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Modeling species occurrence dynamics with multiple states and imperfect detection

DARRYL I. MACKENZIE,[1,5] JAMES D. NICHOLS,[2] MARK E. SEAMANS,[3,4] AND R. J. GUTIÉRREZ[3]

[1]*Proteus Wildlife Research Consultants, P.O. Box 5193, Dunedin 9058 New Zealand*
[2]*United States Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland 20708 USA*
[3]*Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, Minnesota 55108 USA*
[4]*United States Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, Maryland 20708 USA*

Abstract. Recent extensions of occupancy modeling have focused not only on the distribution of species over space, but also on additional state variables (e.g., reproducing or not, with or without disease organisms, relative abundance categories) that provide extra information about occupied sites. These biologist-driven extensions are characterized by ambiguity in both species presence and correct state classification, caused by imperfect detection. We first show the relationships between independently published approaches to the modeling of multistate occupancy. We then extend the pattern-based modeling to the case of sampling over multiple seasons or years in order to estimate state transition probabilities associated with system dynamics. The methodology and its potential for addressing relevant ecological questions are demonstrated using both maximum likelihood (occupancy and successful reproduction dynamics of California Spotted Owl) and Markov chain Monte Carlo estimation approaches (changes in relative abundance of green frogs in Maryland). Just as multistate capture–recapture modeling has revolutionized the study of individual marked animals, we believe that multistate occupancy modeling will dramatically increase our ability to address interesting questions about ecological processes underlying population-level dynamics.

Key words: California Spotted Owl; green frog; multiple states; occupancy modeling; Rana clamitans; *relative abundance; reproductive state; state transition probabilities;* Strix occidentalis occidentalis; *system dynamics.*

INTRODUCTION

Issues of imperfect detection have long plagued studies of species occurrence because of the inability to separate potentially false and true absences of species at survey locations. Imperfect detection not only creates biases in naïve estimates of the true level of occurrence of a species, but also creates biases in estimated magnitudes of regression coefficients reflecting association of occurrence with other factors (e.g., habitat; Tyre et al. 2003, Gu and Swihart 2004) and in estimated probabilities of colonization and local extinction (Moilanen 2002, MacKenzie et al. 2006). Unbiased estimates of colonization and local extinction probabilities are essential to an understanding of the underlying dynamic processes of change in the occurrence of a species over time. Recent methods that allow for direct estimation of detection probabilities from repeated presence/absence (or more correctly, detection/nondetection) surveys each time period (MacKenzie et al. 2003, 2006, Royle and Kery 2007) have made it possible to obtain more reliable inferences about the processes of change in species occurrence.

These methods were developed for the common situation in which scientists or managers are simply interested in the presence or absence of the species across a landscape. However, in many situations it may be possible to further classify locations where the species is present into subcategories that are biologically relevant. Such subcategories could include breeding/nonbreeding, presence or absence of a disease or pathogen within the population, or a categorical index to relative abundance (few/some/many individuals). From a practical perspective though, there may be ambiguity not only in the presence or absence of the species from the field observations, but also in assignment of the correct subcategory. For example, observing the species at a location, but not detecting evidence of breeding, does not imply breeding is not occurring at that location; breeding may be occurring but simply was not identified in that survey. This ambiguity is the result of imperfect detection of the true state of the occupied locations (e.g., breeding/not breeding; imperfect state classification), and with repeated surveys it is possible to account for this additional form of imperfect detection.

State misclassification has been recognized by authors who have been interested in assessing patterns in the multiple states of species occurrence at a single point in time. Royle (2004) and Royle and Link (2005) developed

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[5] E-mail: darryl@proteus.co.nz

models for anuran call index data. In their application, locations were monitored for multiple nights within a season, and even though a location was capable of producing a call index of a particular size (due to the size of the local anuran population), a lower index value may have been observed on any given night due to breeding phenology, weather conditions, etc. For example, the local population may have been of sufficient size to produce a call index of 2 (e.g., intermediate abundance), but during the course of the monitoring the maximum call index reported for that location may have been a 1 (low abundance). Hence, without accounting for imperfect detection the maximum observed call indices may underestimate the true relative abundance level. Nichols et al. (2007) independently developed a reparameterized version of the Royle and Link (2005) model to assess the reproductive success of the California Spotted Owl (*Strix occidentalis occidentalis*) in the central Sierra Nevada, USA. Their interest was not only in whether the owls were present or absent from potential nesting territories, but also in whether owls, when present, successfully reproduced (i.e., further classify presence into present and breeding or present and not breeding). As the evidence required to assess successful reproduction was not guaranteed to be observed on each visit to an owl territory, naïve estimates of reproductive success (i.e., those that do not account for imperfect detection) were likely underestimates.

In this paper we briefly note the similarities between the methods of Royle and Link (2005) and Nichols et al. (2007) and then extend these methods to allow estimation of the dynamic processes of change for both species presence/absence and between states of occurrence (e.g., transitioning from breeding to not breeding between years or from high to low abundance). We believe our approach will result in a clearer understanding of the dynamic processes governing a particular system. We begin with a brief description of the assumed field situation and basic data requirements, provide a common framework, and detail how the dynamic processes of such a system could be modeled. We then apply these methods to two data sets characterized by imperfect detection and investigator interest in multiple states: dynamics of occupancy and reproductive success of the California Spotted Owl in the Sierra Nevada, and dynamics of the distribution and relative abundance of green frog (*Rana clamitans*) populations inhabiting wetlands in Maryland, USA.

ASSUMED FIELD SITUATION AND BASIC DATA REQUIREMENTS

There is some suitably defined geographic unit for which the intent is to establish the presence or absence of the species and, conditional on presence, some appropriate subcategorization or state classification. These units may be naturally occurring (e.g., ponds or patches of habitat) or arbitrarily defined (e.g., quadrats or grid cells). The complete set of units that are of interest comprises the statistical population (e.g., all ponds or grid cells within some specified area). There are S units within this population, of which a sample of s units will be surveyed for the species. The s units are selected in such a manner that it is valid to generalize the conclusions based upon the sample to the greater population. Note that in some situations S may be essentially infinite, while in others S may be very close to s (i.e., the units surveyed for the species represent a substantial fraction of population of interest).

The observed occupancy states of the units are hierarchical in terms of information content about true state, where the lowest observed state has the greatest ambiguity about true state (any true state is possible) and the highest observed state has no ambiguity about true state. For example, we could order the possible states as: 0 = unoccupied or species absence; 1 = occupied and not breeding; and 2 = occupied and breeding. If evidence of breeding is observed (i.e., we observe state 2 on at least one survey) then a unit cannot be in the unoccupied or nonbreeding states (i.e., true state = 2). If animals are detected in the absence of evidence of breeding (i.e., maximum observed state = 1), this precludes the possibility of the unit being unoccupied, but not the possibility that the species may actually be breeding within that unit (i.e., true state may be 1 or 2, but not 0). That is, the potential misclassification of units from the observed data only extends in one direction. Finally, a surveyed site at which the species is not detected during any survey (i.e., maximum observed state = 0) allows the possibility of any of the true states, 0, 1, and 2.

At systematic points in time that correspond with the timescale at which parameters describing the dynamic processes are to be estimated (e.g., annually or twice per year), the s units are repeatedly surveyed within a relatively short period of time, and the observed occupancy state of the species is recorded during each survey. Here we follow MacKenzie et al. (2006) and refer to each of these shorter time periods as a sampling "season," which may or may not correspond to a more biologically relevant definition of a "season." Within each season we initially assume that the occupancy state of each unit does not change; hence the repeated surveys provide multiple opportunities to observe the true occupancy state (see *Discussion* for comments on how this assumption may be relaxed). For example, if unit i is surveyed twice per season over three seasons, the resulting detection history ($\mathbf{h}_i$) for that unit could be denoted as: $\mathbf{h}_i$ = 10 00 21. This history would be interpreted as: in season one the species was detected and state 1 observed in the first survey, and the species was not detected in the second survey (so true state may be either 1 or 2), the species was undetected in both surveys in season two (so true state may be 0, 1, or 2), then detected in both surveys in season three, with evidence of state 2 being observed in the first survey and state 1 observed in the second (so true state has to be 2). Note that the study may be conducted for a single season, in which case only the patterns of occurrence can be investigated, not the processes underlying dynamics (e.g., Royle 2004, Royle and Link 2005, Nichols et al. 2007).

A SINGLE-SEASON MODEL

The methods used by Royle (2004), Royle and Link (2005), and Nichols et al. (2007) have the same basic data requirements outlined above (e.g., repeated survey data) and the same underlying model structure. The main difference is how the models are parameterized. Royle and Link (2005) begin by outlining a very general model parameterization, before reparameterizing the structure of the detection probabilities to suit their application. Nichols et al. (2007) begin with a less general parameterization, but one that is developed to address their biological questions of interest. Here we briefly outline the general approach described by Royle and Link (2005) for single-season data, then demonstrate how the model can be tailored to address specific questions of interest through some reparameterizations. For simplicity, we develop the modeling in terms of three possible states (unoccupied and two occupied states), but note the modeling could be extended to a greater number of states in an obvious manner.

Let $\varphi^{[m]}$ be the probability that a unit is in occupancy state m. As these states are mutually exclusive there is the natural constraint that these probabilities must sum to 1; hence, two of the probabilities may be independently estimated, with the final one obtained by subtraction. For convenience we shall rewrite the probability of a state being unoccupied, $\varphi^{[0]}$, as $1 - \varphi^{[1]} - \varphi^{[2]}$. We can therefore write a state probability vector $\boldsymbol{\phi}_0$ denoting the probability of being in each state immediately before the first season of surveying (i.e., at time $t = 0$) as

$$\boldsymbol{\phi}_0 = \begin{bmatrix} 1 - \varphi^{[1]} - \varphi^{[2]} & \varphi^{[1]} & \varphi^{[2]} \end{bmatrix}.$$

Next, let $p_j^{l,m}$ be the probability of observing unit i in occupancy state l during survey j given the true occupancy state is m (this was denoted as π_{mi} by Royle and Link [2005]). Because we assume that the ambiguity of the observations only extends in the one direction and that for any given true state a survey must result in one of the observed states (i.e., $\Sigma_{l=0}^{m} p_j^{l,m} = 1$), we have the following state detection probabilities:

$$\begin{array}{cc} & \text{Observed state} \\ \text{True state} & \begin{array}{ccc} 0 & 1 & 2 \end{array} \\ \begin{array}{c} 0 \\ 1 \\ 2 \end{array} & \begin{bmatrix} 1 & 0 & 0 \\ 1 - p_j^{1,1} & p_j^{1,1} & 0 \\ 1 - p_j^{1,2} - p_j^{2,2} & p_j^{1,2} & p_j^{2,2} \end{bmatrix} \end{array}$$

which in this format we could define as the detection probability matrix $\mathbf{p}_j$ or, using these detection probabilities, a state-dependent detection probability vector ($\mathbf{p_h}$) can be defined that expresses the probability of observing any particular detection history given the true state of the sampling unit. For example, if $\mathbf{h}_i = 120$, then,

$$\mathbf{p}_{120} = \begin{bmatrix} 0 \\ 0 \\ p_1^{1,2} p_2^{2,2} (1 - p_3^{1,2} - p_3^{2,2}) \end{bmatrix}$$

where the first element is the probability of obtaining this detection history when the true state is 0 (i.e., the sampling unit is unoccupied) and the final element for when the true state = 2. Note that as state 2 was observed in one of the three surveys, this precludes the possibility that the unit may be unoccupied or in state 1; hence the respective elements in the vector are 0. Further, if $\mathbf{h}_i = 010$, then

$$\mathbf{p}_{010} = \begin{bmatrix} 0 \\ (1 - p_1^{1,1}) p_2^{1,1} (1 - p_3^{1,1}) \\ (1 - p_1^{1,2} - p_1^{2,2}) p_2^{1,2} (1 - p_3^{1,2} - p_3^{2,2}) \end{bmatrix}$$

and if $\mathbf{h}_i = 000$,

$$\mathbf{p}_{000} = \begin{bmatrix} 1 \\ (1 - p_1^{1,1})(1 - p_2^{1,1})(1 - p_3^{1,1}) \\ (1 - p_1^{1,2} - p_1^{2,2})(1 - p_2^{1,2} - p_2^{2,2})(1 - p_3^{1,2} - p_3^{2,2}) \end{bmatrix}.$$

Note that when there is ambiguity as to the true occupancy state, there is more than one nonzero element in the detection probability vector. The zero elements in the detection probability vectors indicate the states that are not possible for a site, given the observed detection history.

Rather than use the more general multinomial structure of the occurrence and/or detection probabilities when there are greater than two true states, in their applications Royle and Link (2005) and Nichols et al. (2007) both reparameterized this general model in terms of a series of conditional binomial probabilities. Royle and Link (2005) reparameterized the detection probabilities as follows (note that subscripts denoting survey number have been removed for simplicity):

$$\begin{array}{cc} & \text{Observed state} \\ \text{True state} & \begin{array}{ccc} 0 & 1 & 2 \end{array} \\ \begin{array}{c} 0 \\ 1 \\ 2 \end{array} & \begin{bmatrix} 1 & 0 & 0 \\ 1 - p^{[1]} & p^{[1]} & 0 \\ (1 - \beta^{1,2})(1 - p^{[2]}) & \beta^{1,2}(1 - p^{[2]}) & p^{[2]} \end{bmatrix} \end{array}$$

where $p^{[m]}$ is the probability of correctly observing the true state m and $\beta^{l,m}$ is the probability of observing state l, conditional upon the observed state being less than or equal to l and the true state m (note that the parameters have been denoted slightly differently here to that used by Royle and Link [2005]). Nichols et al. (2007) used a slightly different parameterization, with the multinomial detection probabilities redefined as follows:

$$\begin{array}{cccc} & & \text{Observed state} & \\ \text{True state} & 0 & 1 & 2 \\ 0 & 1 & 0 & 0 \\ 1 & 1-p^{[1]} & p^{[1]} & 0 \\ 2 & 1-p^{[2]} & p^{[2]}(1-\delta) & p^{[2]}\delta \end{array}$$

where $p^{[m]}$ is now the probability of detecting the species (i.e., the observed state is ≥ 1) given the true state is m, and δ is the probability of observing the true state given the species has been detected and the true state $= 2$ (i.e., in their application, the probability of observing evidence of successful reproduction in a survey, given owls have been detected).

Nichols et al. (2007) also reparameterized the multinomial occupancy probabilities, as their objective was to estimate the probability of successful reproduction occurring at a potential territory, given that the territory was occupied. Hence they defined the probability of occupancy as $\psi = \varphi^{[1]} + \varphi^{[2]}$ and the probability of being in state 2, given the site is occupied (i.e., the conditional probability of successful reproduction), as $R = \varphi^{[2]}/\psi$; hence the state probability vector becomes

$$\boldsymbol{\phi}_0 = [1-\psi \quad \psi(1-R) \quad \psi R].$$

We believe that in many situations the conditional binomial parameterizations may be more natural and advantageous, particularly when exploring covariate relationships. However, it is useful to consider the more general formulation of the problem as this provides a framework upon which other reparameterizations or constraints on parameters might be imposed.

EXTENDING TO MULTIPLE SEASONS

Within any given season, conditional upon the true state of a unit, detection probabilities can be defined as noted previously. The most important issue is to consider the transition of a unit from one true state to another between seasons, which can be done by defining a transition probability matrix (TPM). The TPM determines the probability of a unit being in each possible true state at time $t+1$ given the true state at time t. For example, this could be defined as

$$\text{TPM} = \begin{bmatrix} 0 \to 0 & 0 \to 1 & 0 \to 2 \\ 1 \to 0 & 1 \to 1 & 1 \to 2 \\ 2 \to 0 & 2 \to 1 & 2 \to 2 \end{bmatrix}$$

where rows represent the true state of a unit at time t and columns the true state of the unit at time $t+1$. This can be considered as an extension of the MacKenzie et al. (2003) approach, where rather than just two states (presence/absence), there are more than two. Hence, if the probability of a unit transitioning from state m at time t to n at time $t+1$ is denoted as $\varphi_t^{[m,n]}$, then the TPM with three possible states could be defined as follows:

$$\boldsymbol{\phi}_t = \begin{bmatrix} \varphi_t^{[0,0]} & \varphi_t^{[0,1]} & \varphi_t^{[0,2]} \\ \varphi_t^{[1,0]} & \varphi_t^{[1,1]} & \varphi_t^{[1,2]} \\ \varphi_t^{[2,0]} & \varphi_t^{[2,1]} & \varphi_t^{[2,2]} \end{bmatrix}.$$

Note that each row of the TPM must sum to 1, so in practice one value in each row would have to be obtained by subtraction. Further, when there are only two possible states (e.g., presence/absence), then $\varphi_t^{[0,1]}$ is the probability a unit becomes colonized by the species and $\varphi_t^{[1,0]}$ is the probability of the species going locally extinct at the unit.

Once again, dependent upon the biological questions of interest, it may be reasonable to reparameterize the TPM. For example, if state 2 represents occupied with breeding, state 1 occupied with no breeding, and state 0 unoccupied, then the TPM could be defined as

$$\boldsymbol{\phi}_t = \begin{bmatrix} 1-\psi_{t+1}^{[0]} & \psi_{t+1}^{[0]}(1-R_{t+1}^{[0]}) & \psi_{t+1}^{[0]}R_{t+1}^{[0]} \\ 1-\psi_{t+1}^{[1]} & \psi_{t+1}^{[1]}(1-R_{t+1}^{[1]}) & \psi_{t+1}^{[1]}R_{t+1}^{[1]} \\ 1-\psi_{t+1}^{[2]} & \psi_{t+1}^{[2]}(1-R_{t+1}^{[2]}) & \psi_{t+1}^{[2]}R_{t+1}^{[2]} \end{bmatrix}$$

where $\psi_{t+1}^{[m]}$ is the probability of a unit being occupied in season $t+1$ given the unit was in state m in season t and $R_{t+1}^{[m]}$ is the probability of reproduction occurring at a unit in season $t+1$ given the unit was in state m in season t. Such a reparameterization might be advantageous to investigate hypotheses about whether the probability of reproduction occurring in a unit depends on whether reproduction occurred there in the previous year. Finally we note that the TPM can be used as the basis for a population model of occupancy dynamics (Martin et al. 2009), with the transpose of the TPM being analogous to a stage-based population projection matrix in abundance-based population models (e.g., Caswell 2001).

MODELING DATA AND PARAMETER ESTIMATION

To apply the modeling to data, two general approaches are available. The first approach considers the unconditional probability of observing each particular detection history and then determines the joint probability for all units. This joint probability may then be used within a Bayesian method of analysis or considered as the model likelihood, in which case, maximum likelihood estimates of the model parameters could be obtained.

For any observed detection history, the unconditional probability of observing the data simply considers all possible outcomes for the observed data and sums the probabilities for each possible outcome (formally this is known as integrating across the possible outcomes). For example, suppose in a single-season study a unit was surveyed four times. Three possible detection histories are given in Table 1, along with their verbal descriptions and the unconditional probabilities of observing them. Note that to obtain the probability we are simply translating the verbal description into a mathematical

TABLE 1. Example multistate detection histories ($\mathbf{h}_i$) from a single-season study with associated verbal descriptions and the unconditional probabilities of observing them (probability statement).

$\mathbf{h}_i$	Verbal description	Probability statement
1201	The unit was in state 2, with state 1 being observed in the first and fourth survey, state 2 observed in the second survey, and the species was undetected in the third survey.	$\varphi^{[2]}p_1^{1,2}p_2^{2,2}(1-p_3^{1,2}-p_3^{2,2})p_4^{1,2}$
0110	The unit may have been in state 2, with the species undetected in the first and fourth surveys and state 1 observed in the second and third surveys,	$\varphi^{[2]}(1-p_1^{1,2}+p_1^{2,2})p_2^{1,2}p_3^{1,2}(1-p_4^{1,2}-p_4^{2,2})$
	or	
	the unit may have been in state 1, with the species undetected in the first and fourth surveys and state 1 observed in the second and third surveys.	$+\varphi^{[1]}(1-p_1^{1,1})p_2^{1,1}p_3^{1,1}(1-p_4^{1,1})$
0000	The unit may have been in state 2, with the species undetected in all four surveys,	$\varphi^{[2]}\prod_{j=1}^{4}(1-p_j^{1,2}-p_j^{2,2})$
	or	
	the unit may have been in state 1, with the species undetected in all four surveys,	$+\varphi^{[1]}\prod_{j=1}^{4}(1-p_j^{1,1})$
	or	
	the species may be absent from the unit (state 0).	$+1-\varphi^{[1]}-\varphi^{[2]}$

Note: See *A single-season model* for parameter definitions.

expression using the defined model parameters. Whenever an "or" occurs in the verbal description, another term is added to the probability statement.

This same principle can be extended to multiseason data as well. For example, consider the detection history $\mathbf{h}_i = 10\ 21\ 00$ representing a unit that was surveyed for three seasons, with two surveys per season. In the first season, the unit may have been in state 1 with state 1 detected in the first survey and the species undetected in the second survey or the unit was actually in state 2 with state 1 detected in the first survey and nondetection in the second survey. In season two, the unit must have been in state 2, with state 2 being detected in the first survey and state 1 detected in the second survey (so the possible state transitions between seasons are $1 \rightarrow 2$ or $2 \rightarrow 2$). In the final season, the unit may be in any of the three possible states as the species was not detected in either survey (so possible state transitions are $2 \rightarrow 0$, $2 \rightarrow 1$, and $2 \rightarrow 2$). To obtain the probability of observing this detection history we again translate this verbal description of the history using the model parameters (for the more general formulation) defined above, i.e.,

$$\begin{aligned}
&\Pr(\mathbf{h}_i = [10 \quad 21 \quad 00]) \\
&\quad = \Big[[\varphi^{[1]}p_1^{1,1}(1-p_1^{1,1})\varphi_1^{[1,2]} + \varphi^{[2]}p_1^{1,2}(1-p_1^{1,2}-p_1^{2,2})\varphi_1^{[2,2]}] \\
&\qquad \times p_2^{2,2}p_2^{1,2} \\
&\qquad \times [\varphi_2^{[2,0]} + \varphi_2^{[2,1]}(1-p_3^{1,1})^2 + \varphi_2^{[2,2]}(1-p_3^{1,2}-p_3^{2,2})^2\Big].
\end{aligned}$$

Note that the term in the first square brackets represents the probabilities of the unit being in either state 1 or 2 in season one, then transitioning to state 2 in season two. The middle term represents the probability of the observations, given the unit must have been in state 2 in season two, while the final term in the second set of square brackets is the probability of transitioning to any of the three states from state 2 between seasons two and three and the respective probabilities of nondetection.

Following MacKenzie et al. (2003), the unconditional probability can be expressed succinctly using matrix notation, i.e.,

$$\Pr(\mathbf{h}|\boldsymbol{\theta}) = \boldsymbol{\phi}_0\left[\prod_{t=1}^{T-1} D(\mathbf{p}_{\mathbf{h},t})\boldsymbol{\phi}_t\right]\mathbf{p}_{\mathbf{h},T}$$

where $\mathbf{p}_{\mathbf{h},t}$ is the detection probability vector for the portion of the full detection history observed in season t, and $D(\mathbf{p}_{\mathbf{h},t})$ is a diagonal matrix with the elements of $\mathbf{p}_{\mathbf{h},t}$ on the main diagonal (top left to bottom right) and zero elsewhere. Assuming the detection histories are independent for each unit, the joint probability for the data (and the model likelihood) is

$$\Pr(\mathbf{h}_1, \mathbf{h}_2, \ldots \mathbf{h}_s|\boldsymbol{\theta}) = L(\boldsymbol{\theta}|\mathbf{h}_1, \mathbf{h}_2, \ldots \mathbf{h}_s) = \prod_{i=1}^{s}\Pr(\mathbf{h}_i|\boldsymbol{\theta})$$

where $\boldsymbol{\theta}$ denotes all the parameters in the model.

The second approach is to consider the true state of a unit each season to be a latent (unknown) variable and use a state-space approach to predict or impute the true state each season wherever there is ambiguity in the observed data. Practically this necessitates the use of Markov chain Monte Carlo (MCMC) approaches and Bayesian methods of statistical inference. To aid the development of this approach it is convenient to reformulate the model in terms of random variables. In season t, the true state of unit i is a random variable ($z_{i,t}$) from one trial of a multinomial distribution. In season one, the probability of being in each possible state is defined by the vector $\boldsymbol{\phi}_0$, while in subsequent seasons ($t = 2, 3, \ldots, T$) it is the vector given by row

$z_{i,t-1}$ of $\boldsymbol{\phi}_{t-1}(\boldsymbol{\phi}_{t-1}[z_{i,t-1}, \ldots])$, i.e.,

$$z_{i,1} \sim \text{mult}(\boldsymbol{\phi}_0, 1) \qquad z_{i,t}|z_{i,t-1} \sim \text{mult}(\boldsymbol{\phi}_{t-1}[z_{i,t-1}, \ldots], 1).$$

Then, given the (imputed) true state of a unit in season t, the observed state in survey j of unit i is a random variable ($h_{i,t,j}$) from one trial of a multinomial distribution with probabilities given by the appropriate row (based on true state, row $z_{i,t}$) of the detection probability matrix $\mathbf{p}_{t,j}$, i.e.,

$$h_{i,t,j} \sim \text{mult}(\mathbf{p}_{t,j}[z_{i,t}, \ldots], 1).$$

One advantage of the state-space approach is that as the true state of each unit is predicted each season (with different true states being predicted when there is ambiguity as the Markov chain progresses), relevant summaries of the system, such as number of units in state 2, can be calculated relatively easily. Similar approaches have been used by Dupuis (1995) and Schofield et al. (2009) for multistate capture–recapture data, Royle and Kery (2007) for single-occupancy state dynamics problems, and Dorazio et al. (2006) for estimating species richness and accumulation. It is important to realize that the state-space and unconditional probability approaches are equivalent, as the latter also can be developed in terms of latent variables, with the unconditional probability resulting from integrating the probability of observing the detection history across the possible values for the latent variable. Therefore, both approaches yield the same results, although with more complex models the state-space approach will be much easier to implement.

To illustrate that either approach may be used to implement this model, in the following examples we use the unconditional probability approach with maximum likelihood theory to analyze data on California Spotted Owls and the state-space approach on call index data of green frogs from the North American Amphibian Monitoring Program (NAAMP). The maximum likelihood approach can be implemented using Program PRESENCE (*available online*),[6] and we provide our WinBUGS code for implementing the state-space approach as a Supplement to this paper.

COVARIATES AND "MISSING" OBSERVATIONS

Relevant information on factors that may affect occurrence-related and detection-related probabilities may be incorporated through various link functions (functions that transform a regression equation with covariates from the ± infinity scale to the interval [0, 1]). There is a range of possible link functions available, although we note the logit and multinomial-logit link functions may often be preferred, as these correspond to logistic and multinomial-logistic regression. The exact choice of link function depends on parameterization of the model, which is likely to be application-specific. Hence, rather than discuss these options, we simply note that the inclusion of covariates is easily accomplished.

The basic sampling methodology is that within each season, each sampling unit will be surveyed multiple times. MacKenzie et al. (2006) show that there is no requirement of an equal sampling effort across all units, in all seasons. Field logistics may preclude surveying all sites an equal number of times, the study may have been designed such that some units are surveyed more intensively than others, changes in funding may result in more/fewer units being surveyed in certain years, or other unpredicted events (e.g., weather or vehicle breakdowns) may result in some planned surveys not being completed. We consider these possibilities as examples of situations that result in "missing" observations. Essentially the survey occasions that correspond to the missing observations at a unit are skipped with neither a p nor a $1 - p$ being included in the detection probability vector, as there is no information regarding the detection or nondetection of the species. An alternative mathematical explanation for how the modeling deals with missing observations is that for that survey occasion the species was not detected in any state (which occurs with probability $1 - p$), but because no survey was conducted, detection probability for that unit at that occasion was zero, so the probability of nondetection was $1 - 0 = 1$. Provided that the cause for the missing observation is independent of the parameters and quantities of interest in the model, it is not necessary to explicitly account for the missing observations within the analysis. An example in which such a dependency exists (and hence should be avoided) is if budget cuts necessitate a reduction in the number of sampling units being monitored and investigators respond by discontinuing monitoring of those units they think are unoccupied by the species (i.e., knowledge about the likely occupancy state of units is used to determine which ones will become "missing" observations).

EXAMPLE 1: CALIFORNIA SPOTTED OWLS

We apply the above model to data from daytime visits to potential California Spotted Owl territories from April to August 1997–2004 at the Eldorado study area in the central Sierra Nevada, California, USA. Seamans et al. (2001) and Franklin et al. (2004) describe Spotted Owl population dynamics and sampling protocols for this study area. The protocols include locating adult and subadult owls on each visit to a potential territory. Once located, an owl is offered a live mouse and then visually followed after the mouse is taken. Definitive evidence of reproductive activity is provided when owls take mice to a nest or to young and young are observed. Nonreproducing owls usually eat or cache mice, but such behavior during a single visit may not be indicative of a failure to reproduce.

We used the same parameterization as Nichols et al. (2007), in which the probability of a territory being unoccupied, occupied without reproduction, or occupied

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[6] ⟨http://www.mbr-pwrc.usgs.gov/software.html⟩

with reproduction was modeled using two parameters: the probability a site was occupied (ψ) and the probability of successful reproduction occurring at the territory given that the territory was occupied (R). We used this structure for both the initial state vector (probabilistic statement for the state of a site the first year of the study) and for the state transition matrix, TPM, where the occupancy and reproduction probabilities may depend on the true state in the previous year (e.g., probability of a territory being occupied with no reproduction in year $t + 1$ could be different if the territory was unoccupied in year t vs. occupied with reproduction in year t). Detection probabilities were also parameterized as in Nichols et al. (2007), with $p^{[2]}$ defined as the probability of detecting owls in a survey of a territory that was occupied with reproduction, and δ as the probability of observing the evidence of reproduction in a survey given that owls were detected. For simplicity, $p^{[2]}$ and $p^{[1]}$ were assumed to vary among years but not within years (although within-year variation could be allowed), while δ was allowed to have a different value for surveys conducted early in the season (δ_E) vs. late in the season (δ_L). From preliminary modeling, δ_E was found to be essentially zero in all years so only a single value was estimated in the models reported below, while δ_L was allowed to vary among years.

To illustrate the ecological relevance of this type of modeling, here we examine whether the occupancy and reproduction probabilities vary annually and/or depend upon the state of the territory in the previous year. Lack of annual variation in occupancy may suggest the system has reached some point of dynamic equilibrium (as time constancy in the Markovian vital rates results in a stationary distribution), and that was indeed an a priori hypothesis for the owl population, as habitat conditions were relatively stable over the course of the study. Dependency on previous territory state would indicate that system vital rates follow some type of Markov process, although the exact nature of the process would depend upon parameter estimates. Based on the general fidelity of California Spotted Owls to territories, we hypothesized that occupancy would be more likely for territories occupied the previous season. We also predicted that occupancy would be somewhat more likely for territories in which successful reproduction occurred the previous season than for territories in which successful reproduction did not occur. This prediction is based on general evidence for many avian species that fidelity to nesting locations is reduced following unsuccessful reproductive attempts (Greenwood and Harvey 1982, Johnson et al. 1992) and on specific observations of California Spotted Owls (Blakesley et al. 2006). We also predicted that territories that were occupied with reproduction in year t would tend to have higher probabilities of reproduction in year $t + 1$ than territories in the other states in year t. The mechanisms underlying this hypothesis include the possibilities that such territories were of high quality (e.g., they were "sources" [Pulliam 1988]; or they made relatively large contributions to system growth [Runge et al. 2006]) and that high-quality owls show fidelity to territory sites, especially sites at which they were successful the previous season. In contrast, if the probability of reproduction in year $t + 1$ was lower in territories where reproduction occurred in year t compared to other territories, that might suggest a biennial breeding cycle (e.g., see Franklin et al. 2004) or perhaps a "cost" of successful reproduction imposed on subsequent breeding attempts (e.g., energetic costs). Reproductive success is believed to be more sensitive to environmental variation than is occupancy; hence, we did not expect the time constancy models for reproduction to be well supported.

Twenty-four models involving various constraints on the occupancy and reproductive probabilities were fit to the owl data. Note that these constraints were not applied to the occupancy and reproductive probabilities associated with the first year's data because the state of territory in the previous year was unknown. Models were ranked using Akaike's Information Criterion (AIC), with the top two models accounting for 99% of the AIC model weight (Appendix A). Both models had the probability of occupancy in year $t + 1$ depending only on the state of a territory in year t and the probability of reproduction varying by both state in year t and time. In the second-ranked model, with 8% AIC weight, the effect of state on reproduction was consistent in each year (i.e., an additive model) while in the top-ranked model, with 91% AIC model weight, the effect of state on reproduction was different in each year (i.e., an interaction model). All other models had essentially no support, providing very strong evidence that occupancy dynamics were at some point of equilibrium (as time was not an important factor in either model), but reproduction dynamics were not. To account for model selection uncertainty we obtained model-averaged estimates of parameters (Burnham and Anderson 2002). We estimated approximate 95% confidence intervals by calculating symmetric intervals on the logit scale (as ±2 SE), then back-transforming the resulting estimates to the probability scale. This resulted in confidence intervals that were appropriately asymmetric and bounded by 0 and 1; however, if the estimated probability was very near 0 or 1, the resulting confidence interval might be unreliable.

In 1997, the estimated probability of a territory being occupied was 0.89 (95% CI = 0.77, 0.95) and the estimated probability of reproduction occurring was 0.47 (0.31, 0.62). The estimated probability of a territory being occupied in year $t+1$ given its state in year t were 0.17 (0.11, 0.26), 0.87 (0.79, 0.92), and 0.91 (0.83, 0.95) for territories that were unoccupied, occupied without reproduction, and occupied with reproduction in year t, respectively. As predicted, the probabilities of occupancy were much higher for territories occupied the previous year, although the occurrence of reproduction

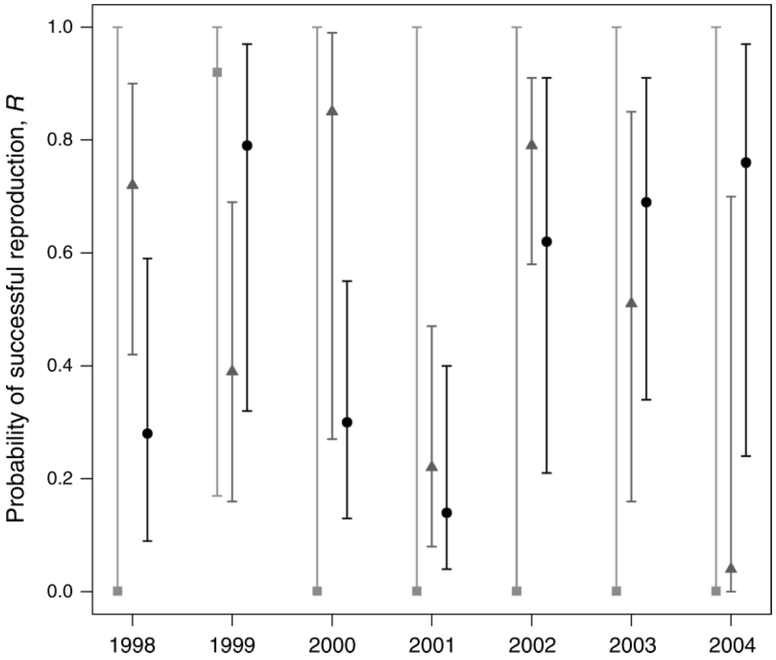

FIG. 1. Model-averaged estimates of the probability of successful reproduction (R) in each year given the occupancy state of a territory in the previous year for California Spotted Owls in Sierra Nevada, California, USA. Squares indicate the probability for territories that were unoccupied in the previous year, triangles for territories that were occupied without successful reproduction, and circles for territories that were occupied with successful reproduction. Error bars indicate approximate 95% confidence intervals.

in the previous year did not appear to be an important determinant of occupancy given the similarity of the latter two estimates.

Fig. 1 presents the estimated probabilities of successful reproduction in each year given the occupancy state of the territories in the previous year. For sites that were unoccupied in year t, the estimated probability of successful reproduction in year $t + 1$ approached 0 for most years, except for $\hat{R}^{[0]}_{1999}$, when one territory was observed to have successful reproduction without the species having been detected there in the previous year. This pattern indicated the relative rarity of colonizing a territory and successfully reproducing the same season. Note that the very wide confidence intervals when the estimated probability was 0 should be ignored and was an artifact of first calculating them on the logit scale. In each case the standard error for each estimate was essentially 0. The probability of successful reproduction for territories that were occupied the previous year showed an interesting tendency to alternate between higher values for territories with and without successful reproduction the previous year. That is, during some years the probability of successful reproduction was higher for territories that were successful the previous year, whereas in other years it was higher for territories that were unsuccessful the previous year. These results were consistent with previous studies of Spotted Owls that show territory quality varies within owl populations (Franklin et al. 2000, Seamans and Gutiérrez 2007*a*) and variability in annual reproduction is highly correlated to environmental variation (Seamans and Gutiérrez 2007*b*).

Estimated detection probabilities (Table 2) were relatively high and tended to be greater for territories in which successful reproduction occurred. The probability of correctly classifying a state when successful reproduction occurs was estimated to be zero for all early-season surveys, but was estimated to be generally high for late-season surveys, except in 1999 and 2003, which highlights the need to consider time specificity of classification probability.

EXAMPLE 2: GREEN FROGS IN MARYLAND

In this second example we fit models to chorus index data gathered under the North American Amphibian Monitoring Program (NAAMP; see Weir and Mossman [2005] for sampling protocol details) for the green frog, *Rana clamitans*, in Maryland, USA, from 2001 to 2005. Royle and Link (2005) present an analysis of the 2001 NAAMP data for the green frog. The NAAMP is an amphibian sampling program consisting of 24.1-km routes along secondary or smaller roads. Each route includes 10 listening stations spaced at least 0.8 km apart. Some routes have assigned equidistant (0.8 km) listening stations, whereas others have listening stations within hearing distance of wetland habitat. Observers

TABLE 2. Model-averaged estimates of detection and classification probabilities (with SE in parentheses) for the California Spotted Owl example.

	Year							
Parameter	1997	1998	1999	2000	2001	2002	2003	2004
$p_t^{[1]}$	0.75 (0.04)	0.56 (0.06)	0.89 (0.08)	0.55 (0.06)	0.66 (0.04)	0.55 (0.08)	0.48 (0.09)	0.62 (0.04)
$p_t^{[2]}$	0.91 (0.03)	0.79 (0.04)	0.30 (0.07)	0.87 (0.03)	0.97 (0.03)	0.79 (0.03)	0.74 (0.05)	0.80 (0.04)
$\delta_{E,t}$	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
$\delta_{L,t}$	0.93 (0.04)	0.79 (0.06)	0.17 (0.15)	0.83 (0.05)	0.85 (0.08)	0.84 (0.04)	0.26 (0.10)	0.85 (0.05)

begin surveys no earlier than 30 min after sunset; they proceed along the route stopping to listen for amphibians for 5 min at each listening station or "stop." Observers record chorus indices of "0" for species that are not detected at a stop, "1" if individuals can be counted, "2" if individual calls can be distinguished with some overlapping, and "3" if a full chorus is present with constant, overlapping calls. It is assumed that each stop is capable of generating a maximum chorus index of either 0, 1, 2, or 3 during a season, which represents the true state of a stop. However, on any given evening when a stop may be surveyed, the level of green frog activity recorded by an observer may be less than or equal to this true maximal value, e.g., local abundance is sufficient to generate a maximum chorus index of 2 during the breeding season, but the level of calling activity at the time of the survey may result in either a 0, 1, or 2 being observed. The number of stops surveyed each year was 240, 280, 250, 270, and 250 from 2001 to 2005, respectively. Each stop was surveyed three times annually with one survey early, middle, and late in the breeding season. We expected within-season variation in detection probabilities because of the frog's breeding phenology.

We implemented the modeling using the state-space (or latent variable) approach described using the software WinBUGS. Rather than using a series of conditional binomial probabilities to model the occupancy state-related probabilities (as in the previous example), we used a general parameterization in which both the initial occupancy state vector $\boldsymbol{\varphi}_0$ and each row of the TPM $\boldsymbol{\varphi}_t$ have a multinomial structure (i.e., we are estimating the parameters $\varphi^{[m]}$ and $\varphi_t^{[m,n]}$ defined earlier). In this context $\varphi^{[m]}$ represented the probability that a stop supported a population of green frogs capable of producing a maximum call index of size m in 2001, and $\varphi_t^{[m,n]}$ represented the probability that the green frog population at a stop that was capable of producing a maximum call index of size m in year t was capable of producing a maximum call index of size n in year $t+1$. We also maintained a general multinomial structure for detection probabilities in which the probabilities were allowed to vary both within a season and among years without any constraints. Naturally simpler models for detection probabilities could be investigated in a detailed analysis, and the influence of such constraints on the results could be assessed.

We specified a uniform prior distribution (equivalent to a beta(1,1) distribution) for probabilities associated with events that have only two possible outcomes and a Dirichlet prior distribution with all parameters equal to 1 for probabilities associated with events with more than two outcomes. The Dirichlet distribution is a multivariate extension of the beta distribution. Two chains of 50 000 iterations were used to approximate the posterior distributions of the model parameters after discarding an initial 10 000 iterations of each chain as the burn-in period. The chains demonstrated good mixing and convergence was achieved rapidly.

We assume that the state variables of interest in this example are the number of stops capable of generating call indices of 0, 1, 2, and 3, with the intent of using this as an index of trends in relative abundance. Note that the numbers of stops within each state each season are not parameters of the model described above; however, these could be obtained by using the output of the model, applying appropriate algebra, and invoking (further) asymptotic approximations to derive standard errors for the resulting estimates. Alternatively, recall that when using the state-space approach with MCMC methods, the true state of a sampling unit is imputed for each iteration of the Markov chain as a useful by-product of estimating the transition probabilities and other parameters. Hence, using the state-space approach to obtain estimates of the number of stops within each state each season requires just a simple summation. The uncertainty in these quantities associated with estimation of the underlying vital rates (transition probabilities) and imperfect detection is automatically accounted for by the MCMC machinery and does not require any asymptotic assumptions. Therefore, it is possible to directly obtain posterior distributions for the estimated number of stops capable of generating each index value each year.

Fig. 2 presents summaries of the posterior distribution for the number of NAAMP stops in Maryland predicted to be capable of generating chorus indices of 0, 1, 2, or 3 from 2001 to 2005. Note that even though a different number of stops were surveyed each year, predictions about the likely state of unsurveyed stops have been made as part of the estimation procedure so no

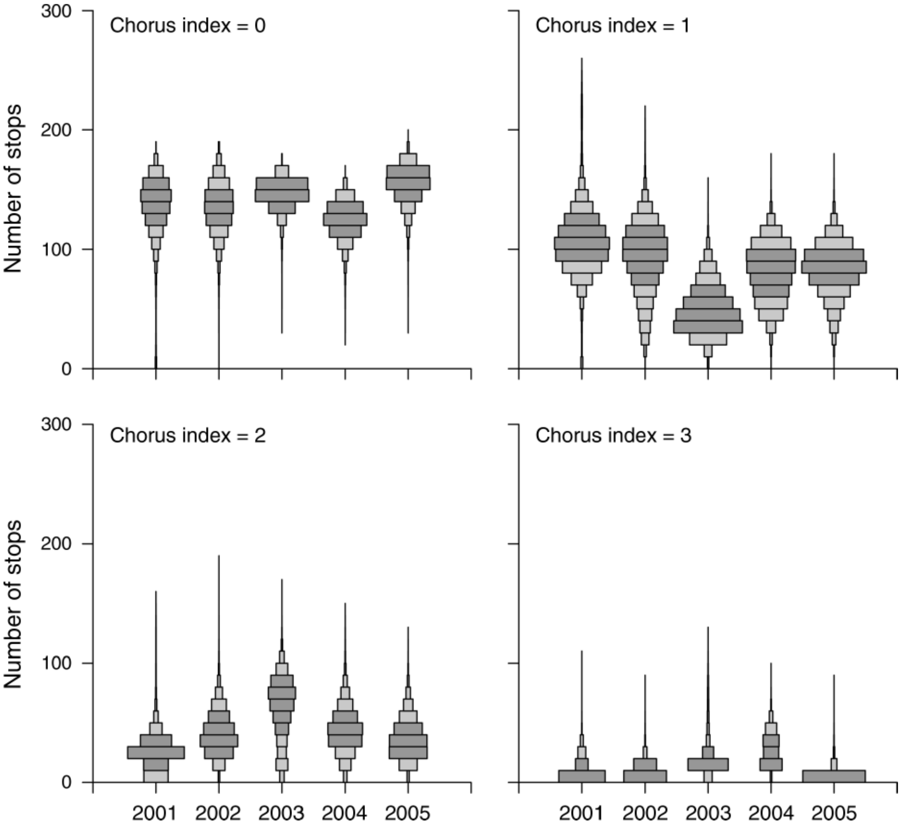

Fig. 2. Posterior distribution for the number of North American Amphibian Monitoring Program (NAAMP) stops in Maryland, USA (from the 280 surveyed), with populations of green frogs capable of generating chorus indices of 0, 1, 2, and 3. Darker shading indicates bars that are within the central 50% of the posterior distribution. The widths of the bars indicate relative frequencies that are comparable between years within each chorus index, but not between indices.

adjustment is needed to account for the unequal sample sizes. From these results, there is little indication of a strong trend in the number of stops of each type, suggesting that perhaps the system is relatively stable, with a reasonably consistent pattern of the number of stops decreasing as the maximum chorus index increases (i.e., most stops are predicted to generate a chorus index of 0, or green frogs are essentially absent, with few stops capable of generating a chorus index of size 3). However, these results are characterized by a relatively large degree of uncertainty about the estimated number of stops in each state. This is due to only three surveys being conducted at each stop per year and the probability of detection generally being fairly low (Appendix B). A greater number of surveys per year would improve the precision on the estimated number of stops capable of generating each chorus index for green frogs. The probability of detection and correct state classification is low in period one and increases in the later periods, reflecting the relatively late breeding of green frogs. Finally note that the probability of nondetection tends to decrease as the true state increases, which is what would be expected if the chorus index is a reasonable indication of relative abundance and if there is abundance-induced heterogeneity in the probability of detection of green frogs (at the species level) among stops.

Discussion

Scientists and managers are often interested in more than just occurrence of a species on a landscape, such as specific types or categories of occupancy (e.g., breeding/nonbreeding or some index of relative abundance). The ability to reliably estimate and model the dynamic processes of change in occupancy states through time, while accounting for imperfect detection, should lead to better scientific understanding of systems and greater information for management decisions. The method we detail above is one approach for situations in which there is ambiguity about the true occupancy state of a sampling unit.

As with all estimation problems, the reliability of parameter estimates depends upon the amount of information contained in the data about those parameters. Obtaining reliable estimates of the probabilities for infrequent transitions will require a larger sample size compared to transitions that occur more frequently. Therefore, as one increases the number of possible occupancy states, required sample sizes will also increase. This is clearly a design issue that should be considered (ideally) before fieldwork commences to determine the level of sampling required that will provide sufficient information for the objectives at hand. However we note that because of imperfect detection, greater improvements to parameter estimates may be obtained by increasing the number of repeated surveys before increasing the number of units sampled. Our examples partially illustrate this point. For the California Spotted Owl we were able to make reasonable inferences about occupancy and reproductive dynamics based on only 66 sampling units (potential territories) but relatively high detection probabilities. Whereas for the green frogs, despite a larger number of sampling units (280), because detection probabilities were low and only three repeat surveys were conducted, resulting estimates still had a relatively high degree of uncertainty.

Although we view the primary use of these models as a means of asking interesting ecological questions, we note that even in the absence of interesting ecology, the use of multistate occupancy models can be viewed as a means of dealing with heterogeneous probabilities of detection, occupancy, and transition parameters (e.g., local extinction and colonization). The basic dynamic occupancy models of MacKenzie et al. (2003, 2006) assume constancy of parameters for all units or at least constant relationships between parameters and sampling unit covariates. Multistate models can be viewed as an approach for dealing with heterogeneity among occupied units by admitting the possibility of different parameter values depending upon occupancy state. Such heterogeneity cannot be dealt with using typical covariate modeling because of the uncertainty associated with the correct covariate value (i.e., true state).

The motivation for developing this modeling approach has come from biologists, and we believe that the approach provides an especially useful framework for assessing questions associated with important ecological concepts such as source–sink dynamics, dynamics of disease spread, and changes in the (relative) abundance distribution of a species. For example, most considerations of source–sink systems view source and sink locations as fixed, with some patches being inherently productive and others inherently unproductive, with status constant over time. Such a view is reasonable for situations in which habitat is the primary determinant of reproductive success at a location and habitat is relatively static. However, if there is temporal variation in habitat quality with respect to reproductive output, then similar temporal variation in the identity of locations that are and are not productive would also be expected. If animals exhibit fidelity to sites of previous breeding, then certain phenotypic "costs of reproduction" (reduced probability of successful reproduction in years following successful reproduction) would be expected to yield specific patterns in state transition parameters: higher probabilities of sites moving from reproductively successful to unsuccessful and unsuccessful to successful. The combination of temporal variation in habitat quality and the existence of reproductive costs could produce patterns of oscillation in state transition probabilities such as those observed for the California Spotted Owls.

In many avian species that are not colonial breeders, an individual's reproductive success in one breeding season is believed to serve as a predictor of reproductive success the next season. Such "predictions" lead to the pattern of higher fidelity to breeding sites for individuals that are successful than for those that are not (e.g., Greenwood and Harvey 1982, Johnson et al. 1992). Even in the absence of substantial habitat variation over time, such behavior would tend to induce a relationship between reproductive state and occupancy. Sites with successful reproduction in one year would tend to be occupied the next, whereas sites without successful reproduction would be less likely to be occupied the next year.

One stated assumption of the modeling is that units are closed to changes in occupancy such that a unit is in the same occupancy state for the period of repeated surveys within a season. This is clearly not true in many situations. However, based on our experience with occupancy and capture-recapture modeling we believe that it is reasonable to relax this assumption provided the interpretation of the parameters is modified accordingly. Note that the consequences of violating the closure assumption is an ongoing area of research; hence our following comments are somewhat speculative. When the occupancy state changes within a season, then detectability is now a combination of the probability the unit is in a particular state at the time of the survey and, given it is in that state, the probability of observing that or a lower order state. When such changes occur at random (i.e., probability of the unit being in each state at the time of surveying does not depend on the true state of the unit at the last survey) then we believe the interpretation of the state-specific occupancy-related probabilities is the probability that that state is the highest reached during the season (i.e., the state of a unit may not always be 2, but 2 is the highest state reached at some point during the surveying). When changes in the occupancy state are expected to be in one direction during the season (e.g., breeding may not commence or evidence of breeding may not be obvious until mid-way through the season, as in the case with the California Spotted Owls), then the occupancy-related probabilities should be interpreted as the probability of being in each state at either the beginning or end of the season, depending upon the nature of the changes. We do not know what effect other types of changes in occupancy state within a season may have on interpretation of the model parameters, and we suspect they may introduce some bias. Importantly, if it is suspected that the closure assumptions are potentially being violated, that suggests a "season" (from the perspective of the modeling) has been defined inappropriately (MacKenzie et al. 2006). Good study design should help avoid such pitfalls. In the case of violation of closure, reduction of the time between surveys within a season is a reasonable design response.

Another assumption is that there is no spatial correlation between units, implying that the occupancy-related vital rates at one unit do not depend upon the current occupancy state at neighboring or nearby units. The extension of these methods to account for such spatial correlation is a current area of research, and while we agree that such spatial correlations will often be present in many situations, we also note that such spatial correlations may not necessarily preclude the use of these and similar methods. Often such spatial correlations may be accounted for by using appropriate covariates, either as a mechanistic explanation for the correlation or as a surrogate for the possible correlation structure. For example, occupancy may appear to be correlated on the landscape, but that is in fact caused by the distribution of habitat on the landscape, i.e., it is the habitat that is spatially correlated and units are relatively independent within habitat types; hence using habitat as a covariate would account for the apparent correlation. In another situation one would often expect different dynamics at units near the edge of a species' range compared to units near its center. This could be expressed as a form of spatial correlation, or it may also be approximated using distance from center of the range as a covariate for the vital rates of change. We also note that if inference is primarily at the population (of sample units) level, provided one has a random sample of units from the population, even if spatial correlation exists then resulting estimates from methods that do not account for it may still be useful if interpreted as average values for the population.

In addition to addressing ecological questions, we believe that multistate occupancy modeling has great potential for use in wildlife management and conservation. Monitoring is an important component of informed management, in general, and adaptive management, in particular (Yoccoz et al. 2001, Williams et al. 2002, 2007). Specifically, population monitoring is used in management to estimate system state for the purpose of (1) making state-dependent decisions, (2) assessing progress towards management objectives, and (3) discriminating among competing hypotheses about population response to management actions (Williams et al. 2002, 2007, Nichols and Williams 2006). However, demographic monitoring (e.g., Franklin et al. 2004) is often not conducted by management agencies because of the cost in terms of the total personnel required, the effort required to obtain suitable measures of response (e.g., survival, reproduction), the requirement of special technical expertise to obtain some forms of data, the overall cost, and the time (both short- and long-term time horizons) required to collect detailed demographic data. If a species can be reliably detected using sign, sight, or sound, then estimation of state-specific occupancy is a potentially useful tool for population monitoring, especially for geographically extensive management and conservation programs. State-specific occupancy (state variables are proportions or numbers of units occupied with and without reproduction; vital rates are the state transition probabilities) is not equivalent to demographic monitoring (state variable is abundance; vital rates are rates of survival, reproduction, and movement), but actually may be more appropriate for some management and conservation programs.

The usual approaches to testing ecological predictions such as those noted here use inference methods that do not deal adequately with nondetection or state misclassification. We thus view models such as those developed here to be important to the progression of ecological science. Multistate capture-recapture models have become enormously useful since their reintroduction to ecologists in the early 1990s (e.g., see reviews in Lebreton and Pradel 2002, White et al. 2006), and this utility is largely attributable to their flexibility in dealing with interesting ecological phenomena. We believe that multistate occupancy models should be similarly attractive to ecologists and expect them to become widely used.

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APPENDIX A

Summary of the model selection process on California Spotted Owl data (*Ecological Archives* E090-056-A1).

APPENDIX B

Posterior distribution summaries for detection probabilities in the green frog example (*Ecological Archives* E090-056-A2).

SUPPLEMENT

WinBUGS 2.2.0 code for the green frog example (*Ecological Archives* E090-056-S1).