ON THE IMPORTANCE OF LANDSCAPE HISTORY FOR ASSESSING EXTINCTION RISK

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Abstract. Assessment of extinction risk may depend not only upon the current state of the landscape and its projected trajectory of change, but also on its past disturbance history. We employed a spatially structured demographic model to evaluate extinction risk for several generic migratory songbirds within landscapes subjected to ongoing habitat loss and fragmentation. We generated different scenarios of dynamic landscape change using neutral landscape models, in which breeding habitat was systematically destroyed at various rates (0.5%, 1%, or 5% per year) and degrees of fragmentation, thus enabling us to determine the relative contribution of these factors to population declines. Extinction risk was assessed relative to the *vulnerability threshold,* the point where the change in population growth rate ($\Delta\lambda$) scaled to the rate of habitat loss (Δh) falls below -1% ($\Delta\lambda/\Delta h = -0.01$). Our model predicts that songbirds are likely to exhibit lagged responses to habitat loss in landscapes undergoing rapid change (5% per year). In such scenarios, the landscape changed more rapidly than the demographic response time of the population, such that population growth rates never exceeded the vulnerability threshold, even though these species inevitably went extinct. Thus, songbirds in landscapes undergoing rapid change might not be assessed as "at risk" until the population's demographic potential has been seriously eroded, which would obviously compromise the success of management actions aimed at recovering the population. Furthermore, our model illustrates how assessment of a species' extinction risk may vary widely among landscapes of similar structure, depending upon how quickly the landscape achieved its current state. Thus, information on the current landscape state (e.g., amount of habitat or degree of fragmentation) may not be sufficient for assessing long-term population viability and extinction risk in the absence of information on the history of landscape disturbance.

Key words: conservation; disturbance; dynamic landscapes; extinction thresholds; habitat fragmentation; habitat loss; landscape history; migratory songbirds; spatially explicit population models.

INTRODUCTION

Landscapes are dynamic systems shaped by a variety of natural disturbances operating across a wide range of spatial and temporal scales (Delcourt and Delcourt 1988). Human land-use activities have significantly altered the disturbance architecture (sensu Moloney and Levin 1996) of many landscapes, in ways that may exceed the rate, severity, and spatial extent of even the largest natural disturbances (Turner and Dale 1998). In particular, human land-use activities have contributed to the rapid loss and fragmentation of native habitats in many landscapes and have been implicated in the decline and extinction of species worldwide (Wilcove et al. 1998).

Observed declines in many migratory bird populations, for example, have been attributed to the loss and fragmentation of breeding habitat (e.g., DeSante and George 1994, Freemark et al. 1995, Coppedge et al. 2001, Donovan and Flather 2002). Habitat loss and fragmentation cause population declines in birds through a combination of factors that reduce population size and reproductive success (Robbins et al. 1989*b*, Askins 1995, Faaborg et al. 1995, Keyser et al. 1998). For example, population density is expected to decline as a function of patch size, and certain area-sensitive species may not occupy small patches that otherwise meet their habitat and territory size requirements (Robbins et al. 1989*a*, Wenny et al. 1993, Hoover et al. 1995). Many species have lower nesting success in habitat fragments owing to higher levels of nest predation and brood parasitism (Paton 1994, Robinson et al. 1995, Flaspohler et al. 2001).

Although these patch-scale effects of habitat loss and fragmentation are well documented, the population status or viability of a species at broader landscape and regional scales cannot be inferred from patch-based metrics alone, particularly if regional persistence is influenced by source–sink dynamics, which appear to characterize many migratory songbird populations (Donovan et al. 1995, Brawn and Robinson 1996). However, two recent studies have contributed to our understanding of how fragmentation effects on distri-

bution and demography translate into population declines of breeding songbirds at the landscape scale (Donovan and Lamberson 2001, With and King 2001). Although they differ in detail, both studies coupled a spatially structured demographic model with a neutral landscape model (With 1997) to explore how habitat fragmentation affected the capacity of the landscape to support populations of a generic migratory songbird. In Donovan and Lamberson (2001), birds varied in area sensitivity, which affected their distribution among habitat patches across the landscape, and in fecundity, with reproductive success varying inversely with patch size. Donovan and Lamberson generated a series of landscapes with the same amount of habitat (30%) but differing in degree of fragmentation. The results of their model demonstrated how area sensitivity (in which individuals preferentially breed in the largest patches) could overcome the adverse local effects of fragmentation on reproductive success, thereby enabling populations to persist ($\lambda \geq 1$), provided the landscape was not extensively fragmented. Thus, Donovan and Lamberson's (2001) study resolved how two life-history traits (area sensitivity and fecundity) interacted with habitat fragmentation to influence population persistence at the landscape scale.

In contrast, With and King's (2001) study evaluated the relative effects of both habitat abundance and fragmentation on population persistence at the landscape scale for generic migratory songbirds differing in life-history traits. As in the previous study, With and King's demographic model included functions for both area sensitivity and fecundity (*edge sensitivity*, where reproductive success declined with increasing patch edge : area ratio). They generated a large array of landscape scenarios in which both the amount of habitat (1–90%) and the degree of fragmentation were varied independently to produce complex landscape patterns along a gradient of fragmentation. As a consequence, they were able to identify thresholds in population persistence (*extinction thresholds*) as the critical level of habitat at which population growth rates fell below replacement levels ($R'_0 < 1$ or equivalently, $\lambda < 1$). Extinction thresholds varied widely depending on the landscape and species in question, which argues against the adoption of general "cookbook prescriptions" regarding how much habitat is enough for population persistence (e.g., the "20% rule"; Fahrig 1997).

Despite this progress toward understanding how the spatial effects of habitat fragmentation ultimately translate into population declines of birds at a landscape scale, we do not yet understand how the dynamics of habitat loss and fragmentation (i.e., temporal effects) interact with avian demography to influence extinction risk. Landscapes were assumed to be static in the two studies just discussed. Even though assessments of extinction risk were made for populations on landscapes along a fragmentation gradient (gradient over space), the landscapes themselves did not undergo a process

of habitat loss and fragmentation (gradient over time). This "space-for-time" substitution is very common in both theoretical and empirical studies of habitat fragmentation, although habitat fragmentation is clearly a time-dependent and ongoing process in many landscapes. Different trajectories of landscape change, such as in the rate of habitat destruction, may give rise to similar landscape patterns, but nevertheless may have different implications for the status and long-term viability of populations within these landscapes. For example, if the rate of landscape change occurs faster than the demographic response time (e.g., generation time) of the species, populations may exhibit a lagged response to habitat loss (i.e., extinction debt; Tilman et al. 1994, Hanski and Ovaskainen 2002, Nagelkerke et al. 2002). Populations in rapidly changing landscapes may initially appear unaffected by habitat loss, but could then decline precipitously years or decades later, even after the disturbance has been halted.

The conservation of migratory songbirds necessarily must be done within a dynamic landscape context, particularly where human land-use activities drive landscape change. Any conservation or land management principles obtained from demographic models based on static landscapes will likely have only limited applicability to situations in which habitat loss is ongoing or occurred in the recent past. We therefore used a modeling approach to assess extinction risk in a dynamic landscape context for several generic migratory songbirds that differ in their sensitivity to fragmentation (area and edge sensitivity). More specifically, our goal was to evaluate the relative effects of habitat loss, fragmentation, and the rate of landscape change on the rate of decline for these hypothetical migratory bird populations. Thus, our model application here is *strategic*, used to generate general insights and to test hypotheses regarding the interaction between avian demography and dynamic landscape change, rather than *tactical*, used to explore the consequences of different land-use change scenarios for particular bird species. Our model results support the prediction of lagged population responses to landscape change, and demonstrate the importance of landscape history for evaluating extinction risk. In practice, population risk assessment will require an understanding of both the spatial and temporal dimensions of landscape disturbance on demography. Such insights ultimately may contribute to the development of general principles and management guidelines for mitigating extinction risk in migratory songbirds within landscapes subjected to ongoing habitat loss and fragmentation.

METHODS

Generation of dynamic landscape scenarios

Scenarios of landscape change were generated using neutral landscape models (With 1997), in which the spatial pattern of disturbance was modeled as a fractal

distribution using the midpoint displacement algorithm (for details, see Gardner 1999). Landscape grids (128 × 128 cells) were initially entirely suitable ($h = 100\%$) for breeding. Breeding habitat is defined here as a single type (e.g., forest, grassland, shrubland). A time series of landscapes was then generated in which a fixed percentage of the initial habitat was destroyed at each time step (year) at a constant rate until the landscape was entirely denuded ($h = 0\%$). Although we explored a variety of habitat loss rates (r), we settled on three levels ($r = 0.5$, 1.0, and 5.0% lost per year) as being representative of the rates of habitat destruction reported for real landscapes (e.g., Spies et al. 1994, Moreira et al. 2001), and also representative of the range of results that we observed in our model. For a given rate of loss, the spatial contagion of disturbance (H) was varied among three levels of fragmentation ($H = 0.0$, 0.5, and 1.0). At one extreme, disturbances were correlated in space ($H = 1.0$), such that habitat loss was concentrated in a particular region of the landscape over time, resulting in the maintenance of large, intact tracts of habitat (i.e., habitat was clumped, not fragmented). At the other extreme, disturbances were negatively correlated ($H = 0.0$), such that habitat loss initially produced small pockets of disturbance scattered across the landscape (i.e., habitat was extensively fragmented) (for examples of fractal landscape patterns, see With and King 2001).

Habitat loss was modeled as an absolute rather than a relative rate, such that a fixed percentage of the original habitat (landscapes were initialized with 100% habitat) was lost each year, rather than a percentage of the remaining habitat on the landscape. Thus, the amount (percentage) of breeding habitat available in a given year is simply the cumulative amount lost over previous years, $h = 100 - rt$, where r is the rate at which habitat is lost and t is the number of time steps (years) over which habitat loss has occurred. Given the rates of habitat loss that we explored in this analysis, the amount of breeding habitat available on the landscape after 20 years of habitat destruction would be 90% ($r = 0.5$), 80% ($r = 1.0$), or 0% ($r = 5.0$). Although habitat fragmentation did not affect the absolute amount of habitat on the landscape, it did affect the suitability of habitat patches for breeding birds through its influence on patch size and shape. Habitat fragmentation could, for example, influence whether individuals would settle in the patch (area sensitivity) and thus could affect population size within individual patches, or the resulting edge effects (a function of patch edge : area ratios) might affect nesting success (edge sensitivity). These relationships between patch size and patch occupancy and between patch geometry and nesting success are described in *Model description*. The combination of habitat loss rates (r) and degree of fragmentation (H) resulted in nine scenarios of landscape change (three rates of habitat loss by three levels of fragmentation). Each scenario consisted of a time series of maps in which the landscape was subjected to the specified rate of habitat loss and level of fragmentation until total denudation. For example, landscape scenarios in which habitat was destroyed at a rate of 0.5% per year required a time series of 200 maps, 100 maps were required to capture a time series in which habitat was lost at a rate of 1% per year, whereas only 20 maps were needed to capture the time series for landscapes subjected to a 5% per year rate of habitat loss. For each scenario of landscape change ($r \times H$), we generated 10 replicate time series. Thus, the experimental design of our simulations represented a 3 × 3 factorial with $n = 10$ replicates. The spatially structured avian demographic model was then run on each of these replicated scenarios of dynamic landscape change.

Model description

The model used here, dSSAD (dynamic Spatially Structured Avian Demography), is a demographic model for territorial, migratory bird populations in dynamic landscapes subjected to chronic habitat loss and fragmentation, and is an extension of the demographic model described by With and King (2001) for migratory songbirds in static landscapes. The model applies to monogamous territorial birds that establish and defend all-inclusive territories within which nesting and most foraging take place (Hinde 1956, Morse 1989). The model can be applied, for example, to most temperate-zone warblers and other Neotropical migrants. In fact, the model was expressly developed as an assessment tool for evaluating the status and future management options for the Henslow's Sparrow (*Ammodramus henslowii*), a migratory songbird, within a heavily disturbed landscape (King et al. 2000). The model structure thus incorporates relevant aspects of a migratory bird's breeding biology, using demographic data that are commonly available in the literature or that could be feasibly collected in the field as part of a population assessment. Demographic and landscape data required for model implementation are also discussed in With and King (2001).

Comparison with conventional avian demographic models.—dSSAD integrates a conventional avian demographic modeling approach with a landscape perspective on how spatial pattern influences demographic rates. Annual changes in the population are described by an age-structured matrix population model parameterized from a demographic life table and life cycle graph analysis. In traditional avian life-table analysis and demographic modeling, the age-specific birth rate b_x, the expected number of female offspring produced per female of age x (or the equivalent maternity function m_x) is a free parameter estimated empirically from data on reproductive success. In the model described here, the birth rate b_x is an explicit function of the spatial pattern of breeding habitat, which is a largely novel feature of our model (With and King 2001). Be-

cause the landscape's spatial pattern changes over time, the resulting demographic model is nonlinear and time dependent. This is in contrast to more traditional avian demography in which the models are often linear and time invariant. The time-dependent calculation of b_t as a function of spatial pattern and the state of the population is described in *Effect of patch structure on the probability of nesting success and fecundity*.

Species-defined landscapes.—Although the spatial dimensions of the landscape are arbitrary in a theoretical investigation such as this, we nevertheless needed to assign dimensions to the grid cells to permit identification of habitat patches suitable for breeding, defined as those patches that fulfill the territory size and minimum area requirements for the species. We set the resolution of the grid to 30 m, consistent with the resolution of commonly available data obtained from satellite imagery (e.g., Landsat Thematic Mapper). As a consequence, the spatial extent of our landscapes (128 × 128 cells) was ~14.5 km² or ~1452 ha. We calibrated the model to ensure that a closed population on a landscape of this size would persist if $h = 100\%$ (see *Assessment of population viability*). Thus, population dynamics are normalized for landscape size and are not scale dependent, such that modeling populations on larger or smaller landscapes would not affect the results of this study.

For each map in a time series of landscape change (see *Generation of dynamic landscape scenarios*), we identified individual habitat patches that could be used for nesting (see *Patch occupancy and breeding densities within patches*). Cells of breeding habitat separated by less than the distance that a nesting pair will readily cross in using and defending their territory (i.e., their gap-crossing ability; Dale et al. 1994) are aggregated into patches. For the purposes of this analysis, all species were assumed to possess the same gap-crossing abilities (<30 m) and territory size (0.5 ha; Table 1). This territory size is consistent with that of many Neotropical migratory songbirds that breed in woodlands (e.g., Morse 1989). A territory of this size incorporates six habitat cells (aligned either adjacently or diagonally) on the model landscape (one cell = 900 m² × 6 cells = 5400 m² or 0.54 ha). Habitat patches smaller than this size are not used for nesting, but the probability that patches of a given size will be occupied (and by how many breeding pairs) is determined by species-specific incidence functions (see *Patch occupancy and breeding density within patches*). Habitat within a patch is perceived as contiguous and homogeneous; there is no within-patch variability in habitat quality. The matrix between patches is not used for nesting.

Patch occupancy and breeding density within patches.—The number of potential nesting sites or territories within patches larger than the species' territory size is determined by an incidence function J_A that describes the probability of encountering a breeding pair (or territory) at a random point in a patch of area A (Robbins et al. 1989a; Fig. 1A). The probability of occurrence J_A is interpreted as the proportion of the patch occupied at stable, equilibrium population densities, and the number of potential nests n^* in patch i is the occupied area divided by territory size, or

$$n_i^* = J_A \frac{A_i}{A_T} \qquad (1)$$

where A_i is the area (ha) of patch i, A_T is territory size (ha), n_i^* is rounded to the nearest integer, and J_A is calculated with a logistic regression model:

$$J_A = \frac{\exp(\beta_0 + \beta_1 \log_{10} A + \beta_2 \log_{10} A^2)}{1 + \exp(\beta_0 + \beta_1 \log_{10} A + \beta_2 \log_{10} A^2)}. \qquad (2)$$

Here β_0, β_1, and β_2 are regression parameters (Robbins et al. 1989a; Table 1). The maximum number of potential nests in a patch is patch area (A_i) divided by territory size (A_T) and occurs when $J_A = 1.0$.

Nesting females are assigned to patches stochastically, with the probability that an individual female will nest in a particular patch being given by the incidence function J_A. At each time step, females returning to the breeding ground are assigned to patches until all females are settled or all potential nesting sites in all patches are occupied. Accordingly, females preferentially settle in larger patches, especially if species

TABLE 1. Parameter values used in the dynamic spatially structured avian demographic model (dSSAD) to characterize bird species types that differ in their sensitivity to patch area and habitat edge.

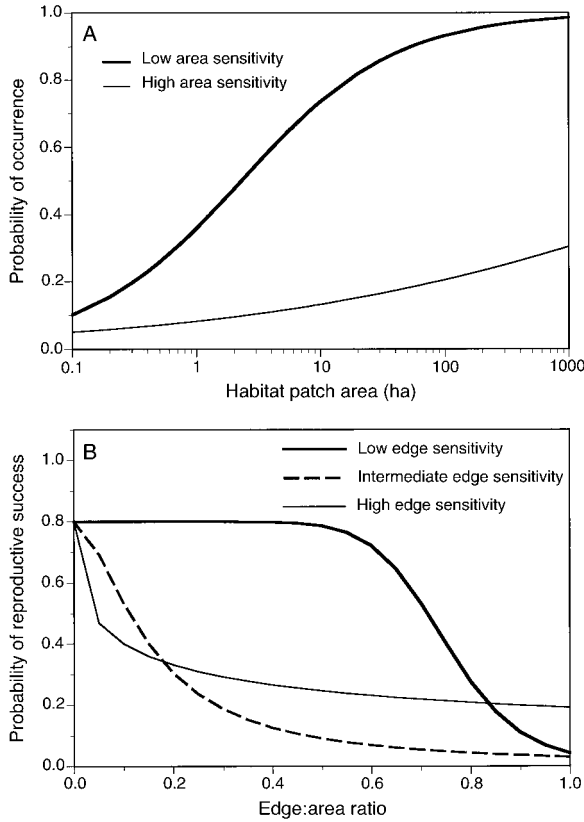| Parameter	Value
Territory size (A_T)	0.5 ha
Gap-crossing ability	<30 m
Juvenile survivorship (s_0)	0.3
Adult survivorship (s)	0.6
Age of first reproduction (α)	1 year
Longevity (L)	8 years
Area sensitivity (Eq. 2)	
Low sensitivity	
β_0	−0.579
β_1	1.596
β_2	0.0
High sensitivity	
β_0	−2.411
β_1	0.528
β_2	0.0
Edge sensitivity (Eq. 3)	
Maximum nesting success (S_{max})	0.8
Low sensitivity	
k	0.75
θ	10.0
Intermediate sensitivity	
k	0.15
θ	1.7
High sensitivity	
k	0.10
θ	0.50

FIG. 1. Life-history functions used to define five types of generic migratory songbirds. (A) Area sensitivity functions (Eq. 2), with occurrence depending on patch area. High area sensitivity is modeled after the Veery (*Catharus fuscescens*), and low area sensitivity after the Red-eyed Vireo (*Vireo olivaceus*) (Robbins et al. 1989*a*). (B) Edge sensitivity functions (Eq. 3), with reproductive success depending on the edge : area ratio.

exhibit a high degree of area sensitivity. Thus, smaller patches are less ''preferred'' and are unlikely to be occupied when population abundance is low. When the size of the landscape population exceeds the number of potential nests in all patches, surplus females are not assigned to nests but remain in the population as nonreproductive ''floaters.'' Floaters do not contribute to actual births (the numerator in Eq. 5), but they necessarily influence the population per capita birth or maternity rate via the denominator in Eq. 5. However, because the populations in these simulations are more demographically limited by survivorship and fecundity than by total habitat or available nests, ''floaters'' are rare or nonexistent except for short periods in the extreme circumstances near the end of the simulations with very little habitat remaining. Consequently, ''floaters'' have little impact on simulated population dynamics, but do function to conserve live females in the closed population.

Effect of patch structure on the probability of nesting success and fecundity.—Nesting success, the proba-

bility that a nest will produce at least one fledgling (Johnson and Temple 1986), is a function of a patch's edge : area ratio. Nesting success is assumed to be lower in patches with a high edge : area ratio, based on empirical studies that have documented lower nesting success in such patches owing to higher rates of nest predation and brood parasitism (Robinson et al. 1995, Flaspohler et al. 2001). Maximum nest success is thus assumed to occur in large patches with relatively little edge. The edge : area ratio is normalized by the edge : area ratio (e_i) of a single grid cell, which yields a maximum value of 1.0 (maximum edge per unit area). An edge index value near 0.0 indicates a patch with minimal edge per unit area.

The probability of nesting success in patch i, S_i, is given by

$$S_i = S_{max} \frac{1}{1 + (e_i/k)^\Theta} \qquad (3)$$

where S_{max} is the maximum probability of nesting success in patches with an edge index approaching zero (i.e., nesting success in the absence of any edge effect), and e_i is the normalized edge index of patch i. The parameter k is the value of e_i where $S_i = 0.5 \, S_{max}$, and Θ is a parameter that determines the rate at which nesting success declines with larger edge : area ratios.

Nesting success in the absence of any edge effect, S_{max}, will always be less than one; some nests will be lost to predation, storms, or other factors regardless of their proximity to an edge. The probability of nesting success will be less than one even in the largest, most contiguous patch of habitat. Some species will be relatively insensitive to edge, at least until patches become mostly edge (i.e., $e_i \rightarrow 1$). We refer to this pattern as a Type I edge response (low edge sensitivity; Fig. 1B). Other species will be very sensitive to edge, and the probability of nesting success will decline very rapidly with increasing edge index (a Type III response; Fig. 1B). Others will show an intermediate response of more gradual decline with increasing edge per unit area, at least initially (Type II; Fig. 1B). Calibration of the parameters S_{max}, k, and Θ enable the nesting success curve of Eq. 3 to be fitted to any observed or hypothesized response to edge within this family of response curves (e.g., Table 1).

Nesting success is evaluated stochastically for each nest in a patch. The probability that a nest in patch i fledges no young is $1 - S_i$. Nests that fledge at least one young are assumed to fledge the entire clutch, so F_{ji}, the number of fledglings from nest j in patch i, is

$$F_{ji} = \begin{cases} C_{ji} & \text{for successful nests} \\ 0 & \text{for unsuccessful nests} \end{cases} \qquad (4)$$

where C_{ji} is the clutch size of nest i in patch j. Clutch size C for each nest is drawn independently from a species- or population-specific frequency distribution. Consequently, clutch size may vary among nests. In

this analysis, we assume that clutch size represents a uniform distribution of 4–5 eggs. The sex of each fledgling is determined stochastically according to the population's fledgling female : male sex ratio. Thus, it is possible for a nest to produce only male or only female fledglings. Cumulatively across all nests in the landscape, however, the ratio of female to male fledglings will approach the population's or species' fledgling sex ratio (normally assumed to be 1:1 or 50% females; Table 1).

The demographic parameter b_t, the expected number of female fledglings produced per female at time t, is

$$b_t = \frac{\sum_{i=1}^{m} \sum_{j=1}^{n_i} F_{ji}}{N_a} \quad (5)$$

where F_{ji} is the number of female fledglings in successful nest j of patch i, and N_a is the total number of adult (reproductive) females in the population, including the non-nesting "floaters." The model assumes that productivity is independent of age after sexual maturity. The maternity function m_x, the number of female fledglings produced by a female of age x, is then $m_x = b_t$ for all ages $x \geq \alpha$, where α is the age of first reproduction. The model assumes no reproductive senescence or decline in fecundity with age (Nichols et al. 1980, Lande 1988, Noon and Biles 1990).

Assessment of population viability.—The maternity function b_t is combined with age-specific survivorship to create a life table for the landscape population (Leslie 1966, Mertz 1971, Nichols et al. 1980, Lande 1988, Noon and Biles 1990). Annual survival probabilities are defined for two age classes: juveniles s_0 and adults s (Table 1). The life table is used to parameterize an age-structured matrix population model that assumes a postbreeding census (Caswell 2001:25). This Leslie matrix is used to project the number of females in the population forward for one year. This new population and the landscape at time $t + 1$ is used to calculate the maternity function b_{t+1} following Eqs. 1–5, and this annual cycle is repeated for the duration of the simulation (until all habitat has been destroyed).

Net lifetime maternity or net reproductive rate R_0 is calculated as

$$R_0 = \sum_{x=\alpha}^{\omega} l_x m_x \quad (6)$$

where R_0 is the expected lifetime production of females by a female fledgling, l_x is the probability of survivorship to age x from the life-history table, α is age of first reproduction (1 year; Table 1), and ω is the age of last reproduction (8 years; Table 1). For a stable age distribution, when $R_0 = 1.0$, a female replaces herself in her lifetime, and the population is stable. If $R_0 < 1.0$, the population is declining, and if $R_0 > 1.0$, the population is increasing.

At each time step, the population's finite rate of increase λ_t is given by the solution of the characteristic equation (Lande 1988):

$$\lambda_t^{\alpha} - s\lambda_t^{\alpha-1} - b_t l_{\alpha} = 0. \quad (7)$$

Here $\alpha \geq 1$ is the age of sexual maturity and $0 < s < 1$. If $\lambda_t = 1.0$, the population is stable. When $\lambda_t < 1.0$, the population is declining, and if $\lambda_t > 1.0$, the population is increasing.

A model run began by placing a population of one of these species in a landscape consisting entirely of suitable breeding habitat ($h = 100\%$). We assumed a stable population with $R_0 = 1.0$, and calculated the corresponding steady-state maternity function $b^* = m_x^*$ (Eq. 6). The matrix model was parameterized with this value of b^*, and the model was "spun" forward in time until both population size and the age class distribution reached steady state (the change in population was <1.0 female per year) and $\lambda = 1.0$. Maximum nesting success S_{max} (Eq. 3) consistent with b^* and the steady-state adult female population N_a^* was calibrated from Eq. 5:

$$\sum_{i=1}^{m} \sum_{j=1}^{n_i} F_{ji} = 0.5(S_{max} n_{max}^* C_{max}). \quad (8)$$

Here n_{max}^* is the maximum number of nests predicted from Eq. 1 for the entire landscape area, and C_{max} is maximum clutch size for the species. This initialization and parameter calibration provided for a stable age distribution and no change in the population in the absence of habitat loss.

Assessment of extinction risk and thresholds in population viability.—Because we initialized the population on a uniform landscape ($h = 1.0$, or 100% habitat) to have both a stable age distribution and population, the population can only remain stable or decline ($\lambda \leq 1.0$) as habitat is destroyed. Populations that exhibit negative growth ($\lambda < 1.0$) are doomed to eventual extinction, especially given the assumption of a closed-landscape population in this analysis (in open landscapes, such populations may function as sinks, which persist because of immigration from outside source populations; With and King 2001). Because of the initial closely calibrated balance at $\lambda = 1.0$, most populations began declining immediately with loss of habitat, and thus the critical level of habitat at which the population crosses the extinction threshold, defined as $\lambda = 1.0$, is of less interest than how rapidly the population growth rate changes as a function of habitat loss. In our analysis, most scenarios of landscape change precipitated a sudden, rapid decline in population growth rates (i.e., a nonlinear response) at some critical level of habitat loss. Intuitively, the prospects for recovery through intervention are likely to be more remote for populations exhibiting rapid rates of decline. Furthermore, the time available for implementing successful recovery plans is severely limited once this
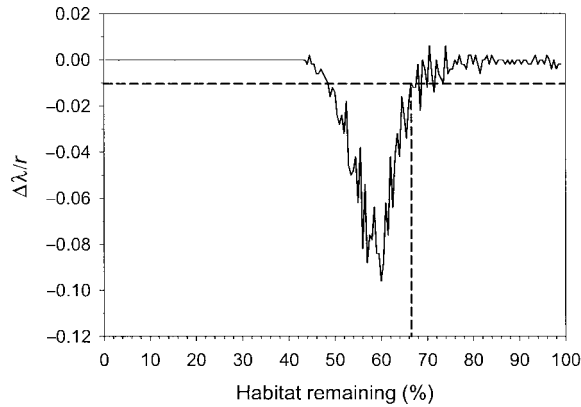
FIG. 2. Change in population growth rates (λ) as a function of the rate of habitat lost per year (r). The vulnerability threshold is defined as the point at which the population consistently falls below a change in the rate of population decline of -1% per year per habitat lost per year ($\Delta\lambda/r = -0.01$). In this example, the change in the population growth rate is gradual until the vulnerability threshold is reached (at 66% habitat; vertical dashed line), at which point there is accelerated change until the population's demographic potential is eroded and the population goes extinct (at 45% habitat).

threshold has been crossed. A rapidly declining population, especially one in which the rate of decline is accelerating, is more vulnerable to extinction, and thus we needed to establish what rate of population decline coincided with a *vulnerability threshold.* By graphing the change in population growth rate per rate of habitat lost per year ($\Delta h = r$)

$$\Delta\lambda/r = (\lambda_{t+1} - \lambda_t)/r \qquad (9)$$

as a function of the amount of habitat h on the landscape, we defined the vulnerability threshold as the point at which $\Delta\lambda/r = -0.01$ (Fig. 2). We chose a conservative value for the threshold analogous to the most conservative IUCN criterion for vulnerability to extinction (e.g., 1% population decline per year; see Caswell [2001], who converted IUCN rates of population decline to values of λ). In effect, $\Delta\lambda/r$ is a measure of the sensitivity of λ to the rate of habitat loss. Our vulnerability threshold values coincided with the point at which population growth rates (λ) began to decline rapidly (i.e., nonlinearly) as a function of habitat loss (Fig. 3).

Analysis of species' responses to dynamic landscape change.—We assessed extinction risk for five generic migratory songbirds that differed in their area and edge sensitivities (Fig. 1), under various scenarios of landscape change (see *Generation of dynamic landscape scenarios*). The five species types exhibited the following combination of traits: (1) low area–low edge sensitivity; (2) low area–high edge sensitivity; (3) low area–intermediate edge sensitivity; (4) high area–low edge sensitivity; and (5) high area–high edge sensitivity. All other demographic parameters were kept constant among these species (Table 1). These are the same

species types used in the spatially structured avian demographic model described by With and King (2001) for static landscapes, with the addition here of a species with intermediate edge sensitivity (Type II; Fig. 1B). This species type was introduced in the current study because it was hoped that it would provide a more sensitive response to landscape change than either extreme (which often produced an ''all or nothing'' response). Data from the Red-eyed Vireo (*Vireo olivaceus*) and Veery (*Catharus fuscescens*) were used to parameterize the incidence functions (Eq. 2) for species with low and high area sensitivity, respectively (Fig. 1A; Robbins et al. 1989*a*), but model results should not be interpreted in the context of these two species because this is only one dimension used to define species types in this analysis. The Red-eyed Vireo also provides a good example of a species with low edge sensitivity, whereas the Ovenbird (*Seiurus aurocapillus*) is an example of a species with high edge sensitivity (Flashpohler et al. 2001). The edge sensitivity functions that we used were not parameterized with empirical data from either of these species, however, and these examples are only provided for illustrative purposes.

A model trial (one for each of the 10 replicated time series for each of the nine landscape scenarios) consisted of 100 realizations of the stochastic model described previously. Model results were averaged across realizations for each trial and these means were averaged across trials. We recorded the mean and standard error of λ for the replicate populations in relation to the amount of habitat remaining.

RESULTS

Effect of disturbance rates on vulnerability thresholds

When habitat was destroyed gradually, at a rate of 0.5% per year ($r = 0.5$), landscape pattern (degree of habitat fragmentation, H) generally had little effect on vulnerability thresholds, except for species with an intermediate degree of edge sensitivity (Fig. 3). For these species, the vulnerability threshold shifted from $h = 66\%$ in clumped landscapes ($H = 1.0$) to 82% in fragmented landscapes ($H = 0.0$). In other words, species with intermediate edge sensitivity exhibited a threshold in vulnerability when only 18% of the habitat had been destroyed if the habitat was also undergoing severe fragmentation, but maintained a relatively steady population growth rate until $\sim34\%$ of the habitat had been destroyed if the landscape was managed so as to preserve large, intact patches of habitat. In general, fragmentation (H) had a greater effect on species with intermediate edge sensitivity than on those with either low or high edge sensitivities (e.g., compare the relative shift in curves among fragmentation levels, H, for the different species types when $r = 0.5$; left-hand column of Fig. 3). Species with low edge sensitivity
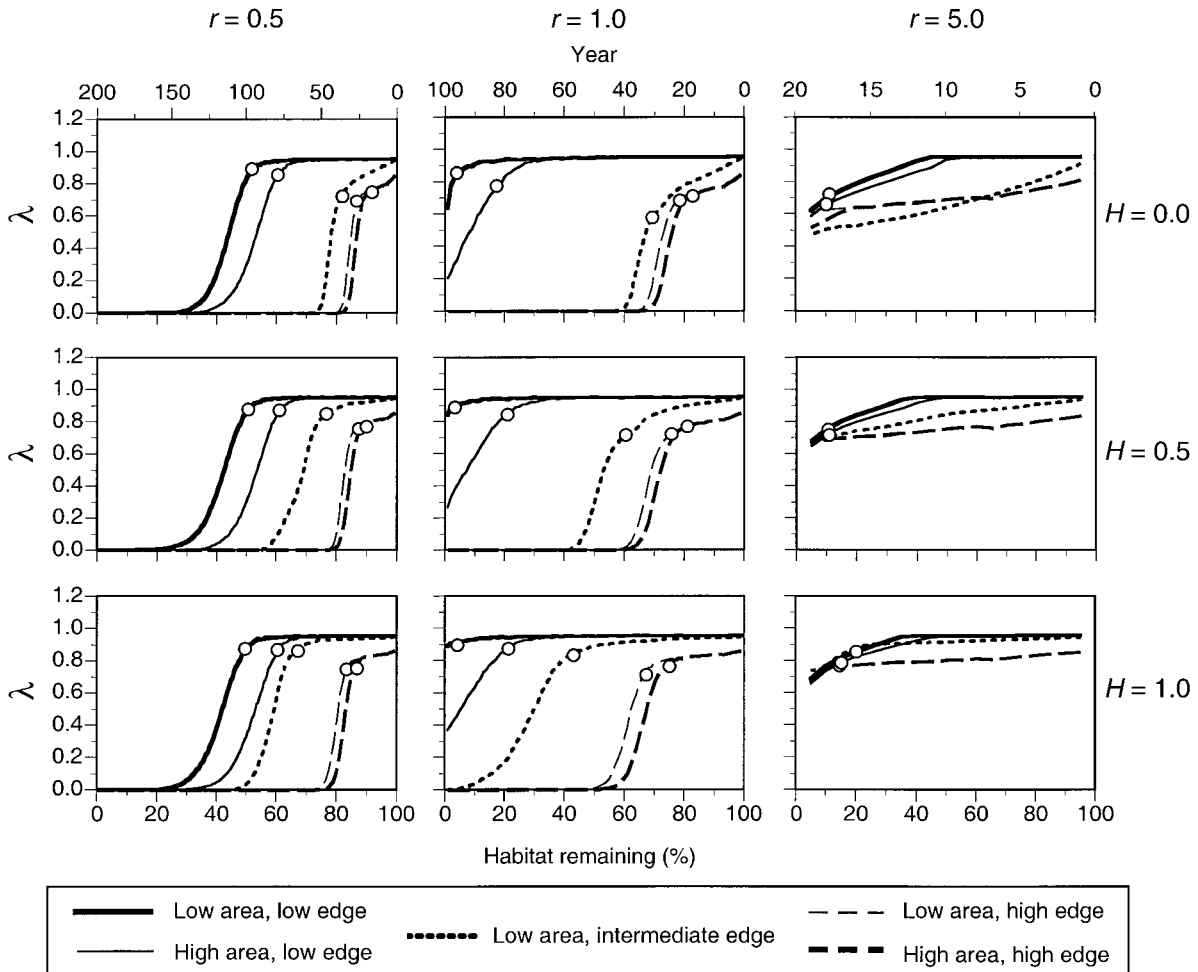
FIG. 3. Effect of landscape fragmentation (*H*) and the rate of habitat loss (*r*), each at three levels, on population growth rates (λ) for species with five combinations of area and edge sensitivities (Fig. 1). Response curves represent the mean of 10 runs on a replicated time series ($n = 10$) for each landscape scenario. The 95% confidence intervals around response curves were extremely small and are not displayed. Nonoverlapping lines can thus be considered statistically significant at the α = 0.05 level. Circles represent the location of the vulnerability threshold of each species–landscape combination (cf. Fig. 2). Note that some species–landscape combinations do not exhibit vulnerability thresholds when habitat loss occurs rapidly (*r* = 5.0).

are so insensitive to edge (given the function that we used in this analysis; Fig. 1B) that the level of fragmentation (*H*) had little effect on population response; populations were more affected by the amount of habitat (*h*). At the other extreme, species with high edge sensitivity are so sensitive (given the function that we used in this analysis; Fig. 1B) that even a little fragmentation had a significant impact on populations. So again, the specific level of fragmentation (*H*) was less important for understanding population response in this species than was the amount of habitat remaining on the landscape (*h*).

All five species types exhibited nonlinear responses to habitat loss, with edge-sensitive species experiencing earlier declines (when 10–16% habitat was destroyed) than species with low edge sensitivity (which only declined after 37–50% of habitat had been de-

stroyed) (Fig. 3). Consequently, the effect of area sensitivity on vulnerability thresholds was much more evident for species with low edge sensitivity. Life-history attributes (edge sensitivity) were generally more important than landscape pattern (degree of habitat fragmentation) in determining vulnerability to extinction when the rate of habitat loss was gradual (i.e., 0.5% of the original habitat loss per year).

The influence of life-history attributes was still evident when the rate of habitat loss was doubled (*r* = 1.0). The magnitude of the effect of landscape pattern on persistence thresholds was again greatest for species with intermediate levels of edge sensitivity (Fig. 3). As the landscape became increasingly more fragmented (*H* = 1.0 → *H* = 0.0), the threshold shifted from ~42% to 69% habitat. In other words, severe habitat fragmentation caused species with intermediate edge sen-

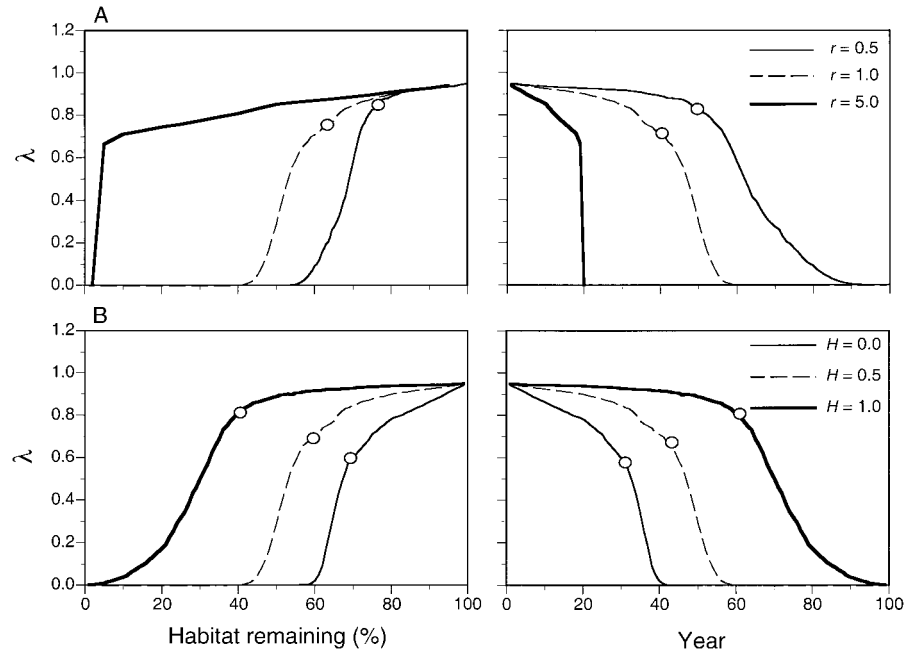FIG. 4. (A) Population growth rates (λ) for species with an intermediate degree of edge sensitivity (cf. Fig. 1B) in landscapes being fragmented ($H = 0.5$) at various rates (r) (left-hand panel), and the growth rates for this species as a function of time in the same landscapes (right-hand panel). (B) Effect of landscape fragmentation (H) on population growth rates for the species with intermediate edge sensitivity in landscapes undergoing a 1% per year loss of habitat ($r = 1.0$) (left-hand panel), and the same data as a function of time in these landscapes (right-hand panel). Circles represent the location of the vulnerability thresholds of each species–landscape combination (cf. Fig. 2). Note that species in landscapes subjected to a rapid rate of habitat loss ($r = 5.0$) in Fig. 4A do not exhibit a vulnerability threshold, as defined by our criterion, although a threshold is apparent in year 20, when the last of the habitat is lost from the landscape.

sitivity to decline rapidly after only 31% of the habitat had been destroyed, whereas population growth rates would otherwise remain steady until 58% of the habitat was lost in a more moderately fragmented ($H = 0.5$) landscape that was managed to preserve larger patches of habitat.

However, when habitat was destroyed rapidly at the rate of 5% per year ($r = 5.0$), such that the landscape was denuded in 20 years, neither landscape pattern (H) nor species life-history attributes (edge and area sensitivities) had very much effect on extinction risk (Fig. 3). All species exhibited linear or near-linear declines in persistence as habitat was destroyed. Threshold effects were conspicuously absent (although a trivial threshold existed at $h = 0$, when $\lambda = 0$).

Time-dependence of vulnerability thresholds

At first glance, it might appear that increasing the rate of habitat destruction actually reduces the population's vulnerability to extinction, by minimizing or eliminating thresholds in the rate of population decline (Fig. 3). This is *not* the case, however, and illustrates a problem with conventional assessments based on how measures of population viability (density or demographic rates) vary solely as functions of static ''snapshots'' of habitat abundance and landscape structure (e.g., level of habitat fragmentation, H) (e.g., Akçakaya

et al. 1995, With and King 2001). The *rate* of habitat loss is also important in interpreting vulnerability thresholds.

For example, a species with intermediate edge sensitivity on a landscape undergoing a moderate degree of habitat fragmentation ($H = 0.5$) appeared to cross the vulnerability threshold at 75% when habitat was lost gradually ($r = 0.5$), but at ~3% when habitat was lost rapidly ($r = 5.0$) (Fig. 4A, left-hand panel). This paradox is resolved when λ is plotted against time, however (Fig. 4A, right-hand panel). When the landscape was being denuded rapidly ($r = 5.0$), the population crossed its vulnerability threshold in less than 20 years, by which time only 3% of the habitat remained. The species' demographic potential (a measure of a population's ability to occupy a landscape, based on life-history characteristics such as reproductive output; Lande 1987) was compromised early, but the population response lagged behind the rapid habitat loss. Rapid landscape change thus decouples demography from landscape structure. In contrast, a population subjected to a slow rate of habitat loss of 0.5% per year would remain relatively stable for ~55 years, with the demographic potential compensating for habitat loss until a threshold was crossed when 75% of the habitat remained (Fig. 4A). Thus, the population would go extinct much sooner in a scenario of rapid landscape

change, as expected. The rate of habitat loss clearly affects the ability of species to persist on landscapes, and the threshold level of habitat at which population decline begins to accelerate (i.e., nonlinearly) is time dependent.

Landscape management might be able to mitigate extinction risk, or at least prolong the time to extinction, for some species in landscapes subjected to chronic habitat loss. For example, a species with intermediate edge sensitivity in landscapes undergoing a 1% per year rate of habitat loss ($r = 1.0$) exhibited greater sensitivity to habitat loss in fragmented ($H = 0.0$) than in clumped ($H = 1.0$) landscapes (Fig. 4B, left-hand panel). The vulnerability threshold shifted from 69% in fragmented landscapes to 42% in clumped landscapes, and the threshold would be reached in 31 years as opposed to 58 years in these two landscape scenarios, respectively (Fig. 4B, right-hand panel). Although the population is declining in either scenario, minimizing fragmentation of the landscape would obviously buy more time for implementing conservation strategies in the hopes of recovering the population.

DISCUSSION

Assessments of extinction risk typically ignore landscape history. Instead, species risk assessments are based either on the capacity of the current landscape to support a viable population (e.g., Akçakaya et al. 1995, Hanski and Ovaskainen 2000, Lindenmayer et al. 2001), or on the probability that the population will persist under various scenarios of future land-use change or proposed land management practices (e.g., Lamberson et al. 1992, Pulliam et al. 1992). Even for assessments that evaluate the effect of future landscape change on population viability, the current landscape condition is generally used as a starting point. This ignores the trajectory by which the landscape achieved its present state (i.e., its disturbance history), or, alternatively, assumes that extant landscapes all lie on the same trajectory of change leading to the present. Consider that the majority of studies (both empirical and theoretical) have attempted to explore the effects of habitat loss on population persistence among landscapes along a gradient in the amount or fragmentation of habitat (e.g., McGarigal and McComb 1995, Fahrig 1997, Trzcinski et al. 1999, Villard et al. 1999, With and King 1999, 2001, Donovan and Lamberson 2001). Implicitly or explicitly, these studies have made a "space-for-time" substitution (Hargrove and Pickering 1992). Disturbance history is ignored, or else all landscapes are assumed to share a similar disturbance history, which is necessary in order to treat each landscape as a treatment that lies along a gradient of "change" (e.g., amount of habitat destroyed). Conclusions are then made as to how "habitat loss" affects population persistence, when, in reality, it is only the effect of habitat difference that is being assayed (i.e., replication in space, rather than in time). Investigation of the effects of habitat loss would require repeated observations of the same landscape over a period of time in which habitat destruction was occurring (replication in time rather than space).

The "space-for-time" substitution is invalid if landscape history is ultimately important for assessing extinction risk. Perhaps the most important implication of our model results is that a species' vulnerability to extinction cannot be predicted simply from the current landscape configuration (i.e., the amount and fragmentation of habitat). Landscapes that have a similar amount of habitat and fragmentation could have arrived at that state via different trajectories with different rates of habitat loss, with very different consequences for species occupying those landscapes. Consider, for example, a population with intermediate edge sensitivity inhabiting a moderately fragmented landscape ($H = 0.5$) in which half of the habitat had been destroyed. Depending upon the rate of habitat loss and how quickly the landscape had arrived at its current state, the rate of population decline may or may not have exceeded the vulnerability threshold (compare different rates of habitat loss at 50% habitat in the left-hand panel of Fig. 4A). Accurate assessment of the population status or viability based on available habitat is impossible unless the history of landscape change (rate of habitat loss) is also known. Most disquieting, this species would not have been assessed as at risk for extinction, at least by our criteria, in the landscape subjected to the most rapid rate of habitat loss, even though time to extinction was actually quickest in this scenario (20 years; right-hand panel of Fig. 4A).

From a slightly different perspective, consider this same species of intermediate edge sensitivity on three different landscapes, each with 50% habitat and moderate fragmentation. The rates of habitat loss are unknown to the assessor or decision maker. Assessment based on relationships between population traits and static landscapes (e.g., With and King 2001) or derived from spatially (rather than temporally) replicated landscapes (the space-for-time substitution) would conclude that the extinction risk was the same for each population and landscape. In reality, however, the status of each population could be quite different, depending on how quickly the landscape was changing and the time that it had taken for the landscape to achieve the current state. With knowledge of the rates of habitat loss, an assessment based on the vulnerability threshold criteria that we have defined here might conclude that one population was not at risk (the vulnerability threshold is not exceeded at 50% habitat), another was at risk (50% habitat was beyond the vulnerability threshold), and another should actually be extinct at 50% habitat (assuming rates of habitat loss of 5.0, 1.0, and 0.5% per year, respectively; left-hand panel of Fig. 4A). Again, note that for landscapes undergoing the most rapid rate of habitat loss (5% per year), the population was not assessed as at risk by our criteria

when 50% habitat remained (10 years postdisturbance), although the population eventually went extinct during the ensuing 10 years (right-hand panel of Fig. 4A). Thus, even after allowing for differences based on rates of landscape change, assessments of population viability based on available habitat at a particular point in time provide an incomplete, and potentially misleading, characterization of the status of the population and its risk for extinction.

Landscape history may thus dictate not only how populations will respond to future landscape change, but also may affect our ability to detect how such changes will affect population viability and extinction risk. When the rate of landscape change exceeds the demographic response time (e.g., generation time) of the species, populations may exhibit a lagged response to habitat loss. Consider that the generic migratory bird species that we modeled had life spans of eight years. When habitat was destroyed rapidly, at a rate of 5% per year, the landscape was denuded in less than nine generations (generation time = 2.3 yr). Although habitat loss and fragmentation caused decreased reproductive rates, there was insufficient time for the reproductive decline to translate into a significant change in the population growth rate ($\Delta\lambda$) exceeding the vulnerability threshold (>1% decline per habitat lost per year) before the landscape was entirely denuded. Birds are still present in the landscape, but are not reproducing successfully. A species in such a landscape is one of the ''living dead,'' which is no longer viable and is doomed to eventual extinction (Tilman et al. 1994, Hanski et al. 1996). In highly mobile species, such as many migratory birds, these populations may exist indefinitely as sinks that are only supported and kept from extinction through immigration from source populations that are able to produce surplus individuals (Donovan et al. 1995, With and King 2001).

Our evaluation of extinction risk was based on the determination of a vulnerability threshold, which was meant to provide a conservative estimate of extinction risk analogous to the criterion used by the IUCN to identify species as vulnerable to extinction (a 1% decline per year in population growth rates; Caswell 2001). Note that our definition of the vulnerability threshold involves accelerated change in the rate of population decline with respect to habitat loss. Area sensitivity (Fig. 1A), which enables birds to settle preferentially in larger patches that provide the greatest reproductive success and thus contribute most to the population, may partially explain the precipitous nature of vulnerability thresholds. The sudden increase in the rate of population decline at the vulnerability threshold probably results from the loss or fragmentation of these critical large patches on the landscape, which had previously supported a substantial fraction of the population (Donovan and Lamberson 2001); this threshold obviously would be reached sooner in a more highly fragmented landscape than in a less fragmented one.

Again, however, we have shown that under certain landscape change scenarios (e.g., very rapid habitat loss), populations may decline to extinction without actually exhibiting a vulnerability threshold as measured by changes in habitat. In these cases, effects of habitat loss and fragmentation on demographic potential (e.g., on fledgling production) are felt quickly (left-hand panel of Fig. 4A), but the expression in changes in λ lags behind the changes in habitat. Demographic change is decoupled from landscape change, and the vulnerability metric defined by their relationship (a ratio of the rate of demographic change to the rate of landscape change) is thus obscured.

The vulnerability threshold represents a threshold in the sensitivity of a species' response to habitat loss; the species' sensitivity to habitat loss increases as more habitat is lost. One value of defining the threshold in this manner is that it highlights the danger in extrapolating extinction risk or time to extinction from one point in time to the next. Because the vulnerability threshold identifies an acceleration in population decline, the assessment of time to extinction is time dependent, becoming shorter and shorter over time as habitat loss continues. Failing to account for this nonlinearity (accelerated decline) obviously would lead to an overestimate of time to extinction, but perhaps more importantly, this implies that assessment of extinction risk is really a ''moving target.'' Whether a species is assessed as at risk of extinction and its time to extinction ultimately depend on where in time this is being assessed. Furthermore, even when a vulnerability threshold has been determined for a species in a landscape for which the past rate of habitat loss is known, that threshold is subject to change if the rate of habitat loss changes (i.e., is not constant as in our simulations).

How then can we identify the vulnerability threshold a priori? In practice this will be difficult, but it is important that the possibility at least be identified, and modeling approaches such as the one that we have presented here can be used in that assessment. The possibility of a vulnerability threshold also indicates the need for demographic (not just population) monitoring and adaptive management in which a species' vulnerability to extinction is continually assessed, rather than deriving assessments of extinction risk from population projections based solely on an assessment at a single point in time or on current landscape configurations that ignore landscape history. For example, managers seeking to estimate a species' vulnerability to landscape change should first determine whether or not the landscape has a history of habitat loss and fragmentation on a time scale relevant to the demography of the population of interest. It is also important to determine whether the expected rates of future change are in sync with the time scale of the population's demographic response, or whether the rates of change are likely to exceed the population's demographic potential, thus decoupling demographic response from land-

scape change. Determination of how tightly coupled are the rates of demographic change and landscape change could inform decision makers on how useful information on the current state of the landscape is for assessment, or whether alternative assessments more focused on the time domain than the spatial domain are needed.

Our study is not the first to hint at the potential importance that the rate of habitat loss might have to bird populations. Hagan et al. (1996) studied birds in a boreal forest in Maine used primarily for forestry. They found that displacement of individuals by habitat loss could lead to temporary crowding within forests adjacent to the disturbed area, which might give the appearance that habitat destruction had little effect on bird populations, or had actually increased them. This illustrates one of the risks of examining highly mobile bird populations at local patch-based scales rather than broad landscape scales. Population density by itself is unlikely to be a good indicator of the status of many migratory bird populations. For example, Hagan et al. also reported that Ovenbird (*Seiurus aurocapillus*) pairing and reproductive success were low in forests fragmented by logging, even though their population densities were higher in such forests than in unfragmented forests. Census data cannot reveal the extent to which demographic potential has been eroded by rapid habitat loss. Although populations exposed to such rapid habitat loss may not exhibit immediate declines in density, our model demonstrates the potential for lagged demographic effects that can greatly increase extinction risk when breeding habitat is destroyed. More generally, delayed population responses to habitat loss have been documented in metapopulation models (Tilman et al. 1994, Hanski 1999), and recent assessments of extinction risk in a dynamic landscape context likewise demonstrate that the rate of habitat loss may be more important to metapopulation persistence than the amount or fragmentation of habitat (Keymer et al. 2000, Nagelkerke et al. 2002).

Although model applications such as ours point to the importance of landscape history in evaluating extinction risk for species such as migratory songbirds, the reality is that information on the history of past disturbances often is not available. Satellite-based remote sensing can quantify landscape change over the past two decades, but longer profiles may be harder to obtain. In many regions of North America, human land use has led to the rapid and dramatic alteration of landscape structure during the past 200–300 years; thus the rate and intensity of habitat destruction have either been documented or can be re-created through various sources such as land surveys (Whitney 1994). Historical landscape composition can also be estimated over much longer time periods (centuries to millennia) using a variety of paleoecological procedures (Delcourt and Delcourt 1988). The importance of landscape history for assessment of population viability argues for concerted programmatic efforts to document past and ongoing changes in land cover, land use, and landscape pattern as an integral part of regional, national, and international species conservation efforts. Reconstructions of landscape history have, in some cases, documented the recent recovery of historically impacted landscapes, such as the reforestation of central New England during the past century (Foster et al. 1998). This offers the hope that populations may recover as habitat recovers, assuming of course that the demographic potential of the population has not been seriously eroded by prolonged periods of widespread habitat destruction (Schrott et al. 2005) and these populations are not already among the ''living dead.''

Literature Cited

Akçakaya, H. R., M. A. McCarthy, and J. L. Pearce. 1995. Linking landscape data with population viability analysis: management options for the Helmeted Honeyeater *Lichenostomus melanops cassidix*. Biological Conservation **73**: 169–176.

Askins, R. A. 1995. Hostile landscapes and the decline of migratory songbirds. Science **267**:1956–1957.

Brawn, J. D., and S. K. Robinson. 1996. Source–sink population dynamics may complicate the interpretation of long-term census data. Ecology **77**:3–12.

Caswell, H. 2001. Matrix population models. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Coppedge, B. R., D. M. Engle, R. E. Masters, and M. S. Gregory. 2001. Avian response to landscape change in fragmented southern Great Plains grasslands. Ecological Applications **11**:47–59.

Dale, V. H., S. M. Pearson, H. L. Offerman, and R. V. O'Neill. 1994. Relating patterns of land-use change to faunal biodiversity in the central Amazon. Conservation Biology **8**: 1027–1036.

Delcourt, H. R., and P. A. Delcourt. 1988. Quaternary landscape ecology: relevant scales in space and time. Landscape Ecology **2**:23–44.

DeSante, D. F., and T. L. George. 1994. Population trends in the landbirds of western North America. Pages 173–190 *in* J. R. Jehl, Jr., and N. K. Johnson, editors. A century of avifaunal change in western North America. Studies in Avian Biology Number 15. Cooper Ornithological Society, Camarillo, California, USA.

Donovan, T. M., and C. H. Flather. 2002. Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. Ecological Applications **12**:364–374.

Donovan, T. M., and R. H. Lamberson. 2001. Area-sensitive distributions counteract negative effects of habitat fragmentation on breeding birds. Ecology **84**:1170–1179.

Donovan, T. M., R. H. Lamberson, A. Kimber, F. R. Thompson, III, and J. Faaborg. 1995. Modeling the effects of habitat fragmentation on source and sink demography of Neotropical migrant birds. Conservation Biology **9**:1396–1407.

Faaborg, J., M. Brittingham, T. Donovan, and J. Blake. 1995. Habitat fragmentation in the temperate zone. Pages 357–380 *in* T. E. Martin and D. M. Finch, editors. Ecology and management of neotropical migratory birds: a synthesis and

review of critical issues. Oxford University Press, New York, New York, USA.

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. Journal of Wildlife Management **61**:603–610.

Flaspohler, D. J., S. A. Temple, and R. N. Rosenfield. 2001. Species-specific edge effects on nest success and breeding bird density in a forested landscape. Ecological Applications **11**:32–46.

Foster, D. R., G. Motzkin, and B. Slater. 1998. Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. Ecosystems **1**:96–119.

Freemark, K. E., J. B. Dunning, S. J. Hejl, and J. R. Probst. 1995. A landscape ecology perspective for research, conservation, and management. Pages 381–427 *in* T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues. Oxford University Press, New York, New York, USA.

Gardner, R. H. 1999. RULE: map generation and spatial analysis program. Pages 280–303 *in* J. M. Klopatek and R. H. Gardner, editors. Landscape ecological analysis: issues and applications. Springer-Verlag, New York, New York, USA.

Hagan, J. M., W. M. Vander Haegen, and P. S. McKinley. 1996. The early development of forest fragmentation effects on birds. Conservation Biology **10**:188–202.

Hanski, I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos **87**:209–219.

Hanski, I., A. Moilanen, and M. Gyllenberg. 1996. Minimum viable metapopulation size. American Naturalist **147**:527–541.

Hanski, I., and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape. Nature **404**:755–758.

Hanski, I., and O. Ovaskainen. 2002. Extinction debt at extinction threshold. Conservation Biology **16**:666–673.

Hargrove, W. W., and J. Pickering. 1992. Pseudoreplication: a sine qua non for regional ecology. Landscape Ecology **6**:251–258.

Hinde, R. A. 1956. The biological significance of the territories of birds. Ibis **98**:340–369.

Hoover, J. P., M. C. Brittingham, and L. J. Goodrich. 1995. Effects of forest patch size on nesting success of Wood Thrushes. Auk **112**:146–155.

Johnson, R. G., and S. A. Temple. 1986. Assessing habitat quality for birds nesting in fragmented tallgrass prairies. Pages 245–249 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. Modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, Wisconsin, USA.

Keymer, J. E., P. A. Marquet, J. X. Velasco-Hernández, and S. A. Levin. 2000. Extinction thresholds and metapopulation persistence in dynamic landscapes. American Naturalist **156**:478–494.

Keyser, A. J., G. E. Hill, and E. C. Soehren. 1998. Effects of forest fragment size, nest density, and proximity to edge on the risk of predation to ground-nesting passerine birds. Conservation Biology **12**:986–994.

King, A. W., L. K. Mann, W. W. Hargrove, T. L. Ashwood, and V. H. Dale. 2000. Assessing the persistence of an avian population in a managed landscape: a case study with Henslow's Sparrow at Fort Knox, Kentucy. ORNL/TM-13734. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.

Lamberson, R. H., R. McKelvey, B. R. Noon, and C. Voss. 1992. A dynamic analysis of Northern Spotted Owl viability in a fragmented forest landscape. Conservation Biology **6**:505–512.

Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. American Naturalist **130**:624–635.

Lande, R. 1988. Demographic models of the Northern Spotted Owl (*Strix occidentalis caurina*). Oecologia **75**:601–607.

Leslie, P. H. 1966. The intrinsic rate of increase and the overlap of successive generations in a population of Guillemots (*Uria aalge* Pont.). Journal of Animal Ecology **35**:291–301.

Lindenmayer, D. B., I. Ball, H. P. Possingham, M. A. McCarthy, and M. L. Pope. 2001. A landscape-scale test of the predictive ability of a spatially explicit model for population viability analysis. Journal of Applied Ecology **38**:36–48.

McGarigal, K. J., and W. C. McComb. 1995. Relationships between landscape structure and breeding birds in the Oregon coast range. Ecological Monographs **65**:235–260.

Mertz, D. B. 1971. The mathematical demography of the California Condor population. American Naturalist **105**:437–453.

Moloney, K. A., and S. A. Levin. 1996. The effects of disturbance architecture on landscape-level population dynamics. Ecology **77**:375–394.

Moreira, F., P. G. Ferreira, F. C. Rego, and S. Bunting. 2001. Landscape changes and breeding bird assemblages in northwestern Portugal: the role of fire. Landscape Ecology **16**:175–187.

Morse, D. H. 1989. American warblers: an ecological and behavioral perspective. Harvard University Press, Cambridge, Massachusetts, USA.

Nagelkerke, K. (C. J.), J. Verboom, F. van den Bosch, and K. van de Wolfshaar. 2002. Time lags in metapopulation responses to landscape change. Pages 330–354 *in* K. J. Gutzwiller, editor. Applying landscape ecology in biological conservation. Springer-Verlag, New York, New York, USA.

Nichols, J. D., G. L. Hensler, and P. W. Sykes, Jr. 1980. Demography of the Everglade Kite: implications for population management. Ecological Modelling **9**:215–232.

Noon, B. R., and C. M. Biles. 1990. Mathematical demography of spotted owls in the Pacific Northwest. Journal of Wildlife Management **54**:18–27.

Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology **8**:17–26.

Pulliam, H. R., J. B. Dunning, Jr., and J. Liu. 1992. Population dynamics in complex landscapes: a case study. Ecological Applications **2**:165–177.

Robbins, C. S., D. K. Dawson, and B. A. Dowell. 1989*a*. Habitat area requirements of breeding forest birds in the middle Atlantic states. Wildlife Monographs **103**:1–34.

Robbins, C. S., J. R. Sauer, R. Greenberg, and S. Droege. 1989*b*. Population declines in North American birds that migrate to the Neotropics. Proceedings of the National Academy of Sciences (USA) **86**:7658–7662.

Robinson, S. K., F. R. Thompson, III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science **267**:1987–1990.

Schrott, G. R., K. A. With, and A. W. King. 2005. Demographic limitations on the ability of habitat restoration to rescue declining populations. Conservation Biology, *in press*.

Spies, T. A., W. J. Ripple, and G. A. Bradshaw. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecological Applications **4**:555–568.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak.

1994. Habitat destruction and the extinction debt. Nature **371**:65–66.

Trzcinski, M. K., L. Fahrig, and G. Merriam. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecological Applications **9**:586–593.

Turner, M. G., and V. H. Dale. 1998. Comparing large, infrequent disturbances: what have we learned? Introduction for special feature. Ecosystems **1**:493–496.

Villard, M.-A., M. K. Trzcinski, and G. Merriam. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. Conservation Biology **13**:774–783.

Wenny, D. G., R. L. Clawson, J. Faaborg, and S. L. Sheriff. 1993. Population density, habitat selection and minimum area requirements of three forest-interior warblers in central Missouri. Condor **95**:968–979.

Whitney, G. G. 1994. From coastal wilderness to fruited plain: a history of environmental change in temperate North America from 1500 to the present. Cambridge University Press, Cambridge, UK.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Assessing the relative importance of habitat destruction, alien species, pollution, over-exploitation, and disease. BioScience **48**:607–616.

With, K. A. 1997. The application of neutral landscape models in conservation biology. Conservation Biology **11**:1069–1080.

With, K. A., and A. W. King. 1999. Extinction thresholds for species in fractal landscapes. Conservation Biology **13**:314–326.

With, K. A., and A. W. King. 2001. Analysis of landscape sources and sinks: the effect of spatial pattern on avian demography. Biological Conservation **100**:75–88.