AREA-SENSITIVE DISTRIBUTIONS COUNTERACT NEGATIVE EFFECTS OF HABITAT FRAGMENTATION ON BREEDING BIRDS

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Abstract. We used a modeling approach to determine the conditions under which fragmentation of breeding habitat can cause landscape-scale population declines in songbirds. The simulated species resided in a system of forest patches (a landscape) and could potentially disperse among patches between breeding seasons. The model combined: (1) the frequency distribution of patch sizes in the landscape, (2) the distribution of individuals across the range of patches in the landscape, and (3) the fecundity of individuals as a function of patch size in the landscape. Simulated landscapes varied in patch size distribution while holding total forest area constant. Three distribution patterns were modeled: the classic ''area-sensitive'' pattern in which density increased as patch size increased, an area-insensitive pattern in which density was independent of patch size, and an ''inverse-area-sensitive'' pattern in which density increased as patch size decreased. We used this model to examine population growth under various landscape, distribution, fecundity, and survival scenarios.

In the ''fragmentation hypothesis'' simulations, in which fecundity decreased as patch size decreased within the landscape, population growth rates were highly sensitive to distribution patterns and to landscape composition. When landscapes consisted of both large and small patches for breeding, populations were either above or below replacement, depending on how individuals were distributed among patches: Classic area-sensitive distributions produced growth rates above replacement levels, whereas inverse-area-sensitive distributions produced growth rates below replacement levels. The results of the model suggest that reduced fecundity associated with habitat fragmentation could lead to population declines when (1) landscapes are highly fragmented, or (2) landscapes offer both large and small patches for breeding, but distribution patterns place a high proportion of the breeding population on small patches that are less favorable for breeding.

Key words: area sensitivity; breeding birds; ecological trap; fecundity; habitat fragmentation; habitat selection; island biogeography; landscape scale; metapopulation; population dynamics; population modeling; source–sink.

INTRODUCTION

Fragmentation of breeding habitat has been hypothesized as a cause of population declines in some migratory bird species (e.g., Brittingham and Temple 1983, Wilcove 1985, Bohning-Gaese et al. 1992; see reviews in Askins et al. 1990, Faaborg et al. 1995). Initially, fragmentation studies focused on patterns of species distribution and abundance in relation to patch size and distance, using the MacArthur and Wilson (1967) model of island biogeography as a guiding framework (reviewed in Faaborg et al. 1995). Species showing a positive association between patch size and density or frequency have been generally considered ''sensitive'' to habitat fragmentation, and area sensitivity traditionally has been viewed as one of the most significant problems associated with habitat fragmen-

tation (see Plate 1). More recently, fragmentation studies have focused on patterns of nesting success (the probability that a nest will fledge genetic young) or fecundity (the number of offspring per adult per year) in relation to patch size or some other index of fragmentation (e.g., Robbins 1979, Brittingham and Temple 1983, Porneluzi et al. 1993, Donovan et al. 1995*b*, 1997, Robinson et al. 1995*b*, Trine 1998). Species showing a positive association between patch size and fecundity have been thought to be sensitive to habitat fragmentation.

These patterns, however, do not necessarily lead to population declines at either the local (subpopulation) or the landscape scale (the system of interacting subpopulations, sensu Pulliam 1988). At a local scale, for example, sink subpopulations on a small forest fragment may not show population declines because they can be ''rescued'' from extinction by receiving immigrants from other locations (e.g., Robbins 1979, Pulliam 1988, Brawn and Robinson 1996). At a landscape scale, overall population growth (the growth rate of the entire source–sink system on the landscape) may not

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PLATE 1. A fragmented landscape near Jonesboro, Illinois (USA). Photo by Peter W. Jones.

be affected significantly by the poor reproductive success of birds on fragments if breeding individuals generally avoid small patches or if the landscape is dominated by larger patches that are used for breeding.

Indeed, some species thought to be severely affected by habitat fragmentation are not declining in numbers. For example, Ovenbirds (*Seiurus aurocapillus*) generally have lower densities and poorer reproductive success on small patches than large patches, but trend estimates suggest that populations are stable or increasing in many parts of their breeding range (reviewed in Van Horn and Donovan 1994). Hence, the observed negative correlations between the amount of forest fragmentation and nesting success or density provide only weak support for the hypothesis that declines in some species are due in part to fragmentation of North American breeding habitat. As yet, the mechanisms by which fragmentation may generate population declines at a landscape scale are poorly understood.

Our goal in this paper is to examine how fragmentation of breeding habitat, distribution of individuals, fecundity, and survival potentially interact to influence population change in birds. We modeled the population dynamics of a hypothetical forest-nesting passerine that nests in a system of forest patches, where individual patches are either sources or sinks and the collection of patches is called a landscape system. Although landscapes varied in patch size distribution, total forest area was held constant in all simulations.

METHODS

Model overview

The model combined: (1) the frequency distribution of patch sizes in a landscape, (2) the distribution of individuals across a range of patch sizes in the landscape, and (3) the fecundity of individuals across a range of patches in the landscape. Model parameters also included adult and juvenile survival values. We considered only the female portion of the population and assumed that adult females in the population were not mate limited. The model was programmed in SAS language (SAS Institute 1990), and a simulation consisted of a given landscape and four life history parameters: patterns of abundance, fecundity, adult survival, and juvenile survival. For each landscape ($n = 10$), we ran 81 different simulations that reflected varying combinations of parameters. Simulation outputs included per capita population growth at the patch level (subpopulation, an indication of whether specific patches within the landscape were sources or sinks), and overall population growth of the entire landscape system.

Model parameters: landscape composition

We began by considering the distribution of patches within a landscape. We used Gardner's (1999) RULE program to develop 10 simulated landscapes that varied in patch composition (Fig. 1). All landscapes consisted of a matrix of cells ($243 \times 243 = 59\,049$ cells), in which 30% of the total cells ($n = 17\,715$ cells) were forest habitat and 70% of the total cells ($n = 41\,334$ cells) consisted of a nonforest matrix within which forest was embedded. Thus, total forest cover was held constant in all landscapes, but landscapes varied in patch size distribution. We selected a landscape with 30% forest cover simply because such a landscape could be "fragmented" in a variety of ways while holding total forest cover constant (Pearson and Gardner 1997), and because habitat fragmentation is thought to have profound effects on population persistence when landscapes consist of relatively "low" amounts of total habitat (Fahrig 1997).

We generated 10 landscapes that varied in fragmentation level, and used the "neighborhood rule" to identify the sizes of each patch within a given landscape (Gardner 1999; Table 1). The neighborhood rule procedure selects a forested cell within the landscape, and then examines cells in each of the four cardinal directions. If a forested cell is located, that cell is assigned as part of the patch and the process is iterated until none of the surrounding cells consisted of forest. The 10 land-
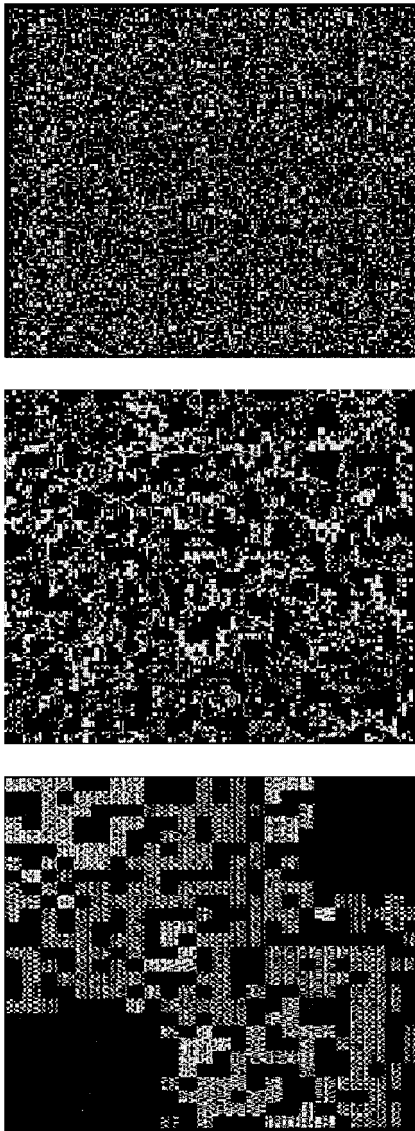
FIG. 1. Landscapes 1 (top), 5 (middle), and 10 (bottom) generated by the RULE program (Gardner, 1999). Forest is depicted by black, and nonforest matrix is depicted by gray. All landscapes are composed of 30% forest cover and 70% nonforest matrix.

scapes represented a gradient from a highly fragmented landscape (Landscape 1) characterized by small patch sizes and small correlation lengths (a measure of the average within-patch distances for the entire map, or the average distance an organism might move without leaving a habitat patch), to a continuous landscape (Landscape 10) characterized by large patch sizes and large correlation lengths, although contiguous landscapes consisted of both large and small patches (Table 1).

Model parameters: distribution of individuals across patches

Next, we defined three types of density distributions that represented how individuals were distributed across forest habitats of varying size within a given landscape. For all landscapes, we assumed that individuals would seek breeding territories by either of two processes. The first process was an ideal-depotic model of habitat selection in which some territorial individuals (the despots) displaced other individuals to suboptimal habitats (Fretwell 1972). In this situation, we assumed that individuals would seek breeding territories in optimal, source habitat first; in most cases, these were located in the largest patches in the landscape. This density-dependent process creates a pattern of distribution of individuals across heterogeneous landscapes, and is thought to be common in nature (Krebs and Davies 1993). Pulliam (1988) also envisioned this process in his classic source–sink model, in which both sources and sinks could be either numerically large or small. The second process of habitat selection was potentially an ''innate'' preference for large or small patches, or preference for a particular patch because of site fidelity. For example, some species readily occur in high densities in small patches and are less abundant in large patches (Donovan et al. 1995b). Regardless of which of the two mechanisms shaped the distribution of individuals across the landscape, our primary interest was in the system-wide consequences of such distribution patterns (see also Pulliam and Danielson 1991).

Three distributions were modeled. The first distribution pattern was an area-insensitive distribution, in which density of individuals was independent of patch size (Fig. 2a, curve x). The next distribution pattern was a classic ''area-sensitive'' pattern, in which densities were low or zero on small patches and gradually increased as patch size increased (Fig. 2a, curve y). The final distribution pattern was also area sensitive, but densities were highest on small patches and decreased as patch size increased. For clarity, we refer to this distribution as ''inverse-area-sensitive'' (Fig. 2a, curve z).

Model parameters: fecundity across patches of varying size

Next, we considered the reproductive success of birds nesting in forest patches of varying size. Variation in nesting success (the probability that a nest will fledge genetic offspring) and fecundity (the number of offspring per adult female) across a range of forest patch sizes has been well documented in midwestern and eastern North America (e.g., Donovan et al. 1995b, Robinson et al. 1995b, Weinberg and Roth 1998). In general, reproductive success of forest-nesting species is positively correlated with percentage of forest cover, percentage of forest interior, and average patch size in a landscape (Robinson et al. 1995b). Populations on small fragments appear to be sinks because of low fecundity of nesting females, even when renesting and multiple brooding are incorporated into fecundity estimates (e.g., Donovan et al. 1995b). In comparison,

TABLE 1. Characteristics of 10 landscapes generated by RULE (Gardner 1999).

Landscape number	Fragmentation level	Largest patch size (no. cells)	Total no. patches	Mean patch size†	Correlation length‡	Forest cover in landscape (%)
1	Fragmented	16	9036	3.5	1.9	30
2		102	2868	22.6	5.1	30
3		254	2081	47.7	7.8	30
4		353	1794	68.3	9.1	30
5		320	625	100.0	9.6	30
6		774	445	264.0	17.1	30
7		1314	815	356.3	25.2	30
8		1541	6480	618.9	23.8	30
9		1949	88	963.3	25.6	30
10	Continuous	2956	90	1319.0	35.4	30

† Area-weighted mean patch size.
‡ A measure of the mean within-patch distances for the entire map, or the mean distance that an organism might move without leaving a habitat patch.

populations on large patches experience high fecundity (Robinson et al. 1995b, but see Trine 1998).

We modeled two fecundity functions that mimic these observations, one in which fecundity (the number of female offspring that successfully fledge per adult female per year) increased linearly as patch size increased (a linear fragmentation effect; Fig. 2b, curve y), and a threshold function in which fecundity sharply increased at a critical minimum patch size (a threshold fragmentation effect; Fig. 2b, curve z). As a control, we also modeled a function in which fecundity did not vary with patch size (Fig. 2b, curve x). Thus, fecundity was a function of patch size in our model, although the model also could have reflected other measures of landscape fragmentation such as percent forest cover, percentage of core habitat, or other metrics that are often highly correlated with patch size.

Model parameters: adult and juvenile survival

Finally, we varied juvenile and adult survival parameters. For this model, we used adult survival values of 0.5, 0.6, and 0.7, which reflected the probability that an adult bird in year t would survive to the census period in year $t + 1$. We used juvenile survival values of 0.2, 0.3, and 0.4, which reflected the probability that a fledgling in year t would survive to the census period in year $t + 1$. These values reflect the average range of survival values documented in songbirds (Roberts 1971, Greenberg 1980, Nichols et al. 1981), and have been used extensively in other models that examine the effect of a management action or anthropogenic disturbance on songbirds (e.g., Temple and Cary 1988, Howe et al. 1991, Davis and Howe 1992, Thompson 1993, Donovan et al. 1995a). The "base model" consisted of adult survival values of 0.6 and juvenile survival values of 0.3 (Noon and Sauer 1992). Variations of the base model included increasing and decreasing adult survival values while maintaining juvenile survival at 0.3, and increasing and decreasing juvenile survival values while maintaining adult survival at 0.6.

Model assumptions

In our modeling exercise, we focused on a single process (habitat fragmentation) that may limit population growth in songbirds, and assumed that patch size and other fragmentation metrics operate independently of other limiting processes. We made three assumptions
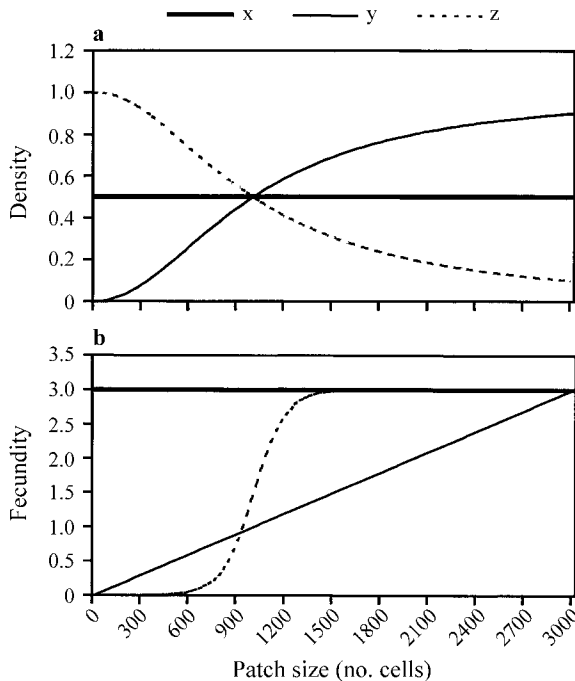

FIG. 2. Density (number of females per cell) and fecundity (number of female offspring per female per year) as a function of patch size. (a) Density distribution patterns depict area-insensitive distributions (heavy line), area-sensitive distributions (light line), and inverse-area-sensitive distributions (dashed line). (b) Fecundity patterns depict models in which fecundity is independent of patch size (heavy line, the "control model"), a linear fragmentation effect (light line), and a threshold fragmentation effect (dashed line).

in our model related to patch size. First, we used our model to assess the influence of the frequency distribution of patch sizes on population growth. As such, we did not assess the importance of the spatial distribution of patches in the landscape, which potentially affects population dynamics (Forman and Godron 1986, With et al. 1997), but has not been well established in birds. Thus, we assumed that all patches in the landscape were accessible to dispersing individuals. Similarly, we did not directly assess the impact of the nonforest matrix habitat on populations (see Wiens 1995). However, the matrix effect was incorporated into the fecundity parameter of the model indirectly because the reproductive success for a given patch size could potentially be influenced by both internal patch characteristics (such as food quality; Burke and Nol 1998) and by characteristics of the nonforest matrix (which may affect predator and brood parasite numbers in both the matrix and the patch itself; Andrén 1995, Donovan et al. 1995b, Robinson et al. 1995a).

Second, we assumed that that the major type of density dependence affecting population dynamics was a result of the ideal-despotic habitat selection. In territorial species, density-dependent processes result in between-habitat dynamics in which not all individuals are able to secure what they perceive to be optimal locations for breeding (e.g., Fretwell and Lucas 1970, Fretwell 1972, Nolan 1978, Holmes et al. 1996, Rodenhouse et al. 1997). Thus, we did not consider the effects of within-patch density on food availability (and assumed that territories within a patch were large enough so that within-patch neighbors would not depress food abundance). Additionally, we did not consider the effects of within-patch density on predation rates, because field studies show that many area-sensitive species experience the highest nesting success in the most densely populated patches (Donovan et al. 1995b).

Third, we assumed that survival was independent of patch size; that is, survival of adults or fledged juveniles was constant across the system and did not change as the patch size changed. Our adult survival estimates reflected the probability that an adult individual will survive from year t to the beginning of the breeding season in year $t + 1$. We did not partition adult survival estimates into breeding ($\sim$2-mo) and nonbreeding ($\sim$10-mo) estimates, because we are unaware of any published studies demonstrating that fragmentation of breeding habitat negatively affects adult survival during the breeding season. Our juvenile survival estimates reflected the probability that a juvenile will survive from the time of fledging to the beginning of the breeding season in year $t + 1$. We are unaware of any published studies that document the effects of fragmentation on postfledging juvenile survival while birds still occupy North American habitats. Documentation of these effects would require the measurement of postfledging survival across a range of fragmentation levels. However, survival studies that examine color-banded or radio-tracked individuals typically occur within a narrow portion of the entire fragmentation spectrum (e.g., Anders et al. 1998).

The model

For a each simulated landscape, we identified the size of all forest patches and the frequency distribution of different patch sizes. Patch sizes ranged from 1 to 2956 cells. For all 10 landscapes modeled, total forest area available was always 17 715 cells, or 30% of the total landscape. The manner in which adult females were actually distributed across forest patches was given by the density distribution function (Fig. 2a). The size of the total population occupying a given landscape in year t was:

$$\text{Population}(t) = \sum_{i=1}^{i=N} \text{total area}_i \times \text{density}$$

where i was a given patch size in the landscape.

Given the distribution of patches and the number of individuals that occupied patches of different sizes, populations on each patch reproduced at a rate specified by the fecundity curve (Fig. 2b). Finally, total population size in the landscape in future years was influenced by the ability of adults and juveniles to survive to breed in the following year. Thus, total population size (prior to the birth pulse) in the landscape in year $t + 1$ was:

$$\text{Population}(t + 1)$$

$$= \sum_{i=1}^{i=N} \text{density}_i(t) \times \text{area}_i$$

$$\times (\text{fecundity}_i \times \text{juvenile survival}_i$$

$$+ \text{adult survival}_i).$$

We then determined the finite rate of increase (λ) by dividing the total population size in year $t + 1$ by the total initial population size in year t. An overall growth rate >1 indicated that the population was increasing, an overall growth rate of <1 indicated that the population was declining, and an overall growth rate $= 1$ indicated that the population was maintained at previous levels.

RESULTS

Landscape composition and distribution patterns

Model results indicated that landscape composition, distribution of individuals, fecundity, and survival interacted in a variety of ways to influence population growth in the landscape system. Moreover, changes in total habitat did not affect our results. That is, we obtained qualitatively similar results when we modified total forest cover in the landscape (e.g., 40% vs. 50% forest cover; T. M. Donovan, *unpublished data*) and held fragmentation levels constant.

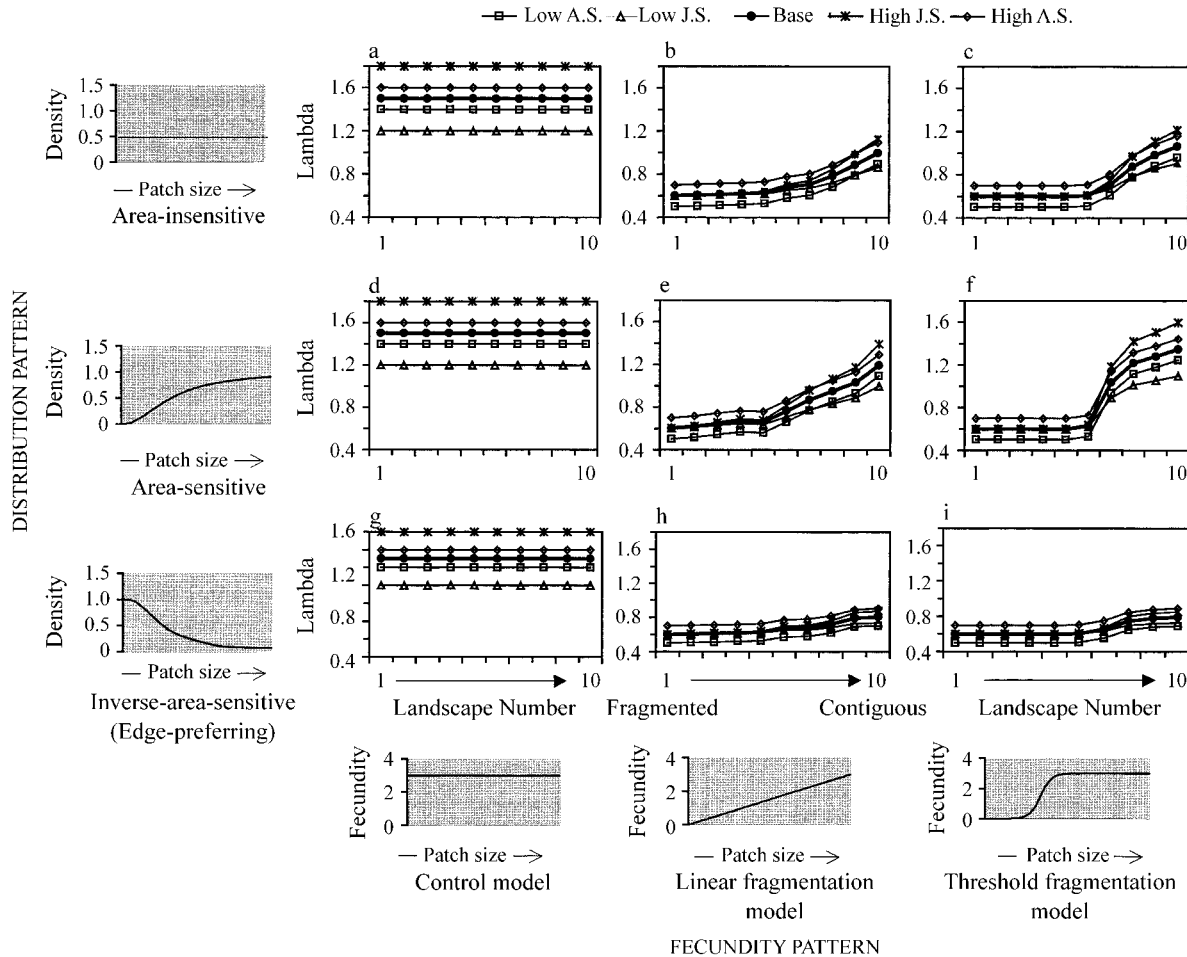Generally speaking, when reproduction was influ-

FIG. 3. Compiled results of 810 model simulations. The far-left column indicates species distribution patterns; the bottom row indicates fecundity as a function of patch size (see Fig. 2). The nine boxes indicate results of varying species distribution and fecundity function models. For each box, lambda values are depicted on the y-axis, and landscape fragmentation is depicted on the x-axis, from highly fragmented landscapes (e.g., landscapes 1–3) to continuous landscapes (e.g., landscapes 8–10). Within each box, five levels of juvenile and adult survival are depicted: base levels (solid circles) consist of adult survival rates (A.S.) of 0.6 and juvenile survival rates (J.S.) of 0.3. Other values represent deviations from base values (e.g., low A.S. = low adult survival, where adult survival = 0.5 and juvenile survival = 0.3). Lambda values = 1 indicate that the population is stable; lambda >1 indicates that the population is increasing; and lambda <1 indicates that the population is declining.

enced by fragmentation (Fig. 3, columns 2 and 3), landscape composition had a large effect on population growth, but its impact depended on how individuals distributed themselves across the landscape. When distributions were either area sensitive or area insensitive, growth increased as landscapes became more continuous (indicated by a positive slope of lambda across the 10 landscapes, Fig. 3, panels b, c, e, and f). That is, as long as landscapes offered enough large patches that were high in quality for breeding, classical area-sensitive distribution patterns counteracted the impacts of reduced fecundity associated with habitat fragmentation in breeding birds.

In highly fragmented landscapes (e.g., Landscapes 1–3), distribution pattern had little effect on population growth when there was a fragmentation effect on fe-

cundity (Fig. 3, panels b, c, e, f, h, and i). That is, when landscapes were highly fragmented, populations were below replacement level no matter how individuals distributed themselves across patches. In contrast, in continuously forested landscapes (e.g., Landscapes 8–10), distribution patterns had large effects on population growth when there was a fragmentation effect on fecundity. In such landscapes, classic area-sensitive distributions produced the highest growth rates and inverse-area-sensitive distributions produced the lowest growth rates. Growth rates in this situation appeared to be driven by the proportion of females in the population that nested in large patches. Because classic area-sensitive females avoided small patches, a greater proportion of their population nested in larger patches that were higher in quality for reproduction. As a result,

more young were produced in the entire system of patches and the population increased (Fig. 3, panels e and f). Similarly, a greater proportion of the area-insensitive population nested in larger patches, not because patch sizes influenced density, but simply because the landscape was dominated by patches that were higher in quality for breeding and individuals distributed themselves proportionately across the landscape (Fig. 3, panels b and c). In contrast, inverse-area-sensitive females readily nested in small fragments and occurred in low densities in the best patches for reproduction. A small number of these females nested in large patches and experienced high fecundity there, but these individuals were not able to compensate for the low growth rates incurred on small patches, and the overall population declined (Fig. 3, panels h and i).

Adult and juvenile survival

Population growth was highly sensitive to adult and juvenile survival values when there were no fragmentation effects on fecundity (based on the ''spread'' of lambda values for varying survival estimates; Fig. 3, control model: panels a, d, g). Population growth rates, however, appeared to be comparatively less sensitive to changes in survival when there were fragmentation effects on fecundity (Fig. 3, panels b, c, e, f, h, i). In this situation, maximum growth was achieved by changing different survival values from the base levels, and these varied depending on landscape composition and distribution pattern. That is, there was an interaction between landscape composition and the survival values that produced the highest overall growth (based on the non-parallel nature of the lambdas produced by different survival rate combinations; e.g., Fig. 3, panel f). Generally speaking, for area-insensitive and area-sensitive distributions, population growth was maximized by increasing adult survival values above base levels in fragmented landscapes, but growth was maximized by increasing juvenile survival above base levels in more continuous landscapes (Fig. 3, panels b, c, e, and f). However, for inverse-area-sensitive distributions, maximum growth rates in all landscapes were achieved by increasing adult survival values above base levels when there were fragmentation effects on fecundity (Fig. 3, panels h and i).

DISCUSSION

Evaluation of the fragmentation hypothesis

The literature on habitat fragmentation is vast, and most studies to date have examined distribution and fecundity patterns independently as a function of fragmentation (summarized in Askins et al. 1990). Yet, few authors have examined the potential effects that area sensitivity and fecundity patterns jointly have on growth in the landscape system. Results from our model suggest that area sensitivity may be a strategy for overcoming the negative effects of habitat fragmen-

tation on reproductive success in birds. That is, in spite of the adverse effects of fragmentation on fecundity, populations are able to persist as long as enough individuals breed in optimal patches. This basic result has not penetrated the conservation literature, where area sensitivity is still seen as a major problem caused by habitat fragmentation (see also Villard 1998) and where poor reproductive success on fragments is taken as strong support for the hypothesis that fragmentation has caused many forest-nesting species to decline in number (Donovan et al. 1995b). A larger, landscape-scale view is needed.

Our population projections occurred over a single generation. However, it is straightforward to envision how population growth would be manifested over multiple generations (assuming a closed population). However, the trajectories of these populations depend on the mechanism shaping the distribution of individuals. In an ideal-despotic situation in which individuals prefer to breed in the larger patches, when $\lambda > 1$, the carrying capacity of source patches is maintained and excess individuals are forced into more suboptimal habitats. The result is a ''flattening'' of the area-sensitive curve into a more or less area-insensitive pattern, and a concomitant decrease in λ. When $\lambda < 1$, populations decline and fewer individuals are displaced into low-quality patches; this modifies the distribution curve into a more extreme area-sensitive pattern, in turn increasing λ. In the ''innate'' habitat selection process, individuals seek breeding territories in either small or large patches; once those patches are filled, excess individuals disperse to the less ''optimal'' patch choice. In this situation, preferences for large patches will result in population changes similar to those described in the ideal-despotic habitat selection model. Preference for small patches, however, will result in a stable population only if the small patches are full, forcing enough individuals into the larger patches to support the entire population. If this population declines, however, a greater proportion of the population will attempt to nest in the small patches, and the population will eventually go extinct.

Although our model is heuristic, examination of how distribution patterns interact with reproductive patterns across patches in a landscape has potentially been limited because ''real'' bird populations are difficult to define spatially. In our model, we used a defined area as a potential landscape that was occupied by our hypothetical species, within which source–sink dynamics occur. In reality, it is unclear what spatial scale is appropriate for evaluating of long-term trends. Clearly, birds potentially can disperse among habitat patches. Consequently, long-term trends at the patch scale, particularly small patches, may not be indicative of patch-specific birth and death rates (Brawn and Robinson 1996). What is less clear, however, is the extent of the geographic ''scale'' that encompasses most of the sub-population interactions (Greenwood and Harvey 1982).

Theory suggests that dispersal in birds should be geographically limited to a small landscape (Shields 1982), but banding recoveries of both adults and juveniles from one breeding season to the next indicate that dispersal can be quite extensive (USGS Bird Banding Lab recapture data, J. Tautin, USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA). Lack of information on dispersal dynamics in migratory birds has hampered ornithologists' ability to predict how landscape-scale population processes affect bird population change.

The few studies that have examined regional-scale (landscape) or range-wide scale decline of species in relation to habitat fragmentation have revealed that long-term trends appear to vary across landscapes (James et al. 1992, Villard and Maurer 1996), and that forest area is not a good predictor of population declines (Flather and Sauer 1996). Our model supports both results. Although we held total habitat area constant in our model (30% of the landscape was forested), changes in total habitat did not affect population growth. With constant total habitat, our model predicts that trends can vary among landscapes and suggests that selection of patches within a landscape, in combination with landscape configuration, may be critical ingredients in determining population change. For a discussion on changing proportions of suitable habitat in a landscape context, see Andrén (1994). Fahrig (1997) discusses on the relative importance of habitat loss vs. habitat fragmentation in species extinctions.

Species distribution patterns, fragmentation, and survival: conservation implications

A general result of our model is that when fecundity decreases as a function of fragmentation, populations will decline either when landscapes are already fragmented or when landscapes offer both large and small patches for breeding, but a large proportion of the individuals occurs on small patches that are unfavorable for reproduction. In our model, growth values above replacement levels can be achieved through a combination of (1) making landscapes more continuous, (2) altering how fecundity is influenced by patch size, (3) altering how individuals distribute themselves among patches, and (4) altering juvenile or adult survival values during the nonbreeding season.

From the management perspective, the first two options, making breeding landscapes more continuous or altering the influence of patch size on fecundity, may be more achievable than the latter two options. Landscapes are altered continuously and land management can produce significant changes in the landscape to benefit birds (e.g., Thompson et al. 1995). Fecundity can also be managed through landscape management and by identifying the mechanisms behind nest loss in fragmented landscapes (e.g., Robinson et al. 1995a). For example, if Cowbird parasitism is a major cause of reproductive loss on small forest patches (e.g., Trine

1998), then management can focus on decreasing Cowbird populations on the landscape by decreasing feeding or roosting opportunities within the landscape (e.g., Robinson et al. 1995a). Increasing juvenile and adult survival values can also benefit populations (Rappole 1995), although quantitative estimations of these vital rates are currently less tractable than reproductive rates.

For vagile organisms such as birds, the ability to disperse may allow individuals to select or sample among a variety of habitats (Whitcomb et al. 1981, Haila et al. 1993, Villard et al. 1995). Habitat selection theory suggests that individuals should attempt to occupy habitats that offer the greatest reward in terms of fitness or survival (Nolan 1978, Møller 1995, Holmes et al. 1996, Newton 1998). In our model, these habitats are large patches that occur in what we have called a continuous landscape. Changes in the carrying capacity of the source patches produce distribution patterns that have profound effects on overall population growth. For area-sensitive species in continuous landscapes, sinks do not strongly influence overall population growth (see also Haila et al. 1993). However, when sources have low carrying capacities, large numbers of individuals are displaced to sinks; in our model, this produces an inverse-area-sensitive distribution.

More interesting, perhaps, is the preference of some species for poor-quality habitats for breeding when higher quality habitats are available. In our model, species that have "innate" preference for small patches over large patches (inverse-area-sensitive patterns) are more threatened by habitat fragmentation than classic area-insensitive or area-sensitive species. Why would females select small patches for breeding when larger patches are available? The perception of what constitutes high-quality habitat for a species is probably formed over evolutionary time scales (Hildén 1965, Cody 1985). Natural selection may have favored individuals that nested in smaller patches in evolutionary time. However, intrinsically preferred habitats developed over evolutionary time may function as sinks in ecological time, because of recent anthropogenic habitat change. Individuals may not perceive sink habitats as low quality if the speed of evolutionary change is slower than the speed of anthropogenic habitat change.

Concluding remarks

Although patterns of distribution and reproductive success of individuals across patches are well documented for many bird species, these patterns are rarely linked to population persistence at the landscape scale. Our results suggest that, in species in which reproductive success is a correlate of patch size or other fragmentation indice, declines could be due to habitat fragmentation, particularly in landscapes that are highly fragmented and for species that select poor-quality patches for breeding. Our model highlights the interplay of landscape structure and habitat selection choices made by individuals across that landscape, and the

need to understand the mechanisms that shape distri-
bution patterns in vagile species. Our results also high-
light the need to understand basic life history charac-
teristics, such as habitat selection, to manage species
with different habitat needs for long-term persistence.

Literature Cited

Anders, A. D., J. Faaborg, and F. R. Thompson III. 1998.
Postfledging dispersal, habitat use, and home-range size of
juvenile wood thrushes. Auk 115:349–358.

Andrén, H. 1994. Effects of habitat fragmentation on birds
and mammals in landscapes with different proportions of
suitable habitat: a review. Oikos 71:355–366.

Andrén, H. 1995. Effects of landscape composition on pre-
dation rates at habitat edges. Pages 225–255 in L. Hansson,
L. Fahrig, and G. Merriam, editors. Mosaic landscapes and
ecological processes. Chapman and Hall, New York, New
York, USA.

Askins, R. A., J. F. Lynch, and R. Greenberg. 1990. Popu-
lation declines in migratory birds in eastern North America.
Pages 1–57 in D. M. Power, editor. Current ornithology.
Volume 7. Plenum Press, New York, New York, USA.

Bohning-Gaese, K., M. L. Taper, and J. H. Brown. 1992. Are
declines in North American insectivorous songbirds due to
causes on the breeding range? Conservation Biology 7:76–
86.

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

Brittingham, M. C., and S. A. Temple. 1983. Have Cowbirds
caused forest songbirds to decline? BioScience 33:31–35.

Burke, D. M., and E. Nol. 1998. Influence of food abundance,
nest-site habitat, and forest fragmentation on breeding Ov-
enbirds. Auk 115:96–104.

Cody, M. L. 1985. Habitat selection in birds. Academic Press,
Orlando, Florida, USA.

Davis, G. J., and R. W. Howe. 1992. Juvenile dispersal, lim-
ited breeding sites, and the dynamics of metapopulations.
Theoretical Population Biology 41:184–207.

Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thomp-
son. 1997. Variation in local-scale edge effects: mecha-
nisms and landscape context. Ecology 78:2064–2075.

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

Donovan, T. M., F. R. Thompson III, J. Faaborg, and J. Probst.
1995b. Reproductive success of migratory birds in habitat
sources and sinks. Conservation Biology 9:1380–1395.

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

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

Flather, C. H., and J. R. Sauer. 1996. Using landscape ecology
to test hypotheses about large-scale abundance patterns in
migratory birds. Ecology 77:28–35.

Forman, R. T. T., and M. Godron. 1986. Landscape ecology.
John Wiley, New York, New York, USA.

Fretwell, S. F. 1972. Populations in a seasonal environment.
Princeton University Press, Princeton, New Jersey, USA.

Fretwell, S. F., and J. L. Lucas, Jr. 1970. On territorial be-
havior and other factors influencing habitat distribution in
birds. I. Theoretical development. Acta Biotheoretica 19:
16–36.

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

Greenberg, R. 1980. Demographic aspects of long-distance
migration. Pages 493–504 in A. Keast and E. S. Morton,
editors. Migrant birds in the Neotropics: ecology, behavior,
distribution, and conservation. Smithsonian Institution
Press, Washington, D.C., USA.

Greenwood, P. J., and P. H. Harvey. 1982. The natal and
breeding dispersal of birds. Annual Review of Ecology and
Systematics 13:1–21.

Haila, Y., I. K. Hanski, and S. Raivio. 1993. Turnover of
breeding birds in small forest fragments: the ''sampling''
colonization hypothesis corroborated. Ecology 74:714–
725.

Hildén, O. 1965. Habitat selection in birds—a review. An-
nales Zoologici Fennici 2:53–75.

Holmes, R. T., P. P. Marra, and T. W. Sherry. 1996. Habitat-
specific demography of breeding black-throated blue war-
blers (Dendroica caerulescens): Implications for popula-
tion dynamics. Journal of Animal Ecology 65:183–195.

Howe, R. W., G. J. Davis, and V. Mosca. 1991. The demo-
graphic significance of ''sink'' populations. Biological
Conservation 57:239–255.

James, F. C., D. A. Wiedenfeld, and C. E. McCulloch. 1992.
Trends in breeding populations in warblers: declines in the
southern highlands and increases in the lowlands. Pages
43–56 in J. M. Hagan III and D. M. Johnston, editors.
Ecology and conservation of Neotropical migrant land-
birds. Smithsonian Institution Press, Washington, D.C.,
USA.

Krebs, J. R., and N. B. Davies. 1993. Behavioral ecology:
an evolutionary approach. Blackwell Scientific, Oxford,
UK.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of
island biogeography. Princeton University Press, Princeton,
New Jersey, USA.

Møller, A. P. 1995. Developmental stability and ideal des-
potic distribution in blackbirds in a patchy environment.
Oikos 72:228–234.

Newton, I. 1998. Population limitation in birds. Academic
Press, London, UK.

Nichols, J. D., B. R. Noon, S. L. Stokes, and J. E. Hines.
1981. Remarks on the use of mark–recapture methodology
in estimating avian population size. Studies in Avian Bi-
ology 6:121–136.

Nolan, V., Jr. 1978. The ecology and behavior of the Prairie
Warbler, Dendroica discolor. Ornithological Monographs
26:1–595.

Noon, B. R., and J. R. Sauer. 1992. Population models for
passerine birds: structure, parameterization, and analysis.
Pages 441–464 in D. R. McCullough and R. H. Barrett,
editors. Wildlife 2001: populations. Elsevier Applied Sci-
ence, New York, New York, USA.

Pearson, S. M., and R. H. Gardner. 1997. Neutral models:
useful tools for understanding landscape patterns. Pages
215–230 in J. A. Bissonette, editor. Wildlife and landscape
ecology: effects of pattern and scale. Springer-Verlag, New
York, USA.

Porneluzi, P., J. C. Bednarz, L. Goodrich, N. Zawada, and J.
Hoover. 1993. Reproductive performance of territorial Ov-

enbirds occupying forest fragments and a continuous forest in Pennsylvania. Conservation Biology **7**:618–622.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist **132**:652–661.

Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. American Naturalist **137**:S50–S66.

Rappole, J. H. 1995. The ecology of migrant birds. Smithsonian Institution Press, Washington, D.C., USA.

Robbins, C. S. 1979. Effect of forest fragmentation on bird populations. Pages 198–212 *in* R. M. DeGraaf and K. E. Evans, editors. Management of north-central and northeastern forests for nongame birds. North Central Forest Experiment Station Publication, U.S. Forest Service General Technical Report **NC-51**.

Roberts, J. O. L. 1971. Survival among some North American wood warblers. Bird Banding **42**:165–183.

Robinson, S. K., S. I. Rothstein, M. C. Brittingham, L. J. Petit, and J. A. Grzybowski. 1995*a*. Ecology and behavior of Cowbirds and their impact on host populations. Pages 428–460 *in* T. E. Martin and D. M. Finch, editors. Ecology and management of neotropical migratory birds. Oxford University Press, Oxford, UK.

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

Rodenhouse, N. L., T. W. Sherry, and R. T. Holmes. 1997. Site-dependent regulation of population size: a new synthesis. Ecology **78**:2025–2042.

SAS Institute. 1990. SAS/SATA user's guide, version 6, fourth edition. Cary, North Carolina, USA.

Shields, W. M. 1982. Philopatry, inbreeding, and sex. State University of New York Press, Albany, New York, USA.

Temple, S. A., and J. R. Cary. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. Conservation Biology **2**:340–347.

Thompson, F. R., III. 1993. Simulated responses of a forest-interior bird population to forest management options in central hardwood forests of the United States. Conservation Biology **7**:325–333.

Thompson, F. R., III, J. R. Probst, and M. G. Raphael. 1995. Impacts of silviculture: overview and management recommendations. Pages 201–219 *in* T. E Martin and D. M. Finch, editors. Ecology and management of neotropical migratory birds: a synthesis and review of critical issues. Oxford University Press, Oxford, UK.

Trine, C. L. 1998. Wood thrush populations sinks and implications for the scale of regional conservation strategies. Conservation Biology **12**:576–585.

Van Horn, M. A., and T. M. Donovan. 1994. Ovenbird (*Seiurus aurocapillus*). *In* A. Poole and F. Gill, editors. The birds of North America, Number 88. Philadelphia: the Academy of Natural Sciences; Washington, D.C., USA, and the American Ornithologists' Union.

Villard, M. A. 1998. On forest-interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. Auk **115**:801–805.

Villard, M. A., and B. A. Maurer. 1996. Geostatistics as a tool for examining hypothesized declines in migratory songbirds. Ecology **77**:59–68.

Villard, M. A., G. Merriam, and B. A. Maurer. 1995. Dynamics in subdivided populations of neotropical migratory birds in a fragmented temperate forest. Ecology **76**:27–40.

Weinberg, H. J., and R. R. Roth. 1998. Forest area and habitat quality for nesting Wood Thrushes. Auk **115**:879–889.

Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, K. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation of avifauna of the eastern deciduous forest. Pages 125–206 *in* R. L. Burgess and D. M. Sharpe, editors. Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, New York, USA.

Wiens, J. A. 1995. Habitat fragmentation: island vs. landscape perspectives on bird conservation. Ibis **137**:S97–S104.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology **66**:1211–1214.

With, K. A., R. H. Gardner, and M. G. Turner. 1997. Landscape connectivity and population distributions in heterogeneous environments. Oikos **78**:151–169.