Perturbation analysis for patch occupancy dynamics

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Abstract. Perturbation analysis is a powerful tool to study population and community dynamics. This article describes expressions for sensitivity metrics reflecting changes in equilibrium occupancy resulting from small changes in the vital rates of patch occupancy dynamics (i.e., probabilities of local patch colonization and extinction). We illustrate our approach with a case study of occupancy dynamics of Golden Eagle (*Aquila chrysaetos*) nesting territories. Examination of the hypothesis of system equilibrium suggests that the system satisfies equilibrium conditions. Estimates of vital rates obtained using patch occupancy models are used to estimate equilibrium patch occupancy of eagles. We then compute estimates of sensitivity metrics and discuss their implications for eagle population ecology and management. Finally, we discuss the intuition underlying our sensitivity metrics and then provide examples of ecological questions that can be addressed using perturbation analyses. For instance, the sensitivity metrics lead to predictions about the relative importance of local colonization and local extinction probabilities in influencing equilibrium occupancy for rare and common species.

Key words: Aquila chrysaetos; Denali National Park, Alaska; detection probabilities; elasticity; Golden Eagles; local extinction and colonization probabilities; patch occupancy models; rarity; sensitivity.

INTRODUCTION

Dynamic patch occupancy models are usually concerned with processes that govern the patterns of patch occupancy (i.e., presence or absence of species or a local population in a patch) in space and time (Simberloff 1969, Lande 1987, Hanski 1999, Moilanen 1999). These models have been widely used to address questions in evolutionary ecology, population ecology, and conservation (Lande 1987, Hanski 1999, Moilanen 1999, Amarasekare and Possingham 2001). The relatively recent development of statistical models to estimate patch occupancy and local rates of patch extinction and colonization, while accounting for detectability, have tremendously increased the potential of patch occupancy models to address ecological questions and conservation problems (MacKenzie et al. 2003, 2006).

A simple model for patch occupancy dynamics is represented by the following equation (e.g., MacKenzie et al. 2006):

$$\psi_{t+1} = \psi_t \times (1 - \varepsilon_t) + (1 - \psi_t) \times \gamma_t \qquad (1)$$

where ψ_t denotes the proportion of patches occupied at time t, and ε_t and γ_t are local probabilities of patch extinction and colonization, respectively. Eq. 1 represents a simple Markov chain model in which state of a

patch (occupied or not) at one time $(t + 1)$ depends on state of the patch the previous time (t). Eq. 1 can also be written in matrix form (MacKenzie et al. 2006):

$$\Pi_{t+1} = \Phi_t \Pi_t \qquad (2)$$

where

$$\Pi_t = \begin{pmatrix} \psi_t \\ 1 - \psi_t \end{pmatrix}$$

and

$$\Phi_t = \begin{pmatrix} 1 - \varepsilon_t & \gamma_t \\ \varepsilon_t & 1 - \gamma_t \end{pmatrix}.$$

When the Markov chain model described in Eq. 1 is written in matrix form it becomes clear that there are some analogies between this model and the matrix population models often encountered in the ecological literature (e.g., $\mathbf{n}(t + 1) = \mathbf{An}(t)$, where $\mathbf{n}$ is a population stage vector and $\mathbf{A}$ is a population projection matrix; see Caswell [2001]).

If local probabilities of extinction and colonization are constant over time ($\varepsilon_t = \varepsilon$, $\gamma_t = \gamma$, $\Phi_t = \Phi$), then a system governed by the above expressions will attain dynamic equilibrium. In this case, equilibrium occupancy, ψ^*, is defined as the first element of the right eigenvector associated with the dominant eigenvalue of Φ, which corresponds to the stationary distribution of the Markov chain (e.g., Caswell 2001). Equilibrium

occupancy can be readily computed by substituting $\psi*$ for both ψ_t and ψ_{t+1} in Eq. 1 and solving:

$$\psi* = \frac{\gamma}{\gamma + \varepsilon}. \qquad (3)$$

Equilibrium occupancy is thus defined by system vital rates (ε and γ) and provides a convenient descriptive statistic reflecting the well-being of a metapopulation system (e.g., Ferraz et al. 2007). We view equilibrium occupancy as an analog of asymptotic rate of population growth, λ, for density-independent populations (e.g., Caswell 2001), and equilibrium population size, $N*$, for density-dependent populations (e.g., Grant and Benton 2003), in the sense that it is a metric that is defined by system vital rates and that can be used to describe system well-being.

A topic of particular interest in the study of system dynamics is the change in dynamics and/or equilibrium state expected to result from changes in system vital rates. Because different system vital rates frequently respond differently to changes in the environment or to conservation efforts, relative system response to the different rates is a topic of special interest. For example, in the case of patch occupancy dynamics, local extinction probability is typically thought to be a function of patch size (among other things), whereas local colonization probability is typically thought to be a function of connectivity with respect to potential sources of colonists (e.g., MacArthur and Wilson 1967, Hanski 1999, Ferraz et al. 2007). Just as sensitivity of population growth rate (λ) to changes in key vital rates (e.g., survival and fertility rates) is important to studies of evolutionary and population ecology (e.g., Gaillard et al. 1998, Pfister 1998, Benton and Grant 1999, Caswell 2001), sensitivity of equilibrium occupancy to changes in probabilities of local extinction and colonization is a topic of interest in studies of patch occupancy dynamics (e.g., see Amarasekare and Possingham [2001] and Kean and Barlow [2004] using different models). Several authors have shown that perturbation analysis in the context of Markov chains is a powerful tool to study community and population dynamics (e.g., Caswell 2001, Hill et al. 2004). Here, our focus is on perturbation analyses of equilibrium occupancy of dynamic patch occupancy models. These models are widely used by ecologists, and recent development of robust statistical estimation models for "presence–absence" survey data (MacKenzie et al. 2003, 2006) has led to an increase in the number of reliable estimates of model parameters.

In this paper, we present expressions for sensitivity and scaled sensitivity (e.g., elasticity [Caswell 2001], variance stabilized sensitivity [Link and Doherty 2002]) metrics reflecting changes in $\psi*$ resulting from small changes in the vital rates (i.e., local patch colonization rate, γ; and local patch extinction, ε). We then consider data from a case study of occupancy dynamics of nesting Golden Eagles (*Aquila chrysaetos*) in Denali National Park (Denali), Alaska. We investigate the hypothesis of

system equilibrium using competing models expressing different hypotheses about the time specificity of the vital rates. We then use vital rate estimates from these models to estimate equilibrium patch occupancy of Golden Eagles. We compute estimates of sensitivity, elasticity, and variance-stabilized sensitivity and discuss their implications for Golden Eagle population ecology and management. We conclude with a general discussion of the intuition underlying some of the sensitivity expressions and of ecological and conservation questions that can be addressed using these types of sensitivity analyses.

SENSITIVITY METRICS

Sensitivity

Sensitivity of $\psi*$ to parameter θ (s_θ) measures the change in $\psi*$ resulting from a very small change in θ; s_θ can be computed as the partial derivative of $\psi*$ with respect to θ, or $\partial\psi*/\partial\theta$ (see Caswell [2001] for discussion of sensitivity of λ to changes in vital rates). Expressions for the sensitivity of $\psi*$ (s_θ) to local probabilities (θ) of colonization (γ), extinction (ε) and persistence (ϕ; i.e., the complement of extinction: $\phi = 1 - \varepsilon$) are presented below:

$$s_\gamma = \frac{\partial\psi*}{\partial\gamma} = \frac{\varepsilon}{(\gamma + \varepsilon)^2} \qquad (4)$$

$$s_\varepsilon = \frac{\partial\psi*}{\partial\varepsilon} = -\frac{\gamma}{(\gamma + \varepsilon)^2} \qquad (5)$$

$$s_\phi = \frac{\partial\psi*}{\partial\phi} = \frac{\gamma}{(\gamma + 1 - \phi)^2}. \qquad (6)$$

Of course sensitivity of $\psi*$ to small changes in colonization (s_γ) and persistence (s_ϕ) are positive, whereas sensitivity to extinction (s_ε) is negative. In order to compare the magnitudes of these metrics we use the absolute values.

Examination of Eqs. 4 and 5 leads to some inferences about the relationship between sensitivities to changes in extinction and colonization. For example, if $\gamma > \varepsilon$, then $|s_\varepsilon| > |s_\gamma|$; if $\gamma = \varepsilon$ then $|s_\varepsilon| = |s_\gamma|$; and if $\gamma < \varepsilon$ then $|s_\varepsilon| < |s_\gamma|$. From Eq. 1, we know that if $\gamma > \varepsilon$, then $\psi* > 0.5$; if $\gamma = \varepsilon$ then $\psi* = 0.5$; and if $\gamma < \varepsilon$ then $\psi* < 0.5$. Therefore, if $\psi* > 0.5$ then $|s_\varepsilon| > |s_\gamma|$; if $\psi* = 0.5$ then $|s_\varepsilon| = |s_\gamma|$; and if $\psi* < 0.5$ then $|s_\varepsilon| < |s_\gamma|$. In contrast, $|s_\varepsilon| = |s_\phi|$ for all values of γ and ε between 0 and 1. Thus, knowledge of either equilibrium occupancy or the rates of extinction and colonization permit inference about the relative magnitudes of the sensitivities of these rate parameters.

Elasticity

Elasticities (see Caswell 2001) are sensitivities that are scaled to represent proportional changes, for example in equilibrium occupancy, resulting from proportional changes in local extinction or colonization. Elasticity

of equilibrium occupancy with respect to parameter θ would thus be defined as

$$e_\theta = \frac{\partial \log(\psi*)}{\partial \log(\theta)} = \frac{\partial \psi*/\psi*}{\partial \theta/\theta} = s_\theta \left(\frac{\theta}{\psi*} \right). \quad (7)$$

Elasticities for local probabilities of colonization, extinction, and persistence are thus

$$e_\gamma = \frac{\gamma}{\psi*} \frac{\partial \psi*}{\partial \gamma} = \frac{\varepsilon}{\gamma + \varepsilon} \quad (8)$$

$$e_\varepsilon = \frac{\varepsilon}{\psi*} \frac{\partial \psi*}{\partial \varepsilon} = -\frac{\varepsilon}{\gamma + \varepsilon} \quad (9)$$

$$e_\phi = \frac{\phi}{\psi*} \frac{\partial \psi*}{\partial \phi} = \frac{\phi}{\gamma + 1 - \phi}. \quad (10)$$

Hence, $|e_\gamma| = |e_\varepsilon|$ and $|e_\phi| \neq |e_\varepsilon|$.

Variance-stabilized sensitivities

Link and Doherty (2002) noted that there are various ways to scale sensitivities and recommended the use of a variance-stabilizing transformation as a basis for scaling. There are several advantages of this approach to scaling. For example, when such scaling is used as a basis for ranking demographic parameters with respect to relative importance, it attributes equal importance to complementary rates (e.g., mortality and survival), whereas proportional scaling (elasticity) does not. We computed the variance-stabilized sensitivities (VSS_θ) of $\psi*$ to changes in θ as follows:

$$VSS_\theta = \frac{\partial [\sin^{-1}(\sqrt{\psi*})]}{\partial [\sin^{-1}(\sqrt{\theta})]} = \frac{\sqrt{\theta(1-\theta)}}{\sqrt{\psi*(1-\psi*)}} \frac{\partial \psi*}{\partial \theta}$$

$$= \frac{\sqrt{\theta(1-\theta)}}{\sqrt{\psi*(1-\psi*)}} s_\theta. \quad (11)$$

Variance-stabilized sensitivities of equilibrium occupancy with respect to local probabilities of extinction and colonization are as follows:

$$VSS_\gamma = \frac{\sqrt{\varepsilon(1-\gamma)}}{(\gamma + \varepsilon)} \quad (12)$$

$$VSS_\varepsilon = -\frac{\sqrt{\gamma(1-\varepsilon)}}{(\gamma + \varepsilon)} \quad (13)$$

$$VSS_\phi = \frac{\sqrt{\gamma \phi}}{(\gamma + 1 - \phi)}. \quad (14)$$

Hence, $|VSS_\phi| = |VSS_\varepsilon|$.

METHODS

Our interest in the perturbation metrics presented above was motivated by an interest in the potential management of Golden Eagles in Denali. Management options include such possibilities as regulations designed to minimize disturbance of nesting birds. Potential nesting territories are viewed as patches, and management objectives may be expressed in terms of a desired proportion of territories occupied by nesting eagles. This focus on occupancy leads naturally to a consideration of the ability of management actions to influence the relevant vital rates, probabilities of local extinction and colonization. Here we use data from occupancy surveys conducted in Denali from 1988 to 2007 to (1) investigate recent dynamics of Golden Eagles in these nesting territories, (2) estimate occupancy and rates of local extinction and colonization, and (3) use these estimates to investigate sensitivity with some of the metrics we have described here.

Surveys

The study area for the Golden Eagles data set covered 1800 km^2 and was located in the northeast portion of Denali National Park, Alaska (see McIntyre and Adams 1999 for details). From 1988 to 2007, Golden Eagles territories were surveyed annually between April and July. We used data for up to three surveys per seasons. The surveys were conducted by helicopter and complemented by foot following methods described in McIntyre and Adams (1999). All potential territories were observed on the first survey each year. Potential territories consisted of the historical nesting sites. The first survey was conducted in late April or early May after most pairs had completed their clutches, before most nest failure occurred, and before any hatching occurred. If evidence of occupation was observed during the first survey (i.e., territorial behavior, eggs in nest, incubating bird, nest construction, nest maintenance), the territory was considered occupied and it was not visited again until late in brood rearing (mid to late July) to assess nesting success and fledging production (but this information was not included in our analysis). On the other hand, if no evidence of occupation was detected on the first survey, it was surveyed again up to two times during the nesting season until evidence of occupation was detected. In other words, occupancy of eagle territories was reported only until eagles were observed for the first time (within a year) in a territory (the so-called "removal design" of MacKenzie et al. 2006). Additional details about data collection are presented in McIntyre and Adams (1999).

Statistical analysis

In the context of the Golden Eagle study, the patches under investigation were the 93 potential nesting territories with detection history data from 1988 to 2007. These data were then modeled as functions of parameters associated with the sampling process and with the underlying process of patch occupancy dynamics. Detection probability, $p_{t,i}$, reflects the probability that nesting eagles were detected during visit i in year t, given that the patch was occupied in year t.

Territory extinction probability, ε_t, is the probability that a territory occupied in year t is unoccupied by eagles in year $t + 1$. Territory colonization probability, γ_t, is the probability that a territory unoccupied in year t is occupied by eagles in year $t + 1$. The probability that a territory is occupied in year t is ψ_t. We applied statistical models proposed by MacKenzie et al. (2003) and implemented in program MARK (White and Burnham 1999).

Our most general model used a parameterization of the following form (see MacKenzie et al. [2003] for details): $\psi(1)\varepsilon(t)\gamma(t)p(t,.)$, where $\psi(1)$ indicates the probability that a territory is occupied at time $t = 1$ (i.e., during the first year), and other parameters are modeled as year specific for all years of the study. Restrictions on the time-specific structure of this general model are denoted as (.), indicating no time variation. We constrained detection probabilities within a year (i.e., among secondary occasions) to remain constant over time; however, we allowed detection probabilities to vary among years (i.e., among primary occasions) or remain constant over the years. Thus, $p(t,.)$ indicated a model where p varied among primary occasions but remained constant among secondary occasions, whereas $p(.,.)$ indicated a model were p remained constant among primary and secondary occasions. We had to constrain p to remain constant among at least some of the secondary occasions because occupancy of eagle territories was reported only until eagles were observed for the first time (within a year) in a territory.

The sensitivity metrics described above pertain to the situation of a stationary Markov process, a process in which the same probabilities of patch extinction (ε) and colonization (γ) apply each year, producing an equilibrium occupancy, ψ^*. Although we believe that the concepts of equilibrium occupancy and associated sensitivities are relevant and interesting even in cases where a stationary Markov process does not exist (see analogous arguments for projection matrix asymptotics in Caswell 2001), we wanted to draw inferences about the existence of stationarity (models with $\psi(1)\varepsilon(.)\gamma(.)$). Note that even if ε and γ remain constant over time, patch occupancy may vary over time because the system has not yet reached the equilibrium (i.e., the system may be experiencing transient dynamics, see MacKenzie et al. [2006]).

We ranked our models based on the Akaike's information criterion adjusted for small sample size; models with the lowest AIC_c were considered to represent the most parsimonious descriptions of the variation in the data (AIC_c [Akaike 1973, Burnham and Anderson 2002]). We used AIC_c weight (w) as a measure of relative support for each model. Values of w range from 0 to 1 (with 0 indicating no support from the data; and 1 indicating maximum support [Burnham and Anderson 2002]). We also present ΔAIC_c (ΔAIC_c for the ith model was computed as $AIC_{ci} - \min (AIC_c)$, see Burnham and Anderson [2002]).

RESULTS

Statistical analysis of territory occupancy for eagles

Models $\psi(1)\varepsilon(.)\gamma(.)p(t,.)$ and $\psi(1)\varepsilon(.)\gamma(.)p(.,.)$ received the most support from the data based on AIC_c weight (w for these two models were 0.8 and 0.2, respectively; ΔAIC_c was 0 and 2.8, respectively; see also Appendix). Based on the model $\psi(1)\varepsilon(.)\gamma(.)p(t,.)$, the estimate of ε was 0.05 (estimated standard error, SE = 0.006), the estimate of γ was 0.25 (SE = 0.026), and the estimate of ψ at time $t = 1$ was 0.87 (SE = 0.04). Models $\psi(1)\varepsilon(t)\gamma(.)p(t,.)$, $\psi(1)\varepsilon(.)\gamma(t)p(t,.)$, and $\psi(1)\varepsilon(t)\gamma(t)p(t,.)$ received considerably less support from the data ($w \sim 0$, $\Delta AIC \geq 15.5$; see also Appendix), consistent with the hypothesis of approximately constant probabilities of extinction and colonization over time.

Equilibrium occupancy and sensitivity metrics for eagles

The equilibrium territory occupancy based on estimates of ε and γ obtained from model $\psi(1)\varepsilon(.)\gamma(.)p(t,.)$, was 0.833. Sensitivity metrics based on estimates of ε and γ obtained from model $\psi(1)\varepsilon(.)\gamma(.)p(t,.)$ were: $s_\varepsilon = -2.8$, $s_\gamma = 0.6$, $VSS_\varepsilon = -1.6$, and $VSS_\gamma = 0.6$. Thus $|s_\varepsilon| > |s_\gamma|$ and $|VSS_\varepsilon| > |VSS_\gamma|$. See Fig. 1 for a graphical representation of the relationships between vital rate θ (i.e., ε or γ), ψ^*, s_θ, and VSS_θ for eagles in Denali.

DISCUSSION

The expressions of sensitivity of equilibrium patch occupancy to changes in vital rates just presented provide some interesting insights about the relationship between sensitivity (s_ε and s_γ), local extinction (ε), local colonization (γ), and equilibrium occupancy (ψ^*). In particular, the value of equilibrium patch occupancy determines whether $|s_\varepsilon|$ will be greater, smaller, or equal to $|s_\gamma|$. This dependence of sensitivity on equilibrium occupancy was predicted, because equilibrium occupancy specifies the proportion of patches exposed to the processes of colonization and extinction. For instance, if ψ^* for a given species is greater than 0.5, then the equilibrium occupancy for this species should be more sensitive to changes in local patch extinction than to changes in local patch colonization. This makes intuitive sense, because when equilibrium occupancy is high ($\psi^* > 0.5$), local patch extinction applies to more patches than does local patch colonization. In contrast, when equilibrium patch occupancy is low ($\psi^* < 0.5$), local patch colonization applies to more patches. Therefore, for this situation it was expected that equilibrium occupancy would be more sensitive to changes in local patch colonization than to changes in local patch extinction. In the case of the eagles in Denali, we found that equilibrium patch occupancy was about 0.83; thus, equilibrium occupancy for this population is more sensitive to small changes in local territory extinction than to small changes in local patch colonization (see also Fig. 1a, b). For the purpose of comparing the sensitivity values for the two vital rates it may be
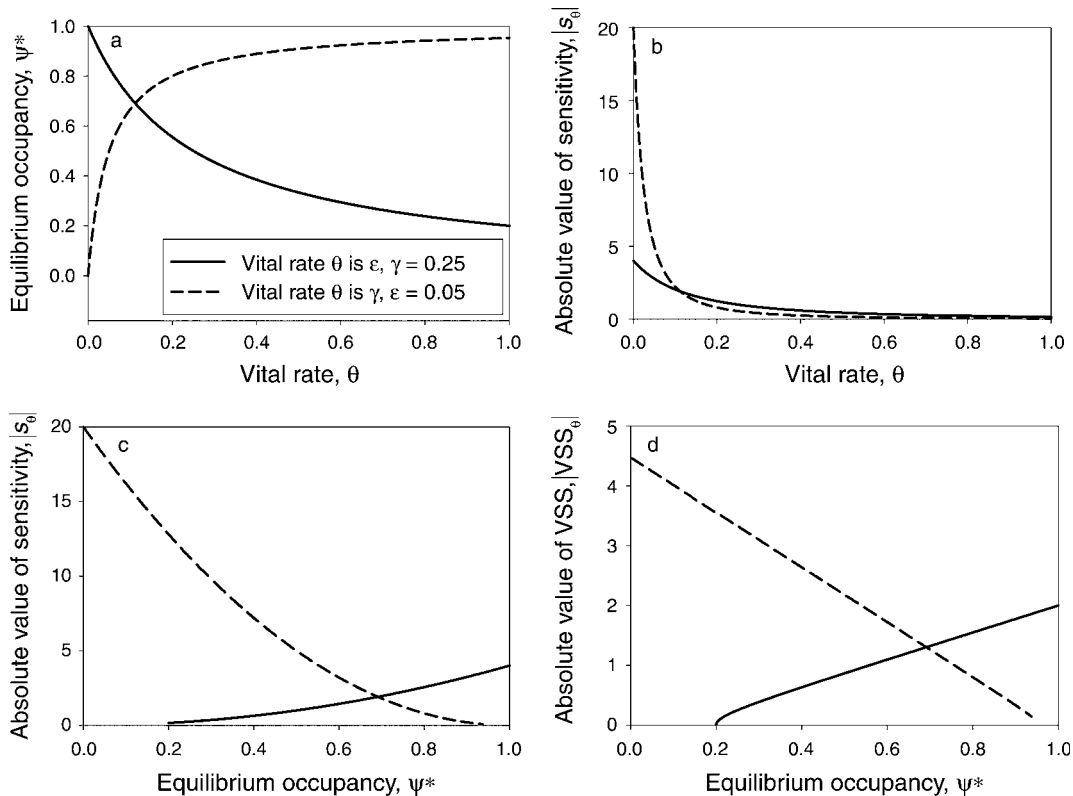
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FIG. 1. Relationships between vital rate θ (i.e., local probability of extinction [ε] and local probability of colonization [γ]), equilibrium patch occupancy (ψ^*), sensitivity of ψ^* to changes in vital rate θ (here we present the absolute value of sensitivity $|s_\theta|$), and variance-stabilized sensitivity (here we present the absolute value of variance-stabilized sensitivity $|VSS_\theta|$) based on estimates of ε and γ for Golden Eagles in Denali National Park. (a) The relationship between ε and ψ^* with γ fixed to 0.25 (solid line), and the relationship between γ and ψ^* with ε fixed to 0.05 (dashed line). (b) The relationship between ε and $|s_\varepsilon|$ with γ fixed to 0.25 (solid line) and the relationship between γ and $|s_\gamma|$ with ε fixed to 0.05 (dashed line). (c) The relationship between ψ^* and $|s_\varepsilon|$ with γ fixed to 0.25 (solid line) and the relationship between ψ^* and $|s_\gamma|$ with ε fixed to 0.05 (dashed line). (d) The relationship between ψ^* and $|VSS_\varepsilon|$ with γ fixed to 0.25 (solid line) and the relationship between ψ^* and $|VSS_\gamma|$ with ε fixed to 0.05 (dashed line).

tempting to compute elasticity (relative sensitivity) of ψ^* to changes in these vital rates (e_γ and e_ε). However, this metric sometimes leads to confusing inferences. For example, the absolute values of elasticities for extinction and its complement (persistence) are different $|e_\phi| \neq |e_\varepsilon|$. Link and Doherty (2002) provide a detailed discussion of this topic in the context of asymptotic population growth rate. Conversely, the variance stabilized-sensitivity metric (VSS$_\theta$; see *Methods* and *Results*) recommended by Link and Doherty (2002) is consistent with the sensitivity metric s_θ in that $|s_\varepsilon| = |s_\phi|$ and $|VSS_\phi| = |VSS_\varepsilon|$ (see Eqs. 5, 6, 13, and 14). The patterns of changes in sensitivity are consistent between these two metrics (see also Fig. 1c, d).

Given that the sensitivity metrics we have described above assume that the system has reached equilibrium occupancy, it makes sense to evaluate the hypothesis of system equilibrium using competing models expressing different hypotheses about the time-specificity of the vital rates. In the case of the eagles in Denali, we found some evidence to support the hypothesis of constant local probabilities of colonization and extinction, which

then yield a constant patch occupancy. However, we believe that the use of sensitivities to gain insight into influences of rate parameters on equilibrium occupancy is a reasonable exercise even for systems not currently at equilibrium.

Sensitivity of λ to changes in key vital rates has proven to be an important tool in the study of evolutionary and population ecology (e.g., Gaillard et al. 1998, Pfister 1998, Benton and Grant 1999, Caswell 2001). Similarly, the relative sensitivities of equilibrium occupancy to changes in probabilities of local extinction and colonization may yield interesting predictions about the relative importance of factors associated with these vital rates for rare vs. common species. For the purpose of this discussion we view rare species as those that occupy a small proportion of patches or habitat within a landscape, as opposed to common species that occupy a large proportion of patches. This is an operational definition, and we recognize that there are other ways to view rarity (e.g., Kunin and Gaston 1997, Kean and Barlow 2004). However, because of its deliberate simplicity (e.g., we ignore local abundance and focus

exclusively on geographic range), this view offers some intuitive insights that would be otherwise difficult to perceive. For example, we noted above that when $\psi^* < 0.5$ (e.g., relatively rare species), $|s_\varepsilon| < |s_\gamma|$, that is, equilibrium occupancy is more sensitive to changes in local colonization than in local extinction probabilities. Therefore, factors that induce changes in dispersal abilities and other attributes associated with colonization are expected to have a greater impact on occupancy of species that tend to be relatively rare across the landscape than to common species (e.g., see Ferraz et al. 2007).

Many investigators have noted the positive relationship between occupancy and abundance (e.g., Brown 1984, Gaston and Blackburn 2000, He and Gaston 2003). Without posing any sort of causal explanation, we note that extinction probability should be more influential than colonization for common species and that this probability is strongly influenced by abundance (e.g., MacArthur and Wilson 1967, Burgman et al. 1993). In addition to the expectation of variation in the relative importance of local extinction and colonization processes for species that tend to be relatively common vs. rare, we also note that populations of a single species tend to have higher occupancy at locations near the center than near the periphery of the species range (e.g., Brown 1995, Brown et al. 1996). Recent macroecological studies have provided some evidence of higher rates of extinction and turnover at peripheral vs. central portions of species ranges (e.g., Karanth et al. 2006). This latter expectation illustrates the point that any characteristics of a patch or sample unit that influence probabilities of local extinction and colonization (e.g., patch size and isolation [Ferraz et al. 2007]) also influence equilibrium occupancy and occupancy dynamics. Thus, there may be no "typical" sensitivity of occupancy for a species. Instead, we expect sensitivity of occupancy to changes in extinction and colonization to be dependent on patch location and other patch characteristics such as habitat.

One motivation for computing s_θ and its scaled analogs is to obtain possible insights about the potential effectiveness of management actions. For instance, if an objective is to find management actions that will be most influential with respect to ψ^*, one may want to favor actions that will affect the vital rates with the highest s_θ or VSS_θ. Other things (e.g., costs) being equal, actions that influence colonization (e.g., provision of corridors) are likely to be more effective for relatively rare species. These inferences have obvious implications for conservation (or control) of desired (or undesired) populations of organisms. For our example of Golden Eagles at Denali, assume that one management action is likely to influence patch extinction probabilities of eagles whereas another influences primarily colonization. Because of the high equilibrium occupancy and resultant higher sensitivity to local extinction, we would be most likely to consider the action expected to influence extinction, other things (e.g., cost) being equal.

Although we believe that sensitivities may provide useful insights to managers, we also agree with authors who have cautioned about the blind reliance on sensitivity metrics to focus management actions (see Heppell et al. 2000, Link and Doherty 2002, Nichols and Hines 2002). For example, the following metric expresses the sensitivity of changes in ψ^* to dollars spent on selected management actions (see Nichols and Hines 2002 for a similar metric in the context of λ):

$$m_\theta = \frac{\partial \psi *}{\partial \theta} \frac{\partial \theta}{\partial x} \frac{\partial x}{\partial y}$$

where x is management action, which can be viewed as a continuous variable (e.g., proportion of eagle nests protected from human disturbance), and y is the cost associated with this action (e.g., expressed in dollars). In addition, $\partial \psi^*/\partial \theta$ is the sensitivity of ψ^* to changes in parameter θ; $\partial \theta/\partial x$ is the sensitivity of parameter θ to changes in action x (which measures how a small change in action x will affect parameter θ); and $\partial x/\partial y$ is the sensitivity of action x to changes in monetary expenditure y (reflects the cost associated with the management actions). Thus, m_θ measures the change in ψ^* resulting from the influence of a small change in management action x on vital rate θ per unit cost associated with the action (see also Nichols and Hines 2002). We believe that this metric, m_θ, provides a reasonable framework for thinking about sensitivity analyses of ψ^* and management actions.

In conclusion, the sensitivities of equilibrium occupancy to changes in probabilities of local extinction and colonization may be useful in the study of patch occupancy dynamics. The sensitivity expressions presented here provided intuitive interpretations that we found useful to our understanding of patch occupancy dynamics. Our development has been focused on the simplest of patch occupancy models, in the sense that a patch is either occupied or not. This development follows the initial theoretical models for patch occupancy dynamics as well as the initial work on estimation of dynamic parameters (MacKenzie et al. 2006). Just as the work on estimation has been extended recently to deal with multistate patch dynamics (e.g., MacKenzie et al. 2006, 2009, Nichols et al. 2007), we believe that sensitivity analyses for patch occupancy can be extended readily to these models. This generalization should prove useful as these more general approaches to estimation and modeling for patch occupancy dynamics become more common.

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APPENDIX

Model selection of patch occupancy models for Golden Eagles in Denali National Park (*Ecological Archives* E090-002-A1).