

MODELING THE ECOLOGICAL TRAP HYPOTHESIS: A HABITAT AND DEMOGRAPHIC ANALYSIS FOR MIGRANT SONGBIRDS

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Abstract. Most species occupy both high- and low-quality habitats throughout their ranges. As habitats become modified through anthropogenic change, low-quality habitat may become a more dominant component of the landscape for some species. To conserve species, information on how to assess habitat quality and guidelines for maintaining or eliminating low-quality habitats are needed. We developed a source–sink population model that depicted the annual cycle of a generalized migratory songbird to address these questions. We determined how demographic factors, landscape composition (the percentage of high- and low-quality habitat), and habitat selection interacted to promote population persistence or extirpation. Demographic parameters, including adult and juvenile survival, nesting success (probability of a nest successfully fledging one or more young), number of nesting attempts, and number of young fledged per nest, interacted to affect population growth. In general, population growth was more sensitive to adult and juvenile survival than to fecundity. Nevertheless, within typically observed survival values, nest success was important in determining whether the population increased, decreased, or was stable. Moreover, the number of nest attempts by females and the number of young fledged per nesting attempt influenced population stability. This highlights the need to obtain more complete demographic data on species than simple nest success to assess habitat quality. When individuals selected high- and low-quality habitats in proportion to habitat availability, populations persisted as long as low-quality habitat did not make up >40% of the landscapes. However, when individuals preferred low-quality habitats over high-quality habitats, populations were extirpated in landscapes with >30% low-quality habitat because low-quality habitat functioned as an ecological trap, displacing individuals from high-quality to low-quality habitat. For long-term conservation, we emphasize the need for basic information on habitat selection and life-history characteristics of species throughout their range.

Key words: *ecological trap; habitat quality; landscape management; neotropical migrant songbirds; population demography; population dynamics; source–sink.*

INTRODUCTION

The earth is a patchwork of habitats. For a population that resides in both high- and low-quality habitat, the presence of low-quality habitat can promote population persistence in a variety of ways. Although reproductive and survival rates are too low to maintain numbers in low-quality “sink” habitats (Pulliam 1988), these habitats may increase the probability that the greater population will persist by “housing” a large number of individuals at any given time, and may serve as a storehouse of genetic information as long as individuals can successfully reproduce at least at some level (Howe et al. 1991; see also Dias 1996, Hanski et al. 1996, Holt 1997). Additionally, a substantial number of young may be produced in low-quality habitats, depending on the number of individuals breeding there (Pulliam 1988).

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It is less clear, however, when the presence of low-quality habitat is a detriment to population persistence. Animals often have the opportunity to select among a variety of habitats that vary in quality; preferred habitats are those that are selected disproportionately to other available habitats (Johnson 1980). If individuals avoid low-quality areas, the presence of low-quality habitats may not negatively influence population persistence. However, if individuals disproportionately select low-quality habitats over available, high-quality habitats for reproduction and survival, then low-quality habitats may function as ecological traps, and their presence may lead to population extirpation (Gates and Gysel 1978).

Organisms tend to be distributed differentially across different habitat types, occasionally with low densities in high-quality habitats and high densities in low-quality habitats. Bobolinks (*Dolichonyx oryzivorus*), for example, have breeding densities up to four times greater in hayfields than in native prairie habitats, and may actively seek out breeding territories in this evolutionarily “new” environment (Bollinger and Gavin 1992). Yet, in most years, hayfields are low-quality habitats

for breeding because nests are often destroyed as fields are hayed prior to fledging. Similarly, California Towhees (*Pipilo crissalis*) occur in greater densities in habitats where reproductive success is lower (Purcell and Verner 1998), and this pattern of distribution is apparently not explained by the density-dependent exclusion of subdominant individuals from high-quality habitats (sensu Fretwell and Lucas 1970). For more examples of potential ecological traps see Dwernychuck and Boag (1972), Best (1986), and Misenhelter and Rotenberry (2000).

The selection of poor-quality habitat over available, high-quality habitats has been documented in species such as Snow Geese (*Chen caerulescens*) and butterflies. Snow Geese experience poor reproductive success in highly degraded, high-density habitats. Yet, because of site fidelity, birds select degraded habitats for breeding year after year, while apparently more suitable habitat remains unoccupied (Ganter and Cooke 1998). Catepillars in the genus *Pieris* also appear to select poor-quality habitats (host plant species) over available, high-quality habitats. In landscapes that offer both native and introduced host species, *Pieris oleracea* readily oviposit on the introduced host plant species that is lethal to larvae (Chew 1978, 1980).

The essence of an ecological trap is that it is low in quality for reproduction or survival and cannot sustain a population, yet it is preferred over other available, higher quality habitats. Low-quality habitat that is not preferred beyond its availability is not likely to have the same effect on a population as an ecological trap, but low-quality habitat may lead to extirpation if it becomes a dominant or sole habitat for reproduction and survival. Traps may become more common as landscapes are dramatically altered, and where populations are not able to adapt behaviorally to new landscapes. Species unable to adapt to rapid changes will become extinct before adaptation to trap habitat occurs.

Management plans are currently being developed to promote long-term viable populations of native bird species across the United States (e.g., Partners in Flight Landbird Conservation Plans, Bonney et al. 1999). Consequently, resource managers and planners are challenged to identify the quality of different habitats and to make recommendations about the maintenance or elimination of low-quality habitats in the region. As a result of recent planning and research efforts, major gaps in our knowledge of "landscape-scale" management have emerged. Several critical questions in songbird conservation have not been explored either theoretically or empirically, including the following. How should habitat quality be assessed? Which demographic factors are most important to measure in determining habitat quality? How does low-quality habitat affect a population's ability to persist? When should low-quality habitats be eliminated, and when do low-quality habitats serve a useful purpose for maintaining populations? When do low-quality habitats function as eco-

logical traps? Should managers target their efforts toward altering the percentage of the landscape in high and low quality, or should they maintain landscape composition and focus on changing habitat features within the landscape?

Our objectives were to assess how population growth of a generalized migratory bird species varied (1) as demographic variables such as survival and reproduction varied within a one-habitat landscape, (2) as the percentage of low- and high-quality habitat in the landscape varied, (3) as differences in productivity between low- and high-quality habitat varied, and (4) as individuals' "preference" for low-quality habitat varied, which included the specific scenario in which low-quality habitat functioned as an ecological trap. Data were scant for some model parameters and we made many simplifying assumptions. Therefore, the model is of value for the relative comparisons that we made and for generating hypotheses about landscape-scale management, but not for predicting specific population responses.

MODEL DESCRIPTION

Our model was based on the generalized population ecology of a neotropical migratory songbird that nested in either low- or high-quality habitat for breeding. The model accommodated different definitions of low- and high-quality habitat. For example, low- and high-quality habitats could have been hayfields and native prairie, small and large forest patches, or edge and interior forest, respectively. Moreover, the model was independent of a specific definition of low-quality habitat. For example, if low-quality habitat was edge, low-quality habitat could have been defined as habitat within 50 m of a habitat edge, habitat within 100 m of a habitat edge, or any other distance related to edge. The model revealed population growth in response to changes in the demographic parameters and the amount of low- and high-quality habitat in the landscape.

We modeled population growth with difference equations modified from a standard, age-structured matrix model (Caswell 1989, Noon and Sauer 1992). This approach allowed us to model the effects of habitat selection and the amount of each habitat while maintaining the basic structure of a traditional Leslie matrix model (Leslie 1945). The analytical solutions of this model are presented by R. H. Lamberson, T. M. Donovan, and J. E. Carroll (*unpublished manuscript*).

We used a female-only model with two age classes: n_0 (individuals <1 yr old), and n_{1+} (individuals ≥ 1 yr old). The model was based on an annual cycle; females were censused at the beginning of the breeding season in year t . After breeding, adults and juveniles migrated to their winter range, overwintered, and then migrated back to their breeding range and reoccupied breeding habitat, at which time they were censused in year $t + 1$. Although two age classes were present in the population over the annual cycle, this is a one-stage model

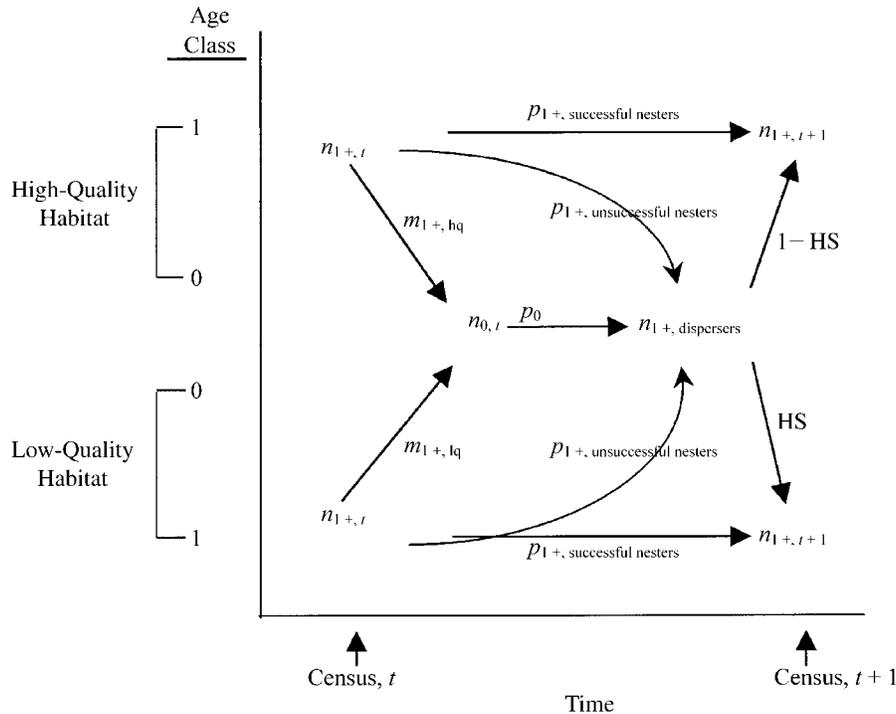


FIG. 1. A time-by-age biplot of the model used to project a migratory songbird population that breeds in two habitats, high and low quality. Symbols are: n , the number of females; m , habitat-specific fecundities; hq, high-quality habitat; lq, low-quality habitat; 1+, birds ≥ 1 yr old; p , survival rates; and HS, habitat selection coefficient. The diagram does not depict the density-dependent effects of carrying capacity; see *Model description* for a further explanation of the model.

because all individuals were considered adults (≥ 1 yr old) when the population was censused. Adults came from two sources: surviving adults and young that were born after the last census and survived to the current census. The simplest form of the difference equation was for the one-habitat model and was:

$$n_{1+, t+1} = n_{1+, t} (p_0 m_{1+}) + n_{1+, t} (p_{1+})$$

where $n_{1+, t+1}$ was the number of females in ≥ 1 yr old in year $t + 1$; p_0 was the survival of young from fledging to the pre-breeding census in the following year (juvenile survival); m_{1+} was the number of female young produced in a breeding season per female, and p_{1+} was the survival of females ≥ 1 yr old from one census to the next (Caswell 1989, Noon and Sauer 1992). The term n_0 does not appear in the model because the model was based on a pre-breeding census; upon their return to the breeding grounds, juveniles were counted as 1-yr-olds (Caswell 1989, Noon and Sauer 1992). We combined the 1-yr-old and older age classes into a single stage because of lack of strong variation in age-specific fecundities (especially after the first year) and little or no reproductive senescence before death in most passerine species (Noon and Sauer 1992). Fecundity was estimated from separate terms for nesting success, number of young fledged per successful nest, and number of nesting attempts (Donovan et al. 1995a, b).

Population projections in the two-habitat model were

based on the same basic difference equation, except that populations in each habitat were projected separately and functions were added to control movements between habitats (Fig. 1). Habitat selection occurred when individuals returned to the breeding grounds, just prior to the population census. We assumed that females that successfully fledged at least one offspring in the previous year returned to the same habitat in the current year. Females that did not successfully reproduce were pooled with returning juveniles into a disperser pool, and then were assumed to select habitats according to a habitat selection coefficient. The habitat selection coefficient was the proportion of the disperser pool that attempted to secure a breeding location in the low-quality habitat (Fig. 1).

Total habitat in the landscape was 1000 ha, with a maximum density of 1 female/ha. We assumed that individuals in excess of 1000 permanently emigrated from the system. This type of ceiling model can be appropriate for populations with contest competition due to territoriality (Akçakaya et al. 1997). This was the only form of density dependence in the one-habitat model. In the two-habitat model, the success of dispersers in attaining a breeding territory in a habitat also depended on how many territories were occupied by older adults that had successfully reproduced in that habitat in the previous year. If K in one habitat was attained, then individuals attempted to breed in the non-

preferred habitat. This type of density dependence produced distribution patterns in which individuals occupied both high- and low-quality habitat (*sensu* Fretwell and Lucas 1970).

We calculated three variables from each simulation. Total population size (N_t) for each year of a simulation was the sum of the number of breeding females in low- and high-quality habitat. The finite rate of increase, λ , was calculated as N_{t+1}/N_t from a series of projected population sizes during a period when the population was growing (or declining) and not influenced by K . We also calculated the population size at equilibrium, which ranged from 0 to 1000 (K) and depended on λ . If $\lambda < 1$, then population equilibrium was always 0 because there was no emigration from outside the system, and the population was extirpated. If $\lambda > 1$, then the population equilibrium was always 1000 (K) because the number of females above K were removed (emigrated) from the population each year. When $\lambda = 1$, the population equilibrium was between 0 and K , which we calculated as the integer value at which the population stabilized during the 100-yr simulation.

MODEL PARAMETERIZATION

Model inputs included the proportion of low- and high-quality habitat, the initial number of females in each habitat, adult and juvenile survival, habitat-specific fecundity values (including nesting success, number of young fledged per successful nest, and number of nesting attempts), and preference for a particular habitat type. The proportion of the total habitat in low-quality habitat ranged from 0 to 1. A proportion scale was used for model calculations, but results are expressed as percentages of low-quality habitat. Initial number of females in each habitat type varied depending on how much habitat was available to be occupied. Initial population size did not affect model outputs because our model was deterministic. Hence, populations grew to carrying capacity, declined to extinction, or stabilized at an equilibrium value between 0 and K , regardless of the initial population size.

Adult survival values ranged from 0.4 to 0.8, reflecting the average known range of survival for migratory passerines (Greenberg 1980). Juvenile survival (the probability of surviving from fledging to the pre-breeding census) values varied, and were one-half of adult rates in most simulations. This relative proportion was supported by empirical data (Greenberg 1980), and has been used in several other models of migrant bird populations (Temple and Cary 1988, Howe et al. 1991, Thompson 1993, Donovan et al. 1995a). Fecundity was defined as the number of female offspring per adult female per breeding season, and depended on nesting success, the number of fledglings per successful nest, and the number of re-nesting attempts. For simplicity, we assumed that individuals had the potential to produce no more than one successful brood during the breeding season. That is, individuals that were suc-

cessful early in the breeding season did not make further breeding attempts. The fecundity inputs varied and the range of values used in the model was derived from empirical data from Donovan et al. (1995b) and Robinson et al. (1995), as well as Temple and Cary (1988), Greenberg (1980), and Porneluzi and Faaborg (1999).

MODEL SIMULATIONS

Our goal was to assess how population growth (λ) varied: (1) as demographic variables such as survival and reproduction varied within a one-habitat system; (2) as the proportion of low-quality habitat in the landscape varied; (3) as differences in productivity between low- and high-quality habitat varied; and (4) as individuals' preference for low-quality habitat varied, with an emphasis on situations in which the habitat selection coefficient for low-quality habitat was greater than the proportion of low-quality habitat in the system (the ecological trap hypothesis). We will describe each of these simulations.

Sensitivity of λ to demographic values in a one-habitat system

We began by evaluating the sensitivity of λ to variation in demographic rates (survival and reproduction) for a system in which low-quality habitats did not exist. This step served as a comparison for the two-habitat models. In this model, "base" inputs simulated a population with adult survival of 0.6, juvenile survival of 0.3, and nesting success of 0.4, where successful nests fledged two female young. There was a maximum of two female offspring per female per year. If a nesting attempt failed, individuals could re-nest up to three times total in the breeding season or until a breeding attempt was successful.

We covaried all of the model inputs (Table 1) and compared the different model outputs (λ) to the base model. Thus, we examined λ in response to changing nest success estimates, changing number of offspring per successful nests, changing number of nesting attempts, and changing survival estimates. The results indicated which of the parameters most strongly affected λ and, hence, which factors have significant management implications for a system with a single habitat type in which immigration is zero.

Sensitivity of λ to proportion of low-quality habitat in the system

Next, we allowed the proportion of low-quality habitat in the system to vary from 0 to 1. In these simulations, we let individuals select habitats in direct relationship to their availability (no habitat selection, i.e., if the landscape contained 10% low-quality habitat, then 10% of the disperser pool attempted to secure breeding territories in the low-quality habitat and 90% attempted to secure breeding territories in the high-quality habitat). We examined λ in response to changing habitat percentages and to demographic variables.

TABLE 1. Parameter values used in model simulations to determine sensitivity of the finite rate of increase to demographic rates in a one-habitat system.

Simulation	Nest success	Survival		No. young fledged per successful nest	Maximum no. nest attempts
		Adult	Juvenile		
Base	0.4	0.6	0.3	2.0	3
Nest success vs. survival	0.2–0.6 (by 0.05)	0.4–0.8 (by 0.05)	adult × 0.5 (all simulations)	2.0	3
Nest success vs. juvenile survival	0.2–0.6 (by 0.05)	0.6	0.2–0.6 (by 0.1)	2.0	3
Nest success vs. no. nest attempts per year	0.2–0.6 (by 0.05)	0.6	0.3	2.0	1–4 (by 1)
Nest success vs. no. young fledged per nest	0.2–0.6 (by 0.05)	0.6	0.3	1.2–2.0 (by 2.0)	3

We covaried nest success and survival rates for six levels of low-quality habitat in the landscape: 0, 20, 40, 60, 80, and 100% (Table 2). In these simulations, nest success in the low-quality habitat was 50% that of nest success in high-quality habitat. Thus, the absolute difference between low- and high-quality habitat remained constant in these simulations. We limited the range of adult survival rates from 0.5 to 0.7, based on results of sensitivity analyses in a one-habitat system.

Sensitivity of λ to reproductive differences between low- and high-quality habitat

Next, we changed the percentage of low-quality habitat, and additionally modified the magnitude of the difference in reproductive parameters between low- and high-quality habitat (allowing differences in nesting success between low- and high-quality habitats to vary from 50%; Table 2). In these simulations, we varied nest success and number of young fledged in low-quality habitat, while maintaining at base levels both

nest success and the number of young fledged per nest in high-quality habitat. This allowed us to examine how the presence of low-quality habitat affected λ differently depending on how inferior those low-quality habitats were for reproduction.

Sensitivity of λ to preference for low-quality habitat: the ecological trap hypothesis

Finally, we examined the effects of habitat preferences for low-quality habitat, with an emphasis on situations in which the habitat selection coefficient for low-quality habitat was greater than the percentage of low-quality habitat in the system (the ecological trap hypothesis). As a comparison, we also modeled the more traditional view that high-quality habitats would be preferred over low-quality habitats (e.g., Dhondt et al. 1992, Wauters and Lens 1995, Ferrer and Donazar 1996). In these simulations, we varied selection for low-quality habitat from 0% to 100% (Table 2). When selection of low-quality habitat was equal to the per-

TABLE 2. Parameter values used in model simulations to determine sensitivity of the finite rate of increase to demographic rates, the amount of high quality (HQ) and low-quality (LQ) habitat, and habitat preference.

Simulation	LQ habitat (%)	LQ preference†	Nest success		Survival		No. young fledged/nest		No. nest attempts
			HQ	LQ	Adult	Juvenile	HQ	LQ	
Base	User-defined	User-defined	0.4	0.2	0.6	0.3	2.0	1.6	3
Nest success vs. survival	0–100 (by 20)	none	0.2–0.6 (by 0.05)	HQ × 0.5 (all simulations)	0.5–0.7 (by 0.05)	Adult × 0.5 (all simulations)	2.0	1.6	3
LQ nest success vs. no. fledged per nest in LQ	0–100 (by 10)	none	0.4	0.1, 0.2, 0.3	0.6	0.3	2.0	1.2, 1.6, 2.0	3
Dispersers selecting LQ (%)	0–100 (by 10)	0–100 (by 10)	0.4	0.2	0.6	0.3	2.0	1.6	3

† LQ preference is the percentage of the pool of dispersers that initially attempt to breed in LQ habitat.

centage of low-quality habitat in the system, the population used habitats in relation to their availability and there was no habitat preference based on quality (no selection). When selection of low-quality habitat was less than the percentage of low-quality habitat in the system, the population avoided low-quality habitat and preferred high-quality habitat (*sensu* Fretwell and Lucas 1970). When selection of low-quality habitat was greater than the percentage of low-quality habitat in the system, the low-quality habitat functioned as an ecological trap.

RESULTS

Sensitivity of λ to demographic values in a one-habitat system

With model parameters at base levels (Table 1), $\lambda = 1.07$, so the population increased 7% per year and stabilized at K (or 1000 individuals). Changing model inputs, however, resulted in either population increase or decline, and the parameters affected λ differently.

Nest success vs. adult survival.—The model was more sensitive to changes in survival rates than to changes in reproductive rates (Fig. 2a). Increasing adult survival values by 0.1 increased λ more than did increasing nesting success by 0.1, particularly when nesting success was high (Fig. 2a). Within the range of adult survival 0.5–0.7, nest success was important in determining whether the population increased, decreased, or was stable (Fig. 2a).

Nest success vs. juvenile survival.—When all other demographic parameters were at base levels, juvenile survival had to be ~ 0.25 for λ to be 1. The model was sensitive to levels of juvenile survival (Fig. 2b). When juvenile survival was within the range 0.2–0.4, nest success was important in determining population stability. High levels of juvenile survival (0.5 and 0.6) produced growth rates of $\lambda > 1$, irrespective of nest success values modeled. When nesting success was very low (0.2), changes in juvenile survival had less impact on population growth than when nesting success was high (0.6).

Nest success vs. number of nest attempts per year.—Increases in the number of nest attempts per year increased λ (Fig. 2c). When the number of nesting attempts per year was limited to one, the population was below replacement levels even when nesting success was high. When nesting success was between 0.25 and 0.4, the number of nesting attempts per year determined whether the population increased, declined, or remained stable. At higher nesting success levels (e.g., 0.6), increasing the number of nest attempts per year beyond two attempts did not increase λ greatly because the vast majority of females experienced reproductive success with their first or second nesting attempt.

Nest success vs. number of young fledged per nest.—The model was not as sensitive to changes in the number of young fledged per successful nest relative to

other demographic parameters (Fig. 2d). However, the number fledged per successful nest was an important demographic factor in determining whether the population would persist with nesting success values ≥ 0.3 . When nest success levels were high (0.6), at least 1.4 female young per successful nest was required for $\lambda > 1$, indicating that clutch size and partial nest loss due to predation, parasitism, or other factors influence population persistence.

Sensitivity of λ to percentage of low-quality habitat in the system

We determined the effect of the percentage of low-quality habitat in the landscape when individuals selected habitats in relation to their availability and when reproductive parameters were 50% lower in low-quality habitat than high-quality habitat (Table 2). The finite rate of increase was < 1 when low-quality habitat comprised $> 40\%$ of the landscape and other demographic parameters were at base levels (Fig. 3). Thus, the population was extirpated when landscapes contained $> 40\%$ low-quality habitat. With base demographic values, $\lambda > 1$ and equilibrium population sizes were 1000 when the amount of low-quality habitat was $< 30\%$ of the landscape (Fig. 4). When the relative amount of low-quality habitat was 30–40%, populations persisted, but equilibrium population size decreased as the percentage of low-quality habitat increased (Fig. 4).

Nest success vs. survival (no habitat preference).—For landscapes with 0–100% low-quality habitat landscape, maximum growth was attained, not surprisingly, when nesting success and survival values were greatest (Fig. 3). Within a given landscape, incremental changes in survival had a greater impact on λ than did incremental changes in nesting success in the high-quality habitat (Fig. 3), particularly in landscapes with a low percentage of poor-quality habitat.

Nest success and percentage of low-quality habitat in the landscape.—As the percentage of low-quality habitat in the landscape increased, higher levels of nest success and/or adult survival in the high-quality habitat were required for $\lambda > 1$. These results changed predictably as the relative amount of low-quality habitat increased in the landscape. When the landscape contained 20% low-quality habitat, with base demographic parameters, 0.35 nesting success in high-quality habitat was adequate to sustain the population at $\lambda = 1$ (Fig. 3b). When the landscape contained 60% low-quality habitat, with base demographic parameters, 0.55 nesting success in high-quality habitat was needed to sustain the population at $\lambda = 1$ (Fig. 3d).

Sensitivity of λ to reproductive differences between low- and high-quality habitat

Not surprisingly, the “quality” of the low-quality habitat strongly influenced λ , but its effect depended on the percentage of the landscape in low-quality habitat (Fig. 5).

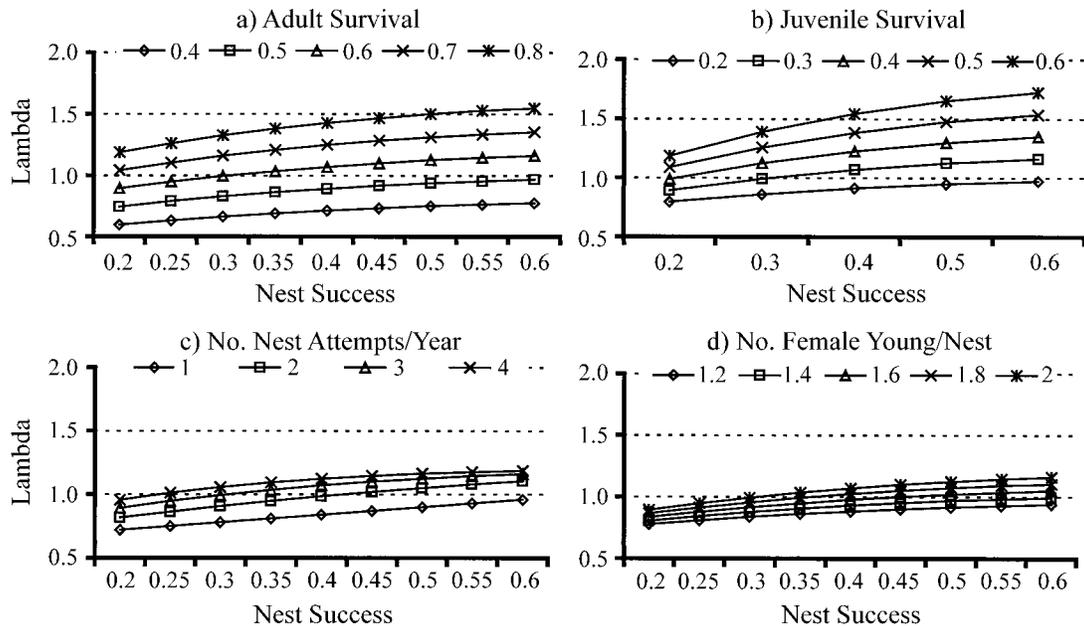


FIG. 2. Sensitivity of λ , the finite rate of population increase, to changes in demographic variables from base levels in a landscape composed of high-quality habitat. Base levels were 0.4 nesting success, 0.6 adult survival, 0.3 juvenile survival, three or fewer nesting attempts, and two female fledglings per successful nest.

Low-quality habitat nest success vs. percentage of landscape in low-quality habitat.—When landscapes contained $\leq 30\%$ low-quality habitat, $\lambda > 1$, regardless of how “poor” nesting success was in the low-quality habitat. However, λ was sensitive to nesting success in the low-quality habitat when landscapes contained $>30\%$ low-quality habitat (Fig. 5). In these situations, logically, λ increased as nesting success increased within the low-quality habitat. However, increasing nesting success in low-quality habitats generally did not allow populations to persist when landscapes contained a very large percentage (e.g., $>80\%$) of low-quality habitat.

Low-quality nest success vs. number of young fledged per nest in low-quality habitat (no habitat preference).—The model was sensitive to the number of young fledged per nest in low-quality habitat, but again, only when landscapes contained $>30\%$ low-quality habitat (Fig. 5). In landscapes with $<30\%$ low-quality habitat, increasing the number of young fledged per nest in low-quality habitats did not change λ , regardless of nesting success in the low-quality habitat. When landscapes contained 30–40% low-quality habitat, an increase in nesting success in the low-quality habitat appeared to have a larger effect on λ than did increasing the number of young fledged per nest. In landscapes with $>40\%$ low-quality habitat, the number of young fledged per nest affected λ , but this effect was more important as nest success increased in the low-quality habitat (Fig. 5). For example, when nest success in the low-quality habitat was 0.1 and the landscape contained $\geq 40\%$ low-quality habitat, increasing the number of

young fledged per successful nest has little impact on λ (Fig. 5a). In contrast, when nest success in the low-quality habitat was 0.3 and landscapes contained $>40\%$ poor-quality habitat, increasing from 1.2 to 2 young fledged per nest determined whether the population would persist or would be extirpated (Fig. 5c).

Sensitivity to preference for low-quality habitat: the ecological trap hypothesis

The percentage of dispersers selecting low-quality habitat and the percentage of low-quality habitat in the landscape interacted to affect λ (Fig. 6). When the contribution of the low-quality habitat was 20% or less of the landscape, $\lambda > 1$, regardless of the percentage of dispersers that selected low-quality habitat. In this situation, even high preference for low-quality habitat resulted in a system in which individuals occurred in both low- and high-quality habitat (because the low-quality habitat was at K , and individuals were “forced” into high-quality habitat).

Habitat preferences became important to population persistence in landscapes that contained a greater amount (e.g., $>20\%$) of low-quality habitat. If landscapes contained $>30\%$ low-quality habitat and $>30\%$ of individuals in the population selected low-quality habitat for breeding, then $\lambda < 1$. That is, the low-quality habitat functioned as an ecological trap and the population was extirpated (Fig. 6).

If the landscape contained $\geq 30\%$ low-quality habitat, but only 0–30% of the population preferred low-quality habitat over high-quality habitat, the population could persist and $\lambda = 1$ (Fig. 6). In this situation, equi-

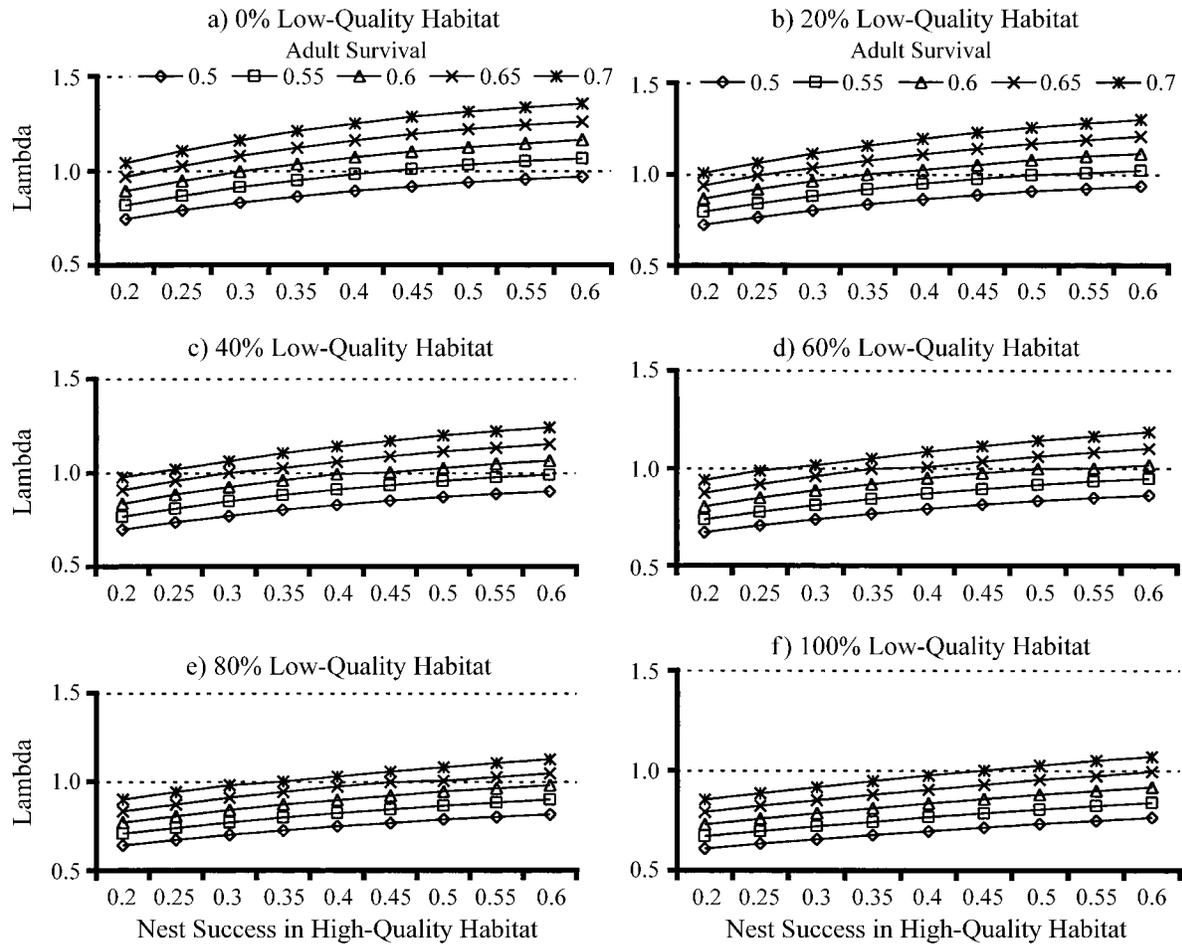


FIG. 3. Sensitivity of λ to changes in the percentage of low-quality habitat in the landscape. Graphs depict the response of λ to five levels of adult survival (0.5–0.7) and nine levels of nesting success (0.2–0.6) within high-quality habitats. Base levels were 0.4 nesting success, 0.6 adult survival, 0.3 juvenile survival, three or fewer nesting attempts, and two female fledglings per successful nest. Individuals selected habitats according to the availability of each habitat type in the landscape (preference = none).

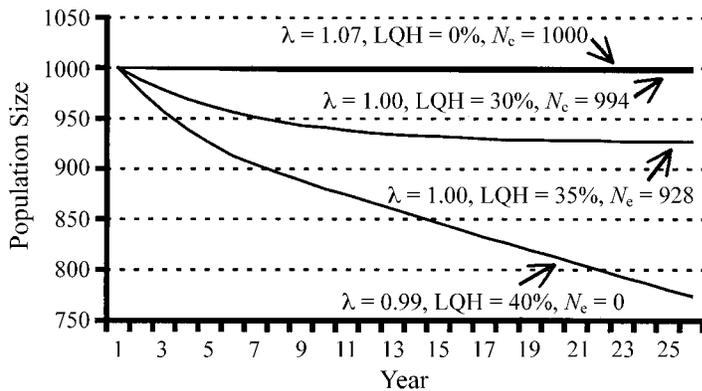


FIG. 4. Population size during a 25-yr simulation in which low-quality habitat (LQH) made up 0–40% of the landscape. N_e is the number of total individuals in the population at equilibrium.

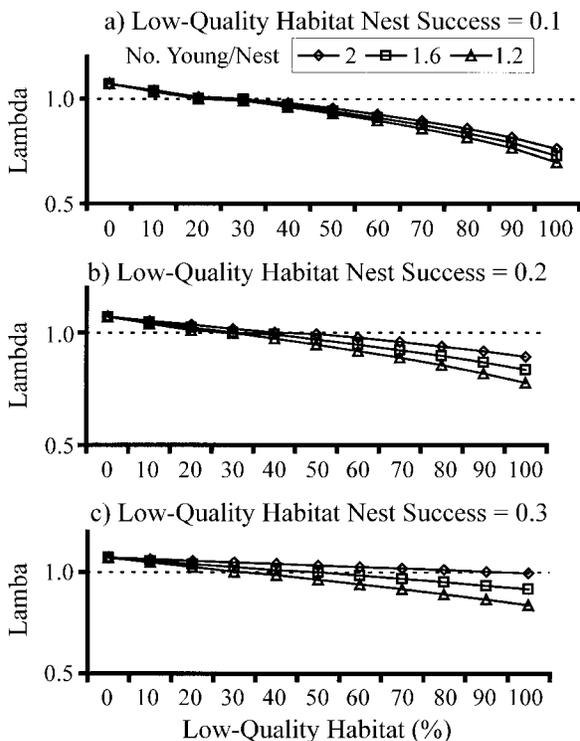


FIG. 5. Sensitivity of λ to reproductive differences (nesting success and number of females fledged per successful nest) between low- and high-quality habitat. Nesting success varied from 0.1 to 0.3 (panels a–c), and number of fledglings per successful nest varied from 1.2 to 2.0. Nest success in high-quality habitat was 0.4 in all simulations.

librium population size depended on the landscape composition (Fig. 7). Equilibrium population size was 1000 in landscapes with $\leq 30\%$ low-quality habitat, suggesting that the presence of low-quality habitats in the landscape did not negatively impact population size in the system. However, when 0–30% of the population preferred low-quality habitats and when landscapes contained 40–90% low-quality habitat, equilibrium population size decreased as the percentage of low-quality habitat in the landscape increased. The majority

of the individuals in all cases occurred in the high-quality habitat because 70% of the individuals preferred high-quality habitats (Fig. 7).

DISCUSSION

Scientists and land managers now recognize the need to address spatial variation in species demographics and to address conservation issues at a landscape and regional scale (Noss 1983, Franklin 1993, Maurer 1993, Freemark et al. 1995, Petit et al. 1995). Through model simulations, we showed how variation in demographic values, habitat availability in a landscape, and habitat preference could affect λ . Our results, however, are essentially untested hypotheses. We made several simplifying assumptions in our model and, hence, results should be cautiously interpreted. For example, in our model, habitat was either high or low quality; gradients in habitat quality did not exist. Because we used a deterministic model, confidence intervals were not produced and, consequently, the statistical and biological significance of the different λ values generated by the model should be cautiously interpreted. Additionally, our model was not spatially explicit and, hence, we did not consider the importance of the spatial arrangement of habitat on reproduction, survival, habitat selection, or dispersal. Moreover, the model assumed that total habitat in the system was constant; that is, we did not consider the effect of habitat loss on population persistence, although habitat loss clearly is a serious threat to population viability (Fahrig 1997). Finally, our model focused on single-species population dynamics, but managers will need to consider the dynamics of multiple species, often with conflicting habitat needs and conflicting definitions of high- and low-quality habitat. In spite of these shortcomings, we discuss some of the major results of the model and make preliminary suggestions for landscape-scale management, with the hope that these hypotheses will be tested and modified as more is learned about songbird population dynamics in heterogeneous landscapes.

Population growth was sensitive to all demographic parameters in our single-habitat model, at least under

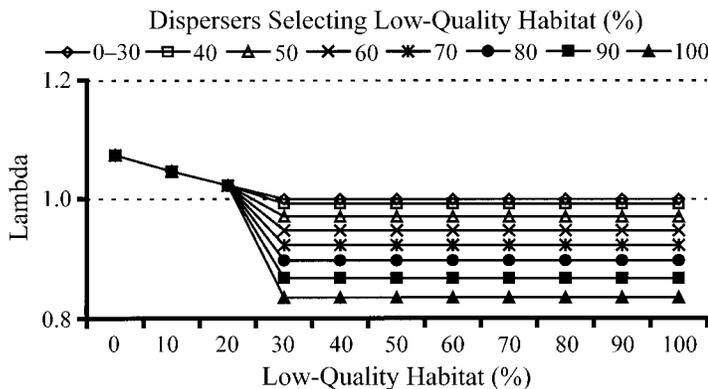


FIG. 6. Sensitivity of λ to the percentage of individuals that select low-quality habitat and the percentage of low-quality habitat in the landscape.

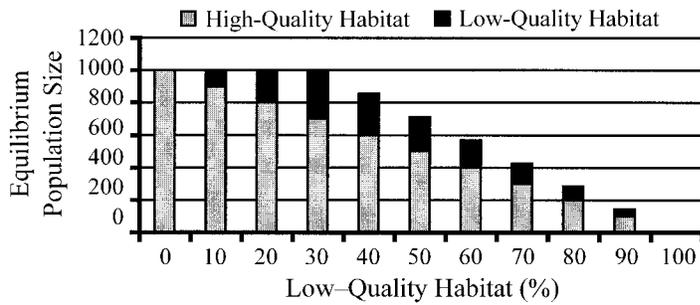


FIG. 7. Equilibrium population size and the distribution of individuals in landscapes containing 0–100% low-quality habitat, where $\leq 30\%$ of the population selected low-quality habitat over high-quality habitat for breeding.

some conditions. Moreover, demographic parameters often interacted with each other to influence population growth in different ways. For example, nest success had a greater impact on λ when juvenile survival was high, and the number of nest attempts per year was more important when nest success was low. The potential effects of the number of nest attempts and the number of young fledged per nest indicate the importance of obtaining more complete demographic data than simple nest success.

In our two-habitat model, the amount of low- and high-quality habitat had important effects on λ and strongly interacted with habitat preference. Under typically observed survival and nest success values (0.6 adult survival, 0.3 juvenile survival, and 0.4 nest success in high-quality habitat), landscapes with intermediate amounts of low-quality habitat (e.g., 40%) supported viable populations, assuming that individuals selected habitats in proportion to their availability or selected high-quality habitats over low-quality habitats. Populations on landscapes with large amounts of low-quality habitats (e.g., 80%) are likely to be extirpated unless nesting success in the high-quality habitat is very high.

If low-quality habitat acted as an ecological trap (i.e., was actually preferred to high-quality habitat), then λ was very sensitive to the amount of low-quality or “trap” habitat. When $>30\%$ of dispersers sought low-quality habitat and the landscape contained $>30\%$ low-quality habitat, then $\lambda < 1$. Of equal interest, however, was that $\lambda > 1$ on landscapes that contained $<30\%$ low-quality habitat, even if the low-quality habitat functioned as a trap. Thus, a population could persist in landscapes with ecological traps as long as there was a large amount of high-quality habitat. A key assumption in our model was that individuals that could not attain breeding territories in the preferred trap habitat would spill over into the high-quality areas (see also Pulliam and Danielson 1991). Without this assumption, the population would show even greater sensitivity to the amount of trap habitat in the landscape.

MANAGEMENT IMPLICATIONS

To the extent that models such as ours reflect the actual population biology of a species, they can help

to determine what factors are limiting population growth. With information on demographic values, our sensitivity analyses can be used to demonstrate how a change in one or more parameters can affect λ , and how increases in one parameter can offset low values in another parameter.

One approach to increasing λ is to increase adult and juvenile survival. Although the model suggests that increased adult and juvenile survival strongly influences λ , managers may have little control over improving these values for their breeding populations. During the breeding season, adult survival appears to be relatively high, based on observations of color-banded individuals throughout the breeding season (e.g., Nolan 1978, Roth and Johnson 1993). Before birds leave breeding locations, land managers can potentially improve juvenile survivorship because the postfledging/pre-migration period can be a critical bottleneck for songbirds (e.g., Anders et al. 1997). Postfledged juveniles often move into areas of dense cover, which potentially can be manipulated on the landscape. Migration and wintering events undoubtedly are critical components of adult and juvenile survival (Moore et al. 1995, Rappole 1995), but once birds leave their breeding areas, monitoring their survival may not be tractable. Similarly, land managers in wintering or migration areas may improve survival values at their sites, but may have little control in manipulating habitats or landscapes that promote high nest survival. These results emphasize the need to develop conservation plans at spatial scales that encompass the life cycle of migratory organisms.

During the nesting season, managers may have several options for increasing λ in their system: increasing the number of young fledged per nest, increasing nesting success in either the high-quality or the low-quality habitat, or increasing the amount of high-quality habitat in the landscape. (At some point, increasing nest success levels within the low-quality habitat will also change the landscape composition). Which of these options is most achievable depends on how much control the manager has in manipulating resources and how easily the different parameters are changed.

In songbirds, nest predation is a major cause of nest failure (Martin 1988), often resulting in complete nest

failure. However, partial nest loss may not be trivial, and is common in areas where brood parasitism by the Brown-headed Cowbird (*Molothrus ater*) is frequent (Lowther 1993). Reducing parasitism pressures may not increase nesting success (but see Arcese et al. 1996), but is likely to increase the number of young fledged per successful nest. Should managers target reducing predation rates, brood parasitism rates, or both? Our model suggests that which strategy to employ depends on the starting conditions of landscape and habitat.

Generally speaking, when landscapes contain a large percentage of low-quality habitat, managers should focus on manipulating the landscape composition by converting low-quality habitat to high-quality habitat. If low-quality habitats have very low nesting success, managers should aim to increase nest success (by decreasing predation) because increasing the number of young fledged per nest (e.g., by reducing brood parasitism) has little effect if few nests survive to fledge young. As nesting success is increased in the low-quality habitats, managers can additionally target partial nest loss, because differences in number fledged per successful nest can determine whether the population will persist or be extirpated.

When landscapes contain a relatively low percentage of low-quality habitat, managers should aim to further decrease the amount of low-quality habitat in the landscape; increasing the number of young per nest and/or increasing nesting success within the low-quality habitat have little impact on λ in such landscapes. Further decreases in low-quality habitat are especially important if the landscape is thought to be a major source of immigrants for other systems.

Managers can address the balance of low- and high-quality habitat for species thought to be potential victims of ecological traps. In our model, 70% of the landscape had to be in high-quality habitat to balance the effects of trap habitat that occupied the remaining 30% of the landscape. If species avoid low-quality habitats, then populations can persist under much greater quantities of low-quality habitat. In these situations, maintenance of low-quality areas can benefit a population by increasing the overall population size (see also Howe et al. 1991).

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