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IMPROVING INFERENCES IN POPULATION STUDIES OF RARE SPECIES THAT ARE DETECTED IMPERFECTLY

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Abstract. For the vast majority of cases, it is highly unlikely that all the individuals of a population will be encountered during a study. Furthermore, it is unlikely that a constant fraction of the population is encountered over times, locations, or species to be compared. Hence, simple counts usually will not be good indices of population size. We recommend that detection probabilities (the probability of including an individual in a count) be estimated and incorporated into inference procedures. However, most techniques for estimating detection probability require moderate sample sizes, which may not be achievable when studying rare species. In order to improve the reliability of inferences from studies of rare species, we suggest two general approaches that researchers may wish to consider that incorporate the concept of imperfect detectability: (1) borrowing information about detectability or the other quantities of interest from other times, places, or species; and (2) using state variables other than abundance (e.g., species richness and occupancy). We illustrate these suggestions with examples and discuss the relative benefits and drawbacks of each approach.

Key words: *abundance; detection probability; occupancy; rare species; species richness.*

INTRODUCTION

Estimation of abundance and related quantities for animal populations requires that investigators deal with two important sources of variation in resulting count data (Skalski and Robson 1992, Lancia et al. 1994, Thompson et al. 1998, Yoccoz et al. 2001, Pollock et al. 2002, Williams et al. 2002). The first source of variation involves spatial sampling. Investigators are frequently interested in inferences about areas so large that they cannot survey or count animals over the entire areas of interest. This problem requires that investigators select a sample of smaller areas on which to conduct survey efforts and that this selection be conducted in a manner that permits inference about the entire area of interest. That is, sample locations must be selected such that counts on these areas can be used to draw inferences about locations that do not appear in the sample (i.e., by using a probabilistic sampling scheme). This problem is not unique to the sampling of animal and plant populations, and ecologists and wildlife managers can use the various sampling designs developed by statisticians in other contexts (e.g., Cochran 1977, Thompson 1992).

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The second source of variation involves the issue of detectability and the fact that even when efforts are made to count animals on sample areas, it is extremely unlikely that the investigator will count every animal in any such area. Instead, the investigator obtains count statistics that represent unknown fractions of animals present in the sampled area. Count statistics, C, reflect the number of animals observed, captured, heard, harvested or otherwise detected by one or more survey methods used by animal ecologists. Count statistics are best viewed as random variables with expectation equal to the product of the true number of animals (N) present in the sample location and the detection probability (p) associated with the count:

$$E(C) = pN. \quad (1)$$

Inference about N requires inference about, or knowledge of, p. For example, estimation of abundance is accomplished by

$$\hat{N} = \frac{C}{\hat{p}} \quad (2)$$

where $\hat{p}$ is the estimated detection probability associated with the specific count statistic. We note that the seemingly diverse abundance and density estimation methods appearing in books such as Seber (1982) and Williams et al. (2002) represent different ways of es-

timating detection probability, but that the final step in abundance estimation involves Eq. 2.

We note that in addition to abundance, estimation of demographic rate parameters also requires consideration of detection probability. For example, reproductive rate is often estimated using age ratios, representing relative abundances of young to adult or young to adult females. If inferences about age ratios are based on raw counts, neglecting detection probabilities, then resulting ratios will reflect a confounded function of true relative abundances and relative detection probabilities (MacKenzie and Kendall 2002, Williams et al. 2002). Estimates of survival and movement probabilities are typically based on marked individuals released at one time and location and estimated to be alive at some later time in the same or a different location. If time- and location-specific detection probabilities are not incorporated into estimation models, then biased estimates of survival and movement can result (Williams et al. 2002).

Rarity will typically increase the difficulties in dealing with both spatial sampling and detectability in the estimation of abundance and related parameters. A species may be considered ''rare'' either because it occurs at very low densities across a broad range, or it could be locally abundant but not widely distributed across the landscape, with the consequence that the species may only occupy a small fraction of spatial sampling units (Gaston 1994). Rarity is also likely to be associated with low probabilities of detecting individuals even in sampling units that are occupied. When detection probabilities are known and not estimated then for a fixed count C, $\widehat{\text{var}}(\hat{N})$ will be larger when p is small (as $\widehat{\text{var}}(\hat{N}) = \widehat{\text{var}}(C)/p^2$; from Eq. 2). Furthermore, detection probability is seldom known, and most methods for estimating p use the count data themselves (e.g., Seber 1982, Williams et al. 2002). Small sample sizes tend to produce large $\widehat{\text{var}}(\hat{p})$ and, hence large $\widehat{\text{var}}(\hat{N})$. Thus, observation-based methods such as distance sampling, multiple-observers, time at detection or temporal removal, and marked subsamples, as well as capture-based methods such as capture–recapture, catch-effort, and change-in-ratio, all perform best with sample sizes that frequently exceed those that can be obtained for rare species (see Williams et al. 2002, and references therein, for details of these various techniques).

There may also be other more practical impediments to estimating abundance for rare species. In order to obtain an accurate count of the number of unique individuals, it must be possible to identify individual animals. Capture–recapture or resighting methods require that individuals detected during one sample period can be recognized as such if they are detected in a subsequent period. If animals can not be reliably identified using natural colorations or patternings, then some form of mark will need to be applied to the animal, which may require animals to be captured and handled. However many rare species are listed as a protected or endangered and in some instances there may be resistance (from a variety of quarters) to handling and marking animals if there is the potential for negative impact on the animals.

In this paper, we focus on the detectability issue and consider approaches to obtaining reliable inferences about animal populations and communities when dealing with rare species and with detection probabilities <1. We discuss two general approaches. First, we briefly present our views on the concept of borrowing information about detectability and relevant state variables from other times, places, and classes of animals (even species). The other approach involves consideration of state variables other than abundance to characterize status and changes in the population. We believe that both approaches hold promise for permitting reasonable inferences about populations and communities of rare species.

Borrowing Information

In some situations, it may be appropriate to share or borrow information about population parameters for rare species from multiple data sources. The general concept is that by combining the data, where appropriate, more precise estimates of the parameters may be obtained. We describe two situations that are distinguished by the similarity of the data being combined. In one situation, data of exactly the same type are aggregated over times, locations, individuals, or species. In the second situation, different kinds of data are combined to yield inferences about a common parameter(s).

The first situation is exemplified by capture–recapture modeling, where it has become common to consider aggregation of capture history data over times, places and individuals (e.g., Seber 1982, Lebreton et al. 1992, Williams et al. 2002). The decision about the appropriate level of aggregation is considered as a problem in model selection, where the task is to select a level that describes the data reasonably well, with the smallest number of parameters and greatest degree of aggregation (Burnham and Anderson 2002). The data are considered jointly, and the model set includes general models with separate parameters for different times and locations, for example, and reduced parameter models in which parameters are constrained to be equal over times and/or locations. The competing models thus represent different levels of aggregation and different degrees to which data are shared. We note that there are other approaches to aggregation than the described approach of equating model parameters (assuming homogeneity) over times, places, and individuals. For example, modeling parameters as function of covariates represents a form of aggregation in which a common relationship (over times, places, individuals, etc.) is assumed between a covariate and the parameter of interest (for closed capture–recapture models, see Pollock et al. [1984], Huggins [1989, 1991], Alho [1990]). Another approach is to assume a distributional

form for variation in a parameter of interest over individuals, for example, and then use a hierarchical modeling approach to estimate parameters of that distribution for an aggregation of individuals (e.g., Dorazio and Royle 2003). Both covariate modeling and hierarchical modeling assume some common form or relationship for the variation in a parameter over individuals, or times, or places, and the task is then to estimate the parameters that describe that form or relationship. As for the case of equality constraints on parameters, model selection approaches are needed to ascertain the appropriateness of different distributions or relationships linking the different data sets.

This general approach to sharing information is relatively common and was used by Boyce et al. (2001) to estimate the number of female grizzly bears (*Ursus arctos*) with cubs-of-the-year in the Yellowstone ecosystem. Capture frequency data from 1986–1998 were fit to truncated negative binomial distributions with various assumptions about constancy of parameters over time. Model selection results favored a model with a heterogeneity in ''sightability'' parameter constant over time, so that information across years was borrowed to yield realistic, annual estimates of abundance. Franklin et al. (2004) conducted capture–recapture studies of California Spotted Owls (*Strix occidentalis occidentalis*) at four sites in the Sierra Nevada mountain range. They conducted a meta-analysis in which they investigated the plausibility of additive location + time models for rate of population increase. The a priori hypothesis was that the different sites might experience different average rates of population increase, but that the sites were exposed to similar environmental conditions and should thus exhibit parallel changes in population size. Indeed, a model with additive location + time effects was appropriate for the data, leading to the interesting biological inference about similar environmental effects and also permitting more precise estimation of rate of population increase than was possible for any single location.

A form of aggregation that is not used very commonly by ecologists involves sharing information across species. For example, Nichols et al. (2000) used double-observer models to estimate detection probability and abundance from avian point count data. They grouped species a priori based on hypothesized similarity of detection probabilities. These models appeared to work well and were used to estimate abundance for relatively rare species for which data were inadequate to compute species-specific estimates of detection probability. M. W. Alldredge, K. H. Pollock, T. R. Simons, and S. A. Shriner (*unpublished manuscript*) have greatly expanded on this idea and have developed sets of models for avian point count data that incorporate various assumptions about similarity of species groups identified *a priori*. They present a unified model selection framework similar to that now used for aggregating over time and space. We believe that this approach of borrowing information from species believed to exhibit similarities in detection or population dynamics will prove to be very useful for rare species.

The second situation in which information is borrowed uses different types of data within a modeling framework that contains shared parameters. Dixon et al. (2005) use such an approach to improve estimates of capture efficiency of wasps by the insectivorous pitcher plant, *Darlingtonia californica*. They had two forms of available data, both of which contained some information about the capture rate of wasps by the pitcher plant. One data set permitted direct estimation of capture efficiency, whereas the other permitted estimation of a function of capture efficiency and visitation rate. Combination of the two data sets permitted use of the information about capture efficiency encoded in the second data set, and thus resulted in more precise estimates. Other examples of this type of approach to borrowing information include recent work on integrating animal count data with capture-recapture data (Besbeas et al. 2002, 2003). Information about survival rate comes from the data on marked animals, whereas information about population growth rate comes from the count data. Population growth rate can also be computed using survival and reproductive rates with a simple population projection model. Thus an integrated estimation approach incorporating the two data types with a population model permits estimation of reproductive rate in addition to population growth and survival (Besbeas et al. 2002, 2003). We expect such efforts to combine data from multiple sources to become more common in the near future (see Schnute 1994, Gallucci et al. 1996, Quinn and Deriso 1999, Elliott and Little 2000, Millar and Meyer 2000, Trenkel et al. 2000, Grove et al. 2002, White and Lubow 2002).

State Variables Other Than Abundance

As indicated above, despite the large number of potential methods for estimating detection probability of individual animals, and hence their abundance and density, rarity will typically translate into small sample sizes and imprecise estimates of relevant parameters. One approach to sample size problems using existing methods is to increase sampling effort. This approach usually increases expenses but is sometimes feasible nonetheless. As another approach, we suggest that, in many cases, it may be appropriate to consider alternative state variables: (1) the number of species present within the area (species richness; perhaps within some taxonomic or other group of interest), or (2) the proportion of the area occupied by a single species (occupancy). As with abundance, we believe that these are relevant state variables that provide important information about systems of ecological and conservation interest. For example, species richness conveys information about community structure and biodiversity, while occupancy provides information about species range, likelihood of extinction (e.g., Lande 1988),

metapopulation dynamics (e.g., Hanski 1999), and abundance. In addition, vital rates associated with dynamics of these state variables can be identified and estimated. The sampling effort required to estimate these two variables and their associated vital rates will typically be smaller (often substantially so) than that required to estimate abundance and rates of birth, death, and movement. Below we expand upon these concepts, provide a brief overview of potential analytical methods and give examples where these alternative state variables have been used in practice.

Species richness

Species richness (the number of species inhabiting a predefined area) is a state variable representing an alternative to abundance that may be useful in studies of groups of rare species. This state variable is aimed more at the community level than at a single species, and is widely used in ecological investigations and in conservation initiatives (e.g., Barbault and Hochberg 1992, Scott et al. 1993, Mangel et al. 1996, Boulinier et al. 1998, 2001, Cam et al. 2002, Doherty et al. 2003*a*, *b*). As in most cases in animal sampling, it is unlikely that all species at a sampling location will be observed. Even if the investigator is simply interested in relative species richness (e.g., computed as the ratio of richness at points in time and/or space), it is unlikely that raw species counts will be useful, as the fraction of any species pool that is observed will likely vary according to such factors as habitat and differences in the local species composition. The problem is then how to estimate species richness in the face of imperfect detectability. Although the bulk of the work on this topic has been relatively recent, the estimation of species richness has been considered many times over the last decade, including reviews by Bunge and Fitzpatrick (1993), Colwell and Coddington (1994), Nichols and Conroy (1996), Williams et al. (2002), and new synthetic contributions by Dorazio and Royle (2005) and Mao and Colwell (2005). Therefore, here we simply provide a brief overview of the various sampling situations that permit estimation of species richness, with reference to key publications that can be sought for further details of the particular methods. We also note that the concept of estimating species richness could be considered as a form of borrowing information: inferences about rare and infrequently encountered species are made by borrowing information about detectability from the other species in the community.

One sampling approach is where a single (or small number) of locations are surveyed multiple times within a relatively short time period. At each survey a list is maintained of the species detected, hence at the conclusion of the sampling it is possible to construct a ''capture history'' for each species, denoting whether the species was detected within each survey. The sampling should be conducted over a reasonably short time period to avoid any potential change in species composition, i.e., the community is assumed to be closed to any species additions or deletions. A species is considered to be analogous to an individual in a single-species, closed population capture–recapture study. Based upon the detection histories of species detected at least once, the number of species that were never detected can be estimated, i.e., an estimate of the total number of species at that location can be obtained. There is a wide range of capture–recapture models that could be used (e.g., Otis et al. 1978, Williams et al. 2002), although generally we would suggest that models permitting heterogeneous detection probabilities will be needed because of the variation in abundances and individual detection probabilities associated with different species.

Another sampling approach involves geographic replication rather than temporal replication. An area of interest is defined, and interest is focused on the community of species (perhaps of a certain taxon or functional guild) associated with that area. Sample locations are randomly selected from the area of interest, and the investigator surveys each such location only once. A capture history for each species can then be formed by denoting whether the species was encountered at each location, and species richness can be estimated as above. The key difference between the two sampling approaches is that one uses temporal replication of surveys, while the other uses spatial replication. Naturally this has some influence on how the results are interpreted, but the mechanics of the estimation procedure are identical.

A third general design is one where the investigator has both temporal and spatial replication. The usual approach to estimation with such data involves two steps. Species richness is estimated for each sampling site using the temporal replication, and then means and other summary statistics are computed for all sites within strata of interest. However, a more integrated approach is to consider prior distributions of individuals and species over space and to estimate parameters of this spatial distribution (see Dorazio and Royle 2005).

A final sampling design for richness estimation involves the so-called empirical species abundance distribution. Sampling is conducted at a single location during a single short time interval so there is neither temporal nor geographic replication. However, the investigator now records the number of individuals for each detected species. So the data used for estimation are the so-called detection frequencies, f_i, indicating the number of species for which exactly one individual was detected (f_1), exactly two individuals (f_2), etc. These data can then be used with a limiting form of the jackknife estimator developed by Burnham and Overton (1979), or other appropriate methods (e.g., Norris and Pollock 1998, or see Bunge and Fitzpatrick 1993).

The previously cited reviews deal almost exclusively with estimation of species richness, itself, and there

has been much less attention devoted to estimation of the vital rates influencing this state variable. Initial approaches to estimate local species extinction probability, number of local colonizing species, colonization rate, and species turnover have been developed by Nichols et al. (1998*a*, *b*; also see Williams et al. 2002). These methods have been used to draw inferences about community dynamics of forest birds exposed to forest fragmentation (Boulinier 1998, 2001), avian community dynamics at the edge and center of species ranges (Doherty et al. 2003*b*), and the relationship between avian community dynamics and sexual dichromatism (Doherty et al. 2003*a*). These analyses are especially relevant to the issue of rare species, as many of the species included in these different analyses were characterized by data that would have been inadequate for single-species inferences.

Finally, we note that an interesting quantity in some community studies is the fraction of the members of some identified species pool that are present in a specific community or location of interest. This problem was considered by Cam et al. (2000; also see Nichols 1998*b*, Chao et al. 2000). Here, we note that there are similarities between this problem and the estimation of the occupancy state variable discussed below, where the intent is to estimate the fraction of sites at which a species is present. By considering each species in the pool (or each species on any a priori reference list) as a ''site,'' the mechanics of the two problems are identical: the nondetection in the sampled community of a species on the list does not imply that the species was absent. Thus, we believe that some of the occupancy estimation and modeling described below (e.g., MacKenzie et al. 2002, 2003, Royle and Nichols 2003) may prove useful in community studies as well.

Occupancy

Occupancy has been used as an alternative state variable to abundance for many inferential purposes ranging from questions about habitat selection (e.g., Reunanen et al. 2002, Scott et al. 2002, Bradford et al. 2003) to questions about population dynamics and distribution (e.g., Hames et al. 2001, Barbraud et al. 2003, Martinez-Solano et al. 2003). Occupancy data are recognized to be especially useful for the study of rare species, although the historical emphasis for such species has been on use of occupancy as an index to abundance, rather than on occupancy as a state variable of interest in its own right (e.g., Diefenbach et al. 1994). When occupancy is viewed as the state variable of interest, focus shifts from ''how many individuals of the species are located at various locations across the landscape?'' to ''what fraction of the landscape does the species inhabit?'' For most species, the two questions should be closely related, as occupancy is simply the proportion of the landscape for which the local abundance distribution for the species of interest is >0. For territorial species, the number of individuals within an area will frequently be directly proportional to the fraction of the area occupied by the species. However, in other situations changes in abundance do not always result in a change in occupancy or species range (i.e., there is only a change in the density of the species). In such instances, occupancy may not be a useful surrogate state variable for abundance. However, we note that for questions dealing with topics such as metapopulation ecology (e.g., Hanski 1999) or geographic range (Brown 1995, Wikle 2003), occupancy is the state variable of primary interest regardless of the relationship between occupancy and abundance.

Occupancy is usually measured as the proportion of the area of interest where the species is present during the sampling. We use the term ''area'' in the sense of a statistical population, namely a collection of all the possible sampling units that we wish to make inference about. The sampling units themselves may represent naturally occurring discrete habitat patches (e.g., remnant patches of forest, islands, or ponds), or arbitrarily defined quadrats (henceforth we shall generically refer to sampling units as sites). The intent is to then survey a fraction of the total area (using an appropriate statistical method for selecting which sites to survey) and determine the presence or absence of the species at each site. However for most species, the investigator can never confirm species absence. There will generally be a non-negligible chance that the species was actually present, but due to chance, was undetected by the survey techniques. This issue of imperfect detectability (as in the case of abundance estimation) must be accounted for if robust inferences about occupancy are to be made. Comparisons of uncorrected, or naïve, estimates of occupancy can be strongly influenced by changes in species detectability, possibly leading to incorrect inferences about changes in occupancy. An observed difference between two naïve occupancy estimates may be due to differences in our ability to detect the species at the two times or places, rather than to a true difference in occupancy. In fact, Moilanen (2002) recently investigated the effect of various assumption violations with respect to metapopulation incidence functions (Hanski 1992, 1999) and found that changes in species detectability were the greatest contributor of bias to the estimated functions.

This issue of imperfect detectability has long been recognized. In an effort to minimize the probability of declaring the species falsely absent, many studies and monitoring programs for rare species conduct repeated surveys of sites over a reasonable timeframe, during which no changes in the occupancy states of sties are thought to occur. With this type of information (repeated surveys) it is possible to account for detection probabilities and obtain corrected, or unbiased, estimates of occupancy.

The development of analytical methods for estimating occupancy at a single point in time has been sporadic over the last 20 years (Geissler and Fuller 1987,

Azuma et al. 1990), but more recently there have been a number of similar methods published (MacKenzie et al. 2002, Royle and Nichols 2003, Tyre et al. 2003, Stauffer et al. 2004, Wintle et al. 2004). Here, we shall briefly review the method presented by MacKenzie et al. (2002), of which Stauffer et al. (2004), Tyre et al. (2003) and Wintle et al. (2004) could be considered special cases. Royle and Nichols (2003) have developed a useful extension that allows for heterogeneity in detection probability between sites caused by differences in local abundance.

Despite this interest in occupancy estimation, until recently, few methods have been developed for estimating changes in occupancy, and the vital rates (local probabilities of extinction and colonization) that produce such changes, that explicitly account for imperfect detectability. Often in metapopulation studies, changes caused by local extinctions and colonizations of patches by the target species are of primary interest (e.g., Hanski 1992, 1999). Only recently has any attempt been made to allow for the possibility of false absences (Moilanen 2002), with arguable success. As noted above, Moilanen (2002) found that issues related to species detectability were the major contributor to bias in estimated incidence functions. Two recent papers (Barbraud et al. 2003, MacKenzie et al. 2003) use similar approaches to estimate local extinction and colonization probabilities directly, whilst allowing for imperfect detection. Given that the data have been collected from monitoring sites over several seasons or years, and within each season sites are surveyed more than once, probabilistic arguments are applied to form a model likelihood that can be used to obtain parameter estimates. The main difference between the two methods is that the approach of Barbraud et al. (2003) is conditional upon the first occasion at which the target species is detected at a site, whereas the approach of MacKenzie et al. (2003) is unconditional, allowing the proportion of sites occupied by the species each season to be estimated.

A general sampling scheme

From the area of interest, U sites are selected to be surveyed for the species using appropriate methods. These sites are surveyed multiple times each season for T seasons (e.g., years). In each survey, detections are regarded as truth (the species is never falsely recorded as being present), but nondetections are recognized as arising from both (1) true absence and (2) presence with nondetection (sometimes referred to as false absences). Within a season, sites are closed to changes in occupancy (i.e., sites are either always occupied or unoccupied by the species). This assumption may be relaxed provided that any changes occur completely at random in which case ''occupancy'' should be interpreted as ''use.'' Sites are repeatedly surveyed (possibly an unequal number of times), with the species either being detected or not detected. Between seasons, changes in occupancy may occur which are referred to as the processes of colonization and local extinction.

The sequence of detections and nondetections recorded at the sites form a detection history ($\mathbf{H}_i$ for site i). For example $\mathbf{H}_i = 101\,000$ represents data collected over two seasons, each with three surveys per season. In the first season, the species was detected in the first and third survey, but undetected in the second. In the second season, the species was never detected at the site during the surveys. The basic procedure for building a model is to develop a verbal description of the observed data, then translate that description into a mathematical equation representing the probability of observing the data using the defined model parameters.

A single season model

MacKenzie et al. (2002) define ψ as the probability that a site is occupied by the species, and p_j is the probability of detecting the species (given presence) during the jth independent survey of a site. To illustrate model construction, consider the detection history 1001. A verbal description of this history would be that the species is present (as it was detected at least once), and it was then detected in the first and fourth surveys of the site, but not in surveys two and three. Translating this into a mathematical equation using the model parameters, the probability of observing this history could be expressed as

$$\Pr(\mathbf{H}_i = 1001) = \psi p_1(1 - p_2)(1 - p_3)p_4.$$

A similar expression can be obtained for detection histories from all sites at which the species is detected at least once. However, for sites where the species was never detected (e.g., $\mathbf{H}_i = 0000$), there are two possibilities that must be accounted for. The verbal description for this history would be, either the species was present but went undetected in the surveys (which has a probability of $\psi \prod_{j=1}^{4} (1 - p_j)$), or the species was genuinely absent from the site (with probability $(1 - \psi)$). As either reason for never detecting the species at the site is possible, the probability of observing this history is the sum of these two components, i.e.,

$$\Pr(\mathbf{H}_i = 0000) = \psi \prod_{j=1}^{4} (1 - p_j) + (1 - \psi).$$

Assuming that the detection histories for all sites are independent, the likelihood function for an estimation model takes the usual form:

$$L(\psi, p \,|\, \mathbf{H}_1, \ldots, \mathbf{H}_U) = \prod_{i=1}^{U} \Pr(\mathbf{H}_i).$$

Note that this requires both the probability of occupancy and each detection probability to be constant across all U sites. If this not the case, then the probabilities are said to be heterogeneous. While it is not possible to estimate site-specific occupancy probabil-

ities, the probabilities may be modeled as a function of measured covariates using the logistic equation

$$\theta_i = \frac{\exp(\mathbf{X}_i\boldsymbol{\beta})}{1 + \exp(\mathbf{X}_i\boldsymbol{\beta})}$$

where θ_i is the probability of interest for site i, $\mathbf{X}_i$ is the row vector of covariate information for site i and $\boldsymbol{\beta}$ is the column vector of coefficients to be estimated. In general, occupancy may be a function of site-specific covariates that are constant throughout the season (e.g., habitat type), while detection probabilities may also be a function of covariates that change through the season (e.g., weather conditions).

However one potential source of heterogeneity that cannot be easily accommodated directly by a covariate is heterogeneity in detection probabilities caused by differences in the species abundance between sites. Royle and Nichols (2003) extend the above approach by arguing that the species is not detected only if none of the N_i individuals at site i are detected. This suggests the probability of detection can be written as a function of abundance, i.e., $p_{ij} = 1 - (1 - r_j)^{N_i}$, where r_i is the probability of detecting an individual of the species in the jth survey. As the N_i are unknown, this approach requires that a distribution for how N_i varies across sites be specified. Estimation under this model permits estimation of occupancy in the face of abundance-related heterogeneity.

An additional comment on the method for estimating occupancy detailed by MacKenzie et al. (2002) is that an equal number of surveys across all sites is not required. By having the ability to deal with ''missing observations,'' MacKenzie et al. (2002) developed a very flexible method that could be used to analyze data from a number of different designs that could be used in practice (e.g., repeatedly surveying only a subset of all sites or surveying only until the species is first detected). Finally, we note that recent work on single-season occupancy modeling includes development of a goodness-of-fit test for the above model (MacKenzie and Bailey 2004) and an approach for modeling and estimating possible dependencies in occupancy patterns (and detection probabilities) of multiple species (MacKenzie et al. 2004).

A multiple season model

MacKenzie et al. (2003) extended the single season model of MacKenzie et al. (2002) to multiple seasons by introducing two parameters that govern changes in the occupancy state of sites over time. These parameters can be viewed as the vital rates associated with occupancy dynamics. Let ε_t be the probability that a site occupied in season t is unoccupied by the species in season $t + 1$ (local extinction), and γ_t be the probability that an unoccupied site in season t is occupied by the species in season $t + 1$ (colonization). Therefore, a matrix of the probability of a site transitioning between occupancy states between seasons may be defined as;

$$\boldsymbol{\phi}_t = \begin{bmatrix} 1 - \varepsilon_t & \varepsilon_t \\ \gamma_t & 1 - \gamma_t \end{bmatrix},$$

where rows of $\boldsymbol{\phi}_t$ represent the occupancy state of the site at t (state 1 = occupied; state 2 = unoccupied), and columns represent the occupancy state at $t + 1$. For completeness, a row vector $\boldsymbol{\phi}_0$ may be defined as $\boldsymbol{\phi}_0 = [\psi_1 \quad 1 - \psi_1]$, where ψ_1 is the probability the site is occupied in the first season ($t = 1$).

To incorporate detection probabilities into the model, define a column vector $\mathbf{p}_{\mathbf{H},t}$ that denotes the probability of observing the portion of the detection history $\mathbf{H}_i$ relevant to season t, conditional upon occupancy state. For instance

$$\mathbf{p}_{101,t} = \begin{bmatrix} p_{t,1}(1 - p_{t,2})p_{t,3} \\ 0 \end{bmatrix}$$

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

where $p_{t,j}$ denotes the detection probability for visit j in season t. Note that whenever the species is detected at least once during a season, the second element of $\mathbf{p}_{\mathbf{H},t}$ will be zero because it is impossible to observe such a history if the site is in the unoccupied state. Similarly, the second element of $\mathbf{p}_{\mathbf{0},t}$ will always be 1, because the all zero history is the only observable outcome if the site is unoccupied.

For any given detection history, the probability of observing such an outcome can be expressed as, $\Pr(\mathbf{H}_i) = \boldsymbol{\phi}_0 \prod_{t=1}^{k-1} [D(\mathbf{p}_{\mathbf{H},t})\ \boldsymbol{\phi}_t]\ \mathbf{p}_{\mathbf{H},K}$, where $D(\mathbf{p}_{\mathbf{H},t})$ is a 2×2 diagonal matrix with the elements of $\mathbf{p}_{\mathbf{H},t}$ along the main diagonal (top left to bottom right), zero otherwise. For example, consider again the detection history $\mathbf{H}_i$ = 110 000 010. The probability of observing this would be

$$\begin{aligned}
&\Pr(\mathbf{H}_i = 110\ 000\ 010) \\
&\quad = \boldsymbol{\phi}_0 D(\mathbf{p}_{110,1})\boldsymbol{\phi}_1 D(\mathbf{p}_{000,2})\boldsymbol{\phi}_2 \mathbf{p}_{010,3} \\
&\quad = [\psi_1 \quad 1 - \psi_1] \begin{bmatrix} p_{1,1}p_{1,2}(1 - p_{1,3}) & 0 \\ 0 & 0 \end{bmatrix} \\
&\qquad \times \begin{bmatrix} 1 - \varepsilon_1 & \varepsilon_1 \\ \gamma_1 & 1 - \gamma_1 \end{bmatrix} \begin{bmatrix} \prod_{j=1}^{3} (1 - p_{2,j}) & 0 \\ 0 & 1 \end{bmatrix} \\
&\qquad \times \begin{bmatrix} 1 - \varepsilon_2 & \varepsilon_2 \\ \gamma_2 & 1 - \gamma_2 \end{bmatrix} \begin{bmatrix} (1 - p_{3,1})p_{3,2}(1 - p_{3,3}) \\ 0 \end{bmatrix} \\
&\quad = \psi_1 p_{1,1} p_{1,2}(1 - p_{1,3}) \\
&\qquad \times \left[(1 - \varepsilon_1) \prod_{j=1}^{3} (1 - p_{2,j})(1 - \varepsilon_2) + \varepsilon_1\gamma_2 \right] \\
&\qquad \times (1 - p_{3,1})p_{3,2}(1 - p_{3,3}).
\end{aligned}$$

The central term in brackets on the final line represents the two possibilities for the species during the second season when it was not detected. Either the species (1) did not go locally extinct between seasons 1 and 2, was undetected in the three surveys during the second season, and continued to occupy the site into season three (with probability $(1 - \varepsilon_1)\ \Pi_{j=1}^{3}\ (1 - p_{2,j})\ (1 - \varepsilon_2)$); or (2) went locally extinct between seasons 1 and 2, and recolonized the site between seasons 2 and 3 (with probability $\varepsilon_1\gamma_2$).

Once the probability of observing each detection history has been established, the model likelihood can be formed as usual, i.e.,

$$L(\psi_1, \varepsilon, \gamma, \mathbf{p} \mid \mathbf{H}_1, \ldots, \mathbf{H}_U) = \prod_{i=1}^{U} \Pr(\mathbf{H}_i).$$

MacKenzie et al. (2003) describe how missing observations and covariate information can be included in the model, and also how the model can be reparameterized to get seasonal estimates of occupancy or estimates of the rate in change of occupancy.

EXAMPLES

To illustrate how the above occupancy estimation methods could be used in practice with respect to rare species, we now consider data collected for the following three species: (1) Mahoenui giant weta (*Deinacrida mahoenui*) from New Zealand, (2) gaur (*Bos frontalis*) from Malaysa, and (3) Blue-ridge salamander (*Eurycea wilderae*) from the eastern United States. Each example is used to demonstrate some aspects of the methods we describe above: single-season occupancy estimation, occupancy at multiple study areas with the concept of borrowing information, and multiple-season occupancy estimation. For brevity, only relatively simple analyses are presented here, but note that more complex analyses could be conducted to further investigate relationships between occupancy (and related parameters) and covariates that have been collected in the field. All analyses have been conducted using Program PRESENCE (*available online*).[7]

Mahoenui giant weta

Weta are one of the more unique and specialized groups of New Zealand insects. More than 70 endemic species of weta survive in New Zealand today. Weta are ancient species of the order Orthoptera (e.g., grasshoppers, crickets, and locusts) and remain almost unchanged from their ancestors of 190 million years ago. All weta are flightless and relatively large, and members of a subgroup called the giant weta are among the largest insects in the world. Most giant weta species are now endangered, with populations having been decimated by the introduction of mammalian predators. Currently, most species only survive on predator-free offshore islands or in protected reserves.

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

The Mahoenui giant weta (*Deinacrida mahoenui*) is endemic to the King Country on the North Island of New Zealand. The main naturally occurring population is restricted to a 240-ha block of reverting farmland at Mahoenui (near the town of Te Kuiti), which is designated as a scientific reserve, with a second population near Otangiwai 20 km to the east. The reserve is characterized by steep-sided gullies and is largely covered by dense gorse, *Ulex europaeus*, a perennial pest plant with sharp spiny stems and bright yellow flowers that can form dense thickets, originally introduced to New Zealand as a hedging plant by the early European settlers. The New Zealand Department of Conservation (DOC) uses goats and cattle to maintain the gorse habitat through browsing. Mahoenui giant weta use gorse as protection from predators and also as a food source.

In order to monitor the population, in March 2004 DOC began a pilot study to assess the effectiveness of using occupancy as the state variable of interest. While ideally DOC would like to monitor abundance of the species, the main impediments are (1) the weta only occur at low densities, hence few individuals are likely to be observed in any given survey; (2) they are not individually identifiable by natural markings; and (3) the weta are usually found in the brittle, dead foliage of a gorse bush, hence attempts to capture and mark them would likely destroy their apparently preferred habitat. Thus the decision was made to try occupancy rather than use unadjusted transect counts as had been done previously.

Between 23 and 27 March 2004, 72 circular plots of 3 m radius where surveyed for the Mahoenui giant weta. The plots were randomly positioned within the more accessible regions of the reserve. This means some caution must be used if the results are generalized to the entire reserve, but restricting the sample frame was determined to be reasonable given it was a pilot study. Each plot was surveyed between three and five times during the 5-d period. Three different surveyors were used and the study was designed such that each surveyor surveyed each site at least once. This allows surveyor-specific detection probabilities to be estimated.

Weta were detected at 35 of the 72 plots (a naïve occupancy estimate of 0.49), however often weta were only detected in one or two of the repeated surveys clearly indicating that detection probabilities are <1. Conceivably, there may be a number of plots where weta were indeed present but were simply never detected during the surveys. Here we use the single-season occupancy model described above to estimate the proportion of plots that may be occupied. We consider four simple models. In each case occupancy probability is assumed to be constant for all plots (denoted as $\psi(\cdot)$), and detection probability was either constant ($p(\cdot)$), different on each day ($p(t)$), varied by surveyor ($p(S)$) or varied by both day and surveyor ($p(t + S)$).

TABLE 1. Summary of models fit to Mahoenui giant weta example.

Model	AIC	ΔAIC	$\hat{\psi}$	SE($\hat{\psi}$)
$\psi(\cdot)p(t + S)$	258.55	0.00	0.64	0.09
$\psi(\cdot)p(t)$	260.80	2.25	0.63	0.09
$\psi(\cdot)p(S)$	263.36	4.81	0.62	0.09
$\psi(\cdot)p(\cdot)$	265.79	7.24	0.62	0.09

Notes: Models are ranked in terms of Akiake's Information Criterion (AIC). The relative difference in values (ΔAIC), estimates of occupancy ($\hat{\psi}$), and its standard error (SE($\hat{\psi}$)) are also given.

The four models are ranked for parsimony in terms of Akiake's Information Criterion (AIC; Burnham and Anderson 2002), with the results summarized in Table 1. In this instance, regardless of the structure used to model detection probability, estimates of occupancy (and its associated standard error) are similar, approximately 30% greater than the naïve estimate. This result is partially due to the design of the study so will not always be the case. There is some evidence that the surveyors differed in their ability to detect weta. If surveyors always sampled the same sites, a form of heterogeneity in detection probability would be introduced, resulting in underestimates of occupancy if not accounted for (Royle and Nichols 2003).

Malaysian gaur

The gaur (*Bos frontalis*) is a large (up to 1000 kg) Asian bovid found in scattered areas of suitable habitat (forests and associated grassy clearings) extending from India and Nepal eastward to Indochina and the Malaysian peninsula. The species is believed to have declined dramatically over the past several decades. It is classified as vulnerable by IUCN, as endangered by the U.S. Department of Interior, and is listed on appendix 1 of CITES (Nowak and Paradiso 1983).

Kawanishi studied tigers (*Panthera tigris*) and potential prey species in three extensive study areas within Taman Negara National Park in Peninsular Malaysia (Kawanishi and Sunquist 2004). A grid with nine 5 × 5 km cells was superimposed on each of the three study areas for the purpose of estimating occupancy by gaur. Each grid cell was sampled monthly for 5 mo using camera traps and ground surveys for animal sign. Virtually all travel was on foot, so the three areas were sampled sequentially over the period 1999–2001.

Gaur were detected in six, five, and one of the grid cells in each of the study areas, leading to naïve occupancy estimates of 0.67, 0.55, and 0.11 respectively. Applying a constant detection single-season occupancy model to the data from each study area separately, we obtain occupancy estimates of 0.86 and 0.60 for the two areas with adequate data. Only one gaur was detected at a single site in the third data set, leaving us uncomfortable with attempting to estimate occupancy separately for this area. In order to improve the estimates of occupancy and obtain some inference about the third study area, here we model the data from the three study areas within a single framework by sharing information about the probability of detecting gaur among the areas. We consider two models for these data: (1) detection probability is the same at all sites, or (2) detection probability at the third area is the average (on the logistic scale) of the other two areas. Note that a third model in which detection probabilities are different at each site is equivalent to fitting the occupancy model to each data set independently, which is the model that does not permit reasonable inference about the third area. For all models we wish to obtain area specific estimates of occupancy.

Table 2 presents a summary of the model selection procedure for each of these models. For the purpose of determining model weights and model averaged estimates of occupancy (Burnham and Anderson 2002), the third model has not been considered due to the concerns of estimator reliability. Note that the model averaged estimates of occupancy for study areas 1 and 2 are reasonably similar to those obtained when each data set is analyzed separately, however the estimate for area 3 appears much more realistic.

Blue-ridge salamander

The Blue-ridge salamander (*Eurycea wilderae*) is one of more than 75 salamander species found in the

TABLE 2. Summary of model selection procedure for the Malaysian gaur example.

			$\hat{\psi}$ (SE($\hat{\psi}$))		
Model	ΔAIC	*w*	Area 1	Area 2	Area 3
ψ(area)$p(\cdot)$	0.00	0.62	0.79 (0.20)	0.66 (0.21)	0.13 (0.13)
ψ(area)p(average)	1.00	0.38	0.90 (0.29)	0.61 (0.19)	0.13 (0.13)
ψ(area)p(area)	1.28		0.86 (0.26)	0.60 (0.18)	1.00 (0.00)
Model-averaged estimates			0.83 (0.24)	0.64 (0.20)	0.13 (0.13)

Notes: Models are ranked in terms of Akiake's Information Criterion (AIC). Presented here are the relative difference in values (ΔAIC), AIC model weights (*w*), estimates of occupancy ($\hat{\psi}$), and its associated standard error (SE($\hat{\psi}$), in parentheses) for each of the three study areas. Model-averaged estimates are based upon the first two models only.

TABLE 3. Parameter estimates and summary of model selection procedure according to AIC for the Blue-ridge salamander (*Eurycea wilderae*) example.

Model	ΔAIC	*w*	$\hat{\psi}_{98}$	$\hat{\gamma}_{98}$	$\hat{\gamma}_{99}$	$\hat{\gamma}_{00}$	$\hat{\varepsilon}_{98}$	$\hat{\varepsilon}_{99}$	$\hat{\varepsilon}_{00}$	$\hat{p}_{98}$	$\hat{p}_{99}$	$\hat{p}_{00}$	$\hat{p}_{01}$
$\psi(98)\gamma(\cdot)\varepsilon(\cdot)p$(yr)	0.00	0.68	0.87	0.16	0.16	0.16	0.22	0.22	0.22	0.52	0.41	0.28	0.28
$\psi(98)\gamma(\cdot)\varepsilon$(yr)$p$(yr)	2.95	0.16	0.87	0.17	0.17	0.17	0.24	0.26	0.06	0.52	0.41	0.29	0.26
$\psi(98)\gamma$(yr)$\varepsilon(\cdot)p$(yr)	3.75	0.10	0.85	0.32	0.16	0.13	0.22	0.22	0.22	0.54	0.41	0.28	0.28
$\psi(98)\gamma$(yr)ε(yr)p(yr)	6.70	0.02	0.84	0.33	0.17	0.14	0.24	0.25	0.06	0.54	0.41	0.29	0.26
$\psi(98)\gamma(\cdot)\varepsilon(\cdot)p(\cdot)$	6.98	0.02	0.94	0.17	0.17	0.17	0.27	0.27	0.27	0.38	0.38	0.38	0.38
$\psi(98)\gamma(\cdot)\varepsilon$(yr)$p(\cdot)$	10.18	0.00	0.93	0.19	0.19	0.19	0.26	0.35	0.21	0.39	0.39	0.39	0.39
$\psi(98)\gamma$(yr)$\varepsilon(\cdot)p(\cdot)$	10.51	0.00	0.94	0.00	0.12	0.21	0.27	0.27	0.27	0.38	0.38	0.38	0.38
$\psi(98)\gamma$(yr)ε(yr)$p(\cdot)$	13.59	0.00	0.94	0.00	0.13	0.23	0.25	0.36	0.21	0.39	0.39	0.39	0.39
Model averaged estimates			**0.87**	**0.18**	**0.16**	**0.16**	**0.22**	**0.23**	**0.19**	**0.52**	**0.41**	**0.29**	**0.28**
Standard errors			0.08	0.14	0.11	0.11	0.07	0.08	0.09	0.06	0.05	0.05	0.05
Naïve estimates			**0.76**	**0.44**	**0.21**	**0.27**	**0.28**	**0.44**	**0.29**	**1.00**	**1.00**	**1.00**	**1.00**

Note: ΔAIC is the relative difference in AIC values from the top ranked model; *w* is the AIC model weight. Bold values are referred to in the text. Subscripts in column heads represent years 1998–2001.

southeastern United States. *E. wilderae* has a dual life phase, with a larvae period lasting 1–2 years in the southern Appalachians (Bruce 1988). Usually considered a stream-side salamander, *E. wilderae* is believed to undergo seasonal migration away from streams during warmer months and can often be found far from running water (Petranka 1998). Because *E. wilderae* potentially uses both aquatic (stream) and terrestrial habitats, it was proposed as a management indicator species (MIS) for National Forests in North Carolina (FY2002 Monitoring and Evaluation Report: National Forests in North Carolina; *available online*).[8] Recently, many proposed amphibian and reptile species have been removed from MIS lists by the Forests Service because count-based statistics for these species show high temporal and spatial variability, thus making inferences about relationships between population and habitat changes unreliable and difficult. *E. wilderae* shares this characteristic and may be considered ''rare'' because it occurs at low densities in terrestrial habitats. For example, in a capture–recapture study in Great Smoky Mountains National Park (GSMNP), Bailey et al. (2004*a*) sampled 15 × 15 m forest plots 14–16 times each of three spring sampling seasons. *E. wilderae* was detected on more plots than any other salamander species (16 out of 20 plots), but the average number of captured individuals per sampling occasion was less than 1. Abundance estimates are impossible for *E. wilderae* without borrowing information from other species, times or locations (see Bailey et al. 2004*a*). Alternatively, occupancy has been proposed as a more appropriate state variable for large-scale salamander monitoring programs in the southeastern United States (Bailey et al. 2004*b*).

We used the multiple season model presented above to estimate occupancy dynamics (vital rates) for *E. wilderae* populations found within a single watershed within GSMNP. In 1998, Hyde and Simons (2001) initiated a salamander study within the Roaring Fork Watershed (Mt. LeConte USGS Quadrangle) and Bailey et al. (2004*b*) continued to sample a subset of 39 sites for a total of four years (1998–2001); only these 39 sites are used in this analysis. Each sample site was sampled with both a natural cover transect (50 m long × 3 m wide) and a parallel coverboard transect consisting of five stations placed 10 m apart (see Hyde and Simons [2001] for details). Sites were located near trails and spaced approximately 250 m apart, beginning at a random point at least 250 m from each trail head. Sites were sampled once per month in 1998 (June–August), then once every two weeks from early April to late June for the remaining three years of the study. Relative abundance information was collected on all salamander species, but we use only detection/nondetection information for *E. wilderae* in this analysis.

We used MacKenzie et al.'s (2003) initial parameterization to estimate initial occupancy (1998), vital rates (colonization and extinction), and detection probabilities. A number of covariates were measured at each site (e.g., elevation and stream proximity) but here we only consider a suite of simple models where vital rates and detection probabilities are year specific or constant across time. We expected yearly differences in all multi-season parameters as rainfall levels varied considerably among years, with total April–June precipitation declining over the last three years of the study. Again for brevity, we assume the probability of detecting *E. wilderae* in a single survey of a site was constant within each year.

Table 3 presents the parameter estimates and summary of the model selection procedure for the eight simple models considered. Note that the models with constant detection probability among years (which is an implicit assumption when comparing naïve counts) constitute <3% of the total AIC model weights. That is, from this analysis there is very strong support for the hypothesis that detection probabilities vary over time suggesting reliable conclusions about the population can only be made if these detection probabilities

[8] ⟨http://www.cs.unca.edu/nfsnc/me2002/fy2002_me_report.pdf⟩

differences are explicitly accounted for. Considering the model averaged estimates, the proportion of sites occupied by *E. wilderae* in 1998 was 0.87, the probability of a site being colonized between years is ≈0.16, and the probability of *E. wilderae* going local-extinct from a site was ≈0.20. By using the fact that sites occupied in the next year are a combination of occupied sites this year where the species did not go locally extinct, and unoccupied sites that the species colonizes (i.e., $\psi_{t+1} = \psi_t (1 - \varepsilon_t) + (1 - \psi_t)\gamma_t$), we can determine the proportion of sites occupied in years 1999–2001. Using the model averaged parameters estimates we obtain the values 0.70, 0.59, and 0.54 respectively, suggesting a downward trend in occupancy over this time frame for *E. wilderae* that is consistent with our a priori expectations based on seasonal rainfall records. It is worth noting that estimated vital rates are lower than naïve estimates, suggesting that some of the apparent turnover is likely the result of nondetection rather than true colonization and extinction events.

Discussion

It is particularly unfortunate that rare species are simultaneously the species for which strong inferences about state variables and vital rates are most needed and the species for which such information is most difficult to obtain. These dual concerns provide a formidable challenge to conservation biologists and wildlife biologists to obtain useful information on which to base management decisions in the face of substantial sampling difficulties. We are pleased at recent efforts to meet this challenge, including this Special Feature and the new edited volume by W. L. Thompson (2004).

We began this paper with a brief summary of statistical principles important in estimating abundance and related parameters of animal populations. The response of many biologists and managers to the poor sample sizes achieved in studies of rare species is to abandon these principles and simply base inference on raw count statistics. We do not believe that this response is satisfactory, so we discussed two general approaches to inference that we hope might be useful for rare species.

The borrowing of information is nothing new and indeed underlies all inferential statistics. Our suggestion is simply to extend the basic idea beyond the units of aggregation typically used in statistics (e.g., individuals, replicate locations) to possibly disparate times and locations, to different data sources, and even to different species. In the case of rare species, such aggregation may permit reasonable inference in situations where it would not be possible with more typical disaggregated treatments.

The use of state variables other than abundance is also not new. In particular, other investigators have used occupancy as a state variable of interest for rare species. However, until the last year or so, these past uses have ignored the issue of detection probability. We described a framework for drawing inferences about occupancy, changes in occupancy, and the vital rates responsible for such changes using models that properly incorporate detection probability. As illustrated by our examples, we believe that these methods hold great promise for use in studies of rare species.

In summary, we recognize that rare species present problems to biologists and managers who wish to study their populations. However, we do not believe that the appropriate response to such problems is to abandon reasonable inference methods. Instead, we recommend consideration of the methods provided in this Special Feature. In particular, we recommend consideration of borrowing information and using state variables such as occupancy as means of dealing with detection probability when studying rare species.

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