ESTIMATING SITE OCCUPANCY, COLONIZATION, AND LOCAL EXTINCTION WHEN A SPECIES IS DETECTED IMPERFECTLY

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Abstract. Few species are likely to be evident that they will always be detected when surveyed (e.g., species that allow for the estimation of site occupancy, colonization, and local extinction probabilities. These population vital rates are often of interest in long-term monitoring programs and metapopulation studies. We present a model that enables direct estimation of these parameters when the probability of detecting the species is less than 1. The model does not require any assumptions of process stationarity, as do some previous methods, but does require detection/nondetection data to be collected and analyzed similar to Pollock’s robust design as used in mark-recapture studies. Via simulation, we show that the model provides good estimates of parameters for most scenarios considered. We illustrate the methods with data from monitoring programs of Northern Spotted Owls (Strix occidentalis caurina) in northern California and tiger salamanders (Ambystoma tigrinum) in Minnesota, USA.

Key words: colonization; detection; local extinction; metapopulation; monitoring; occupancy; population; patch occupancy; robust design; site occupancy.

INTRODUCTION

Estimating the proportion of sites occupied by a target species is important in both long-term monitoring programs and metapopulation studies. In a monitoring context, site occupancy probabilities may be used as a metric reflecting the current state of the population. Although estimates of abundance traditionally are used as a measure of system state (e.g., Williams et al. 2002), abundance estimation often requires more expense and effort than estimation of site occupancy (e.g., Tyre et al. 2001, MacKenzie et al. 2002). In metapopulation and island biogeographic studies, site (or patch) occupancy often is used as a state variable and incorporated into “incidence functions” that may be used to estimate local extinction and colonization probabilities. Sampling a metapopulation over multiple years (e.g., annual breeding seasons in a 5-year study of migratory birds, or days within a week-long study of the study of a single sampling period, between which changes in site occupancy state may occur. Within each primary period, investigators use an appropriate sampling design for monitoring individual sites at a single point in time. This is akin to Pollock’s robust design for mark-recapture studies where k, surveys represent secondary sampling periods within each primary period (Pollock 1982, Pollock et al. 1990).

The target species may or may not be detected at each survey and is not falsely detected when absent. The resulting detection history for each site may be expressed as T vectors of 1’s and 0’s, indicating detection and nondetection of the species. We denote the detection history for the k, surveys of site i at primary sampling period t as Xit, and the complete detection history for site i over all primary periods, as X, Detection histories for the N sites can be used to estimate site occupancy, colonization, and local extinction probabilities using a simple application of likelihood theory.

Statistical model

The situation presented by MacKenzie et al. (2002) could be considered as a special case of those considered here, where multiple surveys of the sites are only conducted for a single primary period. Let Oi be the probability that a site was occupied at time t (t = 1) and p, be the probability of detecting the species, given presence, in survey j within primary period t. (MacKenzie et al. 2002) use a series of data error types on parameter estimates for Stochastic Patch Occupancy Models (SPOMs); the error with the most serious implications was the recording of false absences (because species were not detected with certainty). Molinaren (2002) suggested modifying the probabilities of transition between patch states (occupied and unoccupied) in successive years by incorporating a term that allows for the probability of observing a false absence. Yet Molinaren as-
Consider the detection history **000** (**001**): the species was detected at the site in the first primary period (t = 1) during the third survey only, and was never detected in the second primary period (t = 2). The probability of observing the detection history at t = 1 would be

\[
\operatorname{Pr}(X_1 = 000) = \phi_1 \prod_{t=2}^{T-1} (1 - \phi_t) \prod_{t=T} (1 - \phi_T)
\]

Following this, there are two possibilities: either the species was not detected at t = 2: either it continued to occupy the site and was undetected, or it became locally extinct. The probability of this occurring would be expressed as

\[
\operatorname{Pr}(X_1 = 010) = \phi_1 \phi_2 \prod_{t=3}^{T-1} (1 - \phi_t) \prod_{t=T} (1 - \phi_T)
\]

\[
\operatorname{Pr}(X_1 = 001) = \phi_1 \prod_{t=2}^{T-1} (1 - \phi_t) \phi_T
\]

These representations of the detection history are applied and the vector \( \mathbf{p} \) is adjusted by removing the corresponding \( p_t \) parameter(s). For example, if the history **11** is observed at primary period (where "---" indicates a missing observation), then

\[
\mathbf{p}_{t-1} = \left[ \begin{array}{c} 0 \\ \phi_T \\ 0 \\ \cdots \\ 0 \end{array} \right]
\]

This represents that fact that no information, either detection or non-detection, was gathered at the third sampling occasion of primary period \( t \).

Failure of this assumption introduces heterogeneity, which will lead to biased parameter estimates. Use of covariates enables this assumption to be relaxed somewhat, but heterogeneity created by unknown or unmeasured factors may be problematic.

Note that the probability of occupancy at time \( t \), \( \phi_t \), can be calculated recursively by the relationship

\[
\phi_t = \phi_t (1 - \epsilon_t) + \epsilon_t (1 - \phi_{t-1})
\]

Using this relationship, we can reparameterize the model to estimate \( \phi_t \), directly, by rearranging Eq. 7 to make either \( \epsilon_t \) or \( \gamma_t \), the subject. Similarly, we can imagine that the rate of change in occupancy may be of interest in some situations (e.g., change in the size of the occupied species’ range). By means of analogy with population size, we define such a rate of change as

\[
\lambda_t = \frac{\phi_t}{\phi_{t-1}}
\]

Further, let \( \mathbf{D} \) be the row vector

\[
\mathbf{D}_{t-1} = [1 - \epsilon_t, \epsilon_t, 0, \ldots]
\]

where \( \phi_t \) is the probability that the site is occupied in the first primary sampling period. Let \( \mathbf{P}_{t-1} \) be a column vector where each entry represents the probability of observing the detection history of sites in primary period \( t \)., conditional upon occupancy state. For instance, in the primary period \( t = 1 \), \( \phi_t = \prod_{t=2}^{T-1} (1 - \phi_t) \prod_{t=T} (1 - \phi_T) \).

\[
\begin{align*}
\mathbf{P}_{t-1} & = [1 - \phi_t, \phi_t (1 - \phi_t), 0, \ldots] \\
\mathbf{P}_{t=T} & = [1]
\end{align*}
\]

Whenever the species is detected at least once during a primary period, the second element of \( \mathbf{P}_{t-1} \) will always be zero, as it is impossible to observe such a history if the site is in the unoccupied state.

The probability for an observed detection history could then be calculated as

\[
\operatorname{Pr}(X_t) = \phi_t \prod_{t=2}^{T} D_{t-1} \phi_{t-2} \phi_{t-3} \prod_{t=T} (1 - \phi_T)
\]

where \( D_{t-1} \) is a diagonal matrix with the elements of the primary surveying periods and the probability statements, according to this table, can be applied: and the vector \( \mathbf{D}_{t-1} \) is adjusted by removing the corresponding \( p_t \) parameter(s). For example, if the history **11** is observed at primary period (where "---" indicates a missing observation), then

\[
\mathbf{D}_{t-1} = [1 - \epsilon_t, \epsilon_t, 0, \ldots]
\]

Suitable covariates for site occupancy, colonization, and local extinction probabilities would be site-specific parameters that may change with each primary sampling period (e.g., habitat type or generalized weather patterns such as drought or El Niño years). Such covariates could also be used for detection probabilities, and covariates that may change with each secondary sampling period (e.g., precipitation or air temperature) could also be considered. This is unlike the situation in mark-recapture, where time-varying, individual (site-specific) covariates cannot be used in the modeling of capture histories from open populations because the covariate value is unknown for occasions when the individual is not encountered. In the site occupancy setting, however, the covariate may be measured regardless of whether the species is detected. As mentioned previously, including covariates may account for some forms of heterogeneity.

Model comparisons

Using the general framework just described, one could develop a suite of potential models that may be reasonable explanations of observed data, i.e., time-
specific vs. time-dependent extinction probabilities, or models with and without a covariate of interest. Models in the candidate set could be formulated to reflect competing hypotheses about the system under study. Selecting the better model(s) from the candidate set may proceed either by hypothesis testing (such as likelihood ratio tests) or information-theoretic methods (such as Akaike's Information Criterion, AIC).

Although our approach does not require the assumption of stationarity, one could test whether such an assumption is reasonable by including a model in the candidate set that represents this situation. Using alternative parameterizations of the model (Eqs. 7 and 8), the process would be stationary when the occupancy probability is constant over time, or \( \lambda = 1 \). Such a model can be formally compared with a more general model permitting time-varying \( \lambda \).

**Simulation results**

In some instances (generally \(< 5\%\) the matrix of second partial derivatives could not be inverted; this trend occurred when parameters were estimated to be very close to 0 or 1. On such occasions, we disregarded parameter estimates.

Generally, the parameter estimates appear to be largely unbiased except when both \( k \) and \( p_1 \) are small, in which case occupancy and colonization probabilities tend to be overestimated when \( k \) is low to moderate, and underestimated otherwise. Local extinction probabilities also tend to be overestimated. Increasing \( N \), \( T \), \( k \), or \( p_1 \) improves both the accuracy and precision of estimated parameters.

Estimated standard errors, obtained from the matrix of second partial derivatives, are in good agreement with nominal standard errors calculated from the repeated parameter estimates for each scenario. Full results of the simulations are presented in the Appendix.

We have not assessed the robustness of our model to violations of assumptions such as independent detection histories or heterogeneity in detection probabilities across sites. Undoubtedly violations of such assumptions will influence parameter estimates, but the severity of the resulting problems is unknown and a current area of research.

**Examples**

*Northern spotted owl.* Potential spotted owl territory was monitored to evaluate the presence of breeding pairs since 1985. Here we restrict our analysis to a subset of 55 sites surveyed annually between 1997 and 2001. Each site was surveyed up to eight times (average 5.3 times) during a breeding season to determine whether the territory was occupied by a breeding pair. Survey techniques were consistent from year to year and followed an established protocol (Franklin et al. 1996). However, due to logistical constraints, surveys within sites were not conducted simultaneously across sites.

Our model fit to the data. As there were a number of nested submodels that constrained colonization, local extinction, or detection probabilities to be constant across years. For simplicity, we assume that detection probabilities were constant for all surveys within any given year, although we believe this to be unlikely in practice. Table 2 presents parameter estimates and results of a model selection procedure based upon AIC, an information-theoretic approach to model selection, with parameter estimates and variances.

> Table 2. Summary of model selection procedure and parameter estimates for the Northern Spotted Owl (*Strix occidentalis caurina*).

<table>
<thead>
<tr>
<th>Model</th>
<th>( \Delta AIC )</th>
<th>( w )</th>
<th>( k )</th>
<th>( p_0 )</th>
<th>( T )</th>
<th>( N )</th>
<th>( p_0 )</th>
<th>( p_{det} )</th>
<th>( p_{est} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1997 y/year</td>
<td>0.00</td>
<td>0.57</td>
<td>11</td>
<td>0.63</td>
<td>0.11</td>
<td>0.07</td>
<td>0.39</td>
<td>0.09</td>
<td></td>
</tr>
<tr>
<td>1997 y/year</td>
<td>0.04</td>
<td>0.28</td>
<td>10</td>
<td>0.63</td>
<td>0.11</td>
<td>0.07</td>
<td>0.39</td>
<td>0.09</td>
<td></td>
</tr>
<tr>
<td>1997 y/year</td>
<td>0.03</td>
<td>0.27</td>
<td>10</td>
<td>0.63</td>
<td>0.11</td>
<td>0.07</td>
<td>0.39</td>
<td>0.09</td>
<td></td>
</tr>
<tr>
<td>1997 y/year</td>
<td>0.02</td>
<td>0.26</td>
<td>10</td>
<td>0.63</td>
<td>0.11</td>
<td>0.07</td>
<td>0.39</td>
<td>0.09</td>
<td></td>
</tr>
<tr>
<td>1997 y/year</td>
<td>0.01</td>
<td>0.25</td>
<td>10</td>
<td>0.63</td>
<td>0.11</td>
<td>0.07</td>
<td>0.39</td>
<td>0.09</td>
<td></td>
</tr>
<tr>
<td>1997 y/year</td>
<td>0.00</td>
<td>0.24</td>
<td>10</td>
<td>0.63</td>
<td>0.11</td>
<td>0.07</td>
<td>0.39</td>
<td>0.09</td>
<td></td>
</tr>
</tbody>
</table>

Notes: \( \Delta AIC \) is the difference in AIC values between each model and the low-AIC model; \( w \) is the AIC model weight; and \( K \) is the number of parameters in the model. Model-averaged estimates of detection probability are \( \bar{p}_{det} \) and \( \bar{p}_{est} \). The AIC model with \( \bar{p}_{det} = 0.63 \), \( \bar{p}_{est} = 0.10 \), \( T = 5 \), and \( N = 10 \) was chosen such that the expected level of occupancy is reasonably high probability of detecting a breeding pair at a site during the survey (given presence, due to many repeat surveys per season), by not explicitly accounting for detectability we would have coalesced a higher turnover rate in territory use. This inference is consistent with the simulation results of Mollanen (2002).

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1. "Tiger salamanders.—Forty tiger salamanders were captured on two wetlands in southeastern Minnesota were surveyed for amphibian activity during spring and summer of 2000 and 2001. Dip net surveys were conducted at each visit for larvae and metamorphs of various amphibian species. Here we focus on detection/non-detection data for tiger salamanders, restricting our analysis to data collected from May until the end of the first week in August (as tiger salamander larvae and metamorphs may not be present outside this time frame, which would violate our within-season closure assumption). The 40 ponds were visited 5.0 times on average during 2000, and 30 of these ponds were visited with 3.0 visits on average per pond. Tiger salamanders were detected at 8 ponds in 2000 and 11 in 2001. Naive estimates of occupancy (Table 3) suggest an apparent estimate of 41%. We used model averaging to determine if the model of the model by rearranging Eq. 7 to directly estimate the occupancy probability in 2001, along with the probability of local extinction between 2000 and 1999. For the sake of simplicity we ignore some aspects of the sampling design and assume that detection probabilities are constant within each year. Full details of the study are available.

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2. The template file for this paper is available at the Ecology journal's website.
ing for the fact that probability of detection is <1, a considerably different conclusion is reached concerning the occupancy probabilities in the 2 years compared to the naïve estimates. This difference is largely accounted for by the fact that detection probabilities appear to be unequal in 2000 and 2001.

The third- and sixth-ranked models, with constant and site-specific colonization probability where no changes in the occupancy state of ponds occur between years. Colonization and local extinction probability are zero, and the proposed model reduces to the closed-population model of MacKenzie et al. (2002).

DISCUSSION

The detection and occupancy data to be collected in accordance with Pollock's (1982) robust design may seem restrictive to some. However, repeated surveys are required in order to estimate detection probabilities, which enable direct estimation of the other parameters. If all sites are surveyed once per primary period, then detection probability will be conditioned with the parameters of interest, resulting in estimates that are biased to an unknown degree and unknown direction. Although we have presented the concept of repeated surveys as discrete visits to the site, in practice they may constitute two or more independent surveys conducted during a single visit by one or multiple observers. Also, the repeated surveys may be restricted to a subsample of sites in order to collect sufficient information for estimating detection probabilities, which can then be applied to those sites only visited once.

We believe there is a great deal of flexibility in how the repeated surveys of sites may be carried out.

However, careful attention must be devoted to effects of the proposed study design on likely methods of analysis. If observers' abilities to detect the target species differ substantially and observers only survey a single site, a form of heterogeneity may be introduced that would bias parameter estimates. Where possible, observers should be randomly allocated to different sites on each survey occasion to minimize such an effect, or should be suitably trained to have similar detection abilities. Also, some study designs may restrict the types of models that may be considered. For instance, if a primary period a site is revisited after the species was first detected, then models involving survey-specific detection probabilities cannot be fit to the data and detection probabilities must be assumed constant within a primary period.

We foresee numerous applications of this modeling framework. Incidence function models frequently assume functional relationships between patch-specific extinction probabilities and patch characteristics (e.g., size and perhaps species abundance), and between patch-specific colonization rates and isolation (e.g., as a function of distance to other patches or to a source population; see Hanski 1994, 1997, Molainen 2002). In contrast, our models treat these relationships as hypotheses to be tested, enabling an objective evaluation of the strength of the relationships for extinction and colonization probabilities, without restrictive assumptions about process stationarity and perfect detection.

One may also formally compare various functional forms for extinction and colonization probabilities. For example, do the expressions for these quantities frequently used in metapopulation studies (e.g., Jolly and Dickson 1983, Pollock et al. 1990, Williams et al. 2002).

ACKNOWLEDGMENTS

This research was funded as part of the U.S. Geological Survey's Amphibian Research and Monitoring Initiative, Minnesota Fund, as recommended by the Legislative Commission on Minnesota Resources and the USGS Upper Midwest Ecological Collections.


