

WHAT ARE THE ISSUES WITH PRESENCE–ABSENCE DATA FOR WILDLIFE MANAGERS?

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Abstract: Presence–absence data can be useful to wildlife managers in a wide variety of contexts, from monitoring populations at large spatial scales to identifying habitats that are of high value to specific species of conservation concern. However, a key issue is that a species may be declared “absent” from a landscape unit simply as a result of not detecting the species using the prescribed sampling methods. The effect of this imperfect detection is that parameter estimates will be biased, and any modeling of the data provides a description of the surveyors’ ability to *find* the species on the landscape, not where the species *is* on the landscape. The reliability of so-called “presence–absence” data for making sound management decisions and valid scientific conclusions could therefore be questioned. However, after collecting appropriate data (i.e., repeated surveys of landscape units within a relatively short timeframe), recently developed statistical models can be used to obtain unbiased parameter estimates. Here I provide a nontechnical overview of the issues that pertain to wildlife studies or monitoring programs that seek to make reliable inference about the presence or absence of a target species.

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The presence or absence of a species from a collection of landscape units is a widely used concept by researchers and managers in wildlife-related disciplines. In a monitoring context, the proportion of monitoring sites (e.g., habitat patches or quadrats) within a region where the species is present can be used as a surrogate for population size or species abundance; this is particularly true at large scales, for cryptic, low-density and/or territorial species. The underlying logic is that changes in the proportion of occupied sites (i.e., places where the species is present) will be correlated with changes in the population size, provided sites are defined at an appropriate spatial scale (Zielinski and Stauffer 1996, Trenham et al. 2003, Weber et al. 2004, MacKenzie et al. 2005a). Habitat models and some resource selection probability functions relate presence–absence data to the habitat characteristics of study sites or resource units. Such techniques have been used to identify habitats that may be highly used by the target species, hence they should be of high conservation value and prioritized for protection by management (Manly et al. 2002, Tyre et al. 2003, Johnson et al. 2004, Ball et al. 2005). In many situations the species’ range or distribution may be of direct interest, particularly how the distribution changes

over time. For threatened and endangered species, interest is often directed at range contractions, while for invasive species, interest is in the rate of expansion (Brown et al. 1996, Ceballos and Ehrlich 2002, Wikle 2003). Metapopulation models and incidence functions have been used with presence–absence data to investigate sources of variation in species occupancy and to identify habitat patches with potentially high levels of persistence. As with habitat models, the identified patches may then be prioritized for protection from future development (Hanski 1999, Moilanen 2002). In some applications the “species” is not restricted to the vertebrate and invertebrate members of the animal kingdom, but it may be a disease (e.g., chronic wasting disease, West Nile virus) or presence of species malformations within a region (e.g., amphibian malformations).

While the presence of a target species can often be confirmed at a location, it is generally impossible to confirm species’ absence. An observed absence may simply be the result of the survey method failing to detect the presence of the species that is actually resident at the location (e.g., the species was currently elsewhere within its home range, or failed to call within a 5-min point count). This facet of so-called “presence–absence” data has long been recognized, and the use of terms such as “presence–not detected” has sometimes been used to acknowledge that a nondetection does

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not equate to species absence. However, the use of such a term confuses the biological and sampling processes. Presence–absence is the biological reality of whether the species is resident at a particular location, while detection–nondetection relates to the observed outcome of the sampling process. A more correct term for the data resulting from such surveys would be detection–nondetection, which I use throughout this paper.

The effect of ignoring imperfect detection is that estimates of occupancy and related parameters can be seriously biased, which results in misleading inferences about the system (Moilanen 2002, Tyre et al. 2003, Gu and Swihart 2004, MacKenzie 2006), which can lead to erroneous management decisions. Regardless of the level of complexity in a particular analytic technique, unless detection probability is specifically accounted for, results will pertain to a combination of biological and sampling processes. That is, results represent the surveyors' ability to *find* the species in the landscape, not where the species *is* in the landscape. From a management perspective, the latter is likely to be much more useful than the former.

To minimize the chance of obtaining a "false absence" (i.e., the species was present but undetected) one protocol is to conduct multiple surveys at a location within a relatively short timeframe. For instance, if the probability of detecting the species in a survey of an occupied location is 0.6, there is a 0.4 ($= 1 - 0.6$) probability of a false absence from a single survey (i.e., by not detecting the species). However if 2 surveys are conducted, then the probability of not detecting the species at either survey reduces to 0.16 ($= [1 - 0.6]^2$), and it reduces to 0.064 ($= [1 - 0.6]^3$) if 3 surveys are conducted. One approach is to then assume that sufficient surveying effort has been expended such that the probability of a false absence is negligible. Hence, locations where the species were never detected are regarded as a genuine absence, and standard techniques for binary data are used (e.g., logistic regression). However a more rigorous approach is to use a method of analysis that explicitly incorporates detection probability. Such techniques have been suggested independently by Geissler and Fuller (1987), Azuma et al. (1990), MacKenzie et al. (2002), Tyre et al. (2003), Stauffer et al. (2004), and Wintle et al. (2004). Useful extensions and refinements to these methods have also been suggested by MacKenzie et al. (2003), Royle and Nichols (2003), MacKenzie et al. (2004a), Royle (2004), and Dorazio and Royle (2005).

I discuss these various techniques by providing a brief summary of the issues that are common to many wildlife applications where presence–absence-type metrics are of interest. I begin with a conceptual overview of how such studies could be conducted, and then illustrate the consequences of imperfect detection. I then provide an overview of the potential analytic methods that are now available that explicitly account for detection probability and touch on important points while avoiding finer mathematical details. Next, I give suggestions on how we might use this analytic framework to aid in the design of an occupancy study, with reference to recent and upcoming publications. Finally, I discuss current and future directions of research and how these new methods could be used to improve management decisions.

A General Sampling Scheme

Consider the general situation in which the fraction of landscape units where the target species is present is of interest (occupancy). Landscape units may constitute small regions of an arbitrarily defined size (e.g., grid cells, quadrats) or naturally occurring discrete patches of habitat (e.g., ponds, forest remnants). Inference is to be made about the collection of landscape units and not the population of animals on the landscape (i.e., the landscape units represent the sampling units of a statistical population). A probabilistic sampling scheme is used to select U landscape units that are to be surveyed to establish the presence or absence of the target species. However, as mentioned above, the species is only ever detected imperfectly, hence each landscape unit is surveyed K times within a relatively short timeframe (i.e., a season). Interest may also lie in how the level of occupancy changes over time, hence the U landscape units may be surveyed for multiple seasons with repeated surveys each season.

MacKenzie et al. (2005b; see also MacKenzie and Royle 2005) discuss in great detail implications of defining a "season." An important point is to distinguish between "occupancy" and "use," and to consider how each relates to management objectives. A landscape unit is "occupied" if the species is always physically present somewhere within that unit over a set period of time (the defined season). If the species is physically present within a unit only at random points in time during the season, then that could be defined as "use" rather than occupancy (MacKenzie et al. 2004b). For example, if the size of a landscape unit is small compared to the home range of a

species, then whether the species is physically present within the unit on a given day during a 5-day study period may be considered random. In this case the unit would be defined as "used" by the species because it was not always there during the 5-day period. However, if the landscape unit is similar in size to the species home range, then it may be more appropriate to consider the unit as "occupied" because the species is likely always to be present within it. Alternatively, if a season is defined to be a single day rather than a 5-day period, then it may be appropriate to consider the smaller landscape unit as "occupied" provided it is unlikely for the species to move to another part of its home range during that day. It is important to realize that the fraction of units "used" by the species over a longer timeframe will generally be larger than the fraction of units "occupied" by the species at any given point in time, and consider how that corresponds with management objectives. For example, if the objective is to determine what habitats are being "used" by a wide-ranging carnivore, then a longer season may be appropriate, but if the intent is to employ occupancy as a surrogate for population size, then a much shorter season should be used. That is, a longer season may indicate that carnivores are everywhere because of their wide-ranging nature, which could be misleading in terms of a surrogate for population size, whereas a shorter season would indicate where the carnivores are within the region before they have a chance to move elsewhere. While it is important to distinguish between "use" and "occupancy" in terms of defining season length, both cases are amenable to investigation using the methods I describe below. Hereafter I use the term "occupancy" for both concepts.

How and Why Would Imperfect Detection be an Issue?

As I alluded to earlier, a species may go undetected in a survey of a landscape unit for a number of reasons. For territorial species that have home ranges larger than a landscape unit, a survey may fail to detect the presence of the species because the species is elsewhere within its home range during the survey. Indeed, it was this type of practical situation that Tyre et al. (2003) envisioned when suggesting the use of a zero-inflated binomial model (see also Wintle et al. 2004, Field et al. 2005). They conceptualized the general problem as the consequence of 2 independent Bernoulli processes operating at 2 timescales: (1)

utilization (or use) of a unit by the species over a longer timeframe, and (2) given the species utilizes a unit, that it was present and observed during a survey within that unit. In a situation where the species was likely to be always present at the landscape unit for the duration of the season, then a nondetection will generally occur simply as a result of the survey methods and level of survey effort. For example, a bird species may simply fail to call during a timed audio survey, or an animal may not happen to walk across a tracking plate. This was the situation regarded by MacKenzie et al. (2002) when they assumed the landscape units were closed to changes in occupancy during the season (i.e., landscape units were either always occupied or always unoccupied during the season). Subsequently, MacKenzie (2005*b*; see also MacKenzie et al. 2004*b*, 2005*b*) suggested this assumption could be relaxed to estimate "use" provided the probability of the species being physically present at a landscape unit was random (i.e., the probability did not depend upon whether the species was physically present within that unit at the time of a previous survey), which was the same situation considered by Tyre et al. (2003). Modern technology does not resolve the nondetection issue. For instance, radio and satellite transmitters may be affected by terrain or canopy cover that may result in an animal not being located during a sampling period (Frair et al. 2004).

If not accounted for, imperfect detection of the species will cause parameter estimators to be biased. Suppose the probability of occupancy is ψ and, given a unit is occupied, the probability of detecting the species in a single survey is p . After K surveys the probability of detecting the species at least once will be: $1 - (1 - p)^K$, (i.e., 1 minus the probability of not detecting the species in any of the K surveys). Therefore, the probability of the species being present and detected (i.e., finding the species) at a unit will be $\psi(1 - [1 - p]^K)$. If detection-nondetection data are regarded as representing actual presence-absence, then the relative bias (RB) in an estimate of occupancy that does not explicitly allow for detection probability will be:

$$\text{RB} = \frac{\psi[1 - (1 - p)^K] - \psi}{\psi} \\ = -(1 - p)^K.$$

That is, a naive estimate will always be biased low with the degree of bias being greater when p

and/or K are small. Furthermore, suppose a comparison of occupancy levels at 2 periods (e.g., trend) or places (e.g., different habitat types) may be of interest. It can be quickly shown that the ratio of 2 naive occupancy estimates will only be unbiased if the probability of detecting the species at least once at both times or places are virtually equal. The relative bias in this instance is approximately:

$$RB \approx \frac{[1 - (1 - p_2)^{K_2}]}{[1 - (1 - p_1)^{K_1}]} - 1$$

For example, suppose in a comparison of 2 habitat types the probability of detecting the species is 0.5 in habitat A and 0.4 in habitat B, and in each habitat type 3 surveys will be conducted per landscape unit. The RB in a naive comparison of occupancy will be approximately:

$$\begin{aligned} RB &\approx \frac{[1 - (1 - 0.4)^3]}{[1 - (1 - 0.5)^3]} - 1 \\ &= \frac{0.784}{0.875} - 1 \\ &= -0.104 \end{aligned}$$

i.e., the comparison will be underestimated by 10%.

The effect of nondetection on parameter estimates in specific contexts has been recently investigated by a number of authors. Tyre et al. (2003) showed in a habitat modeling context that when detection–nondetection data was regarded as presence–absence data, habitat-related effects on presence (or occupancy) were underestimated by simple logistic regression. They speculated that if detection probability co-varied with habitat, then positive biases may result. Gu and Swihart (2004) demonstrated exactly that, again in a habitat modeling context. They concluded that using logistic regression on so-called presence–absence data may lead to erroneous conclusions about habitat suitability, even when the level of nondetection is relatively small. MacKenzie (2005a) also illustrated this, where a variable that affected detection probability was mistakenly identified as being important in a resource selection application when using a simple logistic regression approach. In a metapopulation context, Moilanen (2002) concluded that the nondetection of a

species in occupied patches resulted in serious biases of a number of incidence function parameters to the point where the predictive ability of a metapopulation model may be compromised. In some scenarios, the persistence of the metapopulation may be overestimated. Given the general use of these methods (particularly logistic regression) to analyze presence–absence data in wildlife applications, ignoring the nondetection issue may result in false confidence of current management and conservation strategies by under- or overvaluing different habitats or regions. Moilanen (2002), Tyre et al. (2003), Gu and Swihart (2004), and MacKenzie (2005a) all recommend that appropriate field data should be collected such that detection probabilities can be directly incorporated into inferential procedures. Repeated surveying of landscape units within a season allows that to be accomplished.

Summary of Appropriate Analytic Methods

A number of papers discuss obtaining unbiased estimates of occupancy from appropriately collected field data (Geissler and Fuller 1987, Azuma et al. 1990, MacKenzie et al. 2002, Tyre et al. 2003, Stauffer et al. 2004, Wintle et al. 2004). A common element in these papers was recognizing that nondetection of the species at a landscape unit may be the result of 2 distinct processes: (1) the species was present but never detected, or (2) the species was genuinely absent during the season. Simple probabilistic arguments were used to build a model, and parameters may be estimated, generally using likelihood-based methods. The treatment given to the general problem by MacKenzie et al. (2002) was the most comprehensive in that many of the other methods could be considered special cases. When detection probability is assumed to be constant during a season, the modeling approach of MacKenzie et al. (2002) reduces to a zero-inflated binomial process, which was used by Tyre et al. (2003), Stauffer et al. (2004), and Wintle et al. (2004). In addition, if surveying of a unit is halted after the first detection of the target species during a season, the approach of MacKenzie et al. (2002) is conceptually similar to that of Azuma et al. (1990). The main advantages for considering the problem of occupancy estimation in the likelihood-based framework outlined by MacKenzie et al. (2002) are: (1) unequal sampling effort may be used at each landscape unit, (2) both occupancy and detection probabilities may be functions of landscape-unit characteristics (e.g.,

habitat type), (3) detection probabilities may be a function of variables specific to each survey occasion (e.g., localized weather conditions), and (4) being likelihood-based, either frequentist or Bayesian methods of analysis may be used (by equating the model likelihood to the probability of observing the data given the parameters).

The basic approach of MacKenzie et al. (2002) was very simple and similar to the reasoning used in the development of many mark-recapture models. Model parameters were defined to represent occupancy and detection probabilities, a verbal description of the sampling process that was assumed to result in the observed data was developed, and this was then translated into a mathematical equation using the defined model parameters. Below I briefly illustrate this process. For example, let ψ_i be the probability of occupancy at landscape unit i , and p_{ij} be the probability of detecting the species in the j th survey of unit i given the species was present (hence $1 - p_{ij}$ is the probability of not detecting the species given it was present; note the i subscript is used for generality, but it is not possible to estimate distinct probabilities for each unit, see below). Now suppose that at unit 1, 3 surveys were conducted with the resulting sequence of detections (1) and nondetections (0) being {101}. The verbal description would be: the species was present (as it was detected at least once), detected in survey 1, not detected in survey 2, and detected in survey 3. Translating this into a mathematical equation to represent the probability of observing this sequence gives $\psi_1 p_{11} (1 - p_{12}) p_{13}$. Next, suppose that at landscape unit 2, the species was never detected during the 3 surveys giving the sequence {000}. Here, the verbal description would be: the species was present but not detected in any of the surveys, *or* the species was absent. The corresponding mathematical translation is $\psi_2 (1 - p_{21}) (1 - p_{22}) (1 - p_{23}) + (1 - \psi_2)$. The 2 terms are added here because of the 2 possible explanations for the observed data. The model likelihood is then constructed by combining the equations for all of the sampled landscape units (for details see MacKenzie et al. 2002; see also MacKenzie et al. 2004b, 2005a,b).

An assumption common to all the above methods is that occupancy and detection probabilities were the same across all sampled units (i.e., $\psi_i = \psi$ and $p_{ij} = p_j$), the probabilities varied in accordance to a defined function via measured covariates (e.g., via a logistic regression function; $\psi_i = e^{\beta_0 + \beta_1 x_i} / [1 + e^{\beta_0 + \beta_1 x_i}]$), or the probabilities were random

values from a probability distribution (e.g., ψ_i logit-normal[μ, σ^2]). That is, there was no unmodeled heterogeneity in the probabilities. Unmodeled heterogeneity will again introduce bias into parameter estimates. One potential source of heterogeneity is variation in the local abundance of the species (i.e., the number of individuals of the species within each landscape unit). Detection probability of the species would be greater in units with greater local abundance. Royle and Nichols (2003) extended the approach of MacKenzie et al. (2002) by considering how individuals of the species may be distributed across the landscape. Royle (2004) also extended the general approach to situations where, rather than collecting just detection-nondetection data at each survey, repeated counts of the number of individual animals of the species are made at the landscape units. The advantage of such approaches is that it is possible to estimate abundance rather than just occupancy; however, careful consideration must be made as to exactly what "abundance" refers to in specific contexts (i.e., the estimated "abundance" parameter may not be interpretable as the expected number of individuals within a landscape unit).

So far, all the methods I have mentioned deal with the problem of estimating occupancy at a single point in time (e.g., within a single season). Such methods are useful for evaluating the current status of a species or for investigating how a species was distributed across a landscape in relation to measurable covariates; that is, for investigating patterns in occupancy. Often, how occupancy changes over time and the underlying processes of change may be of as much or greater interest. Clearly the only reliable method for investigating the processes of change is to survey the landscape units for multiple seasons (MacKenzie et al. 2003, MacKenzie and Nichols 2004). One approach for analyzing such data is to apply the above models to each season's data either separately or by assuming some functional change in the occupancy parameter over time (e.g., Field et al. 2005). However, such an approach does not consider how the occupancy state of specific units may change over time. These dynamic processes are commonly referred to as local extinction and colonization, respectively. MacKenzie et al. (2003; see also MacKenzie et al. 2004b, 2005a,b for details) extended the single-season approach of MacKenzie et al. (2002) to explicitly incorporate these processes while simultaneously accounting for imperfect detec-

tion. Their multi-season model had all the same advantages of the single-season model (i.e., likelihood-based, ability to incorporate information on measured covariates, unequal sampling effort) and resulted in a very flexible method of analysis. A similar approach was suggested by Barbraud et al. (2003) using mark-recapture models where landscape units may be considered as individual marked animals, but this method required equal sampling effort across all units and did not consider units where the species was never detected. Note that the processes of local extinction and colonization may induce a form of temporal autocorrelation as units that were occupied in season t may be more likely to be occupied in season $t + 1$. Also note that MacKenzie et al. (2005b) have recently shown that applying a series of single-season models to multi-season data (e.g., Field et al. 2005) makes a de-facto assumption that changes in the occupancy state of units between seasons occur at random (i.e., the probability that a unit is occupied in season t is the same regardless of the whether the unit was occupied or unoccupied in season $t - 1$). Hence, methods of analysis that explicitly incorporate the processes of local extinction and colonization are likely to provide more reliable results than those that do not. Furthermore, the method of MacKenzie et al. (2003) allows detection probability to vary within and between seasons, which is likely to be a biological reality.

From a management perspective, one quantity that may be of interest in some situations is the probability that the species was present at a landscape unit given it was never detected there. From Bayes theorem we have:

$$\frac{\text{PR}(\text{species present} \mid \text{species not detected})}{\text{PR}(\text{species present and not detected})} = \frac{\text{PR}(\text{species not detected} \mid \text{species present})}{\text{PR}(\text{species not detected})}$$

$$= \frac{\psi_{i,t} \prod_{j=1}^2 (1 - p_{i,j,t})}{(1 - \psi_{i,t}) + \psi_{i,t} \prod_{j=1}^2 (1 - p_{i,j,t})}$$

This can be simply calculated from the estimated parameters. For example, suppose that in season t (for generality) unit i was surveyed twice, and the species was never detected. From the results of the analysis, the probability of occupancy was estimated as $\hat{\psi}_{i,t} = 0.65$ (this may have to be calculated recursively in a multi-season study; see MacKenzie et al. 2003 for details), and

detection probabilities were $\hat{p}_{i,1,t} = 0.4$ and $\hat{p}_{i,2,t} = 0.6$. The estimate for the probability of the species being present given it was never detected at the unit would be:

$$\begin{aligned} & \frac{\hat{\psi}_{i,t} \prod_{j=1}^2 (1 - \hat{p}_{i,j,t})}{(1 - \hat{\psi}_{i,t}) + \hat{\psi}_{i,t} \prod_{j=1}^2 (1 - \hat{p}_{i,j,t})} \\ &= \frac{0.65 \times (1 - 0.4) \times (1 - 0.6)}{(1 - 0.65) + 0.65 \times (1 - 0.4) \times (1 - 0.6)} \\ &= \frac{0.65 \times 0.6 \times 0.4}{0.35 + 0.65 \times 0.6 \times 0.4} \\ &= \frac{0.156}{0.506} \\ &\approx 0.31. \end{aligned}$$

That is, the unconditional estimate of the species being present was 0.65, but by taking into account that the species was not detected after 2 surveys, the estimated probability of presence was reduced to 0.31. An approximate standard error for this conditional probability can be obtained using the delta method (MacKenzie et al. 2005b). Had detection probabilities been smaller, then the reduction in the probability of presence would not have been so great, but conversely had they been larger or had more surveys been conducted, the conditional probability of presence would have been smaller (i.e., the probability of a false absence would have been smaller if the probability of detecting the species at least once was greater).

Implications for the Design of Studies and Monitoring Programs

The imperfect detection of a species may seriously impede our ability to make reliable, informed management decisions. Not allowing for detection probability has been shown to lead to erroneous conclusions about the system under consideration, whether using back-of-the-envelope calculations (as above), extensive simulation studies (Moilanen 2002, Tyre et al. 2003, Gu and Swihart 2004) or the analysis of real data (MacKenzie 2006). The use of repeat surveys within a season provides the relevant data allowing detection probabilities to be estimated. Clearly, when logistical resources are limited (as is often the case) the necessity of conducting repeat surveys may reduce the total number of landscape units that can be surveyed per season. A question that naturally arises is "How many repeat surveys should be conducted?" However, before addressing this question, it is important to

consider other more fundamental issues related to the design of a study or monitoring program.

The first is the *why*, *what*, and *how* of the intended study/monitoring program (Yoccoz et al. 2001, MacKenzie and Royle 2005). The *why* component relates to establishing a clear objective for sampling the wildlife population. The exact purpose of the sampling determines what aspect of the population should be measured and how one should conduct the sampling. For example, it would not be useful for me to design a good occupancy study if I really wanted to estimate the survival probabilities of individuals. Similarly, as I discussed previously, the choice of season length may depend upon whether "use" vs "occupancy" of landscape units by a wide-ranging carnivore was of interest. A good objective should provide some statement as to the program's general intent (e.g., measure status or trends in the population) and the level of acceptable uncertainty. Moreover, a good objective provides a link between the collection of data and the advancement of science or implementation of management actions. For example, is the intent of the study to distinguish between competing hypotheses about the ecology of the species such as whether recruitment is density dependent or not (say), or simply to estimate the current level of recruitment to determine whether management should begin a captive breeding program? Similarly, is the intent of the study simply to estimate the current level of occupancy for a species within a management region, or is more detailed information required to identify which habitats are highly used by the species to prioritize them for conservation? In each of these 2 examples, the 2 subtly different objectives would require very different designs (and very different levels of effort) to provide the relevant information. Clearly defining *why* one is sampling a wildlife population greatly aids the entire study design process.

Here the issue of *what* to measure about the population is occupancy (or a related metric), but other options may include abundance or species richness (MacKenzie and Royle 2005; MacKenzie et al. 2005a,b). The choice of which aspect of the population (or wider ecological community) to measure is related to the study's objective and to available logistical resources. Generally, abundance-related measures tend to be most costly, followed by occupancy and species richness-related metrics.

How to design the study is the issue that usually receives the greatest focus, as it is where the

specifics of the design (e.g., sample sizes, field protocols, etc.) are generally considered. For occupancy-type studies, I suggest considering a number of issues: (1) what is an appropriate landscape unit, (2) season length, and (3) how should landscape units be selected for surveying. These issues are inextricably linked to *why* and *what*, hence they should only be considered once these questions have been suitably addressed. For example, if the intent of the study was to determine whether a species prefers one form of habitat over another, one approach would be to randomly select units only from those areas of the landscape with those types of habitats. Another approach would be to randomly select units from the entire landscape that may (or may not) contain one of the habitat types of interest. While either design may provide the relevant information, I think it would be prudent to use the former approach considering the objective of the study. However, if the main objective of the sampling was simply to measure occupancy across the entire landscape, and habitat relationships were of secondary importance, then I suggest using the latter approach because it allows inference to be made to the entire landscape rather than just those portions of the landscape with 2 habitat types. My further comments (and associated references) relate to many of the *how* questions that are commonly raised during the design of an occupancy study, although some can only be considered on a case-by-case basis given the specifics of *why* and *what*.

In terms of designing an occupancy-based study or monitoring program, the necessity of conducting repeat surveys of a landscape unit may not always translate into multiple discrete visits to the unit. That is, the requirement of repeat surveys may be incorporated into a program without substantially impacting upon the total level of effort or resources. Options for collecting the repeated survey data include: (1) multiple discrete visits, (2) multiple observers surveying independently, (3) single observer conducting multiple surveys separated by an appropriate time interval, and (4) surveying multiple plots within a larger landscape unit (e.g., multiple short transects within a 25-ha unit). Whether a particular method is appropriate in a given situation depends very much on how the model assumptions relate to the biology of the target species. Key issues to consider are available survey techniques, the timescale over which detection probability may change (e.g., daily due to weather pat-

terns, or within a day due to activity), whether the species is likely to continuously occupy a unit during a season (i.e., use vs. occupancy), and the meaningful definition of a landscape unit. It is of particular importance to consider whether a proposed study design is likely to introduce detection heterogeneity between units due, for example, to observer effects or surveying different units at different times of the season (MacKenzie et al. 2004b, 2005b; MacKenzie and Royle 2005).

A current area of research is seeking general results in terms of allocation of survey effort between the number of units to sample and number of surveys per unit. Little has been published to date, the exceptions being Field et al. (2005) and MacKenzie and Royle (2005).

MacKenzie and Royle (2005) considered the problem of designing an efficient study for estimating occupancy in a single season, where efficiency may either be defined as achieving a desired level of precision for minimal total survey effort or maximizing precision (i.e., minimizing the variance) for a fixed level of survey effort. They showed that regardless of the definition used, there are an optimal number of repeat surveys that should be conducted at a unit for specified occupancy and detection probabilities. This optimal number was independent of the number of units surveyed; hence, regardless of whether 50 or 50,000 units are to be surveyed, the same number of repeat surveys should be conducted. They also considered 3 general study designs: (1) a standard design where all units are surveyed an equal number of times; (2) a double-sampling design where a subset of units are surveyed repeatedly, with other units only surveyed once; and (3) a removal design where units are surveyed up to a set maximum number of times, but surveying halts once the species is first detected (i.e., the design considered by Azuma et al. 1990). They found that the removal design was generally the most efficient (followed by a standard design, then the double-sampling design) because detecting the species for the first time at a unit was the most important piece of information in terms of establishing occupancy; although they speculated the removal design may be less robust to assumption violations than a standard design. As a compromise between efficiency and robustness, they suggested a hybrid design in which the removal protocol is used on some units and a standard design on others. The final recommendations of MacKenzie and Royle (2005) were that (1) as a general strategy for rare species, more landscape units should be surveyed

less intensively, while for common species, fewer units should be surveyed more intensively; (2) unless a removal design is to be used, units should be surveyed a minimum of 3 times when detection probability is anticipated to be >0.5 , and that minimum should be increased for smaller detection probabilities; and (3) increasing spatial replication with insufficient repeat surveys may not yield a more precise estimate of occupancy than surveying fewer units with greater intensity (e.g., they provided an example where the same expected standard error for the occupancy probability could be achieved by either surveying 80 landscape units 5 times or 500 units only twice).

Field et al. (2005) considered a different situation, with a slightly different approach to study design, where a trend in occupancy (specifically a decline) over a 3 season time period was of interest, subject to budgetary constraints. Based upon a hypothesis testing objective, they assessed the effect the number of repeated surveys had on the power of the test to detect a decline (assuming that increasing the number of repeat surveys decreased the number of units that could be sampled, given a fixed budget). For the scenarios considered, they found that power was maximized when 2 surveys per season were conducted at each site, but they recommended a greater number of surveys if detection probability was low or if the species was more common (i.e., occupancy was higher). Subsequent investigations have shown that this result holds where the main consideration was the variance of the trend estimate rather than the power of a hypothesis test (A. Tyre, School of Natural Resources, University of Nebraska, personal communication). However, the methods used by Field et al. (2005) assumed detection probability was equal in each of the 3 seasons (i.e., all of the repeat surveys over the 3 seasons contributed to estimating a single detection probability). Experience and the analysis of empirical data sets (e.g., MacKenzie et al. 2003, 2005a; Bailey et al. 2004; Olson et al. 2005) suggest that detection probability will likely vary between seasons (and possibly within seasons also). The consequence of this is that a greater number of repeat surveys may be required per season, hence I suggest that the above recommendations of MacKenzie and Royle (2005) also be used where the study/monitoring program is to be continued over multiple seasons (i.e., ≥ 3 surveys per unit when $p > 0.5$).

In some multiple season studies or monitoring programs it may be possible to consider a trade-

off between number of units sampled per season and the number of seasons for which the study is to be conducted. The coefficient of variation (CV) of the estimated trend in occupancy (on the logistic scale and ignoring the processes of colonization and local extinction for simplicity) decreases as the number of seasons of data collection increases (Fig. 1). A similar level of precision can be achieved by surveying more units over fewer seasons vs. surveying fewer units over a longer period (e.g., 200 units for 4 seasons vs. 50 units for 8 seasons; Fig. 1). The implication for designing programs to inform management is that if precise information is required within a short timeframe then more sampling effort will be needed each season (however "season" is defined), whereas if management has the luxury of a longer timeframe and short-term fluctuations are not of interest, then less sampling effort per season may be required. An alternative viewpoint is that if available funding only permits a small number of landscape units to be surveyed each season, then management (and stakeholders) must understand that a longer timeframe will be required to provide decisive information about the system, hence they must be prepared to make a long-term commitment to the program. While I believe this tradeoff to exist more generally, the magnitude of this tradeoff has only been considered for a single situation (Fig. 1) and it should be evaluated on a case-by-case basis.

A related issue in multiple-season studies is whether the same landscape unit should be surveyed each season or different units surveyed as in a rotating panel design (Urquhart and Kincaid 1999). I recently compared (D. MacKenzie, Proteus Wildlife Research Consultants, unpublished data) a number of potential designs for multiple season occupancy studies and found that the precision of an estimated trend in occupancy was generally similar for rotating panel-type designs and designs where the same units were surveyed each season. I found that the key determinant of the precision of the trend estimate (given sufficient

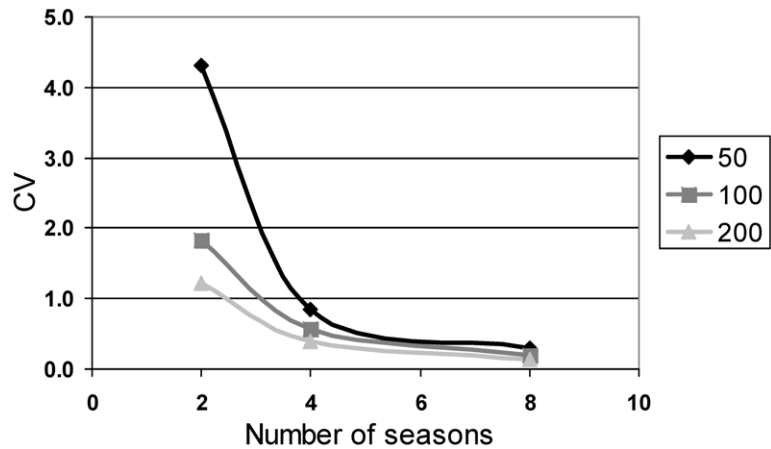


Fig. 1. Simulation-based coefficient of variation (CV) for estimated trend in occupancy (on the logistic scale) where 50, 100, or 200 landscape units are each surveyed 3 times per season, for multiple seasons. Solid lines are solely for ease of interpretation.

repeat surveys within each season) was the number of units surveyed per season, not the total number of units surveyed. However, I argue against the use of rotating panel-type designs from the perspective that spatial and temporal changes in occupancy may become confounded. That is, if occupancy was estimated as different each season using a rotating panel design, it may be due to (1) a change in occupancy across the landscape over time, (2) the fact that different units within the landscape were sampled, or (3) a combination of both. It may not be possible to make strong statements about a trend in occupancy because it could be reasonable to argue that the observed change was a result of surveying different locations, particularly when the number of seasons was small (<5). While some of these issues could be accommodated through appropriate modeling, I point out that the inclusion of additional parameters in the model will reduce the precision of the trend estimate, and a simpler approach would be to survey the same units each season. Where the main objective is to measure trend in occupancy, I suggest that rotating panel-type designs may be unnecessarily complicated and recommend they not be used unless the continual surveying of the same units over time would lead to the degradation of those units (i.e., the act of monitoring was having a negative effect on the units).

DISCUSSION

I have summarized the current literature on occupancy-related applications that explicitly incorporate detectability. There is a greater body

of literature on occupancy-related applications that ignores issues of detectability that I have, in turn, ignored. To me, the issue of imperfect detection is both common sense and fundamental, and hence it cannot be ignored if one wishes to make reliable inferences about the biology (i.e., presence-absence) rather than the sampling (i.e., detection-nondetection) of the species. It is ironic that complicated methods of analysis have often been developed for so-called presence-absence data, but the developers have failed to grasp the influence that imperfect detection may have on their analyses.

I am similarly critical of indices that do not take into account the sampling methods that have given rise to the observed data. A commonly stated virtue of such indices is that they are relatively assumption free compared to other estimation approaches. It is true that they often require very few calculations. However, to draw inferences about the population based on an index, assumptions are required, and the assumptions are typically more restrictive than those required of more direct estimation procedures (see Conn et al. 2004 for a recent treatment of the subject). What is most frustrating is that often studies that have been designed around an index would only require minimal additional effort (or sometimes only a reallocation of effort) to provide appropriate data that would permit direct estimation about the aspect of the population of interest.

Given the flexible methods of analysis that have now been developed for detection-nondetection data and the increasing weight of evidence in the literature that detectability matters, I would expect to see more widespread use of the methods I have discussed, both in terms of robust study designs and statistical analysis. I would also expect to see further development of these methods in the future. Already, the extension to count data by Royle (2004) should prove to be a very useful method in situations where it is possible to obtain repeated counts of unique individuals across a number of landscape units, although as I noted earlier, careful attention must be paid to the modeling assumptions in order to interpret the abundance parameter correctly in any given application. Issues of detectability can also be problematic with inferences about the co-occurrence of species, particularly when the level of detectability differs among species. MacKenzie et al. (2004a) recently considered this problem and extended the single-season occupancy model of MacKenzie et al. (2002) in an effort to address it.

Based on the above methods, Dorazio and Royle (2005) have developed a conceptual framework for estimating occupancy and species richness by taking a community-level approach to modeling.

The prospect of combining occupancy-type thinking with other sources of information also promises some exciting developments. In situations where a landscape unit may be occupied by a small number of individuals that effectively behave as a single entity (e.g., a breeding pair), mark-recapture data could be used to provide information on whether the same individual(s) returns each season or whether turnover occurs (MacKenzie and Nichols 2004). Issues such as population sources and sinks could thus be addressed using empirical data. In other contexts, if mark-recapture studies were conducted at some landscape units the mark-recapture data could be used to augment the estimation of how local abundance may vary across units, using the ideas presented by Royle and Nichols (2003) to incorporate abundance-related heterogeneity in detection probability.

The scope for using occupancy-type thinking in wildlife disciplines is huge, much greater than I realized when I first became interested in the topic in early 2001. Then, my only exposure to the occupancy metric was for use as a surrogate to abundance for a large-scale monitoring program I was loosely associated with. Now I realize the basic concept is widely used in many facets of ecological research and management. Over the past 5 years there seems to have been some realization that not accounting for detection probability may lead to misleading conclusions, and interest in the general topic has been renewed (this special section is evidence of that fact). This has led to rapid methodological developments that we presented in important papers throughout the literature. I have referred to and summarized many of the key papers above, but it is impossible to provide a detailed overview of these methods in a single paper. For a much more complete synthesis of the current literature, interested readers are directed to MacKenzie et al. (2005b).

MANAGEMENT IMPLICATIONS

Presence-absence data can provide wildlife managers and researchers with useful information about a species in a variety of contexts (e.g., changes in species distributions or identifying habitats of high intrinsic value to a species). However, a key issue that has largely been ignored or overlooked until recently is the imperfect detec-

tion of a species and the consequences it has on resulting inferences. To make reliable, informed management decisions, studies and monitoring programs must be designed to provide information about detection probability (i.e., landscape units being repeatedly surveyed) and appropriate methods of analysis must be used.

Finally, in my capacity as a consulting biometrician I am often reminded that conducting monitoring programs and wildlife studies can be costly, particularly at large spatial scales. Before uttering the statisticians' knee-jerk reaction that unattainably large sample sizes will be required, I find it helpful to become familiar with the proposed study site, field methods, etc., to get some idea of what may be practically achieved within a given financial budget. I also encourage clients to think laterally about alternative field methods or aspects of the population that could provide similar information at a reduced cost. However, to effectively monitor a population, there will always be a minimal level of information that needs to be collected from the field, and the cost of doing so may be beyond current budgets. How to proceed in such situations is difficult; one approach is to downscale the objectives or lengthen the time-scale over which the objective is to be evaluated.

There is also the issue of the cost of not having an effective monitoring program. What is the monetary, ecological, cultural, and political impact of not having reliable information about the target species? For example, at the completion of a multi-million dollar habitat restoration project, what would be the cost if it cannot be reliably demonstrated that the habitat restoration has been beneficial to the population? Would future funding be jeopardized? Would there be any social or political fallout for stakeholders who supported or were opposed to the initial project? In a different context, what would be the cost of not having sufficient data to identify that a particular invasive species was becoming established within a region? How much disruption or damage might be caused to the ecosystem? How much more money would be required to control a well-entrenched invasive species, rather than beginning control operations earlier that may have been possible if a more effective monitoring program had been in place? Inherently, reliable knowledge is valuable, the issue is how valuable. Different stakeholders may have different perceptions, but sometimes the potential value of reliable information can only be ascertained by considering the cost of not having that knowl-

edge. In some instances, when the cost outweighs the budget of a proposed design, additional funding can be found. In other situations, consideration of these costs may help to define a more realistically achievable objective.

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