d)\epsilon(year + d)$	2.41	0.23	31	44,408.50
$\gamma(year \times d)\epsilon(year)$	12.72	0.00	30	44,420.81
$\gamma(year \times d)\epsilon(\cdot)$	14.62	0.00	26	44,430.71
$\gamma(year + d)\epsilon(d)$	29.25	0.00	23	44,451.35
$\gamma(year + d)\epsilon(year + d)$	31.03	0.00	27	44,445.12
$\gamma(year + d)\epsilon(year)$	40.70	0.00	26	44,456.79
$\gamma(year + d)\epsilon(\cdot)$	47.44	0.00	22	44,471.54

TABLE 8.3 Estimated regression coefficients ($\hat{\beta}$) and associated standard errors (SE($\hat{\beta}$)) for the probability house finch were present at a Breeding Bird Survey route in 1976, on the logit-scale, i.e., $logit(\psi_{76,i})$. Given are the estimates from the two models ranked highest by AIC (Table 8.2). w is the AIC model weight for each model. Distance from Long Island (d) was measured in 1000 km units, to the nearest 100 km

Term	Model 1: $w = 0.77$		Model 2: $w = 0.23$	
	$\hat{\beta}$	$SE(\hat{\beta})$	$\hat{\beta}$	$SE(\hat{\beta})$
Intercept	−0.83	0.41	−0.81	0.41
d	−1.22	0.48	−1.17	0.53

The estimated regression coefficients for each parameter type, on the logit-scale, are given in Tables 8.3–8.6 from the two highest AIC-ranked models. There is generally very good agreement in the estimated effect sizes from the two models, especially considering the magnitude of the standard errors associated with the estimates. As predicted, the estimated effect of distance on occupancy in 1976 is negative (Table 8.3), indicating the probability of house finch being present at a BBS route was lower farther away from the release point. The interaction terms for the year and distance covariates on colonization ($year_y$:d; Table 8.4) indicate how the effect of distance on colonization is different in the respective years compared to the effect of distance in 1996 (the reference year in this case; d). To obtain the effect of distance in each year, the

TABLE 8.4 Estimated regression coefficients ($\hat{\beta}$) and associated standard errors (SE($\hat{\beta}$)) for the probability house finch colonize a Breeding Bird Survey route between survey periods t and $t+1$, on the logit-scale, i.e., $logit(\gamma_{t,i})$. Given are the estimates from the two models ranked highest by AIC (Table 8.2). w is the AIC model weight for each model. Year effects $year_t$ are additive terms for the indicated years, distance from Long Island (d) was measured in 1000 km units, to the nearest 100 km, and $year_t$:d are the interaction terms between year and distance

Term	Model 1: $w = 0.77$		Model 2: $w = 0.23$	
	$\hat{\beta}$	$SE(\hat{\beta})$	$\hat{\beta}$	$SE(\hat{\beta})$
Intercept	0.54	0.53	0.63	0.55
$year_{76}$	0.89	0.80	0.83	0.82
$year_{81}$	1.79	0.71	1.63	0.71
$year_{86}$	1.76	0.72	1.52	0.72
$year_{91}$	0.13	0.72	0.03	0.73
d	−0.74	0.34	−0.78	0.34
$year_{76}{:}d$	−7.44	3.15	−7.37	3.13
$year_{81}{:}d$	−3.50	0.85	−3.33	0.85
$year_{86}{:}d$	−1.38	0.49	−1.26	0.48
$year_{91}{:}d$	0.10	0.44	0.15	0.45

main effect of distance and the interaction terms must be added together. For example, from the top model:

$$\begin{aligned} d_{76} &= d + year_{76}{:}d \\ &= -0.74 - 7.44 \\ &= -8.18, \end{aligned}$$

$$\begin{aligned} d_{81} &= d + year_{81}{:}d \\ &= -0.74 - 3.50 \\ &= -4.24, \end{aligned}$$

$$\begin{aligned} d_{86} &= d + year_{86}{:}d \\ &= -0.74 - 1.38 \\ &= -2.12, \end{aligned}$$

$$\begin{aligned} d_{91} &= d + year_{91}{:}d \\ &= -0.74 + 0.10 \\ &= -0.64, \end{aligned}$$

and

$$\begin{aligned} d_{96} &= d \\ &= -0.74. \end{aligned}$$

Clearly, these models suggest the effect of distance on colonization generally increased over time, as predicted. For extinction probability, the estimated effect of distance is positive from both models (Table 8.5) so local extinction probability was estimated to be higher farther away from Long Island, the location of the population 'source', which is biologically reasonable. The year effects in the second-ranked model suggests some temporal variation in the overall level of extinction, although this model is not well supported. The estimated regression coefficients for detection probability (Table 8.6) suggest that the effect of distance on detection also increased over time, similar to colonization probability, so house finch were more detectable at greater distances from Long Island as time progressed. This may have been due to local abundance increasing over time after house finch colonized an area. The estimated effect of f is positive, hence house finch were more detectable in a survey after being detected at >10 stops on a BBS route in a previous year.

The model averaged estimates of occupancy, colonization and extinction probabilities in each year are presented in Fig. 8.3. The occupancy probabilities in 1976 were estimated directly in the modeling, while the values for subsequent years were derived from the estimated colonization and extinction probabilities in each year, and occupancy probabilities for the preceding year, using Eq. (8.4). No measure of uncertainty has been presented for clarity of

TABLE 8.5 **Estimated regression coefficients ($\hat{\beta}$) and associated standard errors (SE($\hat{\beta}$)) for the probability that house finch went locally extinct from a Breeding Bird Survey route between survey periods t and $t+1$, on the logit-scale, i.e., $logit(\epsilon_{t,i})$. Given are the estimates from the two models ranked highest by AIC (Table 8.2). w is the AIC model weight for each model. Year effects $year_t$ are additive terms for the indicated years, and distance from Long Island (d) was measured in 1000 km units**

Term	Model 1: $w = 0.77$		Model 2: $w = 0.23$	
	$\hat{\beta}$	$SE(\hat{\beta})$	$\hat{\beta}$	$SE(\hat{\beta})$
Intercept	−3.39	0.26	−2.93	0.33
$year_{76}$			0.33	1.29
$year_{81}$			−0.13	0.72
$year_{86}$			−1.17	0.68
$year_{91}$			−0.60	0.37
d	1.17	0.25	1.00	0.26

TABLE 8.6 **Estimated regression coefficients ($\hat{\beta}$) and associated standard errors (SE($\hat{\beta}$)) for the probability house finch were detected on a Breeding Bird Survey route at which they were present in survey period t, on the logit-scale, i.e., $logit(p_{t,ij})$. Given are the estimates from the two models ranked highest by AIC (Table 8.2). w is the AIC model weight for each model. Year effects $year_t$ are additive terms for the indicated years, distance from Long Island (d) was measured in 1000 km units, to the nearest 100 km, $year_t{:}d$ are the interaction terms between year and distance, and f is the effect on detection of house finch being detected at >10 stops in a previous year**

Term	Model 1: $w = 0.77$		Model 2: $w = 0.23$	
	$\hat{\beta}$	$SE(\hat{\beta})$	$\hat{\beta}$	$SE(\hat{\beta})$
Intercept	−2.09	0.05	−2.09	0.05
$year_{76}$	−0.26	0.21	−0.26	0.21
$year_{81}$	0.29	0.10	0.29	0.10
$year_{86}$	0.62	0.08	0.62	0.08
$year_{91}$	0.66	0.06	0.66	0.06
$year_{96}$	0.18	0.06	0.18	0.06
d	−0.43	0.05	−0.43	0.05
$year_{76}{:}d$	−9.76	2.00	−9.86	2.01
$year_{81}{:}d$	−2.85	0.43	−2.86	0.43
$year_{86}{:}d$	−1.75	0.24	−1.76	0.24
$year_{91}{:}d$	−0.41	0.08	−0.41	0.08
$year_{96}{:}d$	0.08	0.07	0.08	0.07
f	0.94	0.03	0.94	0.03

the plots. The odds-ratio rate of change in occupancy in each year (λ'_t, Eq. (8.5); lower right) highlights at what distances were the fastest rates of change between years. Note that colonization, extinction, and rate of change are between season processes, thus there are $T - 1$ season-specific values, while there are T season-specific values for occupancy. This same information could also be presented in terms of maps. For example, Fig. 8.4 presents the model averaged occupancy probabilities estimated at different distances overlaid with a map of the eastern USA. Similar maps could be created for the other parameters if desired. Maps could also be produced in more complex situations involving additional covariates, e.g., habitat or elevation, although we stress, as noted previously, ideally one would not only present maps of estimates, but also some measure of uncertainty (e.g., standard error, confidence interval limits, or CV) to convey to the reader how reliable the estimates might be in different areas.

In this example, we have modeled expansion of house finch distribution as a function of distance from its release point at Long Island, allowing the relationship between distance and the model parameters to change over time. This enabled us to make inferences about the underlying processes associated with

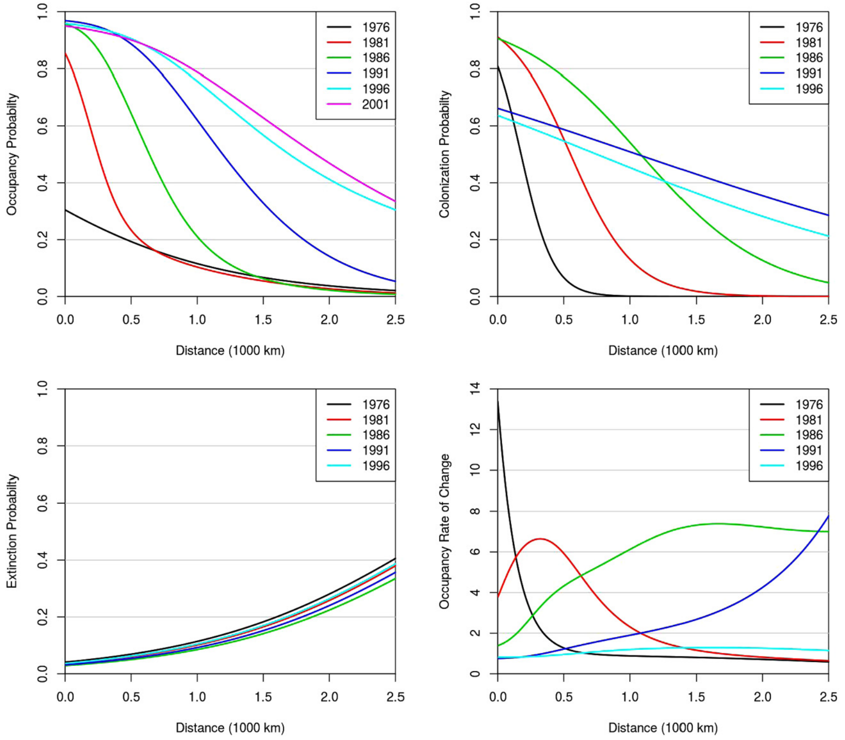

FIGURE 8.3 Model averaged estimates of occupancy (upper left), colonization (upper right), and extinction (lower left) probabilities for house finch at Breeding Bird Survey routes in the eastern USA, as a function of distance from the Long Island release point, in each year. The derived odds-ratio based rate of change in occupancy as a function of distance is also presented (lower right).

changes in the house finch distribution with respect to distance from Long Island, including rates of change as a function of distance. The underlying logic easily transfers to other covariates that might be of interest in other applications. For example, how is a species distribution changing over time relative to elevation, and at what elevations are the fastest rates of change in the species distribution? Such information would provide insights about how species are responding to changes in the environment.

We believe that the general topic of range expansion and contraction will become increasingly important in the future with the spread of invasive species and range changes induced by climate change. Monitoring programs designed to permit estimation of occupancy will be ideally suited to study these changes. We would like to extend these methods to more mechanistic models of range expansion. In particular, we would like to use an approach similar to that of Wikle (2003) to model colonization as a function of occupancy of nearby sample

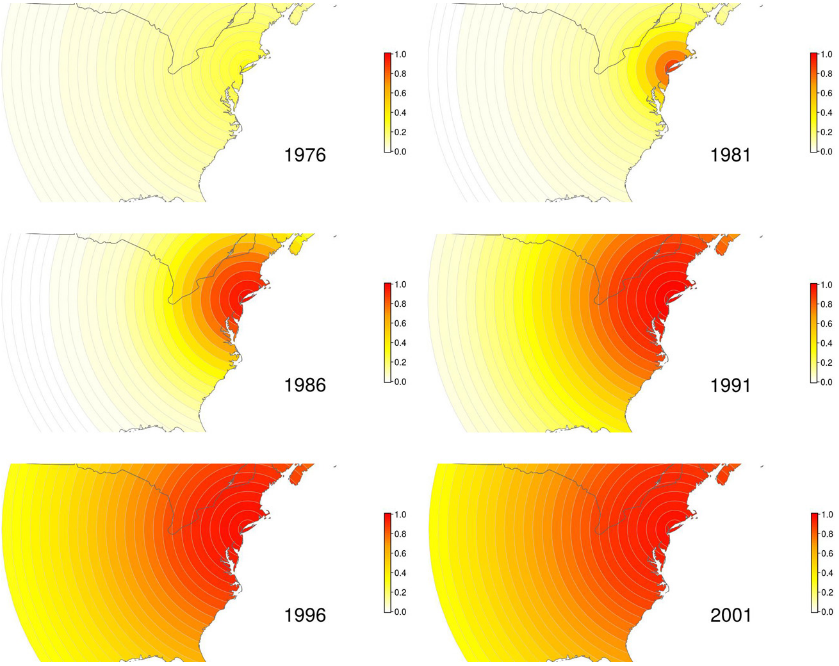

FIGURE 8.4 Maps of the model averaged occupancy probabilities in each year for house finch at Breeding Bird Survey routes in the eastern USA.

units, rather than simply as a time×distance interaction. Incorporating spatial correlation in the underlying occupancy dynamics would be one approach for doing so (e.g., Bled et al., 2011, 2013; Yackulic et al., 2012; Eaton et al., 2014; Chapter 10).

Before finishing with this example, we would like to point out that there were a number of practical challenges associated with its preparation that users should be aware of. These challenges were actually anticipated at the beginning of our modeling effort because of the nature of the invasion process that we sought to model. In early years following release, we knew that there were very few data for medium to large distances from the release site. Specifically, with very low occupancy at even intermediate distances, extinction events are expected to be rare, as extinction is conditional on species presence. Similarly, colonization simply did not occur at greater distances until later in the time series. The point is that we were trying to model rate parameters corresponding to rare events (hence little data), and this will always be a difficult task. With our treatment of year as a categorical variable, we were on the verge of asking too much of the data. We found that the likelihood function for many of the models considered exhibited multiple maxima, and the optimization routines used by the `RPresence R` package, and also used by Program PRESENCE, would sometimes converge to different maxima depending on the starting values used for the regression coefficients. Our solution was to use five random sets of starting values for each model, and use the results from the set that converged to the highest likelihood value. In our experience the issue of multiple maxima is more problematic for more complex models, and we advise practitioners to check for the possibility of multiple maxima with their data. We did not check how sensitive the optimization routines used by other software were to multiple maxima with these data, but this is a general issue for any application of maximum likelihood estimation so we expect all software to exhibit some degree of sensitivity to it. Another practical issue we encountered related to how we coded the *year* categorical covariate, in particular, which year was treated as the standard or reference category. Initially the first category (1976) was used, but we found that in doing so, the software had numerical problems obtaining the variance–covariance matrix (from which standard errors are obtained) for the estimated regression coefficients. Recoding the *year* covariate such that the final year was used as the reference category removed this issue. This is likely due to the fact that at the beginning of the time series for these data, there were many fewer detections than later in the time series. We therefore recommend that when using a categorical covariate, you should choose your reference category to be one that has a fair number of detections associated with it, and not choose one with relatively few detections.

The files used for this example can be downloaded from http://www.proteus.co.nz.

8.4 VIOLATIONS OF MODEL ASSUMPTIONS

The assumption of no unmodeled heterogeneity in any of the parameters (occupancy, colonization, extinction or detection probabilities) is one of several assumptions for the multiple season models presented in the chapter. Additional assumptions include: (1) occupancy state at each unit does not change over surveys within a season; that is, consistent with Pollock's robust design, units are 'closed' to changes in occupancy within seasons or primary periods, (2) detection of species and detection histories at each location are independent, and (3) the target species are never falsely detected (i.e., species are identified correctly).

If these assumptions are not met, some or all estimators may be biased, and inferences about factors that influence both occupancy and occupancy dynamics may be erroneous. Even within the capture–recapture arena, there has been little investigation of effects of heterogeneity on robust design estimators; rather, it is believed that these estimators behave in a manner similar to those for separate closed and open capture–recapture models (Williams et al., 2002).

Assumption violations for single-season (closed) models were presented in Section 4.4.9. In this section we briefly review anticipated impacts of occupancy closure violations and possible solutions and then focus primarily on the impacts of assumption violations on rate parameters estimated between seasons (i.e., during the open periods). We caution readers that there have been few formal investigations of assumption violations within the occupancy context, and that information in this section is based mostly on the analogy with capture–recapture population models that may not always have parallels to occupancy studies.

As mentioned in previous chapters, the closed occupancy state assumption within seasons can be relaxed, provided changes in occupancy are random (sensu Kendall et al., 1997; Kendall, 1999). The species of interest is viewed as having some non-negligible probability of being present in the unit at the time of any survey, which is unaffected by whether the species was present at the previous survey (that would be non-random or Markovian changes within a season). When there are random changes within each season, the occupancy estimator is approximately unbiased, but interpreted as the probability units are *used* by the target species, and detection probability is the probability the species is present at the time of the survey and detected at occupied or used units. Therefore, changes in ‘occupancy’ should be interpreted as changes in ‘use’, and colonization and local extinction probabilities are the underlying dynamic parameters governing changes in use.

Nonrandom movement of a species in and out of sample units likely causes bias in occupancy estimators; nevertheless, if movement is always either only in or only out of the unit(s) (i.e., immigration or emigration only) then Kendall (1999) describes ways in which surveys can be combined to likely eliminate bias in occupancy estimators. As noted in Section 4.4.9, Kendall’s (1999) recommendations involve pooling survey data into two surveys per season and then using models with survey-specific detection probabilities. Specifically, for the case of only emigration, the first survey is retained for each unit, and the last $K - 1$ surveys are combined into a second ‘survey’. In the case of only immigration, the first $K - 1$ surveys are combined and treated as the initial survey, and survey K becomes the second survey. Under this approach, approximately unbiased estimates can likely be obtained for either occupancy at the beginning of each season, for emigration-only situations, or occupancy at the end of each season for immigration-only situations (see Section 4.4.9 and Kendall, 1999, for details). Kendall (1999) also mentions that this pooling approach is valid within the robust design context, yielding unbiased estimates of survival rate between primary periods. In the context of multiple season occupancy models, we would anticipate that similar pooling to accommodate emigration- or immigration-only movement within seasons would yield approximately unbiased estimates of extinction and colonization probabilities. Bias in occupancy estimates will likely remain if analyses are conducted using more than two surveys per season or models with constant detection probability (Section 4.4.9; Kendall, 1999). Kendall's (1999) work suggests that unmodeled heterogeneity or permanent trap response (see below) in detection probabilities will cause bias in occupancy and vital rate estimators.

Another option to deal with the closure assumption is to restrict the data to include surveys between times when the availability of the species is uninterrupted (i.e., during periods of closure) as demonstrated by MacKenzie et al. (2003) with tiger salamanders in Minnesota. Here detection/nondetection information was only included during a time period where the life history of the species dictated that individuals would be confined to the pond (eggs, larvae and early metamorphs). Time periods when adults may be migrating to ponds or when metamorphs may be transitioning to a terrestrial life phase were not included in the analysis. Again, investigators should use their knowledge about the phenology of the target species and design their studies to try to minimize violations in the closure assumption.

The impact of unmodeled variation in occupancy, colonization, and extinction probability among units is virtually unexplored, and more thorough simulation studies are still needed. Effects of heterogeneous survival rates have been investigated for open population capture–recapture estimators (Nichols et al., 1982; Pollock and Raveling, 1982; Pollock et al., 1990). However, the analogy between extinction and the complement of survival is not sufficiently close that we are comfortable in drawing inferences about effects on extinction estimators based on inferences about survival estimators. Recall, for example, to use capture–recapture models to estimate parameters of occupancy dynamics, Barbraud et al. (2003) equated temporary emigration parameters with colonization and extinction. We are aware of no investigation of the effects of heterogeneity on the temporary emigration estimators presented by Kendall et al. (1997), so we conclude that the effects of heterogeneous rates of extinction and colonization are a topic of future investigation.

There are some extensions of the multi-state occupancy models discussed so far that may be more appropriate when some of the above model assumptions are suspected to be violated. These are discussed in the next two chapters. We would also point out that, to the best of our knowledge, robust methods for assessing model fit, and thereby identifying evidence of assumption violations, are yet to be developed for multi-season models.

8.5 DISCUSSION

We believe that this chapter may be the most important in the book. Although most previous occupancy studies have focused on single-season patterns (the topic of Part II), the objectives of most of these previous investigations involved dynamic processes (see review of Chapter 2). Because of the difficulties inherent in attempts to infer process from observation of pattern (see Chapters 1 and 2), we believe that studies of units extending over multiple seasons are likely to provide the strongest inferences about occupancy dynamics and the processes that produce these dynamics. We thus believe that the models of this chapter should see a great deal of use and that future work should focus on extensions and elaborations of these approaches.

The implicit dynamics modeling approach of Section 8.2 essentially involved multiple applications of the single-season models of Chapter 4 to species detection data from a sequence of seasons. However, if occupancy dynamics are best viewed as a Markov process (i.e., non-random changes in occupancy over time), as will be reasonable in many situations, then the explicit dynamics models of Section 8.3 should provide better descriptions of the data. In cases for which they are appropriate, the implicit dynamics models of Section 8.2 yield time-specific estimates of occupancy, as well as estimates of rate of change or 'trend' in occupancy. Trend estimates are the focus of many current animal monitoring programs, and are justified as providing a basis for prioritization of conservation efforts. Species and areas in which rapid reductions in occupancy are occurring make prime targets for conservation efforts. However, estimation of trends does not provide much information about the causes of observed declines or, more importantly, about the kinds of management actions that are likely to reverse them. It is possible to model rate of change in occupancy as functions of environmental or management covariates, and such modeling can prove useful. Although, we believe that direct modeling of the processes governing change is likely to be even more useful.

The models of Section 8.3 explicitly incorporate parameters for the vital rates responsible for changes in occupancy, rates of local extinction and colonization. Covariate modeling can be used to investigate effects of environmental variables and management actions on these rate parameters. We believe that the models of this chapter deserve much more attention than they have thus far received, as they permit direct investigation of such topics as metapopulation dynamics, range dynamics, and the relationship between occupancy dynamics and habitat change. These models also provide alternative means of investigating population dynamics that do not require detailed studies of marked individuals. For example, Barbraud et al. (2003) were able to draw inferences about bird movement (shifting of colony units) by modeling the vital rates in one location as a function of vital rates in a neighboring location. These inferences were indirect, and thus not as strong as those based on observed movements of marked animals (e.g., Nichols, 1996; Kendall and Nichols, 2004). However, such indirect inferences can be obtained for areas too large to permit comprehensive capture–recapture studies, thus providing a useful complement to more detailed intensive investigations. Finally, we discussed some of the consequences of model assumption violations.

The models presented in this chapter can be used not only as a basis for parameter estimation and data analysis, but also for prediction of species distributions into the future or under alternative scenarios for the underlying dynamic processes. Such prediction is based on the transition probability matrix, $\boldsymbol{\phi}_t$, and we revisit this topic during the next two chapters.

In the following chapters we discuss a number of useful extensions and applications of these dynamic occupancy models, including multi-state models (Chapter 9), false-positive detections, spatial correlation, investigation of the fundamental properties of the stochastic processes governing changes in occupancy, heterogeneous detection probabilities (Chapter 10), and study design considerations (Chapter 12). In Chapter 13 we present an approach that enables joint modeling of both habitat and occupancy dynamics, allowing for some form of dependence between the two sets of processes. The multi-species cooccurrence dynamics model outlined in Chapter 14 should prove very useful, for example for dealing with competition between native species of conservation concern and related species experiencing range expansions (Olson et al., 2005; Yackulic et al., 2014). Finally, we believe that similar models of occupancy dynamics hold great promise for investigations of such topics as multi-species community dynamics (Chapter 15).