

Analysis of landscape sources and sinks: the effect of spatial pattern on avian demography

Kimberly A. With^{a,*}, Anthony W. King^b

^aDepartment of Biological Sciences, Bowling Green State University, Bowling Green, OH 43403, USA

^bEnvironmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831, USA

Abstract

To develop theoretical insights into the relationship between spatial pattern and demography, we coupled a spatially structured demographic model with neutral landscape models to investigate how landscape structure affected population persistence and the source–sink potential of landscapes for a generalized, territorial migratory songbird. Four species-types, with different sensitivities to habitat area and edge effects, were simulated on replicated landscapes across a range of habitat abundance (1–90%) and fragmentation or spatial contagion (random, fractal with minimal contagion, and fractal with maximum contagion). For each species-type in each landscape, the expected number of female offspring produced per female (fecundity, b) was modeled as an explicit function of habitat area and spatial structure (patch edge-to-area ratio). Fecundity estimates (b) were combined with survivorship in a life-table analysis to estimate the net lifetime reproductive output (R_0) for the population of each landscape. Landscapes for which $R_0 < 1$ were identified as population sinks, and as potential population sources when $R_0 > 1$. As expected, reproductive output (R_0) was generally highest on fractal landscapes with maximum clumping (minimum fragmentation) and lowest on random landscapes (maximum fragmentation), especially for species with high edge sensitivity. For species with low edge sensitivity, population persistence was unlikely when the landscape had <40% habitat (i.e. $R_0 < 1.0$ in these landscapes and were population sinks). Thus, thresholds in population persistence could be identified for different species in these landscapes, but the level of habitat required for persistence ranged widely from 5 to 90% depending upon the species' response to habitat fragmentation (edge sensitivity) and the specific landscape pattern. Our results caution against the adoption of general rules or 'cookbook prescriptions' in conservation regarding the amount of habitat required for population persistence (e.g. the '20% rule'). Landscape configuration (the 'details of how habitat is arranged') can mitigate the effects of habitat loss and enhance population persistence in fragmented landscapes.

© 2001 Elsevier Science Ltd. All rights reserved.

1. Introduction

Conservation biologists have been grappling with the problem of how to assess the regional status of a species from observations of local population dynamics within habitat patches. The local, patch-based scale of most ecological studies may obscure or exaggerate regional declines that are now occurring for many species, because it is difficult to infer a species' regional status from its occurrence or abundance in isolated habitat fragments (Brawn and Robinson, 1996). This is particularly true for populations in sink habitats, which are not self-sustaining, but which persist owing to immigration

from outside source populations (Pulliam, 1988). Protection of source populations or habitats, in which reproduction exceeds mortality, is obviously critically important for the long-term persistence of a species (Dias, 1996). Because it has been hypothesized that fragmented landscapes may be dominated by sink habitat, owing to edge effects that reduce demographic rates (Temple and Cary, 1988; Donovan et al., 1995a,b), it is imperative that we determine the levels of habitat loss and fragmentation that can be tolerated by native species. The relative abundance of source and sink habitat may affect population persistence at the landscape scale (Pulliam and Danielson, 1991; Donovan et al., 1995b, 1997; Brawn and Robinson, 1996), and thus a broader perspective is ultimately required to assess the source–sink dynamics of populations and to evaluate how changes in landscape structure (e.g. habitat fragmentation) affect these dynamics.

* Corresponding author at present address: Division of Biology, Kansas State University, Manhattan, KS 66506. Tel.: +1-785-5325040; fax: +1-785-5326653.

E-mail address: kwith@ksu.edu (K.A. With).

Although previous source–sink models have examined how the vital rates of populations vary in space, these models are typically spatially implicit (Pulliam, 1988; Howe et al., 1991; Pulliam and Danielson, 1991), including those that have attempted to understand the effect of habitat fragmentation on source–sink populations (e.g. Donovan et al., 1995a, but see Temple and Cary, 1988; Ritchie 1997). Although landscape structure is known to affect reproductive success in many species (Donovan et al., 1995b, 1997), demographic factors (e.g. fecundity, b) are usually treated as fixed input parameters in most population models. If demographic parameters are truly dependent upon spatial structure, varying such parameters independently of landscape pattern in population models may give misleading results about the status of the population (King et al., in press). Spatially explicit approaches that examine how landscape structure affects demography and the source–sink dynamics of populations have not been well developed. A notable exception is the simulation of edge effects on nest success for populations of a hypothetical forest-interior bird in three different landscapes (unfragmented, moderately fragmented and severely fragmented) by Temple and Cary (1988). They tracked population sizes through time across the entire landscape and within habitats that differed in quality (edge–distance categories); the three landscapes varied in the relative amounts of good, marginal and poor-quality habitats, with the unfragmented landscape containing mostly (97.8%) good-quality habitat (nesting territories) and the severely fragmented landscape comprising mostly (80.5%) poor-quality habitat. Although published before the term ‘source–sink population’ was popularized, it was clear that Temple and Cary were thinking along these lines, especially since they additionally ran simulations on these landscapes that included a limited amount of immigration from outside populations. Their conclusion:

Populations of forest-interior birds living in a severely fragmented landscape may be unable to maintain their numbers intrinsically; their continued existence in the fragmented landscape may then be dependent on recruitment by immigrants that disperse into the area from regions where fragmentation is not severe and reproduction is adequate to produce a surplus (Temple and Cary, 1988: 346).

Today we would classify the latter as a population source and the former as a population sink.

Despite this early attempt, general principles regarding how landscape structure affects demography and the ensuing consequences for population persistence have been slow to emerge. Our goal in this paper is to

develop theoretical insights into the relationship between landscape structure and demography, and to understand how this ultimately affects population persistence for species that differ in their response to habitat fragmentation. To accomplish this, we couple a spatially structured demographic model developed for territorial migratory songbirds (King et al., in press) with neutral landscape models. Neutral landscape models are raster maps in which habitat patterns are generated by theoretical spatial distributions (Gardner et al., 1987; With, 1997; With and King, 1997). Our coupled model provides a generalized, spatially explicit framework for assessing the relationship between demography and spatial pattern, thus permitting an analysis of landscapes as overall population sources or sinks. Our approach is unique in that it explicitly incorporates the effect of patch structure on reproductive success.

Neotropical migrants that breed in the temperate forests of Eastern and Midwestern North America are the focus of this analysis because they represent a group of special concern to conservation biologists and land managers (Freemark et al., 1995; Petit et al., 1995) and we wanted to develop a spatially explicit theory relevant to those concerns. Many species have been extirpated from parts of their range or have suffered significant declines owing to widespread habitat destruction and fragmentation (e.g. Robbins et al., 1989a; Askins et al., 1990; Robinson et al., 1995). Because our spatially structured demographic model provides an assessment of whether landscapes represent population sources or sinks, it is possible to evaluate what types of management options are necessary, or even feasible, to restore landscapes from sinks to sources for a given species. By examining the sensitivity of demographic parameters to landscape structure, we can determine the magnitude of landscape change necessary to ensure population persistence. For example, land managers might be able to alter patterns of timber harvest so as to generate landscape configurations that would enhance reproductive output. Although it is perhaps obvious that large patches of contiguous forest with less edge would have this effect, the model can provide quantitative estimates of the magnitude of change needed to achieve the desired goal and indicate which alternative landscape configurations are most likely to achieve this objective.

1.1. Objectives

Our main objective is to distill general principles about how spatial pattern affects demography, and thus how landscape structure affects population persistence. This will also permit us to evaluate the scenarios under which a landscape functions as a population source or sink for a given species. An application of this model for the management of Henslow’s Sparrows (*Ammodramus henslowii*) in fragmented landscapes will be presented

elsewhere (King et al., in press). Specifically, our goals are to:

- Explore the relationship between demography and landscape pattern by generating quantitative predictions of population persistence on spatially structured landscapes for species that vary in their response to habitat fragmentation.
- Provide an assessment of landscapes as population sources or sinks for a given species type. Demographic indices, such as expected net lifetime reproductive output (R_0), can be used to infer the source–sink potential of landscapes. Because this index is calculated for the population of the entire landscape, this analysis provides an assessment of population persistence and source–sink status at the landscape scale.
- Assess what types of landscape configurations can potentially serve as population sources and determine the magnitude of change required to transform landscape sinks into landscape sources for species that vary in their response to habitat fragmentation.

2. Model description

2.1. The landscape template

Landscapes were modeled as binary raster maps (256×256 -cell grid) of breeding habitat versus non-breeding habitat. Breeding habitat was distributed either as randomly selected grid cells or as fractally-distributed patches generated by the midpoint displacement algorithm (Saupe, 1988). This fractal algorithm permits the creation of spatially realistic landscape patterns across a range of habitat abundance (h) and fragmentation or spatial contagion (H) (With, 1997; Fig. 1). Ten replicate maps were generated at each of 11 levels of habitat abundance ($h = 0.01, 0.05, 0.1, 0.2, \dots, 0.9$) for random landscapes and for fractal landscapes at two levels of habitat fragmentation ($H = 0.0$ or 1.0 ; fragmented vs clumped, respectively), for a total of 330 landscapes. Highly fragmented fractal landscapes ($H = 0.0$) are representative of habitat destruction that occurs at a fine scale, resulting in small gaps. Clumped fractal landscapes ($H = 1.0$) are indicative of coarse-scale habitat destruction in which large gaps are created,

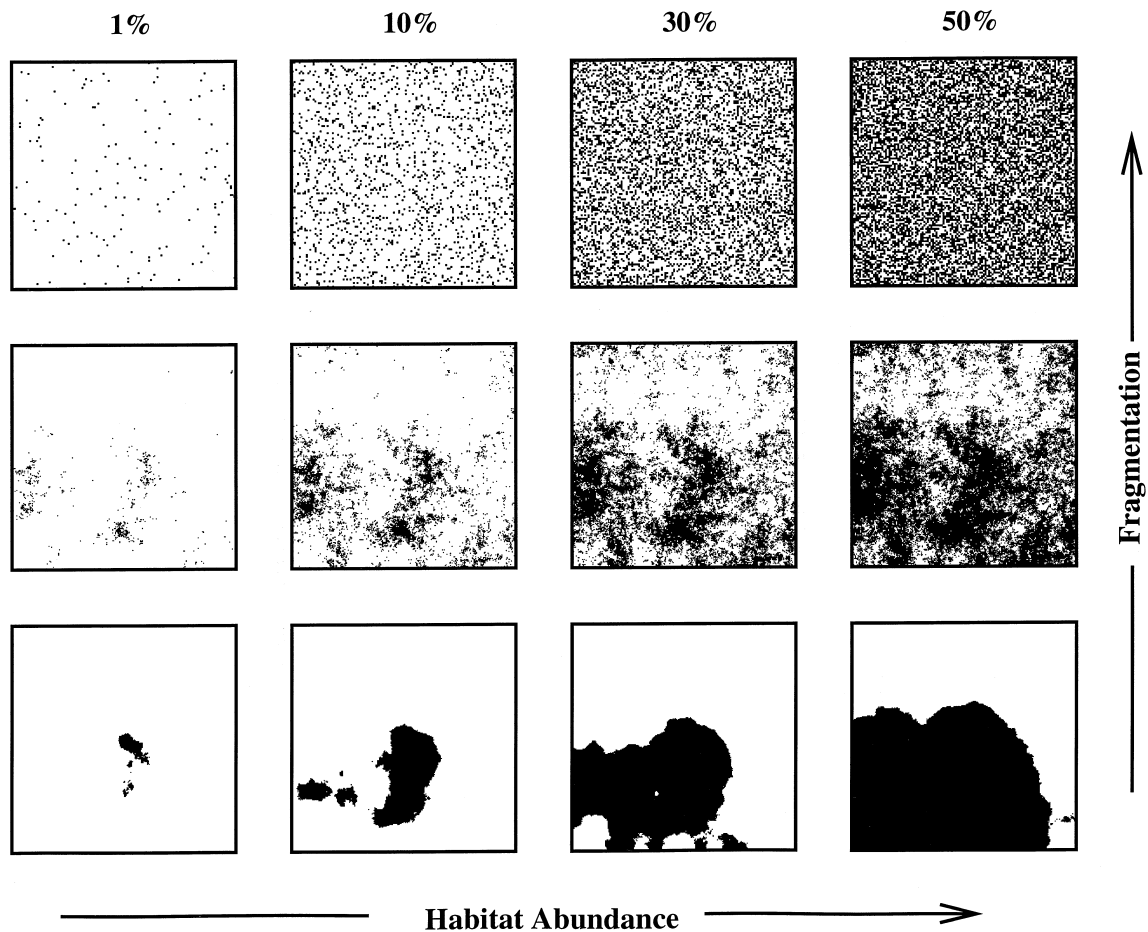


Fig. 1. Random (top) and fractal neutral landscapes across a gradient of habitat destruction. Fractal landscapes were generated at two levels of spatial contagion to produce fragmented ($H = 0.0$, middle) and clumped ($H = 1.0$, bottom) habitat distributions.

but large blocks of contiguous habitat are also preserved as a consequence (Fig. 1).

Although the absolute size of neutral landscapes is arbitrary, it was necessary to assign a size to the maps in this application because the availability of habitat on the landscape was ultimately based on the minimum area requirements (ha) of breeding pairs (see Section 2.2). The resolution of individual grid cells was therefore set at 30 m, which is consistent with the resolution of widely available remotely sensed data (e.g. Landsat TM images). Thus, each grid cell was 0.09 ha (30×30 m) and the overall landscape was ~5900 ha or ~60 km². Because we first calibrated the model to ensure that all populations on a landscape of this size would persist if $h=1.0$ (see Section 2.5), the absolute size of the landscape is not important for the objectives of this analysis, and map size (area) does not affect the probability of persistence. Nevertheless, the size of these neutral landscapes exceeds that of some landscape-scale studies (e.g. 3 km², McGarigal and McComb, 1995; 6.25 km², Villard et al., 1999).

2.2. Identification of available breeding habitat

Habitat fragmentation affects the availability of suitable breeding habitat on the landscape (e.g. Van Horn et al., 1995). Available breeding habitat is defined here as functionally connected habitat meeting the individual minimum area requirements (MAR) for a given species (Dale et al., 1994; With, 1999). In this study we have equated MAR with an individual breeding territory. Habitat need not be contiguous to be considered part of a territory if the individual has the ability, and willingness, to traverse gaps of unsuitable habitat in the maintenance and use of that territory (home-range gap-crossing ability, Grubb and Doherty, 1999). Habitat within the gap-crossing range of the individual is thus functionally connected and integrated into the organism's assessment of available breeding habitat. The availability of suitable breeding habitat declines much faster and more precipitously as a function of habitat abundance in fragmented fractal landscapes ($H=0.0$) than in clumped fractal landscapes ($H=1.0$), especially for species with large MAR (With, 1999). The effect of fragmentation on habitat availability is mitigated for species that are able to cross gaps of unsuitable habitat, however. For example, a gap-sensitive species (unable to cross gaps of unsuitable habitat) with a MAR = 100 ha would perceive nearly all (99.6%) of the habitat on a 10% clumped fractal landscape as available, but would view less than half (46.2%) of the habitat as available for breeding on a 10% fragmented fractal landscape (With, 1999). If the species has good gap-crossing abilities (i.e. individuals can traverse at least three cells of unsuitable habitat), then most (88.9%) of the habitat in the 10% fragmented landscape would become available for breeding (With, 1999).

In the present analysis, availability of breeding habitat on a given landscape was assessed by determining which habitat clusters were of sufficient size to fulfill the territory requirements of a breeding pair with a MAR = 0.5 ha, which is consistent with the territory size of many Neotropical migratory songbirds that breed in woodlands (e.g. Morse, 1989). Habitat clusters (patches) were defined as habitat cells that were contiguous either orthogonally or diagonally (i.e. neighborhood size = eight cells; next-nearest neighbor or 'rule 2,' With, 1997); that is, individuals were unwilling to incorporate gaps of unsuitable habitat ≥ 30 m into their territory. Even highly vagile species such as migratory songbirds may be reluctant to cross gaps formed by roads and streams once they settle on territories (Lidicker and Koenig, 1996). The patch structure of the landscape was thus defined by the species' perception of available breeding habitat.

2.3. Probability of patch occupancy

The probability that habitat patches of sufficient size to fulfill the MAR of a species are occupied was determined by an incidence function, J_A :

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

where β_0 , β_1 and β_2 are model parameters in a logistic regression (Robbins et al., 1989b; Table 1). We wanted

Table 1
Parameter values used in the demographic model to characterize bird species-types that differ in their sensitivity to patch area and habitat edge

Parameter	Value
Territory size (A_T)	0.5 ha
Gap-crossing ability	< 30 m
Juvenile survivorship (s_0)	0.3
Adult survivorship (s)	0.6
Age of first reproduction (α)	1 year
Longevity (L)	8 years
<i>Area sensitivity^a</i>	
Low sensitivity:	
β_0	-0.579
β_1	1.596
β_2	0.0
High sensitivity:	
β_0	-2.411
β_1	0.528
β_2	0.0
<i>Edge sensitivity^b</i>	
Maximum nesting success (S_{\max})	0.8
Low sensitivity:	
k	0.75
θ	10.0
High sensitivity:	
k	0.10
θ	0.50

^a Parameters used in logistic regression model to calculate incidence function of patch occupancy from Eq. (1) in text.

^b Parameters used to define edge sensitivity from Eq. (2) in text.

to capture the extremes in possible species' responses to habitat fragmentation based on available data for Neotropical migratory songbirds, and thus we selected two species that appeared to differ in their area sensitivity to characterize our general species-types (Robbins et al., 1989b). One species-type exhibited low area sensitivity, and had a high probability ($\geq 75\%$) of nesting in patches > 10 ha (Fig. 2). The second species-type had high area sensitivity, and was rarely encountered (31% probability) even in large (1000 ha) patches. For reference, values for the red-eyed vireo (*Vireo olivaceus*) were used to characterize the species-type with low area sensitivity, and values for the veery (*Catharus fuscescens*) were used to characterize the species with high area sensitivity (Table 1; data from Robbins et al., 1989b). Thus our parameterization uses realistic values. We do not relate model results to these specific species, however, because area sensitivity is only one dimension that we use to characterize different species-types for the purpose of our analysis.

Because J_A describes the probability of encountering a breeding pair (territory) at a random point in a patch i of size A (Robbins et al., 1989b), we use the incidence function to estimate what proportion of patch A_i is occupied. Thus, the number of territories T within patch i is $T_i = J_A A_i / A_T$, where A_T is territory size (MAR).

2.4. The demographic model: assessing reproductive success in habitat fragments

Avian demography is affected in complex ways by habitat fragmentation. Fragmentation produces edge effects that decrease available habitat area for forest-interior bird species and increase nest predation and

brood-parasitism rates by brown-headed cowbirds (*Molothrus ater*) within forest fragments (e.g. Askins, 1995; Robinson et al., 1995). Reproductive success, the probability that a pair on a territory will produce at least one offspring, was therefore assumed to be highest in large patches with little edge. A normalized index of patch geometry was obtained by dividing the edge-to-area ratio for each patch on the species-defined landscape by the maximum ratio possible, which is that of a single habitat cell in these raster-based landscapes. Thus, a normalized index of 1.0 indicates the maximum edge per unit area, whereas 0.0 indicates a patch with minimal edge. As landscapes become increasingly fragmented (e.g. random or $H=0.0$), they are dominated by patches with greater edge-to-area ratios.

Reproductive success in a given patch, S_i , can then be obtained as

$$S_i = S_{\max} \frac{1}{1 + (e_i/k^\theta)} \quad (2)$$

where S_{\max} is the maximum probability of reproductive success in the absence of edge effects (normalized patch edge-to-area ratio $\rightarrow 0.0$). This was set at $S_{\max}=0.8$ in this analysis (see Section 2.5). The parameter e_i is the normalized edge-to-area ratio of patch i and k is the value of e_i where $S_i=0.5 S_{\max}$. The parameter θ determines the rate at which reproductive success declines as a function of increasing edge (i.e. edge effects). We considered a family of hypothetical responses to increasing edge. For example, reproductive success may be little affected by edge in some species. Other species may exhibit linear declines in reproductive success as a function of

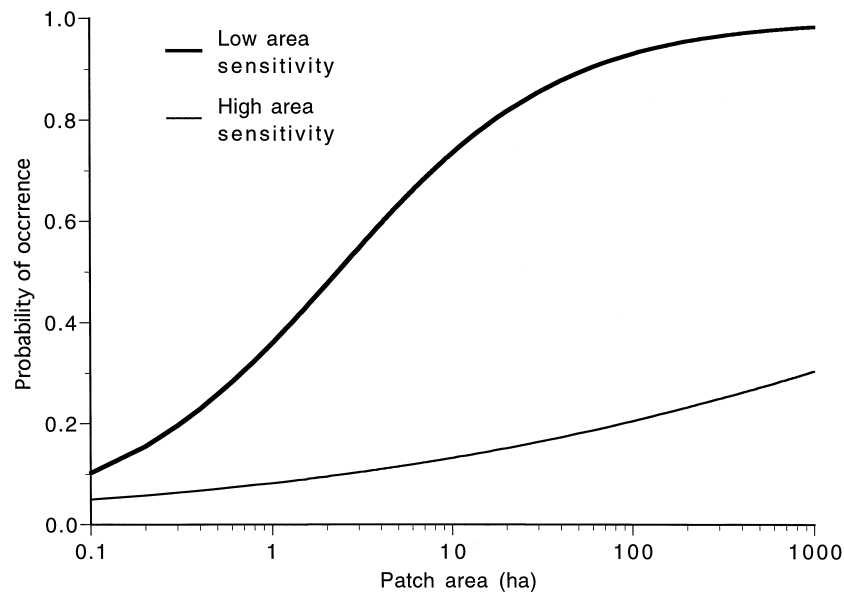


Fig. 2. Incidence functions for species that vary in sensitivity to patch area. Parameter values used in the logistic model [Eq. (1)] that generated these functions are presented in Table 1. Data from Robbins et al. (1989b) for the red-eyed vireo (*Vireo olivaceus*) were used to characterize a species with low area sensitivity and data for the veery (*Catharus fuscescens*) were used to characterize a species with high area sensitivity.

increasing edge, while others may be extremely sensitive to edge. We chose to model the extremes in this analysis, such that species had either high edge sensitivity or low edge sensitivity (Table 1, Fig. 3). Note that because the parameter θ controls the rate at which reproductive success declines as a function of edge, it could also be interpreted in the context of how different edge types or landscape matrixes influence edge effects for a particular species (e.g. Donovan et al., 1997). We have defined reproductive success to be a patch-scale phenomenon that is applied to all nests in a given patch. This formulation makes modeling the explicit location of each territory with respect to the edge unnecessary, and thus we are not modeling edge effects on reproductive success as a function of distance from the edge. Reproductive success is modeled phenomenologically as an aggregate response to patch structure, and is therefore assessed on a per-patch rather than per-nest basis.

The combination of area sensitivity [Eq. (1), Fig. 2] and edge sensitivity [Eq. (2), Fig. 3] yields four species-types: low area sensitivity–low edge sensitivity, high area sensitivity–low edge sensitivity, low area sensitivity–high edge sensitivity, and high area sensitivity–high edge sensitivity. A life-history table combining age-specific reproduction and survivorship was then constructed for each of the four species-types on the landscape. The expected number of female offspring produced per female, b , for the landscape population was calculated as

$$b = \frac{\sum_{i=1}^n \sum_{j=1}^{N_i} F_{ji}}{\sum_{i=1}^n N_i} \quad (3)$$

where F_{ji} is the number of female offspring produced in territory j of patch i , N_i is the number of territorial females in patch i , and n is the total number of patches. The number of female fledglings (F_{ji}) is the product of the number of territories in patch i (T_i), species-specific clutch size (uniform distribution of four or five eggs), the probability of reproductive success for patch i [S_i , Eq. (2)], and the fledgling sex ratio (1:1). The total number of reproductive females (N_i) was assumed to be equivalent to the number of territories (T_i) for simplicity. Another simplification was to assume that reproduction is independent of age after sexual maturity. The maternity function m_x , the number of female offspring produced by a female of age x , was then $m_x = b$ for all age classes beyond the age of first breeding, which was assumed to be 1 year as is typical for passerines. While age-specific survivorship could be incorporated into the model, we again simplified the analysis by assuming that there were just two survivorship classes: non-reproductive juveniles and reproductive adults. Survivorship then needed to be specified only for fledged juveniles (s_0) and adults (s); the latter was assumed to be constant after the age of first reproduction was reached (i.e. 1 year). Adult survivorship was set at $s = 0.6$ and juvenile survivorship at $s_0 = 0.3$, consistent with available information on adult and juvenile survivorship for Neotropical migrants (Greenberg, 1980; Karr et al., 1990; Martin and Li, 1992; Anders et al., 1997) and parameter values used in other avian demographic models (e.g. Temple and Cary, 1988; Donovan et al., 1995a). Although our modeling approach is unique in considering the effect of landscape structure on fecundity (b), the effect of landscape pattern on survivorship was not considered. In

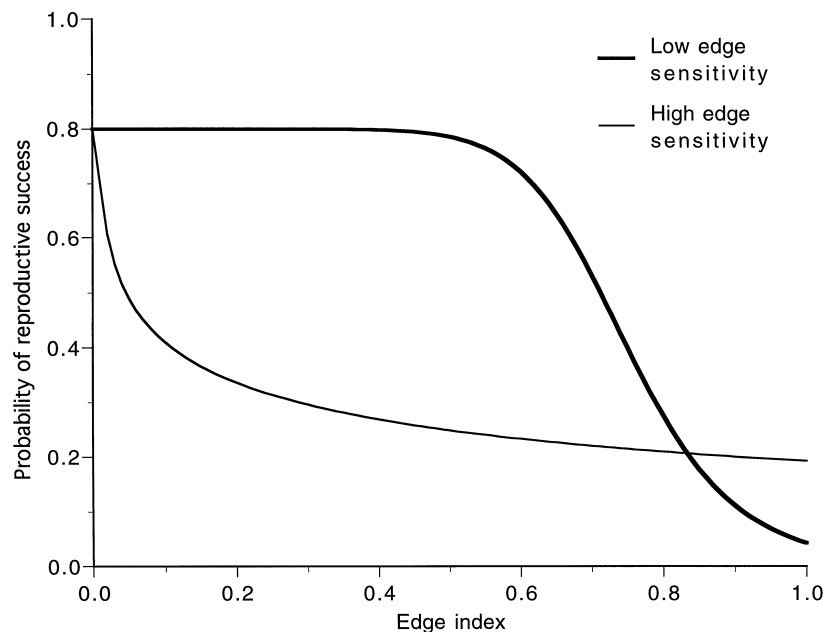


Fig. 3. Response curves for two hypothetical species that differ in their sensitivity to edge. The edge index characterizes the complexity of patch shape; patches with an edge index $\rightarrow 1.0$ are dominated by edge. Parameter values used in the function [Eq. (2)] that generated response curves are presented in Table 1.

birds, at least, effects of fragmentation on population persistence appear to be driven primarily by declines in reproductive success (Robinson et al., 1995). Furthermore, there are no data to suggest that survivorship is lower for females in fragments than in more contiguous habitat, and virtually nothing is known about how fragmentation affects survival once juveniles leave the nest (Donovan et al., 1995a).

2.5. Analysis of landscapes as population sources or sinks

To review, the demographic parameter, b , was calculated for each of the four species-type in each landscape. A life-table combining fecundity (b) and survivorship (s_0 and s) was then constructed for each combination of species-type and landscape. We then calculated the expected net lifetime reproductive output (R_0), which permits a simple characterization of the landscape as either a population source or sink. Net lifetime reproductive output is the expected lifetime production of female offspring by a female and is obtained as

$$R_0 = \sum_{x=0}^{\infty} l_x m_x = l_a b / (1.0 - s) \quad (4)$$

where l_a is the survivorship to the age of first breeding. The population is stable when $R_0 = 1.0$, declining when $R_0 < 1.0$ (landscape is a sink) and increasing when $R_0 > 1.0$ (landscape is a source).

Maximum nesting success [S_{max} , Eq. (2)] was adjusted so that $R_0 \geq 1$ for a homogeneous landscape of breeding habitat ($h = 1.0$). This calibration with the resulting value of $S_{max} = 0.8$ assured population persistence on a landscape of continuous breeding habitat.

3. Results

The expected net lifetime reproductive output (R_0) was generally higher in fractal landscapes than in random ones, especially if species had high edge sensitivity or when $h \leq 0.4$ for species with low edge sensitivity (Fig. 4). Even the most fragmented fractal landscapes ($H = 0.0$) are inherently more clumped than random landscapes, and thus have larger patches with less edge (With and King, 1999a). Species with low edge sensitivity were able to persist in landscapes with as little as 1% habitat if it was arrayed as a clumped fractal distribution ($H = 1.0$, left side of Fig. 4). In contrast, this species-type

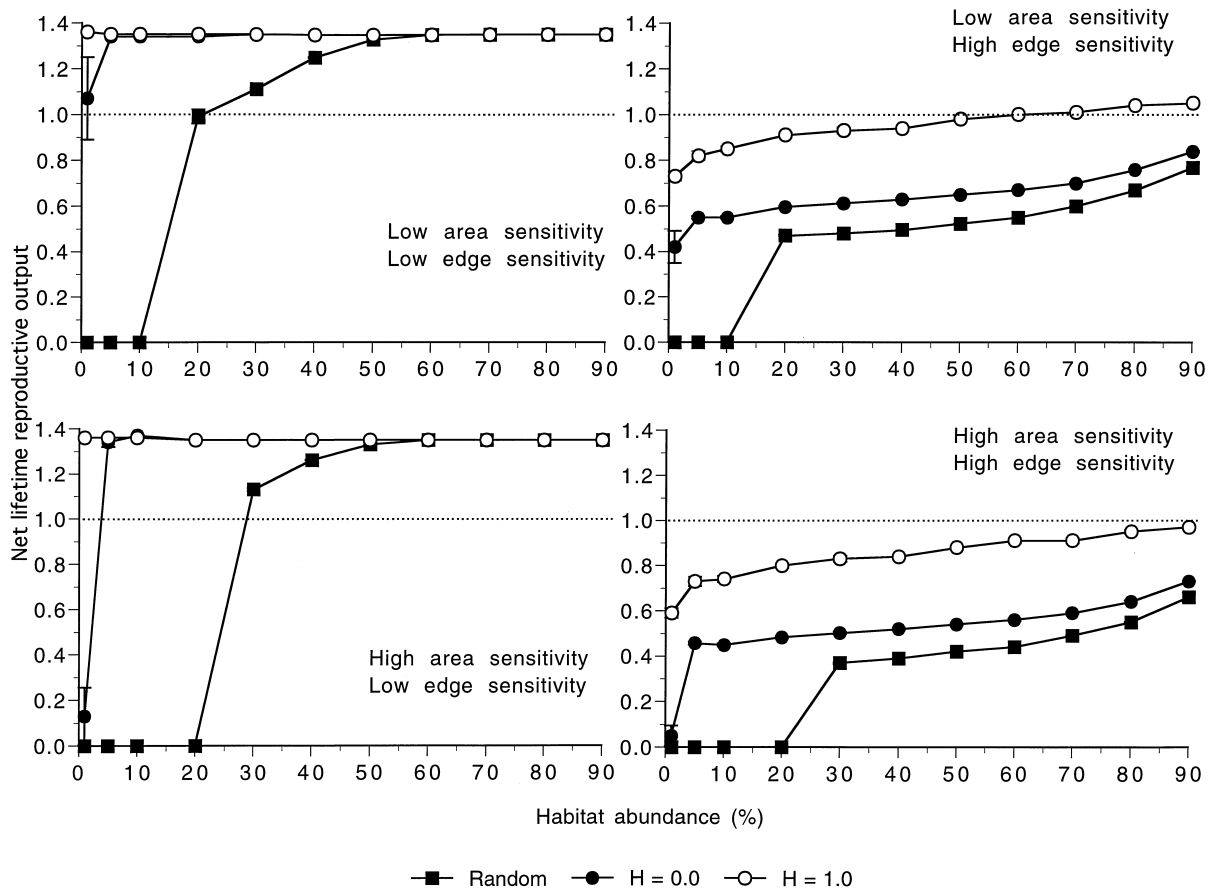


Fig. 4. Effect of habitat abundance and landscape structure (random, fragmented fractal $H=0.0$, clumped fractal $H=1.0$) on net lifetime reproductive output (R_0) for species-types that differ in their sensitivity to patch area (Fig. 2) and habitat edges (Fig. 3). Populations in which $R_0 \geq 1.0$ (dashed horizontal line in each graph) are stable or increasing. Each point represents the mean \pm SE for 10 landscapes (error bars are smaller than symbols in most cases).

was unable to persist on random landscapes once habitat fell below 20 or 30%, depending on area sensitivity. Species with high edge sensitivity were only able to persist on landscapes with a clumped fractal habitat distribution exceeding 50%, and then only if they had low area sensitivity (right side of Fig. 4). Edge sensitivity thus had the greatest effect on whether populations persisted in a given landscape, with area sensitivity having less of an effect, primarily shifting the level of habitat at which thresholds in population persistence occurred in random landscapes.

Species with high edge–high area sensitivities were unable to persist unless habitat was clumped (fractal, $H=1.0$) and very abundant ($\geq 90\%$; Fig. 4), given the levels of survivorship we used in this analysis (Table 1). Higher rates of survivorship would permit persistence of this species-type on fractal landscapes with less

abundant habitat. An increase in juvenile survivorship (s_0) from 0.3 to 0.4, or adult survivorship (s) from 0.6 to 0.7, would substantially reduce the amount of habitat required for population persistence on fractal landscapes (Fig. 5). This species-type would be unable to persist on random landscapes with $< 20\%$ habitat, however, even with elevated levels of survivorship (Fig. 5). Large increases in survival rates would be required to ensure persistence in even the 90% random landscapes (e.g. $s_0=0.46$ and $s=0.72$). In contrast, species with low edge–low area sensitivities persisted in random landscapes with $> 10\%$ habitat, although decreases in survivorship would increase the amount of habitat required for persistence (Fig. 6). Populations were secure in landscapes with clumped habitat distributions (Fractal, $H=1.0$) with even minimal habitat ($\geq 1\%$) unless $s_0 < 0.2$ or $s < 0.4$ (Fig. 6).

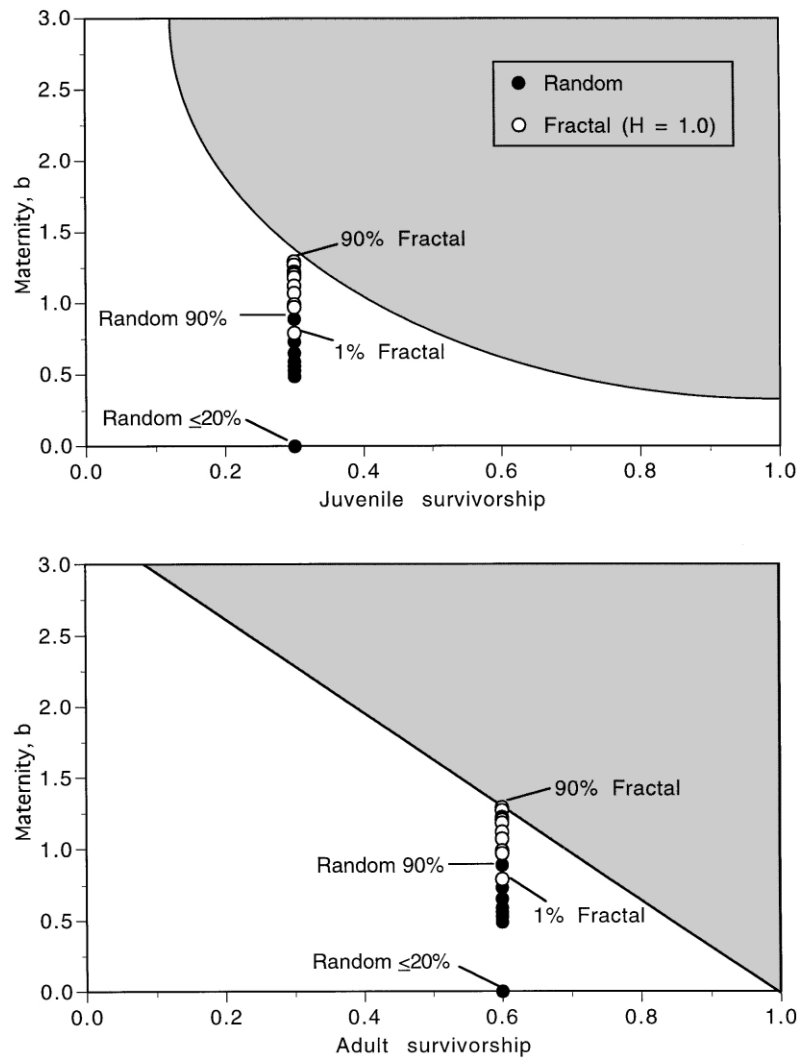


Fig. 5. Net lifetime reproductive output (R_0) as a function of age-specific maternity, b , and juvenile survivorship (s_0 , top) or adult survivorship (s , bottom) for species with high edge–high area sensitivities in random and clumped fractal ($H=1.0$) landscapes at different levels of habitat abundance. The shaded region indicates where $R_0 \geq 1.0$, in which the population is stable or increasing. The population will decline outside this region ($R_0 < 1.0$). Juvenile survivorship, $s_0 = 0.3$, and adult survivorship, $s = 0.6$ in this analysis, consistent with available information on survivorship estimates in Neotropical migrants.

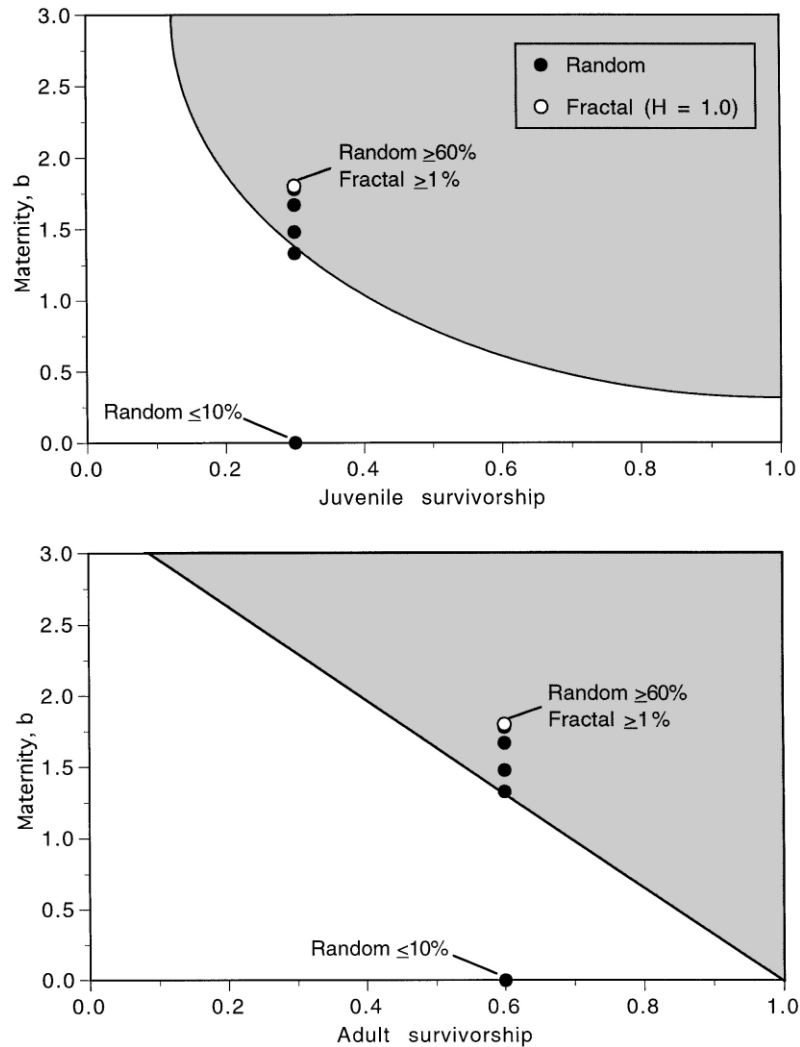


Fig. 6. Net lifetime reproductive output (R_0) as a function of age-specific maternity, b , and juvenile survivorship (s_0 , top) or adult survivorship (s , bottom) for species with low edge–low area sensitivities in random and clumped fractal ($H = 1.0$) landscapes at different levels of habitat abundance. Rest of figure as in Fig. 5.

4. Discussion

4.1. The relationship between landscape structure, demography and conservation

Conservation strategies to reverse regional declines in Neotropical migratory bird populations will require detailed knowledge of how demographic and landscape factors interact to create population sources and sinks (Rosenberg et al., 1999). Forest breeding birds have been shown to respond in different ways to habitat destruction and fragmentation (McGarigal and McComb, 1995; Villard et al., 1999), and thus the effect of landscape structure on avian demography is highly species-specific. This may initially frustrate conservation biologists and land managers hoping to develop a single comprehensive strategy that would encompass the entire breeding bird community, but this goal may be attainable if the most sensitive species are targeted. Species

expected to be particularly sensitive to changes in landscape structure are those with large minimum area requirements or high area sensitivity and which suffer from edge effects (reduced reproductive success in habitat fragments; Faaborg et al., 1995). In our analysis, edge sensitivity had a greater effect on population persistence than area sensitivity. This is because edge sensitivity directly affects the reproductive success within a patch, whereas area sensitivity merely affects patch occupancy or the degree to which patches of a given size are saturated by breeding pairs. While both of these factors contribute to the relative source or sink potential of a landscape, edge sensitivity appears to be a more important determinant of whether the population persists at the landscape scale.

Our model predicted that a species with high edge sensitivity would have a difficult time persisting even in landscapes with minimal edge (clumped fractal landscapes). Combining high edge sensitivity with high area

sensitivity made persistence tenuous at best, at least with the survivorship rates we used. Would higher survivorship rates for adults or juveniles improve the prognosis for these types of species? From a management standpoint, survivorship might be enhanced, particularly for juveniles after they leave the nest, through predator-control programs on the breeding grounds. For example, predation was the greatest factor affecting post-fledgling survivorship in wood thrushes (*Hylocichla mustelina*); half of all fledglings were depredated within 8 weeks of leaving the nest (Anders et al., 1997). Interestingly, the predators of fledglings were different from the suite of nest predators, such as mice (*Peromyscus* spp), raccoons (*Procyon lotor*), blue jays (*Cyanocitta cristata*) and American crows (*Corvus brachyrhynchos*), which are commonly associated with fragmented landscapes and forest edges (Donovan et al., 1997; Rosenberg et al., 1999). Instead, the main predators of fledglings were the Cooper's hawk (*Accipiter cooperii*) and broad-winged hawk (*Buteo platypterus*), which are both forest-nesting species with large area requirements. Thus, it is not clear what measures could be taken to enhance postfledgling survivorship, particularly since juvenile survivorship (estimated at $s_0 = 0.29$, and thus equivalent to the rate used in our model) was ultimately not responsible for the shift in this population's status from a source (Donovan et al., 1995b) to a sink (Anders et al., 1997). Reproductive success had declined, owing to higher predation rates on eggs and chicks, which again argues for concentrating primarily on the relationship between landscape structure and fecundity, rather than survivorship, in birds.

For highly vagile organisms such as Neotropical migratory songbirds, reproductive failure is usually a more serious consequence of habitat fragmentation than a disruption in dispersal (Donovan et al., 1995b). This is consistent with the results of a recent modeling synthesis of metapopulation and neutral landscape models, which found that reproductive output (R_0) was more important than dispersal in ameliorating extinction risk for populations on fractal landscapes (With and King, 1999b). Dispersal success (search for a suitable unoccupied territory) was generally high on fractal landscapes owing to the greater spatial contagion of habitat (With and King, 1999a), and thus did not affect population persistence as much as reproductive output. Our current modeling approach, which couples a simple stage-structured demographic model with neutral landscape models, provides an extension of this previous work and permits us to parse R_0 into its constituent parts (survivorship and fecundity), to investigate in a more refined way the interaction of these demographic parameters with landscape structure to predict the effects of habitat abundance and fragmentation on population persistence.

4.2. When is landscape structure important in predicting population persistence?

The importance of landscape pattern for population persistence depends upon the sensitivity of species to habitat fragmentation. For species with low edge sensitivity, the effect of landscape structure (random vs fractal) on population persistence was most pronounced below 10–20% habitat, depending on the species area sensitivity, where populations plunged from potential sources to sinks in random landscapes. To conserve such species on managed landscapes, the best strategy might be to maintain habitat abundance above 30%, or for landscapes that have less habitat, preserve clumped habitat distributions characteristic of fractal landscape patterns. Even at 1% habitat, clumped fractal landscapes functioned as population sources for these species.

Landscape structure always had a significant effect on species with high edge sensitivity, although most landscapes supported population sinks of these species. Such species could only persist on clumped fractal landscapes ($H = 1.0$) with at least 50% habitat for species with low area sensitivity or 90% for species with high area sensitivity. Edge-sensitive species should obviously be managed by preserving large amounts of habitat with maximum clumping. Predator control or other management programs to enhance survivorship and reproductive success would also increase the likelihood of persistence (Fig. 5). Our results thus demonstrated that landscape structure can affect population persistence for some species, contrary to recent statements that the “details of how habitats are arranged are unlikely to mitigate the risks of habitat loss” (Fahrig, 1997: 609).

Is there empirical evidence that landscape structure — apart from the amount of habitat present on the landscape — significantly affects population persistence in breeding birds? Because of the additional effort required to obtain demographic data on the effects of landscape structure on population persistence, most studies have examined instead the relative effects of habitat abundance and fragmentation (spatial configuration of habitat) on the occurrence or abundance of species in different landscapes. For example, McGarigal and McComb (1995) found that breeding bird abundances were generally related to the cover of late-seral forest, and only secondarily to the configuration of forest cover (landscape structure), in the intensively managed landscapes of western Oregon. Species varied widely in their responses to landscape structure, however. Four species were affected only by habitat configuration; these were ‘edge species’ such as the olive-sided flycatcher (*Contopus borealis*) and western wood-pewee (*Contopus sordidulus*). Slightly more than half of the remaining species ($8/15 = 53.3\%$) exhibited a significant response to both habitat area and configuration, but configuration only explained an additional 11–28% of

the variation in bird abundance once the effects of habitat area were removed. In agricultural-dominated landscapes, however, Villard et al. (1999) found that forest cover and configuration were equally good predictors of the presence of most (9/15 = 60%) of the bird species they studied on fragmented landscapes in eastern Ontario, Canada. McGarigal and McComb (1995) pointed out that the population dynamics of birds in landscapes being fragmented by commercial timber management are likely to differ from those being fragmented by urbanization and agriculture. Managed forests of the Pacific Northwest are dynamic mosaics of regenerating stands of uneven age, unlike the static landscapes of the Midwest where forest fragments (woodlots) stand in sharp contrast to the surrounding land use. Thus, McGarigal and McComb (1995) concluded that, “it is not too surprising that we did not detect stronger relationships”, between bird abundance and habitat configuration, given that, “it seems likely that vertebrate responses to habitat fragmentation would be less pronounced” in the managed forested landscapes in which they worked. Nevertheless, another survey of forest breeding birds on agricultural landscapes in southern Ontario and Quebec found little effect of fragmentation on species’ presence or absence (Trzcinski et al., 1999). Most species (25/31 = 81%) responded significantly to the amount of forest cover, and cover almost always explained more of the variation in species occurrence than fragmentation for species that responded to both cover and fragmentation (5/6 = 83%). Only the presence of the hermit thrush (*Catharus guttatus*) on these landscapes was predicted better by the degree of fragmentation (hermit thrushes were negatively affected by fragmentation).

Differences in the scale of the study area may have contributed to the contradictory findings in these two investigations in agricultural landscapes (6.25 km², Villard et al., 1999; 100 km², Trzcinski et al., 1999). Trzcinski et al. suggested that fragmentation effects might be evident at finer ‘patch’ scales than the landscape scale of their study, and certainly Villard et al. found significant fragmentation effects at their finer scale of analysis. Nevertheless, Villard et al. also viewed their study as being conducted at a landscape scale because it was sufficient to encompass “demographic units that are relatively independent.” While this underscores the importance of defining ‘landscape’ relative to the scale of the organism or ecological phenomenon of interest (Wiens, 1989), it further illustrates that no consensus has yet emerged on the relative importance of landscape structure on either the occurrence or persistence of breeding birds on landscapes.

Identifying when landscape structure can mitigate extinction risk — and when it cannot — is an important task in conservation biology, particularly if the current emphasis on mitigating fragmentation effects detracts

from the larger issue of wholesale habitat destruction (Fahrig, 1997, 1998). Nevertheless, we caution against making blanket statements that landscape structure generally cannot mitigate the effects of habitat loss and enhance population persistence. Our analysis demonstrates that species respond in different ways to landscape structure, such that population persistence emerges as a complex interaction between demography and landscape structure. This complicates the assessment of the effects of habitat fragmentation on species, but at least permits an assessment of the landscape conditions under which the effects of habitat loss can be mitigated and for which species.

4.3. *Threshold responses to landscape structure*

This is not to say that landscape structure is always important for predicting population persistence, however. The spatial arrangement of habitat may influence the source–sink potential of a landscape only when habitat reaches some critical level. A threshold in population persistence occurs at $R_0 = 1.0$. Above this threshold ($R_0 > 1.0$), the population is increasing and the landscape may function as a source of immigrants to populations in other landscapes. Below the persistence threshold ($R_0 < 1.0$), the population is declining and the landscape may function as a sink for emigrants from source landscapes. The transition from landscape source to sink may be a linear function of habitat abundance (e.g. edge-sensitive species with low area sensitivity in clumped fractal landscapes), or non-linear in which small differences in habitat abundance have dramatic consequences for population persistence (e.g. species with low edge sensitivity in random landscapes; Fig. 4).

Identification of threshold responses to habitat loss and fragmentation has become a major research agenda in conservation biology (With and Crist, 1995; With, 1997; Andr n, 1999; M nkk nen and Reunanen, 1999; With and King, 1999b). When do such thresholds in population persistence occur and how are they affected by habitat fragmentation? It has been stated recently that, “when breeding habitat covers more than 20% of the landscape, survival is virtually ensured no matter how fragmented the habitat is” (Fahrig, 1997: 608). Although Fahrig acknowledged that, “the exact value of the threshold will depend to some extent on the demographic potential of the organism,” she concluded that, “for large landscapes, the 20% rule is probably realistic.” We also found persistence thresholds around 10–20% habitat in our analysis of populations on large simulated landscapes, which is consistent with the 20% rule, but only for certain species-types in a particular landscape type (i.e. edge-insensitive species in random landscapes). For other species and in different landscapes, thresholds ranged from 5% (species with low edge-high area sensitivity in fragmented fractal landscapes) to 90%

(species with high edge-high area sensitivity in clumped fractal landscapes). Thresholds in persistence did not even occur for some species (e.g. species with low edge sensitivity in clumped fractal landscapes). Thus, our results do not provide general support for a ‘20% rule.’

Fahrig’s main point of contention had to do with the current emphasis in conservation biology on mitigating fragmentation effects (e.g. by enhancing connectivity of isolated habitat patches or reserves via corridors) when it is the sheer loss of habitat that is the real driving force behind the current extinction crisis. Her point is well-taken, and ideally conservation efforts should focus primarily on the protection and restoration of habitat. Nevertheless, designation of a ‘20% rule’ sets a dangerous precedent for management, because it implies that up to 80% of the habitat can be destroyed before populations are in danger of going extinct. This runs the risk of becoming a ‘cookbook prescription’ for conservation that will be applied blindly to all species, much as the 50/500 rule (Franklin, 1980; Soulé, 1980) was for determining minimum viable population size. Furthermore, there is little theoretical or empirical evidence to warrant the establishment of a ‘20% rule.’

Evidence in support of the ‘20% rule’ is generally taken from a survey of the effects of habitat fragmentation on birds and mammals, in which a threshold response to habitat loss occurred between 10 and 30% habitat (Andrén, 1994). Below this level, fragmentation effects related to increased distances among patches may disrupt dispersal and prevent the successful colonization of habitat fragments, thus reducing population sizes and enhancing extinction probabilities. Interestingly, thresholds in dispersal success have been found to coincide with thresholds in interpatch distances below 20% habitat on fractal landscapes (lacunarity thresholds, With and King, 1999a). In addition to the analysis of population persistence we present in this paper, other spatially explicit metapopulation (patch occupancy) models have also demonstrated that extinction thresholds are critically dependent upon landscape structure (random; fractal, $H=0.0$; fractal, $H=1.0$) and the demographic potential of the species (Hill and Caswell, 1999; With and King, 1999b). For example, extinction thresholds occurred at greater levels of habitat loss for species on clumped fractal landscapes than in random or fragmented fractal landscapes. Thresholds were not found for populations in clumped fractal landscapes if the species had reasonably high reproductive output ($R_0 > 1.10$; With and King, 1999b). The absence of threshold responses to habitat loss and fragmentation has also been found for real species in real landscapes. Villard et al. (1999) found that threshold responses to habitat loss were generally absent for birds in forest fragments in agricultural-dominated landscapes, except for the ovenbird (*Seiurus aurocapillus*) and black-and-white warbler (*Mniotilta varia*), which had a low probability of

occurring in landscapes with <10% mature forest cover. The lack of a threshold response is thus further evidence against the generality of the 20% rule. Finally, a re-analysis of Andrén’s (1994) data set revealed that landscape context (forested vs agricultural-dominated landscape) contributed significantly to the assessment of the relative importance of habitat loss and fragmentation (Mönkkönen and Reunanen, 1999), as had been suggested for forest-breeding birds in different land-use contexts (McGarigal and McComb, 1995; Villard et al., 1999). The 10–30% threshold for birds and mammals is thus not well-substantiated (Andrén, 1999; Mönkkönen and Reunanen, 1999).

4.4. Implementation of the model as an assessment tool

Although we have used the model here in an exploration of theory, the model is amenable to application in a management or assessment context. The model can be, and has been, applied to real species in actual landscapes (King et al., in press). Indeed, the model was originally designed explicitly as an assessment tool (King et al., in press). Model inputs and the data needed to test the model are parameters and variables that can be collected as part of a population assessment, or can be derived from literature on avian demography. Application of the model requires: (1) a raster map of breeding habitat; and (2) values for the parameters in Table 1. Acquiring the habitat map is not trivial, but is straightforward in this modern era of remote sensing and geographical information systems (GIS). Obtaining landscape- and population-specific values for the parameters in Table 1 is admittedly more difficult. Such values may not be immediately available for a particular application, but that situation is by no means unique to the model here. Any age-structured population viability analysis or demographic assessment will require most of the same parameters (e.g. survivorship) and will face the same data limitations. It is important, however, to recognize that these demographic parameters can be, and have been, estimated with the appropriate application of resources (e.g. Nichols et al., 1980; Noon and Biles, 1990). Similarly, the incidence function parameters [Eq. (1), Table 1] can be, and have been, determined for specific landscapes and species (e.g. Robbins et al., 1989; Herkert, 1994). Territory and clutch size are often estimated in the field, and home-range gap-crossing ability can be determined empirically (Grubb and Doherty, 1999).

The model we have used here decomposes the maternity parameter b into a function of landscape pattern. In more traditional avian demography, b is a free parameter which must be specified. Our calculation of b involves an estimate of nesting success for each patch as a function of that patch’s edge-to-area ratio [Eq. (2)]. The functional description of edge-sensitivity in Eq. (2)

is non-traditional, and the parameters for that function (Table 1) will likely not be available a priori for a particular management application. Again, however, they *can* reasonably be obtained for a specific landscape and population. Field surveys would be used to estimate nesting success for individual patches, and GIS analysis would be used to calculate patch edge-to-area ratios. A fit of Eq. (2) to those data would provide estimates of the edge-sensitivity parameters in Table 1. Even data not specifically gathered for that purpose can be used to parameterize Eq. (2), albeit with greater uncertainty; King et al. (in press) parameterized Eq. (2) using data on nesting success from Johnson and Temple (1986).

In summary, application of the model in a management context for specific landscapes and species is beyond the scope of our objectives in this theoretical study. Nevertheless, the model can be applied to specific cases, and thus allows for the future testing and inductive investigation of the theory we have explored here.

Acknowledgements

We thank Sharon Collinge for inviting us to contribute to this special issue on spatial ecology and conservation. K. A. With's research on the conservation applications of neutral landscape models has been supported by the National Science Foundation, most recently through grants DEB-9532079 and DEB-9610159. A. W. King was supported by the Strategic Research and Development Program (SERDP) through US Department of Defense Military Interdepartmental Purchase Requisition Nos. W74RDV73223578 and W74RDV83528676 and the Office of Biological and Environmental Research, US Department of Energy, under contract DE-AC05-96OR22464 with Lockheed Martin Energy Research Corp. We thank R. H. Gardner, Appalachian Environmental Laboratory, University of Maryland, Frostburg for the use of RULE, the FORTRAN program used to generate neutral landscape patterns and to analyze the patch structure of species-defined landscapes. We thank Moric Schwartz and an anonymous reviewer for their comments on the manuscript.

References

Anders, A.D., Dearborn, D.C., Faaborg, J., Thompson III, F.R., 1997. Juvenile survival in a population of Neotropical migrant birds. *Conservation Biology* 11, 698–707.

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., 1999. Habitat fragmentation, the random sample hypothesis and critical thresholds. *Oikos* 84, 306–308.

Askins, R.A., 1995. Hostile landscapes and the decline of migratory birds. *Science* 67, 1956–1957.

Askins, R.A., Lynch, J.F., Greenberg, R., 1990. Population declines in migratory birds in eastern North America. *Current Ornithology* 7, 1–57.

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

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

Dias, P.C., 1996. Sources and sinks in population biology. *Trends in Ecology and Evolution* 11, 326–330.

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

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

Donovan, T.M., Jones, P.W., Annand, E.M., Thompson III, F.R., 1997. Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* 78, 2064–2075.

Faaborg, J., Brittingham, M., Donovan, T., Blake, J., 1995. Habitat fragmentation in the temperate zone. In: Martin, T.E., Finch, D.M. (Eds.), *Ecology and Management of Neotropical Migratory Birds*. Oxford University Press, New York, pp. 357–380.

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

Fahrig, L., 1998. When does fragmentation of breeding habitat affect population survival? *Ecological Modelling* 105, 273–292.

Franklin, I.R., 1980. Evolutionary changes in small populations. In: Soulé, M.E., Wilcox, B.A. (Eds.), *Conservation Biology: An Evolutionary–Ecological Perspective*. Sinauer Associates, Sunderland, Massachusetts, pp. 135–149.

Freemark, K.E., Dunning, J.B., Hejl, S.J., Probst, J.R., 1995. A landscape ecology perspective for research, conservation, and management. In: Martin, T.E., Finch, D.M. (Eds.), *Ecology and Management of Neotropical Migratory Birds*. Oxford University Press, New York, pp. 381–427.

Gardner, R.H., Milne, B.T., Turner, M.G., O'Neill, R.V., 1987. Neutral models for the analysis of broad-scale landscape pattern. *Landscape Ecology* 1, 19–28.

Greenberg, R., 1980. Demographic aspects of long-distance migration. In: Kease, A., Morton, E. (Eds.), *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution and Conservation*, Smithsonian Institution Press, Washington, DC, pp. 493–504.

Grubb Jr, T.C., Doherty Jr., P.F., 1999. On home-range gap-crossing. *Auk* 116, 618–628.

Herkert, J.R., 1994. The effects of habitat fragmentation on mid-western grassland bird communities. *Ecological Applications* 4, 461–471.

Hill, M.F., Caswell, H., 1999. Habitat fragmentation and extinction thresholds on fractal landscapes. *Ecology Letters* 2, 121–127.

Howe, R.W., Davis, G.J., Mosca, V., 1991. The demographic significance of sink populations. *Biological Conservation* 57, 239–255.

Johnson, R.G., Temple, S.A., 1986. Assessing habitat quality for birds nesting in fragmented tallgrass prairie. In: Verner, J., Morrison, M.L., Ralph, C.J. (Eds.), *Modeling Habitat Relationships of Terrestrial Vertebrates*. University of Wisconsin Press, Madison, pp. 245–249.

Karr, J.R., Nichols, J.D., Klimkiewicz, M.K., Brawn, J.D., 1990. Survival rates of birds of tropical and temperate forests: will the dogma survive? *American Naturalist* 136, 277–291.

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

- Lidicker Jr., W.Z., Koenig, W.D., 1996. Responses of terrestrial vertebrates to habitat edges and corridors. In: McCullough, D.R. (Ed.), *Metapopulations and Wildlife Conservation*. Island Press, Washington, DC, pp. 85–109.
- Martin, T.E., Li, P., 1992. Life history traits of open-versus cavity-nesting birds. *Ecology* 73, 579–592.
- McGarigal, K.J., McComb, W.C., 1995. Relationships between landscape structure and breeding birds in the Oregon coast range. *Ecological Monographs* 65, 235–260.
- Mönkkönen, M., Reunanen, P., 1999. On critical thresholds in landscape connectivity: a management perspective. *Oikos* 84, 302–305.
- Morse, D.H., 1989. *American Warblers: An Ecological and Behavioral Perspective*. Harvard University Press, Cambridge, Massachusetts.
- Nichols, J.D., Hensler, G.L., Sykes Jr, P.W., 1980. Demography of the Everglade Kite: implications for population management. *Ecological Modelling* 9, 215–232.
- Noon, B.R., Biles, C.M., 1990. Mathematical demography of spotted owls in the Pacific Northwest. *Journal of Wildlife Management* 54, 18–27.
- Petit, L.J., Petit, D.R., Martin, T.E., 1995. Landscape-level management of migratory birds: looking past the trees to see the forest. *Wildlife Society Bulletin* 23, 420–429.
- Pulliam, H.R., 1988. Sources, sinks, and population regulation. *American Naturalist* 132, 652–661.
- Pulliam, H.R., Danielson, B.J., 1991. Sources, sinks and habitat selection: a landscape perspective on population dynamics. *American Naturalist* 137, S50–S66.
- Ritchie, M., 1997. Populations in a landscape context: sources, sinks, and metapopulations. In: Bissonette, J.A. (Ed.), *Wildlife and Landscape Ecology: Effects of Pattern and Scale*. Springer, New York, pp. 160–184.
- Robbins, C.S., Sauer, J.R., Greenberg, R., Droege, S., 1989a. Population declines in North American birds that migrate to the Neotropics. *Proceedings of the National Academy of Sciences USA* 86, 7658–7662.
- Robbins, C.S., Dawson, D.K., Dowell, B.A., 1989b. Habitat area requirements of breeding forest birds of the middle Atlantic states. *Wildlife Monographs* 103, 1–34.
- Robinson, S.K., Thompson III, F.R., Donovan, T.M., Whitehead, D.R., Faaborg, J., 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267, 1987–1990.
- Rosenberg, K.V., Lowe, J.D., Dhondt, A.A., 1999. Effects of forest fragmentation on breeding tanagers: a continental perspective. *Conservation Biology* 13, 568–583.
- Saupe, D., 1988. Algorithms for random fractals. In: Petigen, H.-O., Saupe, D. (Eds.), *The Science of Fractal Images*. Springer, New York, pp. 71–113.
- Soulé, M.E., 1980. Thresholds for survival: maintaining fitness and evolutionary potential. In: Soulé, M.E., Wilcox, B.A. (Eds.), *Conservation Biology: An Evolutionary-Ecological Perspective*. Sinauer Associates, Sunderland, Massachusetts, pp. 151–170.
- Temple, S.A., Cary, J.R., 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conservation Biology* 2, 340–347.
- Trzcinski, M.K., Fahrig, L., Merriam, G., 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecological Applications* 9, 586–593.
- Van Horn, M.A., Gentry, R.M., Faaborg, J., 1995. Patterns of oven-bird (*Seiurus aurocapillus*) pairing success in Missouri forest tracts. *Auk* 112, 98–106.
- Villard, M.-A., Trzcinski, M.K., Merriam, G., 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conservation Biology* 13, 774–783.
- Wiens, J.A., 1989. Spatial scaling in ecology. *Functional Ecology* 3, 385–397.
- With, K.A., 1997. The application of neutral landscape models in conservation biology. *Conservation Biology* 11, 1069–1080.
- With, K.A., 1999. Is landscape connectivity necessary and sufficient for wildlife management?. In: Rochelle, J., Lehmann, L.A., Wisniewski, J. (Eds.), *Forest Fragmentation: Wildlife and Management Implications*. Brill, Leiden, The Netherlands, pp. 97–115.
- With, K.A., Crist, T.O., 1995. Critical thresholds in species' responses to landscape structure. *Ecology* 76, 2446–2459.
- With, K.A., King, A.W., 1997. The use and misuse of neutral landscape models in ecology. *Oikos* 79, 219–229.
- With, K.A., King, A.W., 1999a. Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. *Landscape Ecology* 14, 73–82.
- With, K.A., King, A.W., 1999b. Extinction thresholds for species in fractal landscapes. *Conservation Biology* 13, 314–326.