Demographic Limitations of the Ability of Habitat Restoration to Rescue Declining Populations

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Abstract: *Habitat restoration is often recommended in conservation without first evaluating whether populations are in fact habitat limited and thus whether declining populations can be stabilized or recovered through habitat restoration. We used a spatially structured demographic model coupled with a dynamic neutral landscape model to evaluate whether habitat restoration could rescue populations of several generic migratory songbirds that differed in their sensitivity to habitat fragmentation (i.e., severity of edge effects on nesting success). Simulating a best-case scenario, landscapes were instantly restored to 100% habitat before, at, or after habitat loss exceeded the species' vulnerability threshold. The vulnerability threshold is a measure of extinction risk, in which the change in population growth rate ($\Delta\lambda$) scaled to the rate of habitat loss (Δh) falls below -1% ($\Delta\lambda/\Delta h \leq -0.01$). Habitat restoration was most effective for species with low-to-moderate edge sensitivities and in landscapes that had not previously experienced extensive fragmentation. To stabilize populations of species that were highly edge sensitive or any species in heavily fragmented landscapes, restoration needed to be initiated long before the vulnerability threshold was reached. In practice, habitat restoration is generally not initiated until a population is at risk of extinction, but our model results demonstrate that some populations cannot be recovered at this point through habitat restoration alone. At this stage, habitat loss and fragmentation have seriously eroded the species' demographic potential such that halting population declines is limited more by demographic factors than the amount of available habitat. Evidence that populations decline in response to habitat loss is thus not sufficient to conclude that habitat restoration will be sufficient to rescue declining populations.*

Key Words: demographic models, extinction risk, habitat loss, habitat fragmentation, migratory birds, neutral landscape models

Limitaciones Demográficas de la Capacidad de la Restauración de Hábitat para Rescatar Poblaciones en Declinación

Resumen: *A menudo, la restauración del hábitat es recomendada en conservación sin evaluar previamente si las poblaciones están limitadas por el hábitat y por lo tanto si las poblaciones en declinación pueden ser estabilizadas o recuperadas mediante la restauración del hábitat. Utilizamos un modelo demográfico estructurado espacialmente acoplado con un modelo de paisaje neutral dinámico para evaluar si la restauración del hábitat podría rescatar poblaciones de varias aves migratorias genéricas con distinta sensibilidad a la fragmentación del hábitat (i.e., severidad de los efectos de borde sobre el éxito de anidación). Al simular el mejor escenario, los paisajes fueron restaurados instantáneamente a 100% hábitat ya sea antes, durante o después de que la pérdida de hábitat excedió el umbral de vulnerabilidad de las especies. El umbral de vulnerabilidad es una medida del riesgo de extinción, en la el cambio en la tasa de crecimiento poblacional ($\Delta\lambda$) en relación con la tasa de pérdida de hábitat (Δh) es menor a 1% ($\Delta\lambda/\Delta h \leq -0.01$). La restauración del hábitat fue más efectiva para especie con sensibilidad al borde baja o moderada y en paisajes que no habían experimentado fragmentación extensiva previamente. Para estabilizar poblaciones de especies que fueron muy sensibles al borde o de cualquier especie en paisajes muy fragmentados, era necesario comenzar*

la restauración mucho antes de que se llegara al umbral de vulnerabilidad. En la práctica, la restauración de hábitat generalmente no se inicia hasta que una población está en riesgo de extinción, pero los resultados de nuestro modelo demuestran que algunas poblaciones no se pueden recuperar en este punto solo mediante la restauración del hábitat. En esta etapa, la pérdida de hábitat y la fragmentación han erosionado seriamente al potencial demográfico de la especie a tal grado que detener la declinación de poblaciones está más limitado por factores demográficos que por la cantidad de hábitat disponible. Por lo tanto, la evidencia de que las poblaciones declinan en respuesta a la pérdida de hábitat no es suficiente para concluir que la restauración del hábitat no será suficiente para rescatar poblaciones en declinación.

Palabras Clave: aves migratorias modelos de paisaje neutrales, fragmentación de hábitat, modelos demográficos, pérdida de hábitat, riesgo de extinción

Introduction

Anthropogenic destruction and fragmentation of natural habitats have put many species at risk of local or global extinction (Wilcox & Murphy 1985; Turner 1996). Conservation plans for small or declining populations often recommend habitat restoration as a means of increasing carrying capacity and lowering extinction risk (e.g., Root 1998; Ferreras et al. 2001; Wisdom et al. 2002). Such recommendations are often made without assessing how much, if at all, habitat restoration would benefit the population (e.g., Foin et al. 1997; Roy et al. 1998). It is simply assumed that habitat recovery will lead to population recovery.

In some population models habitat restoration facilitates the survival and reintroduction of small populations of rare species (Armstrong & Ewen 2002) or is useful in reducing extinction risk in sharply declining populations (Root 1998; Wisdom et al. 2002). For example, Lindenmayer and Possingham (1996) modeled habitat restoration through natural succession following the cessation of timber harvesting in a southeastern Australian forest and found that it was possible to achieve long-term viability for a population of Leadbeater's possum (*Gymnobelideus leadbeateri*). Other models, however, show that increasing carrying capacity through habitat restoration may not be effective to reduce extinction risk. This is especially true for populations in "sink" habitat, in which the population is not able to sustain itself without immigration (Ferreras et al. 2001), because simply creating more habitat of this type will not help the population recover. In practice, habitat restoration projects are sometimes unsuccessful in re-creating high-quality habitat for a species (Foin et al. 1997; Wisdom et al. 2002) and can be expensive and difficult to implement (Jordan et al. 1987; Gilbert & Anderson 1998). For example, Rushton et al. (2000) found that the amount of restoration necessary to achieve an extinction risk of < 10% over 15 years in a water vole (*Arvicola terrestris*) population would be too costly to be practical. Even when cost-effective and practical, habitat restoration may not be effective in recovering populations unless accompanied by other management

actions that increase recruitment or survivorship (e.g., providing secure nesting sites, control of predators or competitor species; Franzreb 1997). Finally, some models demonstrate that although restoration can increase the amount of "source" habitat (where birth rates exceed death rates) and halt or reverse population declines, it may take much longer for the population to achieve its predisturbance levels than it took to decline in the first place. Full population recovery may not be achieved at all in some instances (Acosta & Perry 2002).

Whether habitat restoration will lead to successful population recovery is conditional, but the conditions for successful recovery are poorly understood. It is reasonable to assume that if habitat loss has contributed to population declines, then habitat restoration should lead to population recovery. Habitat loss and fragmentation have been implicated in the decline of many migratory songbirds (DeSante & George 1994; Donovan & Flather 2002); thus, these species should be good candidates for recovery through habitat restoration. Given the limits to our current understanding of population responses to habitat recovery, however, this assumption is best viewed as a hypothesis to be tested. Here, we adopted a spatially structured avian demographic model to explore in a general way the interaction between demography and dynamic landscape change for migratory songbirds that differ in their sensitivity to fragmentation. Our objective was to determine whether one can assume that populations that are sensitive to landscape change (i.e., they decline in response to habitat loss) are necessarily habitat limited and can therefore be rescued by habitat restoration. In effect, we used simulation experiments to test the hypothesis that species declining in response to habitat loss can be rescued by habitat restoration. We also sought to clarify how the timing of habitat restoration relative to the species' vulnerability threshold—a measure of the sensitivity of species' responses to habitat loss—affects the ability to stabilize declining populations. Evidence of population declines in response to habitat loss and fragmentation was not sufficient to conclude that habitat restoration will be able to rescue these populations from extinction.

Methods

Overview of Model

The model dSSAD (dynamic Spatially Structured Avian Demography) is a demographic model of territorial, migratory bird populations in dynamic landscapes in which the amount and the spatial pattern of habitat change over time. The dSSAD is an extension of the demographic model described by With and King (2001) for migratory songbirds in static landscapes. It applies to territorial birds that are monogamous on the breeding grounds and establish and defend all-inclusive territories within which nesting and most foraging take place (Morse 1989). The model assumes a closed population with no immigration or emigration.

The dSSAD model integrates conventional avian demographic modeling with a landscape perspective on how spatial pattern influences demographic rates. Annual changes in the population are described by an age-structured Leslie matrix population model parameterized from a demographic life table and life-cycle graph analysis (Leslie 1966; Lande 1988; Caswell 2001). The model is a classical Leslie matrix model for avian demography (Lande 1988), but the maternity term b is a function of landscape pattern (With & King 2001). This unique feature of the model distinguishes it from most other avian demographic models, including those that explore the effect of landscape pattern (habitat loss and fragmentation) on bird populations. Usually, birth rate (b, expected number of female offspring produced per adult female) is a fixed parameter estimated from data on reproductive success (i.e., it is a model input). In dSSAD, b is a function of landscape pattern (i.e., it is a model output; see section on Landscape-Dependent Reproductive Success). Because in a dynamic landscape the spatial pattern of habitat changes over time, b changes with time (b_t), and the resulting demographic model varies with time and is nonlinear because b_t also changes with changes in the size of the adult female population. This is in contrast to more conventional models of avian demography, which are often time invariant and linear.

Many of the calculations leading to the computation of b_t are stochastic (e.g., the clutch size of an individual nest); thus, b_t is a stochastic parameter. Each stochastic realization of b_t is used to parameterize a deterministic life table and age-structured Leslie projection matrix. Each realization of b_t yields a new matrix parameterization and a new simulation in what is effectively a Monte Carlo simulation of demographic stochasticity (Morris & Doak 2002) that also includes trends in the environment (habitat loss) leading to trends in the vital rate b.

REDISTRIBUTION OF INDIVIDUALS ON LANDSCAPES

The demographic model is implemented on a dynamic landscape in which breeding habitat is destroyed and subsequently restored (see section on Restoration Scenarios). These raster landscapes are 128×128 cells, with a cell size of 30×30 m, for a total landscape area of approximately 14.5 km^2 (1452 ha). Cells of breeding habitat separated by less than the distance the pair will readily cross in using their territory (i.e., their gap-crossing ability, Dale et al. 1994) are aggregated into patches. Habitat within a patch is contiguous and homogeneous; there is no within-patch variability in habitat quality. The matrix between patches is not used for nesting. Patches of nesting habitat smaller than the species' territory size are not used for nesting. For this analysis, all species were assumed to have the same limited gap-crossing ability (<30 m) and the same territory size (0.5 ha) (Table 1). These values are consistent with those of many Neotropical migratory songbirds that breed in temperate forests (Morse 1989).

The number of potential territories within patches is determined by an incidence function J_A that describes the probability of encountering a territory at a random point in a patch of area A (Robbins et al. 1989). Incidence is calculated with a logistic regression model

$$J_A = \frac{\exp\left(\beta_0 + \beta_1 \log_{10} A + \beta_2 \log_{10} A^2\right)}{1 + \exp\left(\beta_0 + \beta_1 \log_{10} A + \beta_2 \log_{10} A^2\right)}, \quad (1)$$

where β_0, β_1, and β_2 are regression parameters (Table 1). We used the parameter values of the Red-eyed Vireo (*Vireo olivaceus*) provided by Robbins et al. (1989)

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[a]	
$\quad \beta_0$	-0.579
$\quad \beta_1$	1.596
$\quad \beta_2$	0.0
Edge sensitivity[b]	
$\quad$ maximum nesting success (S_{max})	0.8
$\quad$ low sensitivity	
$\quad k$	0.75
$\quad \Theta$	10.0
$\quad$ intermediate sensitivity	
$\quad k$	0.15
$\quad \Theta$	1.7
$\quad$ high sensitivity	
$\quad k$	0.10
$\quad \Theta$	0.50

[a]*Parameters used in logistic regression model to calculate incidence function of patch occupancy from Eq. 1 in text. Parameter values are for the Red-eyed Vireo (*Vireo olivaceus*) from Robbins et al. (1989), for which β_2 is 0.*

[b]*Parameters used to define edge sensitivity from Eq. 3 in text.*

in all model runs as a canonical example of a species with low area sensitivity. Area sensitivity has less effect on species' responses to habitat loss and fragmentation than edge sensitivity (defined in section on Landscape-Dependent Reproductive Success; With & King 2001; Schrott et al. 2005); thus, we standardized area sensitivity among species in our simulation experiments.

The probability of occurrence J_A (calculated by Eq. 1) 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

$$n_i^* = J_A \frac{A_i}{A_T},\qquad(2)$$

where A_i is the area (ha) of patch i, A_T is territory size (ha), and n_i^* is rounded to the nearest integer. The maximum number of potential nests in a patch is A_i/A_T, which occurs when $J_A = 1.0$.

At population densities above the equilibrium steady state, nesting habitat is saturated at a nesting density of n_i^*/A_i, and n_i, the number of nests in patch i at time t, is equal to n_i^*. At population densities below the equilibrium steady state, $n_i < n_i^*$ and potential nest sites or territories are unoccupied. Nesting females are assigned to patches stochastically, with the probability that an individual female nests in a particular patch given by the incidence function J_A. At each time step ($= 1$ year), 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. Probabilistically, females preferentially settle in large patches, and thus smaller patches are "less preferred" and 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."

LANDSCAPE-DEPENDENT REPRODUCTIVE SUCCESS

Nesting success, the probability that a nest will produce at least one fledgling (Johnson & Temple 1986), is a function of patch geometry defined by its edge-to-area ratio. Nesting success is assumed to be lower in patches with proportionately more edge per unit area, based on documentation that higher rates of nest predation and brood parasitism are associated with increased amounts of edge and that edge has a negative effect on nesting success (e.g., Robinson et al. 1995). Maximum nesting success is thus assumed to occur in large patches with relatively little edge. The edge-to-area ratio of a patch is normalized by the edge-to-area ratio of a single grid cell, which yields a maximum value of 1.0 (maximum edge per unit area). An edge-index value (e_i) near 0.0 indicates a patch with minimal edge per unit area. The boundary of the finite, closed landscape is also an edge for patches along that boundary.

Nesting success in the model is evaluated stochastically for each nest in a patch. The probability that a nest in patch i fledges no young is $1 - S_i$, where S_i is the probability of nesting success in patch i 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-to-area index of patch i. The parameter k is the value of e_i, where $S_i = 0.5S_{\max}$, and Θ is a parameter that determines the rate at which nesting success declines with larger edge-to-area ratios.

Nesting success in the absence of any edge effect, $S_{\max}$, will always be < 1; some nests will be lost to predation, weather, or other factors, regardless of their proximity to an edge. The probability of nesting success will be <1 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., $e_i \to 1$; low edge sensitivity, Fig. 1). Other species will be very sensitive to edge, and the probability of nesting success will decline rapidly with an increasing edge index (high edge sensitivity, Fig. 1). Others will show an intermediate response of more gradual decline with increasing edge per unit area, at least initially (intermediate edge sensitivity, Fig. 1).

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

$$b_t = \frac{\sum\limits_{i=1}^{m} \sum\limits_{j=1}^{n_i} F_{ji}}{N_a},\qquad(4)$$

where F_{ji} is the number of female fledglings from successful nest j of patch i, m is the number of patches, n_i is the number of nests in patch i, and N_a is the total number of
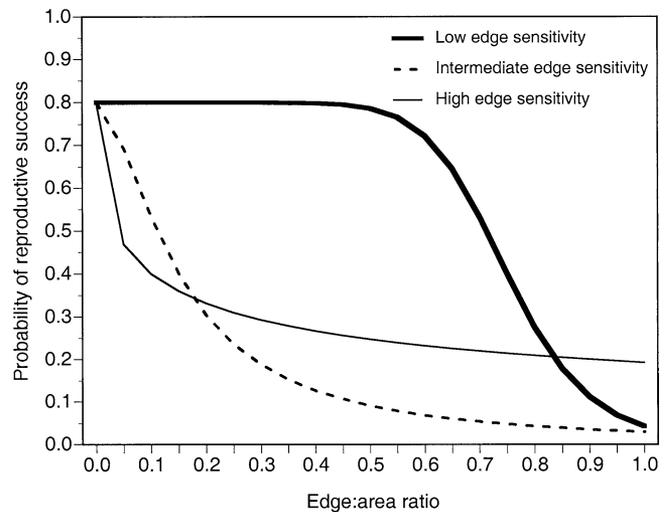
Figure 1. Edge-sensitivity functions (Eq. 3).

females of reproductive age in the population, including the non-nesting floaters.

Nests that fledge at least one young are assumed to fledge the entire clutch, so the maximum number of female fledglings from a successful nest is the clutch size C_{ji} of that nest. The sex of each fledgling, however, is determined stochastically according to the population's fledgling female:male sex ratio (1:1 in these simulations). On average $F_{ji} = 0.5C_{ji}$ for successful nests ($F_{ji} = 0$ for unsuccessful nests). Clutch size C for each nest is drawn independently from a species-specific frequency distribution. Consequently, clutch size and the number of female fledglings may vary among nests. In this analysis, we assumed that clutch size represents a uniform distribution of 4–5 eggs.

The model assumes productivity is independent of age after sexual maturity. The number of female fledglings produced by a female of age x, b_x, is then $b_x = b_t$ 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. Age-independent productivity following maturity is a common assumption in demographic models of short-lived birds (Nichols et al. 1980; Lande 1988).

POPULATION DYNAMICS

The birth rate b_t is combined with age-specific survivorship to create a life table for the landscape population. Annual survival probabilities are defined for two age classes: juveniles s_0 and adults s (Table 1). Following Caswell (2001), the life table is used to parameterize an age-structured matrix population model that assumes a post-breeding census. This Leslie matrix is used to project the number of females in the population forward for 1 year. This new population and the landscape at time $t + 1$ is used to calculate the birth rate b_{t+1}, following Eqs. 2–4, and this annual cycle is repeated for the duration of the simulation or until all habitat has been removed.

Net lifetime maternity (net reproductive rate) is calculated from the life table as:

$$R_0 = \sum_{x=\alpha}^{\omega} l_x b_t, \qquad (5)$$

where R_0 is the expected lifetime production of females by a female fledgling, l_x is the probability of survivorship to age x, 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.

The second demographic index is the finite rate of increase λ given by the solution of the characteristic equation (Lande 1988):

$$\lambda^{\alpha} - s\lambda^{\alpha-1} - b_t l_{\alpha} = 0, \qquad (6)$$

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

ASSESSMENT OF EXTINCTION RISK

Because restoration success might vary with the rate of population decline, we used a vulnerability threshold based on the sensitivity of the population growth rate (λ) to the rate of habitat loss ($r = \Delta h$) to evaluate extinction risk. The vulnerability threshold is where the change in population growth rate ($\Delta\lambda$) scaled to the rate of habitat loss (Δh) falls below -1% ($\Delta\lambda/\Delta h = -0.01$). We chose a conservative value for the threshold analogous to the World Conservation Union's most conservative criterion for evaluating a species' vulnerability to extinction (Caswell 2001: 595). The vulnerability threshold is species and landscape specific and was determined prior to model runs (Schrott et al. 2005) so that restoration could be initiated either before, at, or after the vulnerability threshold (see section on Restoration Scenarios).

MODEL INITIALIZATION

We initialized and calibrated the model to ensure both a stable age distribution and an initial steady state population size ($\lambda = 1.0$) for a closed population on a landscape of the size modeled here assuming 100% breeding habitat ($b = 100\%$). We assumed a stable population with $R_0 = 1.0$ and calculated the corresponding steady state maternity function $b^* = m_x^*$ from Eq. 5. 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. 4 with

$$\sum_{i=1}^{m} \sum_{j=1}^{n_i} F_{ji} = 0.5\left(S_{\max} n_{\max}^* C_{\max}\right), \qquad (7)$$

where $n_{\max}^*$ is the maximum number of nests predicted from Eq. 2 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. Population dynamics are thus normalized for landscape size and are not scale dependent. Although the assumption of a closed, steady state population may rarely apply to real bird populations, it allowed us to control for the potentially confounding effects of immigration and environmental stochasticity, thereby isolating the endogenous demographic processes linked to habitat change that

we sought to understand. The assumption of steady state population growth ($\lambda = 1.0$) is also a reasonable and conservative assumption regarding the long-term dynamics of a persistent population on a homogeneous landscape of 100% habitat.

Restoration Scenarios

We assessed the effects of habitat restoration on populations of three generic migratory bird species that differed in their sensitivity to habitat fragmentation (edge sensitivity; Eq. 3, Fig. 1). For each species, a model run began with a steady state population size and stable age distribution (see Overview of Model, Model Initialization) in a "pristine" landscape (100% suitable breeding habitat). The landscape was then subjected to one of six possible disturbance regimes generated by combining different rates of habitat destruction ($r = 0.5\%$ or 1.0%/year) and levels of fragmentation in a factorial design (2 rates of habitat destruction × 3 levels of fragmentation = 6 landscape disturbance regimes). Landscapes were generated using a fractal algorithm (midpoint displacement) in which we varied the degree of fragmentation by adjusting the parameter (H) in that algorithm that controls the spatial autocorrelation of disturbance (With 1997). We produced landscape patterns that were highly fragmented ($H = 0.0$; disturbances were only weakly correlated in space), moderately fragmented ($H = 0.5$), or relatively unfragmented ($H = 1.0$; disturbances were highly correlated in space) (see With & King [2001] for examples of fractal landscape patterns). The combination of species (3 types defined by relative edge sensitivity) and landscape disturbance trajectories (6 trajectories defined by r and H) produced 18 species-landscape disturbance scenarios.

For each species-landscape disturbance scenario, population dynamics were simulated for 200 years ($t = 0$, 200), with restoration occurring at some point in time t_R, where $0 < t_R < 200$. Before t_R habitat loss continued at a constant rate r. At t_R the landscape was instantaneously restored to its "pristine" state (100% habitat). Although this scenario of habitat restoration is not realistic for most ecosystems, it represents an experimental test of the best-case scenario. If this level of restoration cannot avert extinction, then extinction cannot be averted by habitat restoration.

We restored landscapes according to one of three scenarios: (1) restoration was delayed until habitat destruction exceeded the species' vulnerability threshold ($t_R > t_V$), (2) habitat restoration was initiated at the vulnerability threshold ($t_R = t_V$), and (3) restoration occurred before the species' vulnerability threshold (i.e., before the species was assessed as being at risk of extinction [$t_R < t_V$, where t_V is when the vulnerability threshold occurred]). As a baseline, runs were also made in which no habitat restoration occurred. Because the vulnerability thresh-

old is landscape and species dependent (Schrott et al. 2005), the specific year at which restoration was initiated varied among scenarios. Timing restoration relative to the vulnerability threshold normalizes the effects of habitat restoration on population dynamics.

Model trials consisted of 100 realizations of the stochastic demographic model (see Overview of Model) on each of 10 replicated time series for each species by landscape disturbance by restoration scenario (3 species × 6 landscape disturbance regimes × 3 restoration scenarios = 54 total scenarios). Model results were averaged across realizations for each trial, and these means were averaged across trials. At each time step, we recorded the mean and standard error of λ for the replicate populations.

Assessment of Restoration Success

Given the assumption of an initial steady state population ($\lambda = 1.0$) and the associated calibration to this initial condition, the best-case scenario following restoration of the initial landscape condition (100% habitat) would be a return to this steady state. We therefore defined restoration success in the context of our model results as the ability of habitat restoration to stabilize the population (i.e., a return to $\lambda \approx 1.0$). This is a valid and appropriate criterion for evaluating the success of habitat restoration because the risk of extinction for a stable population is 0 (i.e., time to extinction $\rightarrow \infty$) regardless of the resulting population size. We thus define this recovery to a steady state, persistent population as evidence for the ability of habitat restoration to rescue declining populations from extinction (i.e., successful restoration).

Because the demographic parameter b_t is both landscape and time dependent, we expect that restoration success will be determined by the extent to which the demographic potential has been eroded by past landscape change. Before restoration, habitat loss and fragmentation erode the demographic potential of the population to varying degrees depending on the rate of habitat loss, the degree of fragmentation, the species' edge sensitivity, and the length of time before restoration occurs. The demographic potential of the population (b_t) at the time of habitat restoration (t_R) thus bears the legacy of past landscape change. Therefore, restoration of habitat may not produce a restoration of demographic potential (i.e., $b_R \neq b_o$). In such cases, restoration success is demographically limited.

Results

If complete habitat restoration was implemented at a population's vulnerability threshold ($t_R = t_V$), habitat restoration was successful in stabilizing declining populations of species with low to intermediate edge sensitivities
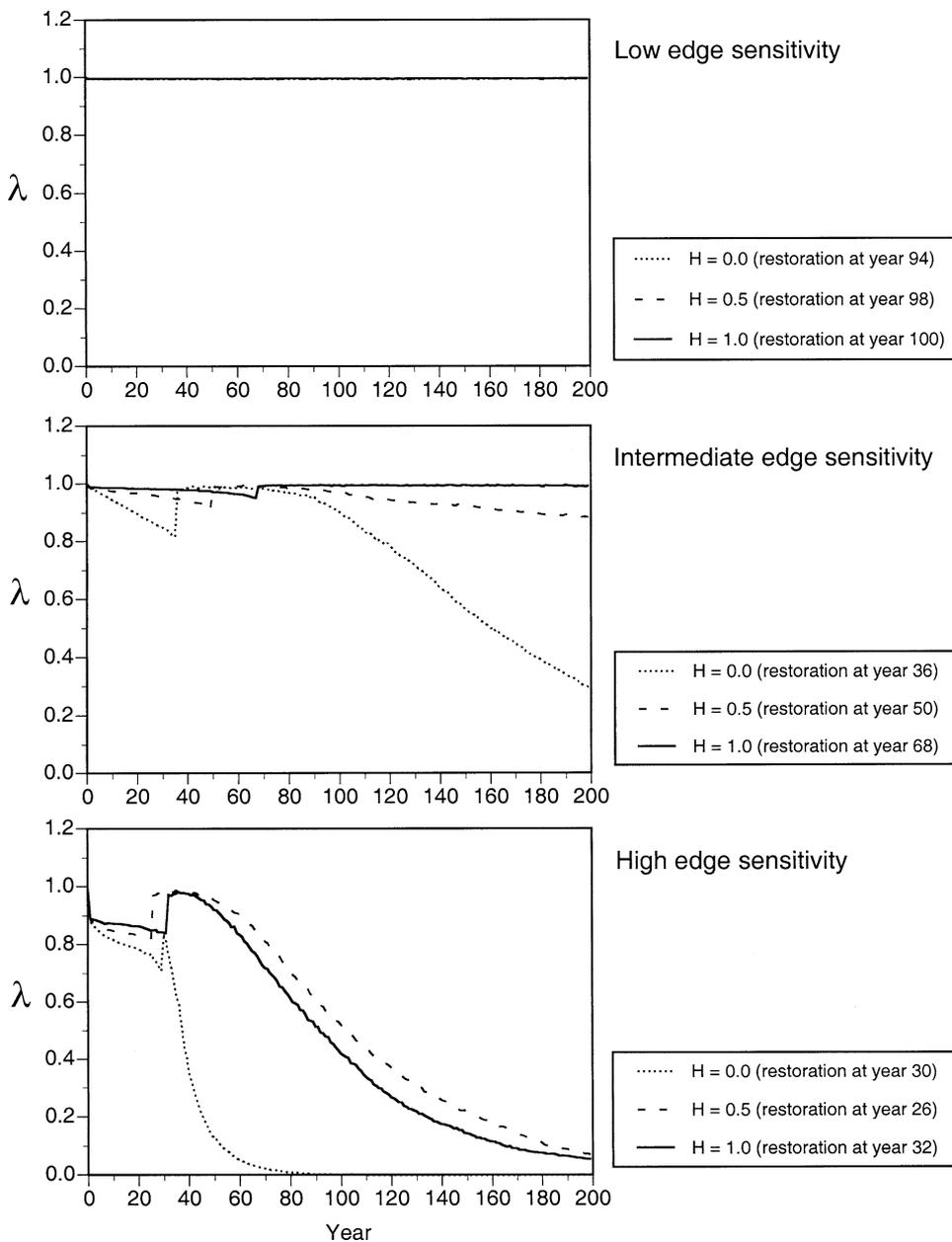
Figure 2. *Effects of habitat fragmentation (H) on population growth rate (λ) for all three levels of edge sensitivity when restoration occurs at the vulnerability threshold. The rate of habitat loss before restoration (r) = 0.5%/year. Response curves represent the mean of 10 runs on a replicated time series (n = 10) for each landscape scenario. The 95% CIs around response curves were extremely small and are not displayed. Nonoverlapping lines can thus be considered statistically significant at α = 0.05.*

in landscapes where habitat destruction had occurred gradually (r = 0.5%/year) and fragmentation had been minimized (H = 1.0; Fig. 2). Habitat restoration also initially stabilized declining populations for highly edge-sensitive species in less-fragmented landscapes (H = 0.5, 1.0), but populations ultimately began declining again within several decades (Figs. 2–3). Lagged population responses are thus possible in edge-sensitive species if restoration is initiated at the vulnerability threshold. Even species with low-to-intermediate edge sensitivity could exhibit lagged declines, which may not occur until 40–45 years after restoration appeared to have stabilized populations, in landscapes that were extensively fragmented (H = 0.0, r = 0.5, intermediate edge sensitivity) or where

habitat loss had been rapid (r = 1.0, H = 0.0, low edge sensitivity) (Figs. 2–3).

Different rates of habitat destruction obviously affected the amount of habitat remaining at the time of restoration, which helps explain these lagged effects and the limitations of habitat restoration to stabilize declining populations in these landscapes. For example, when restoration was implemented at the vulnerability threshold for species with intermediate edge sensitivity, complete habitat restoration occurred at year 36 (t_R = 36) in landscapes destroyed at a rate of 0.5%/year and at year 31 when the rate of habitat destruction was doubled (1%/year; Fig. 3). Total loss of habitat before restoration was 18% and 31%, respectively, for these two landscape-disturbance
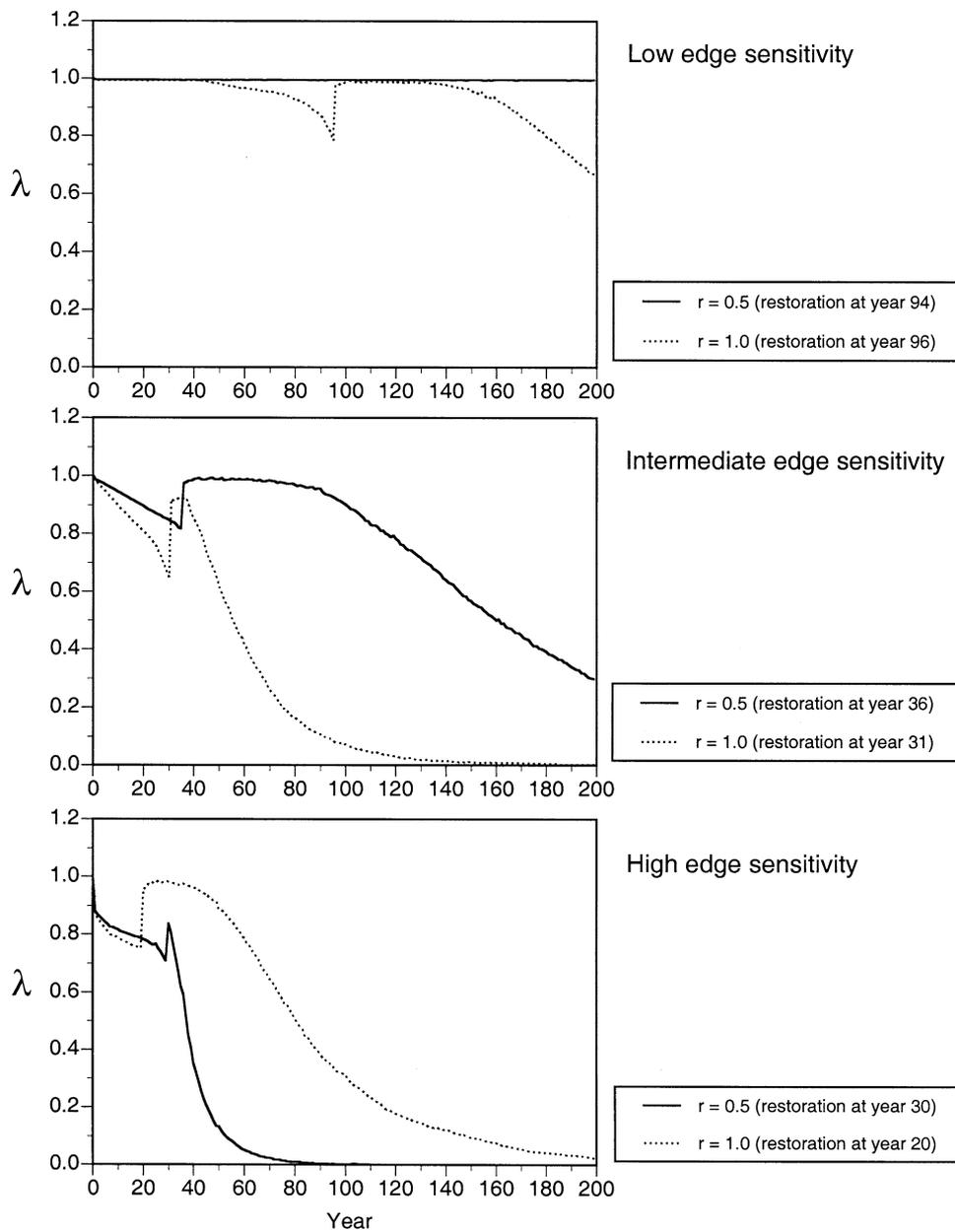
Figure 3. Effects of habitat loss rate before restoration (r) on population growth rate (λ) for all three levels of edge sensitivity when restoration occurs at the vulnerability threshold. The landscapes are highly fragmented (H = 0.0).

scenarios. Thus, although restoration was implemented at approximately the same time, more habitat remained on the landscape just before restoration in the former scenario (82% vs. 69%).

Accordingly, stabilizing a population should be easier to achieve in the scenario of 0.5%/year habitat loss, assuming that population size is proportional to habitat area. This was generally true, except in species with high edge sensitivity, in which reproductive success was severely affected by edge effects (Fig. 3). For these species, even though more habitat remained at the time of restoration when the rate of loss was initially 0.5%/year (15% lost before the vulnerability threshold was reached), restoration at the vulnerability threshold occurred later (year 30) than when habitat was destroyed faster (1%/year; 20% habitat lost before restoration implemented at year 20).

Given the 8-year lifespan of these generic songbirds, with a generation time of 2.3 years, about 13 generations would have been subjected to the demographic effects of habitat destruction and fragmentation in the former scenario as opposed to <9 generations in the latter scenario. Population sizes were thus lower at the point of restoration in the landscapes subjected to gradual loss of habitat owing to death of breeding adults and limited fledgling recruitment (a consequence of this species' high edge sensitivity). The demographic potential (number of productive nesting females and fledgling production) of these populations was eroded ("unsuccessful" restoration, Fig. 4),
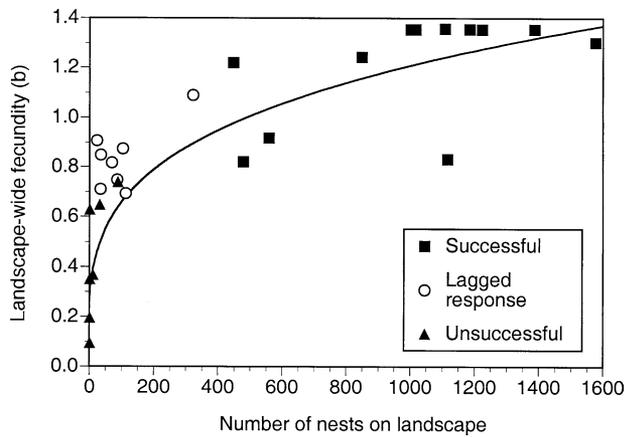
Figure 4. Demographic limitations to restoration success. Landscape-wide fledgling production (b) relative to the size of the nesting female population (number of nests on landscape) just before restoration ($t_R - 1$) for those populations and landscape scenarios depicted in Figs. 2, 3, 5, and 6. "Successful" scenarios are those in which habitat restoration succeeded in stabilizing populations (i.e., a return to steady state, $\lambda = 1.0$). Lagged-response scenarios are those in which habitat restoration produces a short-term return to steady state, but the population eventually declines. Unsuccessful scenarios are those in which habitat restoration failed to stabilize populations. A power function has been fitted to the data ($R^2 = 0.299$).

population growth rates were lower, and the population decline was steeper than when habitat was initially destroyed more quickly ($r = 1.0$; Fig. 3). Thus, population recovery was demographically limited rather than habitat limited in this case.

Although it may not be possible to stabilize or slow population declines if habitat restoration is delayed until the vulnerability threshold, restoration may be more successful if initiated earlier. For example, restoration could not mitigate population declines in species with high edge sensitivity when implemented at the vulnerability threshold (Figs. 2–3). Nevertheless, population growth rates could be stabilized if restoration was initiated earlier, some 16 years before the vulnerability threshold, in scenarios where landscapes experienced gradual habitat destruction ($r = 0.5$) and intermediate levels of fragmentation ($H = 0.5$) (high edge sensitivity, year 10; Fig. 5). Restoration implemented 6 years before the vulnerability threshold (year 20) stabilized populations for nearly 60 years, but recovery could not be sustained owing to demographic limitations produced by the initial habitat destruction ("lagged response" to restoration, Fig. 4).

The history of landscape change ultimately affects whether habitat restoration can stabilize population declines. For species with high edge sensitivity in extensively fragmented landscapes ($H = 0.0$), restoration

needed to occur sooner, some 20 years before the vulnerability threshold, if habitat destruction occurred at a rate of 0.5%/year, than when habitat was destroyed at a rate of 1%/year (where to stabilize populations restoration needed to occur 10 to 15 years before the threshold was reached; Fig. 6). Although it might appear here that restoration needed to be initiated earlier in scenarios where habitat loss was more gradual (0.5%/year vs. 1%/year), the timing of restoration was actually similar in these two scenarios. The species' vulnerability threshold occurred at year 30 in landscapes subjected to gradual ($r = 0.5$%/year) but extensive fragmentation ($H = 0.0$), such that restoration needed to be implemented within 10 years of the initial landscape disturbance to stabilize populations. Similarly, although the species' vulnerability threshold in fragmented landscapes subjected to a higher rate of habitat destruction ($r = 1.0$%/year) was reached sooner (at year 20), habitat restoration still needed to occur within the first 5 to 10 years to be successful. For species with high edge sensitivity in fragmented landscapes, habitat restoration sometimes needed to be initiated years before the species was at risk for extinction (i.e., before the vulnerability threshold) to overcome demographic limitations on the ability of habitat restoration to rescue declining populations.

Discussion

The observation that populations decline in response to habitat loss leads to the reasonable expectation that habitat restoration will be able to rescue these declining populations. Our model results demonstrate that this may not be the case when the populations are demographically limited rather than habitat-limited, however. We have demonstrated that the ability of habitat restoration to stabilize declining populations is strongly affected by the degree to which the species' demographic potential (a function of the number of nesting females and fledglings produced) has been eroded by habitat loss and fragmentation, which in turn is influenced by the species' sensitivity to fragmentation (edge sensitivity). Although edge-sensitive species were expected to benefit most from habitat restoration, such populations could not be rescued unless restoration was initiated well before the vulnerability threshold (i.e., well before the population is formally declared to be at risk of extinction). In practice, conservation measures such as habitat restoration would probably not be undertaken, or even proposed, until the population was assessed as being at risk from extinction. At this point, however, habitat restoration might be a case of too little too late, especially when one considers that we modeled habitat restoration as an absolute best-case scenario (all habitat instantaneously restored to the landscape). More modest restoration efforts would thus offer even less benefit.
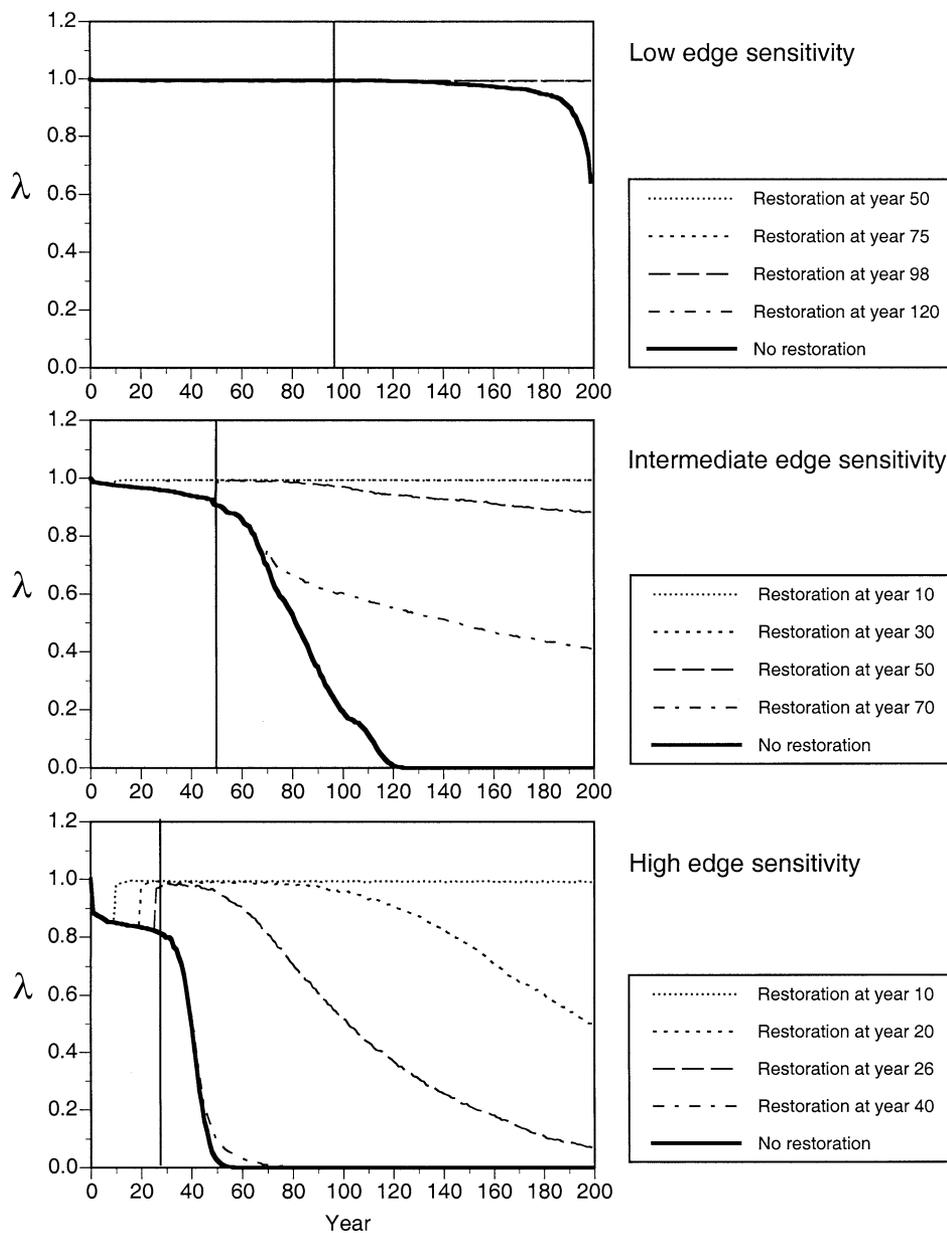
Figure 5. Effects of time of habitat restoration on population growth rate (λ) for all three levels of edge sensitivity. The landscapes are of intermediate fragmentation (H = 0.5), and the rate of habitat loss before restoration (r) = 0.5%/year.

This is not to say that habitat restoration can never recover populations of migratory songbirds, only that we need to shift the burden of proof and first demonstrate that populations are habitat limited and thus that declining populations are capable of being rescued through the restoration of habitat. Observation of population declines in response to habitat loss cannot be taken as evidence that populations are habitat limited, as our model shows.

Although habitat loss and fragmentation had a negative impact on productivity (b_t), the nesting capacity of the landscape (number of nesting females at steady state) was not limited by the amount of available habitat. This was not an a priori assumption of the model; rather, it was an emergent consequence of the model's demographic balance between maternity and survivorship. In other

words, the population was habitat sensitive in that it declined in response to habitat loss, but it was not habitat limited (the number of females needed to achieve demographic balance was not limited by available nesting habitat). Once habitat loss and population turnover (death of adult females) reduced available nesting females below a number coincident with the vulnerability threshold, even full habitat restoration was insufficient to rescue the population. The reproductive output of the remaining females was insufficient to fill restored nesting habitat and the population continued to decline.

In the model results depicted, this demographic threshold appears to occur when the number of nesting females falls below 400 and when $b < 0.8$ (Fig. 4). Populations declining from habitat loss and fragmentation may thus
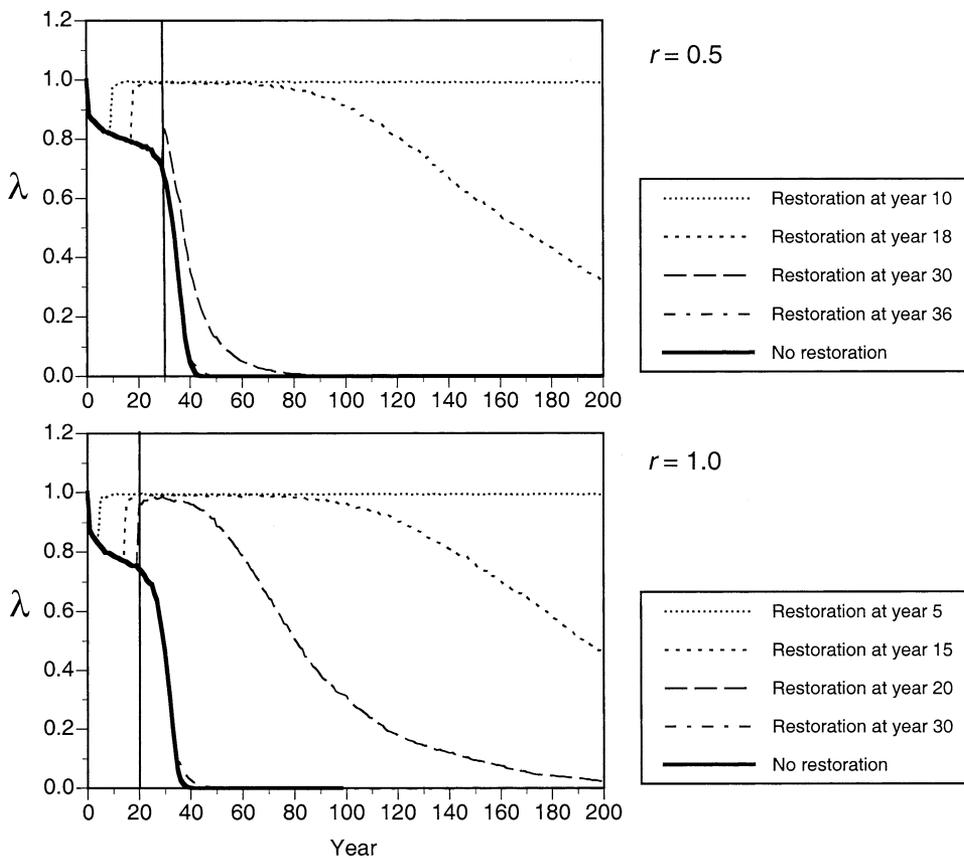
Figure 6. Effects of the rate of habitat loss before restoration (r) on the population growth rate (λ) of species with high edge sensitivity when habitat restoration occurs before, at, or after the vulnerability threshold. The landscapes are highly fragmented (H = 0.0).

have a "restoration threshold" where, once crossed, habitat restoration alone would no longer be sufficient to stabilize the population. This point would almost certainly occur at a higher level of remaining habitat than the vulnerability threshold. In this case, the population is demographically limited rather than habitat limited. Restoration might slow the decline of such populations, but will not be sufficient to prevent their extinction.

Further conservation measures aimed at increasing the demographic potential of the species must be applied, such as decreasing adult mortality through predator control, increasing fecundity through the control of brood parasites or by captive propagation, or increasing immigration either through reintroductions or by managing landscape connectivity to facilitate dispersal from source patches. In the case of many migratory songbirds, whose persistence depends on regional source-sink dynamics, a high level of connectivity among landscapes (meta-landscape connectivity) is essential for maintaining local populations within landscapes undergoing habitat loss and fragmentation (Robinson et al. 1995; K. A. With et al. *unpublished data*).

Several other researchers foresee difficulties in recovering declining populations solely through means of habitat restoration. Breininger et al. (1999) modeled extinction risk in the Florida Scrub-Jay (*Aphlecoma coerulescens*) with the RAMAS/stage program and found that populations recovered very slowly in restored habitat (and not at all if restoration did not succeed in creating high-quality habitat) because there were a limited number of birds available to colonize the new habitat. Root (1998), however, concluded that without habitat restoration the Florida Scrub-Jay would become extinct over much of its range owing to habitat degradation. Acosta and Perry (2002) used a spatially structured demographic model to examine the response of the Everglades crayfish (*Procambarus alleni*) to restoration of habitat by reestablishing a more natural hydroperiod in the south Florida wetlands. The simulated populations did not fully recover to their original numbers up to 50 years after habitat restoration, and the populations increased much more slowly than they had initially declined. These results provide further illustration of how demographic constraints and lag effects can limit a population's ability to recover even when habitat is increased by restoration.

Because habitat restoration projects are often difficult and expensive to execute, it is desirable to assess the likely success of such projects on the populations of species targeted for recovery. Spatially structured population models of the Iberian lynx (*Lynx pardinus*) indicate that restora-

tion will only reduce the extinction risk of the population if source habitat could be created and that increasing the amount of sink habitat will not increase population persistence (Gaona et al. 1998; Ferreras et al. 2001).

There are few published studies assessing the results of habitat restoration on small populations of birds. Kristan et al. (2003) concluded that restoration at the edge of habitat patches is of little benefit to edge-sensitive species such as the California Thrasher (*Toxostoma redivivum*) and Sage Sparrow (*Amphispiza belli*) in the coastal sage scrub of California. The California Gnatcatcher (*Polioptila californica*) and Cactus Wren (*Campylorhynchus brunneicapillus*), on the other hand, are more strongly affected by habitat degradation associated with edges than the existence of edge itself and so could potentially benefit from such restoration. Franzreb (1997) documented management efforts that successfully restored an extremely small population of Red-cockaded Woodpeckers (*Picoides borealis*) at a site in South Carolina. These efforts included habitat restoration, predator control, removal of competitor species, translocations, and the provision of artificial nest sites. The last directly reduced an important demographic constraint (nesting sites) somewhat independently of the more general restoration of the longleaf pine habitat used by this species. Although these combined efforts increased the size of the woodpecker population by an order of magnitude within a decade, it is impossible to assess the relative impacts of the creation of habitat and measures designed to increase survivorship, immigration, and fecundity on their recovery because they were undertaken simultaneously. Based on the results of our model, however, it seems unlikely that habitat restoration alone will be sufficient to stabilize or recover critically small, demographically challenged bird populations.

We identified circumstances in which populations are habitat sensitive (decline in response to habitat loss and fragmentation) but nevertheless cannot be rescued through habitat restoration because of demographic limitations. This is an important finding because it (1) presents a challenge to the general assumption that habitat restoration can recover populations, (2) makes an important distinction between habitat sensitivity and habitat limitation that is generally ignored, (3) suggests that populations may in some cases be demographically limited rather than habitat limited, and (4) raises the question of when populations are expected to be demographically limited as opposed to habitat limited. All these have important implications for restoration and conservation. Fully testing the hypothesis that habitat restoration can recover populations may be difficult in practice, but some combination of field observations, pilot studies, experiments, and model analysis is warranted at the planning stage of a restoration project to determine that the target population is indeed habitat limited and not demographically limited.

Acknowledgments

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