



Efficient Species-Level Monitoring at the Landscape Scale

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Abstract: *Monitoring the population trends of multiple animal species at a landscape scale is prohibitively expensive. However, advances in survey design, statistical methods, and the ability to estimate species presence on the basis of detection-nondetection data have greatly increased the feasibility of species-level monitoring. For example, recent advances in monitoring make use of detection-nondetection data that are relatively inexpensive to acquire, historical survey data, and new techniques in genetic evaluation. The ability to use indirect measures of presence for some species greatly increases monitoring efficiency and reduces survey costs. After adjusting for false absences, the proportion of sample units in a landscape where a species is detected (occupancy) is a logical state variable to monitor. Occupancy monitoring can be based on real-time observation of a species at a survey site or on evidence that the species was at the survey location sometime in the recent past. Temporal and spatial patterns in occupancy data are related to changes in animal abundance and provide insights into the probability of a species' persistence. However, even with the efficiencies gained when occupancy is the monitored state variable, the task of species-level monitoring remains daunting due to the large number of species. We propose that a small number of species be monitored on the basis of specific management objectives, their functional role in an ecosystem, their sensitivity to environmental changes likely to occur in the area, or their conservation importance.*

Keywords: abundance, detectability, occupancy, range

Monitoreo Eficiente a Nivel de Especie en la Escala de Paisaje

Resumen: *El monitoreo de las tendencias poblacionales de múltiples especies animales en la escala de paisaje es prohibitivamente costoso. Sin embargo, los avances en el diseño de muestreo, métodos estadísticos y la habilidad para estimar la presencia de especies con base en datos de detección-no detección han aumentado considerablemente la factibilidad del monitoreo a nivel de especie. Por ejemplo, avances recientes en el monitoreo hacen uso de datos de detección-no detección que son relativamente baratos, datos de muestreo históricos, y nuevas técnicas de evaluación genética. La habilidad para utilizar medidas indirectas de la presencia de algunas especies incrementa enormemente la eficiencia del monitoreo y reduce costos de muestreo. Después de ajustes por ausencias falsas, la proporción de unidades de muestreo en un paisaje en los que una especie es detectada (ocupación) es una variable de estado lógica a monitorear. El monitoreo de la ocupación se puede basar en observaciones en tiempo real de una especie en un sitio de muestreo o en la evidencia de que la especie estuvo en la localidad de muestreo en algún momento del pasado reciente. Los patrones temporales y espaciales de los datos de ocupación están relacionados con cambios en la abundancia de animales y proporciona ideas de la probabilidad de persistencia de una especie. Sin embargo, aun con la eficiencia obtenida cuando la ocupación es la variable de estado monitoreada, la tarea del monitoreo a nivel de especie sigue siendo desalentador debido al gran número de especies. Proponemos que un reducido número de especies sea monitoreado con base en objetivos de manejo específicos, en su papel funcional en el*

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ecosistema, su sensibilidad a cambios ambientales que probablemente ocurran en el área o en su importancia para la conservación.

Palabras Clave: abundancia, detectabilidad, ocupación, rango

Introduction

Estimates of the effects of land-use change, human population growth, and climate change on biological diversity are essential to inform the development of sound environmental policy. However, monitoring changes in species diversity at landscape scales is seldom done because it is viewed as fundamentally infeasible due to the large number of species involved and the costs of traditional survey methods. For these and other reasons, there are few examples of long-term monitoring of individual species at the landscape scale (e.g., Sauer et al. 2003; Forsman et al. 2011).

The lack of commitment to landscape-scale species-level monitoring is exemplified by the major federal land management agencies in the United States (Forest Service and Bureau of Land Management). With notable local exceptions, these agencies do not have scientifically defensible, geographically extensive, long-term monitoring programs in place for animal species that occur on the lands they manage (>160 million ha). Even if they were committed to species-level monitoring, funds to assess the status and trend of all species are lacking. For example, the 7 national forests in the Sierra Nevada ecosystem in the western United States provide habitat for >550 vertebrate species, many with poorly known life histories. In general, restricting assessment to a small set of species may be the only pragmatic solution to evaluating the species component of biological diversity at broad spatial scales (Wiens et al. 2008; Noon et al. 2009; Caro 2010).

Agencies managing large landscapes often use a coarse-filter approach to address the conservation of biological diversity (e.g., Haufler et al. 1996) (i.e., remote monitoring of vegetation communities and their successional stages). Putative changes in the status of animal species are inferred from changes in the vegetative components of their habitats. However, the limitations of a coarse-filter approach have been known for some time (Noon et al. 2005, 2009). In a review of the degree to which coarse-filter models can be used to infer animal occurrence, Schlossberg and King (2009, p. 609) concluded that "...observed error rates were high enough to call into question any management decisions based on these models." These authors also state that coarse-filter "models oversimplify how animals use habitats, and the dynamic nature of animal populations." The coarse-filter approach is a necessary component of a comprehensive assessment of biological diversity, but it is insufficient if

not accompanied by some direct species-level assessment (Noon et al. 2009).

In the last decade, there have been significant advances in survey design, statistical methods, and interpretation of distribution data that are based on patterns of species detection and nondetection derived from direct counts of animals or indirectly from animal sign (Vojta 2005; MacKenzie et al. 2006; Royle & Dorazio 2008). In these surveys, the state variable of interest is occupancy (i.e., the proportion of sample units estimated to be occupied by the species). Collectively, improvements in survey and statistical methods and interpretation of data make species-level monitoring at landscape scales considerably more feasible than in the past and provide reliable inference to land uses that influence species distribution and occupancy dynamics.

Our objectives in this paper were to discuss the importance of species-level monitoring; propose a logical monitoring framework that addresses financial constraints and efficiency; and explain how occupancy, as a measure of a species' spatial distribution, is a valid state variable for quantifying a species' status and probability of extinction over time. We reviewed the literature on the relations among abundance, persistence likelihood, geographic distribution, and occupancy; explained how occupancy models can be used in long-term monitoring programs; considered survey design; reviewed current advances in the use of animal sign, particularly genetic signatures; and considered the selection of species to monitor.

Importance of Species-Level Monitoring

The key reason to monitor at the species level is that species are the fundamental agents of transfer of matter and energy in ecosystems. The dynamics of ecosystems are often driven by a small number of species that have uneven effects on ecosystem processes (e.g., Estes et al. 2011). Knowledge of the status and trends of such species are essential to effective ecosystem management. Results of many empirical and theoretical studies show that more diverse plant and animal communities support less variable ecosystem outputs and provide more ecosystem services (Naeem et al. 2009). Ecosystem resilience is strongly related to native species diversity and functional redundancy (the degree to which multiple species perform similar ecosystem functions [Walker 1992]). Species redundancy buffers ecosystems from disturbance because the role of critical species can be taken over by other

species in the ecosystem (e.g., Palumbi et al. 2008). In general, ecosystems with greater native species diversity are more resistant to disturbance, recover more quickly following disturbance, and are less likely to experience irreversible changes than communities with lower diversity of native species (Cottingham et al. 2001; Hooper et al. 2000; Naeem et al. 2009).

In addition to the consensus view that species' functional characteristics strongly influence ecosystem properties (Hooper et al. 2000), there are often more immediate reasons for monitoring at the species level. These include the role of species as indicators of changes in the chemical or physical conditions of the environment (Simberloff 1998; Caro 2010), the use of status and trend information from proxy species as surrogates for unmeasured species (e.g., Wiens et al. 2008), legal requirements to assess the effects of land management at the species level (e.g., U.S. Endangered Species Act and National Forest Management Act), and almost universal value that humans assign to species persistence.

Theoretical Justification for Occupancy as a State Variable

The probability of persistence of a species is strongly related to the mean and variance of its growth rate, overall abundance, number of local populations, and the geographic distribution of those populations (e.g., Lande 1993; Foley 1994). Justification for the use of species occurrence data in monitoring is based on the statistical relations among a species' abundance, persistence likelihood, and the spatial distribution of its occurrences.

Relations between Extinction Likelihood and Population Abundance

Abundance is a common state variable for wildlife monitoring programs (e.g., Pollock et al. 2002). This is logical given the link between abundance and population persistence and because maintaining populations, or metapopulations, of species well distributed throughout large landscapes is fundamental to the conservation of biological diversity. In stable environments, the theoretical mean time to extinction (MTE) of local populations, subject only to demographic stochasticity, increases exponentially with abundance (Ovaskainen & Meerson 2010):

$$\text{MTE} = C_1 \exp(bK), \quad (1)$$

where K is carrying capacity (individuals), C_1 is a fitted constant, and $b > 0$ determines how MTE depends on K . Assuming a self-regulating population, $b = r/v_d$, where r is the intrinsic growth rate and v_d is variance in the growth rate due to demographic stochasticity (Leigh 1981). Even small populations (>100 individuals) are relatively free from extinction threats due to demographic

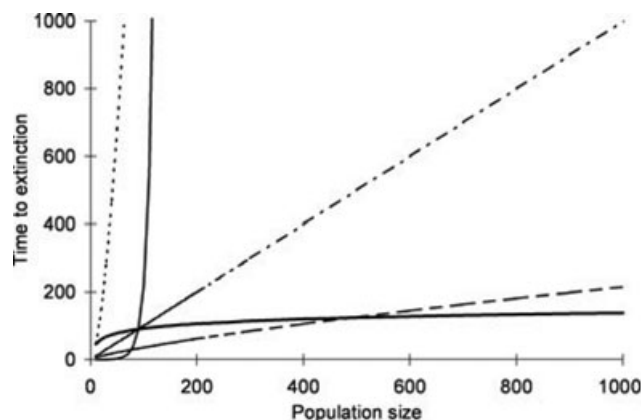


Figure 1. Relation between extinction time and population size under demographic stochasticity (solid line), deterministic decline at $r = -0.05$ (heavy solid line), and environmental variation in which environmental variance = 0.05 and $r = 0.04$ (dashed line), $r = 0.05$ (dashed and dotted line), and $r = 0.06$ (dotted line) (reprinted with permission from Mace et al. [2008]).

stochasticity. General relations between extinction times and abundance under various demographic scenarios have been recently summarized by Mace et al. (2008) (Fig. 1).

Under conditions of environmental stochasticity (random temporal variation in birth and death rates), MTE increases as a power function of abundance (Ovaskainen & Meerson 2010):

$$\text{MTE} = C_2 K^c, \quad (2)$$

where C_2 is a fitted constant and $c = 2r/v_s$ (v_s , temporal variation of the growth rate) (Lande 1993). Equation 2 demonstrates that high levels of environmental stochasticity can lead to high extinction risk even for large populations, particularly if population growth rate (r) is small (Fig. 1). Collectively, Eqs. 1 and 2 capture the strong positive relation between MTE and population size and the role of stochasticity. Reliable estimates of abundance to infer MTE are also fundamental to the estimation of minimum viable population sizes (Traill et al. 2007).

Occupancy (Range Size)-Abundance Relations

The positive relation between the regional abundance of a species and its range size (proportion of sites occupied) is one of the most consistent macroecological patterns (e.g., Brown 1984; Gaston et al. 2000; Zuckerberg et al. 2009). Positive intraspecific and interspecific correlations have been demonstrated for many taxa across a range of spatial scales (Borregaard & Rahbek 2010). These relations have been proposed as an empirical ecological rule for macroecology (Lawton 1993; Gaston & Blackburn 2000).

Thirteen mechanisms have been proposed to explain complex interspecific and intraspecific occupancy–abundance relations (Borregaard & Rahbek 2010). The many mechanisms are not mutually exclusive, and several may act in concert to produce observed patterns. However, complex explanations are unnecessary because the occupancy–abundance relation arises from an inherent statistical relation between these variables (Royle & Nichols 2003) that is unrelated to processes underlying patterns of occupancy and abundance.

Detection of the target species on a sample unit can be expressed as a function of the number of individuals present on the unit. Consequently, the relation between occupancy and abundance arises from first principles. This relation can be expressed as (Royle & Nichols 2003):

$$p_i = 1 - (1 - r)^{N_i}, \quad (3)$$

where p_i is the probability of detecting ≥ 1 individual of the target species on sample unit i , r is the probability that a given individual is detected, and N_i is the number of individuals present on unit i . Royle and Dorazio (2008:130) refer to p_i as the “net probability of detection.”

Occupancy–abundance relations can take several forms, including intraspecific spatial, intraspecific temporal, and interspecific. Interspecific relations are the most studied and easiest to envision—each data point in a regression is based on an estimate of a species’ range size (area encompassed by occupied sites) and its abundance within the estimated range. Abundance is usually extrapolated to the estimated range on the basis of a subset of surveyed locations (e.g., Gaston et al. 1997). Interspecific regressions of range size on abundance generally show significant positive relations, although the amount of explained variance varies widely (e.g., Gaston 2003; Buckley & Freckleton 2010). Because estimates of range size are strongly scale dependent (Kunin 1998; Hurlbert & Jetz 2007), the lack of explained variance and the variability in slope estimates in both intraspecific and interspecific analyses may be associated with differences in survey methods (Wilson 2008, 2011).

Because a species can have only one geographical range, the sampling methods for investigating intraspecific and interspecific relations differ. Abundance–distribution patterns within a species are revealed through measures of local abundance and occupancy at multiple locations. Alternatively, abundance and occupancy can be estimated at a single location over time (intraspecific temporal). Venier and Fahrig (1998) conducted an intraspecific spatial analysis of the relation between abundance and occupancy of 20 species of boreal birds at 131 landscapes across eastern Canada. They estimated abundance and occupancy for each species for multiple landscapes, where distinct landscapes were identified by regional discontinuities in the distribution of

forest habitat. They found all 20 species to show positive abundance–occupancy relations.

For species-level monitoring, the focus is on intraspecific temporal relations (i.e., how occupancy for a given species change over time). In addition, evaluating changes in the spatial pattern of occupancy over time may provide insights into causal relations between changes in distribution and land use, including management practices.

Extinction Risk–Occupancy Relations

Geographic range size is usually measured by overlaying a grid on a map of the species’ putative geographic distribution (e.g., from a range map) and determining the number of occupied cells from survey data (e.g., Gaston et al. 1997). Estimates of range size, however, can be highly variable because they are strongly dependent on the size of grid cells (Gaston & Fuller 2009). Even though numerous studies have estimated species’ geographic ranges, no extensive body of literature relates the risk of extinction to range size (Gaston 2003). Nevertheless, some authors claim that range size is the single best predictor of a species’ risk of extinction (Manne & Pimm 2001; Harris & Pimm 2008). Schemes that rank species by risk of extinction often use information on range size as a ranking factor (e.g., IUCN) (Mace et al. 2008). Species with broad geographic ranges are believed to have higher persistence likelihood because there is a positive relation between occupancy and a species’ abundance; an extensive spatial distribution decouples the dynamics of local populations and increases regional persistence (den Boer 1981); and for fixed patch-level extinction and colonization rates, a greater number of occupied patches results in a lower probability of all becoming extinct (MacKenzie et al. 2006). These same attributes characterize metapopulations with high persistence likelihoods (Hanski 1994).

Few landscape-scale monitoring programs will span a species’ entire range. However, numerous distributional boundaries may occur within a species’ range because habitat is seldom continuously distributed throughout the geographic range. The result is many local range boundaries that vary dynamically as local abundance changes. For example, the positive relation between occupancy and abundance at large spatial extents is also observed at local extents (Venier & Fahrig 1998). As a result, local extinction risk is negatively related to local occupancy (Hanski et al. 1993; Holt et al. 1997; Gaston et al. 1999; Gaston & Blackburn 2000).

Occupancy as a Monitoring State Variable

The proportion of sample units in the management area occupied by the target species (occupancy, ψ) may be an alternative to monitoring abundance as a state variable (MacKenzie & Nichols 2004). Determining the proportion of occupied sites will generally be much less

expensive than estimating the abundance of the target species at multiple sites. An early example of an occupancy approach is the survey methods used to assess possible effects of timber harvesting on territorial Northern Spotted Owls (*Strix occidentalis caurina*) (Azuma et al. 1990).

The justification for occupancy as an acceptable proxy for abundance is that at an appropriate spatial scale these 2 variables are positively related (Royle & Nichols 2003; MacKenzie & Nichols 2004). Abundance and occupancy measure 2 different but related aspects of population dynamics—the number of individuals of the target species in the landscape and the proportion of the landscape occupied by the target species, respectively (MacKenzie & Nichols 2004). The result is that changes in abundance may not always be reflected as occupancy changes. The strength of the linkage between abundance and occupancy is strongly scale dependent (Royle & Dorazio 2008).

Naïve occupancy values, calculated as the proportion of sampled units where the species was detected, are subject to a negative bias if a species is present but not always detected. The consequence is that changes in naïve occupancy of the target species between 2 periods could be the result of a true change in the species' distribution or simply a change in detectability (MacKenzie et al. 2002).

One important consequence of the relation between detection (p_i) and local abundance (N_i) (Eq. 3) is that it allows for the estimation of a distribution of site-specific abundances on the basis of heterogeneity in detection probabilities among sites (Royle & Nichols 2003). Given any discrete probability distribution for N (e.g., Poisson, $g[N|\lambda]$), the probability of occupancy is derived directly as $\psi = \Pr(N > 0) = 1 - g[N = 0|\lambda]$. Stated simply, occupancy probability is a discrete characterization of a species' abundance distribution (Royle et al. 2005).

Occupancy as discussed here is an estimate of the percent sampled landscape occupied, not necessarily the percent habitat occupied. This distinction is important; for example, a species could occupy 80% of its habitat in 2 periods even if 25% of its habitat has been lost in the interim. Occupancy estimated at the landscape-scale would reflect this change because the sample frame is composed of habitat and nonhabitat (see Flather & Bevers 2002). Moreover, recent advances allow for modeling habitat and occupancy dynamics simultaneously (MacKenzie et al. 2011).

Addressing Species Abundance and Persistence

Scale Issues

Occupancy probability is influenced by the size of the sample unit, where a sample unit may be a discrete habi-

tat patch or relatively continuous habitat that is divided using a grid of cells. In the latter case, if occupancy estimates are to be compared across study areas, species, or time, the size of the sample unit should be held constant. However, selecting an appropriate sample-unit size for occupancy surveys is difficult, particularly in multi-species monitoring programs in which each species may interact with the environment at a different scale (Wiens 1989).

The following survey design could be used to estimate occupancy. The surveyed area is a landscape intersected by a grid that is of sufficient extent to encompass local range boundaries for the target species. Such boundaries occur if the extent of the grid includes habitat that is patchily distributed. Grid cells represent candidate sample units, some of which are surveyed for occupancy. The size of the cells is scaled to the species' pattern of space use estimated from movement data or on the basis of allometric relations. To retain a close relation between occupancy and abundance, the sample unit could be set equal to the average size of an individual's average home range (MacKenzie & Nichols 2004). Grid cells that are too large could support many individuals, and occupancy would be relatively insensitive to changes in abundance. Use of the Royle and Nichols (2003) model (Eq. 3) and expansions of this model that include repeated visits to each sample unit, provide information about the local abundance distribution from the heterogeneity in p_i arising from variation in N_i . However, in Eq. 3 p_i asymptotically approaches 1.0 when $N_i > 15$, unless r is small ($r < 0.1$) (Fig. 2). Therefore, if estimating abundance as well as occupancy is a goal, it may be useful to restrict sample unit size to the range over which p_i and N_i remain functionally dependent.

Occupancy Modeling

Advances in occupancy modeling have expanded the use of detection-nondetection data in monitoring programs. Such data are relatively inexpensive to acquire, include historical survey data (e.g., Tingley & Besissinger 2009), and can be gathered through multiple methods, including genetic analyses (e.g., MacKenzie et al. 2005; Nichols et al. 2008). Species occupancy and the processes that cause change in occupancy (e.g., local extinction and colonization) are a direct measure of a species' spatial distribution within a defined landscape. Temporal and spatial variation in species' occupancy patterns and associated dynamics allow inference to changes in abundance (MacKenzie & Nichols 2004).

Methods exist for surveys of single or multiple species over one or more "seasons" (e.g., years [MacKenzie et al. 2006]). These methods are based on the assumptions that species are not always detected when present and that reliable inference can be made from independent surveys if detection, occupancy, and occupancy dynamics are

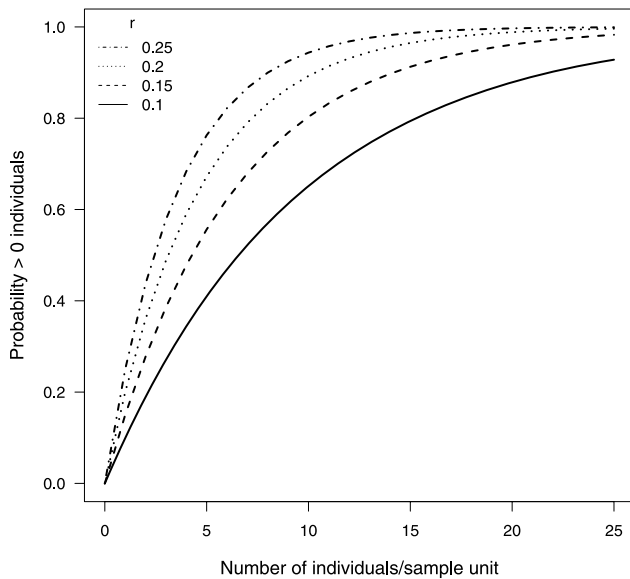


Figure 2. Effects of changes in the number of individuals per sample unit and net detection probability for 4 levels of individual detection probability on the basis of the Royle-Nichols model (Eq. 3).

simultaneously estimated. As such, these methods represent a substantial improvement over logistic-regression models that ignore imperfect detection (Gu & Swihart 2004; MacKenzie et al. 2006).

Occupancy-based monitoring programs typically encompass large areas containing numerous sampling units or sites. These sites may be naturally occurring patches of habitat (i.e., wetlands or stream reaches) or independent subunits of a specified size (e.g., grid cells). A subset of sites is chosen with probabilistic sampling, and multiple independent surveys are conducted over a period of time during which there is assumed to be no change in the occupancy status of the sites (i.e., sites are either occupied or unoccupied by the target species during the sampling period). These surveys can take many forms, including repeated visits, independent observers, multiple-detection methods, or spatial subsampling (but see Kendall and White [2009] for potential biases). During each survey of a site the target species is recorded as detected (1) or undetected (0), which creates a detection history for each sampled site that is then used to model species occurrence and detection probabilities.

MacKenzie et al. (2002) define 2 types of parameters for occupancy models: ψ_i , the probability that site i is occupied by the target species, and p_{ij} , the probability of detecting the species at site i during the j th survey of the site. For example, if 4 surveys at site i resulted in the observed detection history of 1 0 1 0, a probability statement describing the data would be

$$\text{Pr}(1010) = \psi_i p_{i,1}(1 - p_{i,2})p_{i,3}(1 - p_{i,4}).$$

The site is occupied by the target species, detected during the first and third survey, but not detected during the second and fourth survey. Sites where the detection history consists of all zeros (0, 0, 0, 0) are ambiguous with regard to species occurrence. For each of these sites, the species may be present, but not detected, or the species may not occur at the site (i.e., the site was unoccupied). Written as a mathematical expression, each of these sites would have the following probability:

$$\begin{aligned} \text{Pr}(0000) = & \psi_i(1 - p_{i,1})(1 - p_{i,2})(1 - p_{i,3})(1 - p_{i,4}) \\ & + (1 - \psi_i). \end{aligned}$$

Such detection-history data and the corresponding probability model are combined to form a likelihood function, and estimates are obtained via software programs, such as MARK (White & Burnham 1999) or PRESENCE (MacKenzie et al. 2006).

Alternatively, a hierarchical modeling approach may be taken, and would apply especially if spatial units are aggregated across multiple levels (e.g., sites within a landscape and among multiple landscapes). In a hierarchical framework, one set of model components apply to the true spatial process of species occurrence across the sampled sites; then conditional on this true spatial process, a sampling component models the detection process. These hierarchical components (process and sampling) are combined under a Bayesian framework, and statistical inference is achieved with Markov chain Monte Carlo (MCMC) methods (e.g., Royle & Dorazio 2008). Both the likelihood and Bayesian frameworks allow species occurrence and detection to be modeled as a function of covariates (e.g., habitat features), which are often the focus of management decisions and biological inference regarding factors influencing changes in occupancy.

If temporally replicated surveys are conducted over a period when the population can be considered demographically and geographically closed, hierarchical models may be used to estimate parameters describing the distribution for local abundance (Royle 2004; Royle & Dorazio 2008). For example, local abundance among sites (N_i) may be modeled with a Poisson distribution with mean λ , where λ denotes the average abundance of individuals per site. In this case, λ may be modeled as a function of site-specific covariates and occupancy is a derived parameter, where $\psi = 1 - \exp(-\lambda)$. Such methods are especially useful for detection-nondetection data if variation in local abundance is likely to result in site-specific variation (heterogeneity) in species detection probabilities (Royle & Nichols 2003). Moreover, these models emphasize the direct relations among detection probability, local abundance, and occupancy while accounting for imperfect detection (Royle et al. 2005).

Recent advances in occupancy models allow for the estimation of multiple occupancy states (e.g., unoccupied, occupied at low or high abundance [Nichols et al.

2007]) and incorporate the possibility of false-positive detections that may be present in multispecies monitoring programs (McClintock et al. 2010; Miller et al. 2011).

Estimation of Occupancy Vital Rates

We propose that landscape-scale monitoring programs focus on how species' distributions change over time. The dynamic processes of local extinction and colonization result in changes in species occurrence over time and space. MacKenzie et al. (2003) extend the so-called single-season occupancy models discussed above to include 2 dynamic parameters: ε_t , the probability that an occupied site in season t becomes unoccupied in season $t + 1$ (local extinction), and γ_t , the probability that an unoccupied site in season t is occupied by the target species in season $t + 1$ (local colonization). These multiseason models still require that multiple independent surveys be conducted on all (or a subset of) sites within a season, over a period in which the occupancy state at each site is static. Probability models and likelihoods are developed in the usual fashion, and inference can be based on either maximum likelihood or MCMC implementation of hierarchical models. Environmental covariates can be modeled and constraints can be imposed that address hypotheses about factors believed to influence extinction and colonization probabilities (MacKenzie et al. 2003, 2006).

Recent extensions of the basic dynamic occupancy model include multiple occupancy states (e.g., occupied with and without breeding [MacKenzie et al. 2009]) and joint modeling of habitat and species dynamics (e.g., Martin et al. 2010; MacKenzie et al. 2011). These extensions allow one to investigate the causal factors leading to changes in occupancy and the effects of management activities.

The fundamental relation between occupancy and abundance (Eq. 3 & Fig. 2) is also apparent when one considers extinction and colonization dynamics of survey sites over time. Under equilibrium conditions, occupancy is $\Psi^* = \frac{\gamma}{\gamma + \varepsilon}$. For fixed colonization rate (γ), an increase in abundance decreases extinction probability (ε) (Fig. 1) and increases Ψ^* . Thus, system-level extinction probability is a function of average occupancy probability.

Surveys of Animal Sign

Abundance modeling generally involves repeated sampling of populations for which the identity of individuals is often required. Occupancy modeling, however, only requires species identification. Thus, detection-nondetection data can be created from a much broader array of detection methods, which makes collection of these data both more efficient and applicable to many species.

Detection-nondetection data can be obtained in various ways, including direct (visual) or indirect (acoustic or photographs from remote cameras) detections at a site during a survey and detections of evidence that the species was at the survey location sometime in the recent past (e.g., tracks, hair, scat, or other species-specific sign). However, the period to which the sign can be referenced may be more ambiguous for some types of signs than for others. One of the most significant advances in detection-nondetection monitoring takes advantage of the ability to confirm the presence of a species at a site based on its genetic signature (e.g., derived from hair or scat samples) (Waits 2004; Schwartz et al. 2006). Much of the emphasis in recent noninvasive survey methods has been directed at abundance estimates, and these methods have revolutionized monitoring of rare and elusive species such as large carnivores (Long et al. 2008). However, abundance estimation requires high-quality samples and amplification of multiple regions of the nuclear genome and collected samples must conform to the requirements of capture-mark-recapture estimation (i.e., multiple identifications per individual). In contrast, because occupancy modeling does not require individual identification, costs of DNA analyses are significantly lower (Waits 2004).

Genetic identification at the species level, generally on the basis of unique patterns in the mitochondrial genome, has a number of appealing features. First, individual cells generally have many mitochondria; therefore, the number of copies of mitochondrial DNA (mtDNA) in a sample is generally orders of magnitude greater than nuclear DNA. From a practical standpoint, this means that even poor samples can produce reliable species identifications, which increases the potential ways in which these samples can be collected and reduces the need to obtain fresh, high-quality samples (e.g., Haile et al. 2009).

Second, for species identification, the same areas of the genome are amplified to identify multiple species. For example, identical primers amplify the same variable region of mtDNA for all mammals (Kocher et al. 1989). Thus species-specific primers often are not required for species identification. If amplifying species-specific shorter subregions is necessary, designing these primers is straightforward because the entire region can be sequenced on the basis of the existing primers and has been sequenced for many species already. Recently, this concept has been expanded with the idea of identifying or barcoding all species by using the same area of the mitochondria. Ratnasingham and Hebert (2007), for example, identified a 648 base-pair region of cytochrome c oxidase I (COI) as a barcode area for all animal species.

Multiple species can also be identified from a single sample with the same assays (Pegard et al. 2009). In addition, sequences associated with species identification (i.e., DNA sequences unique to a species but invariant within the species) have been identified for thou-

sands of species, and the many published DNA-based phylogenies (which generally use these same areas of mtDNA) provide the raw material to develop new species-level identifications on the basis of existing data.

Third, many species are morphologically cryptic in the field, and their identification requires destructive sampling and often microscopic observation for positive identification. For cryptic species, track and scat identification and particularly DNA sequences provide by far the most reliable, least expensive, and least invasive means of identification.

Target Species

Even with the efficiencies gained by monitoring occupancy as a state variable, the task of species-level monitoring remains daunting due to the large number of species. A requirement to monitor the population status of all species, even if monitoring is restricted to vertebrates, places an impossible burden on most land-management agencies. Modern approaches that are based on genetic sampling and occupancy estimation make that mandate more achievable today, but only if monitoring is restricted to a relatively small number of species. Lack of funding alone restricts monitoring to a subset of native species.

It was beyond the scope of our work to fully review methods for selecting species for monitoring. There has been considerable debate in the ecological literature about the feasibility of using surrogate species as a basis for inferences about the entire species pool (e.g., Landres et al. 1988; Simberloff 1998; Andelman & Fagan 2000). For example, the assumption that individual species can act as direct surrogates of other, unmeasured species is untenable unless those species share very similar population drivers (Landres et al. 1988; Cushman et al. 2010). Nevertheless, surrogate approaches are a pragmatic necessity for assessing overall plant and animal diversity (Wiens et al. 2008; Noon et al. 2009; Caro 2010). Caro (2010; see also Wiens et al. 2008) proposes species be considered for monitoring if they can be used to identify areas of conservation significance or to document effects of environmental change on biological systems or are used in public-relations exercises (e.g., game species).

Ultimately, the choice of which subset of species to monitor will be based on management objectives. The hope is that such decisions are transparent, that the monitored species inform conservation decisions made by agencies, and that the monitoring program produces data that can be used to make reliable inferences about the effects of management decisions on a larger suite of species.

Summary

Knowledge of the status of animal species at a landscape scale is difficult to acquire. Estimates of abundance, or

its underlying processes (survival and reproduction), are expensive to acquire, require extensive field surveys and often the capture and marking of animals. Monitoring programs in which abundance is the state variable for multiple species are impractical. However, recent advances in methods of data analyses, animal detection techniques, and changes in state variable from estimates of abundance to occupancy make it more feasible to monitor species at the landscape scale.

Estimating a species' occupancy requires significantly fewer resources than estimating its abundance. Data on occupancy, as a measure of spatial distribution, in some cases allows inference to changes in a species' abundance and provides a means to assess the effects of management and land use. Landscape-scale monitoring on the basis of presence-absence data has been proposed previously (e.g., Bart & Klosiewski 1989; Manley et al. 2004, 2005; Pollock 2006). Recent advances in survey methods and statistical models allow for the correction of false absences in such data by estimating detectability (MacKenzie et al. 2006) and provide unbiased estimates of a species spatial distribution. Advances in noninvasive survey methods have increased the efficiency of detection-nondetection survey methods that are based on animal sign (Schwartz et al. 2006; Long et al. 2008).

Our focus has been on individual species. However, there are some species groups that lend themselves to omnibus surveys (i.e., true multispecies surveys). In these cases (e.g., breeding birds), multispecies monitoring is feasible (Manley et al. 2004) and occupancy methods have been developed for multispecies surveys (MacKenzie et al. 2006; Zipkin et al. 2010). In addition to providing indirect insights to changes in abundance of several species, information from multispecies occupancy surveys can be used to test the assumption that the species selected for monitoring provide insights into the large suite of unmonitored species (Flather et al. 2009).

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