

# How much habitat is enough?

L. Fahrig\*

*Ottawa-Carleton Institute of Biology, Carleton University, Ottawa, ON, Canada, K1 S 5B6*

## Abstract

If conservation efforts are to be successful, it is critical that we understand the relationship between habitat loss and the probability of population extinction. Available evidence suggests a threshold amount of habitat loss at which the probability of population extinction increases from near-zero to near-one following a small additional loss of habitat. The main factors thought to determine this extinction threshold are reproductive rate of the organism, rate of emigration of the organism from habitat, habitat pattern in the landscape (fragmentation), and matrix quality (survival rate of the organism in non-habitat areas). Effective conservation measures require knowledge not only of what factors determine the threshold, but also the relative magnitudes of their effects. Therefore, the purpose of this study was to determine the relative effects of these four factors on the extinction threshold, using a spatially-explicit simulation model. Reproductive rate had the largest potential effect on the extinction threshold. The rate of emigration from habitat also had a very strong predicted effect on the extinction threshold; the higher the rate of emigration, the more habitat was needed for persistence. Matrix quality had a moderate effect, and habitat pattern had a very small predicted effect. The simulations predicted that under certain circumstances up to 58% less habitat is required for population persistence, if a matrix of very low quality is converted to a matrix of very high quality. Matrix quality can be improved by maintaining heterogeneous landscapes with a diversity of vegetated features, and by reducing factors causing direct mortality of dispersers such as road traffic and pesticides. In summary, the simulations suggest that (i) the first priority for conservation should be habitat preservation and restoration, (ii) information on movement rates of organisms is critical for predicting extinction thresholds and (iii) conservation strategies should consider the quality of the whole landscape, including the matrix. © 2001 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

Habitat loss is the largest factor contributing to the current global species extinction event (Groombridge, 1992; Bibby, 1995; Ehrlich, 1995; Thomas and Morris, 1995). The recent increase in habitat loss is due to growth of the human population leading to expansion of human activities into formerly natural areas (Sisk et al., 1994). At the same time, there has been a growing interest in conservation of species and ecosystems (Gore, 1992). Given the pressures on habitat, for conservation efforts to be successful, the most important question that must be answered is: how much habitat must be conserved to ensure persistence of populations?

In the conservation biology literature, this question is often addressed at the patch scale, i.e. what is the mini-

mum (or ‘critical’) patch size necessary to maintain a viable population (e.g. Beier, 1993; Wenny et al., 1993; Howells and Edwards-Jones, 1997; Marshall and Edwards-Jones, 1998)? Modelling studies suggest that the critical patch size depends on a combination of reproductive rate of the organism, rate of emigration from the patch, population genetics of the organism, and stochastic factors such as disturbances (Soulé and Simberloff, 1986; Lande, 1987; Schneider and Yodzis, 1994; Wissel and Zschke, 1994; Bevers and Flather, 1999).

In the past decade it has become apparent that patch size alone is not sufficient for predicting population persistence; patch context, i.e. the nature of the landscape surrounding a patch, is also important (Dingle, 1991; Merriam, 1991; Dunning et al., 1992; Hansson, 1992; Wiens, 1994; Hinsley et al., 1995; Sjögren-Gulve and Ray, 1996; Gustafson and Gardner, 1996; Watts, 1996; Andrén, 1997; Jonsen and Fahrig, 1997; Sisk et al., 1997; Pope et al., 2000). Patch context determines

\* Tel.: +44-613-5202600×3856.

E-mail address: lfahrig@ccs.carleton.ca (L. Fahrig).

the rate of immigration into a patch through (i) the amount of occupied habitat in the area around the patch that is within the dispersal range of the organism and (ii) the quality of the intervening nonhabitat area ('matrix') for survival of dispersing individuals. To incorporate the effects of landscape structure on population persistence, the question 'how much habitat is enough?' has, therefore, also been addressed at the multiple-patch or landscape scale (Kareiva and Wennergren, 1995; Bascompte and Solé, 1996; Hanski et al., 1996; Hill and Caswell, 1999; With and King, 1999). These studies typically predict an 'extinction threshold', or a minimum amount of habitat below which the equilibrium population size is zero. In a stochastic model, the threshold can be illustrated as the minimum amount of habitat below which population extinction is inevitable over some finite time (Fig. 1; see Fahrig, in press). Previous studies suggest that the main factors determining the extinction threshold are reproductive rate of the organism, rate of emigration of the organism from patches, habitat pattern in the landscape (habitat fragmentation), and matrix quality (i.e. survival rate of the organism in non-habitat areas).

Effective conservation measures require knowledge of not only what factors affect population persistence, but also the magnitudes of their effects. For example, if habitat pattern has a large effect on the extinction threshold, then attention to habitat pattern (e.g. in forestry cutting plans) is important for conservation. However, if its effect is small then it may be much more effective to focus conservation strategies in other areas (e.g. improving matrix quality). The purpose of this study was to determine the relative effects of reproductive rate, dispersal rate, habitat pattern, and matrix quality on the extinction threshold, at a landscape scale.

## 2. Methods

### 2.1. The model

I used a general, stochastic, individual-based, spatially-explicit model of population dynamics and movement of

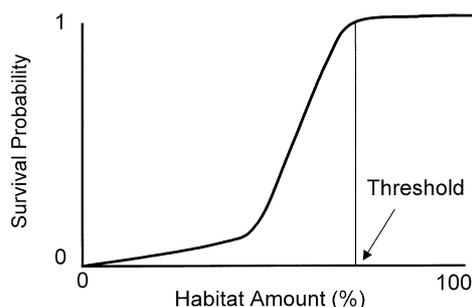


Fig. 1. Illustration of extinction threshold. When habitat amount is reduced to below the threshold the probability of population survival drops precipitously.

a hypothetical organism in a hypothetical landscape. The model is a slightly modified version of the model described in Fahrig (1997, 1998); the only difference is that in the current version, reproduction is modelled using a binomial probability distribution (see below).

The population is simulated on a grid of  $30 \times 30$  cells. In the current runs, the maximum capacity of each cell on the grid is 10 individuals. When the cell population rises above 10 individuals, excess individuals are killed off randomly. This represents the only density-dependent component in the model. Each cell is either 'habitat' or 'matrix'. The main difference between habitat and matrix cells is that the organism can breed only in habitat cells. Depending on the parameter values chosen, individuals in habitat and matrix cells can also have different survival and movement rates (below). The amount of habitat and the pattern of habitat (habitat fragmentation) are specified at the beginning of each simulation run (see Fahrig, 1997 and 1998 for fragmentation algorithm).

One time step in the model equals the time to reproductive maturity for the organism. In each time step, each individual has a chance of reproducing (if in a habitat cell), dying, and moving. The order of these three possibilities is random per individual per time step. Reproduction is determined by selecting a random value for each reproducing individual in each time step, from a binomial distribution, where the mean is the expected number of offspring reaching reproductive age (i.e. the next time step), per time step, per reproducing individual. In the current simulations, the probability of mortality in breeding habitat cells was held constant among all runs. Therefore, two simulation runs that varied only in the reproductive parameter (expected value of the binomial) represented either (i) two species with different intrinsic population growth rates or (ii) the same species in two landscapes containing different qualities of breeding habitat (resulting in different growth rates). The mortality probability is assumed to be higher in matrix than habitat.

In each time step, each individual may or may not move out of its current grid cell. The probability of movement depends on whether the individual is in a matrix cell or a habitat cell. Individuals in matrix cells always move, since they are assumed to be trying to reach habitat cells. Movement occurs as a random walk. Each time step a random angle and random distance, up to a maximum distance (four cells in the current simulations), is chosen for each moving individual.

### 2.2. Simulation experiment

The goal of the simulation experiment was to determine the relative importance of four predictor variables — reproductive rate, dispersal rate, matrix quality, and habitat pattern — on the extinction threshold. The four

predictor variables were labelled GROWTH (expected number of offspring reaching reproductive age, per reproducing individual, per time step), MOVEHAB (probability of an individual in a habitat cell leaving that cell, per time step; recall that all individuals in matrix cells move each time step), MATQUAL (probability of an individual in a matrix cell surviving to the next time step), and FRAG (degree to which the habitat is broken apart into patches).

The simulations consisted of a factorial experiment with three levels of each of the four predictor variables, and 21 levels of habitat amount, i.e. proportion of the grid in habitat (called COVER). The COVER levels were 0.01, 0.05, 0.1, 0.15, 0.2...0.8, 0.85, 0.9, 0.95, 0.99. This allowed me to determine extinction thresholds to within 5%. The three levels for each of the predictor variables were: GROWTH: 0.07, 0.1, 0.5; MOVEHAB: 0.01, 0.1, 1; MATQUAL: 0.05, 0.5, 0.95; FRAG: 0.01, 0.1, 0.99. For MOVEHAB, MATQUAL, AND FRAG, the possible values ranged from 0 to 1 and the three chosen values covered most of this range. For GROWTH, the lower level was the minimum value that resulted in at least some probability of population survival for some parameter combinations. Beyond the upper value of 0.5, population survival was ensured, no matter what how little habitat there was (COVER as low as 0.01). All other parameters in the model were held constant at values that were found in previous simulations (Fahrig, 1998) to maximize the effect of habitat fragmentation on population persistence.

Each simulation run began with 500 individuals randomly distributed over the grid, and each run ran for 500 time steps. By distributing the initial 500 individuals over the whole grid (not just the habitat cells), I ensured that the initial density of individuals in breeding habitat was independent of amount of habitat on the landscape. The output from each run was recorded as zero if the population went extinct within 500 time steps (i.e. no individuals remaining) and one if it persisted for the 500 steps. Five hundred steps was judged a sufficient length of time to determine persistence because preliminary runs indicated that populations that persisted for 500 time steps persisted for at least 2000 time steps. Due to the stochastic nature of the model, small populations inevitably went extinct within 500 time steps.

For each combination of the predictor variable values, at each COVER level, 20 replicate simulation runs were conducted. The proportion of these 20 runs for which the population persisted was recorded as the population survival probability, for a population with that set of predictor values at that COVER level. Three replicates of the whole experiment were conducted. Therefore, the total number of runs was:  $[3(\text{GROWTH values}) \times 3(\text{MOVEHAB values}) \times 3(\text{MATQUAL values}) \times 3(\text{FRAG values}) \times 21(\text{COVER values}) \times 20(\text{replicate runs}) \times 3(\text{replicate experiments})] = 102\ 060$

runs. The total simulation time was about 8 months on a Sparc 20 workstation (300 MHz CPU).

### 2.3. Analysis of simulation output

For each of the 81 predictor variable combinations, I plotted the relationship between habitat amount ( $x$ -axis) and probability of population survival ( $y$ -axis). From these plots I determined the minimum habitat amount for which the estimated population survival probability was one (i.e. for which 20 of 20 runs had populations that persisted for the full 500 time steps). This was my estimate of the extinction threshold for that set of predictor variable values (Fig. 1). Because of the three replicate experiments, I had three estimates of the threshold value for each predictor variable combination, giving a total data set of  $81 \times 3 = 243$  threshold values for the statistical analysis.

I analyzed the threshold values to determine the relative effects of the four predictor variables (GROWTH, MOVEHAB, MATQUAL, FRAG) on the extinction threshold. I knew a priori that GROWTH has the largest potential effect on the threshold. As stated above, preliminary runs showed that GROWTH values below 0.07 resulted in population extinction, no matter how much habitat was available (i.e. threshold  $> 0.99$ ), and GROWTH values above 0.5 resulted in population persistence, no matter how little habitat there was (i.e. threshold  $< 0.01$ ). However, I included GROWTH along with the other variables in the analysis, to determine interaction effects between GROWTH and the other parameters, on the extinction threshold. To determine the relative importance of the other three variables (MOVEHAB, MATQUAL, FRAG) and to determine interaction effects among the four variables, I conducted a four-way ANOVA on the habitat amount threshold. I included all possible two-way interaction terms in the model.

## 3. Results

All the simulated populations showed very distinct extinction thresholds; Fig. 2A shows a typical plot. There was very little variation in the extinction threshold among replicate experiments at the same predictor variable levels. Thresholds varied somewhat in steepness (e.g. compare Figs. 2A and B). Threshold values ranged over the whole span of habitat amount, depending on the parameter values (e.g. Fig. 3A).

Apart from GROWTH, which was known a priori to be the most important variable (see above), the order of importance of the other three variables was: MOVEHAB, MATQUAL, and FRAG, where FRAG had only a small effect on the threshold location (Table 1). The mean, minimum, and maximum effects of shifting

Table 1

ANOVA of effects of four predictor variables — GROWTH, MOVEHAB, MATQUAL and FRAG — and their two-way interactions, on the extinction threshold<sup>a</sup>

	d.f.	Type III SS	<i>F</i>	<i>P</i>
FRAG	2	0.06940247	10.34	0.0001
MATQUAL	2	2.70846173	403.61	0.0001
MOVEHAB	2	16.22055556	2417.15	0.0001
GROWTH	2	5.08483210	757.73	0.0001
FRAG*MATQUAL	4	0.02264691	1.69	0.1541
FRAG*MOVEHAB	4	0.01841975	1.37	0.2446
FRAG*GROWTH	4	0.00211358	0.16	0.9594
MATQUAL*MOVEHAB	4	1.17276790	87.38	0.0001
MATQUAL*GROWTH	4	0.28338025	21.11	0.0001
MOVEHAB*GROWTH	4	2.03723457	151.79	0.0001

<sup>a</sup> Results are based on a factorial experiment with each predictor variable at three levels and each parameter combination replicated three times. Model  $R^2 = 0.975$ ,  $n = 243$ .

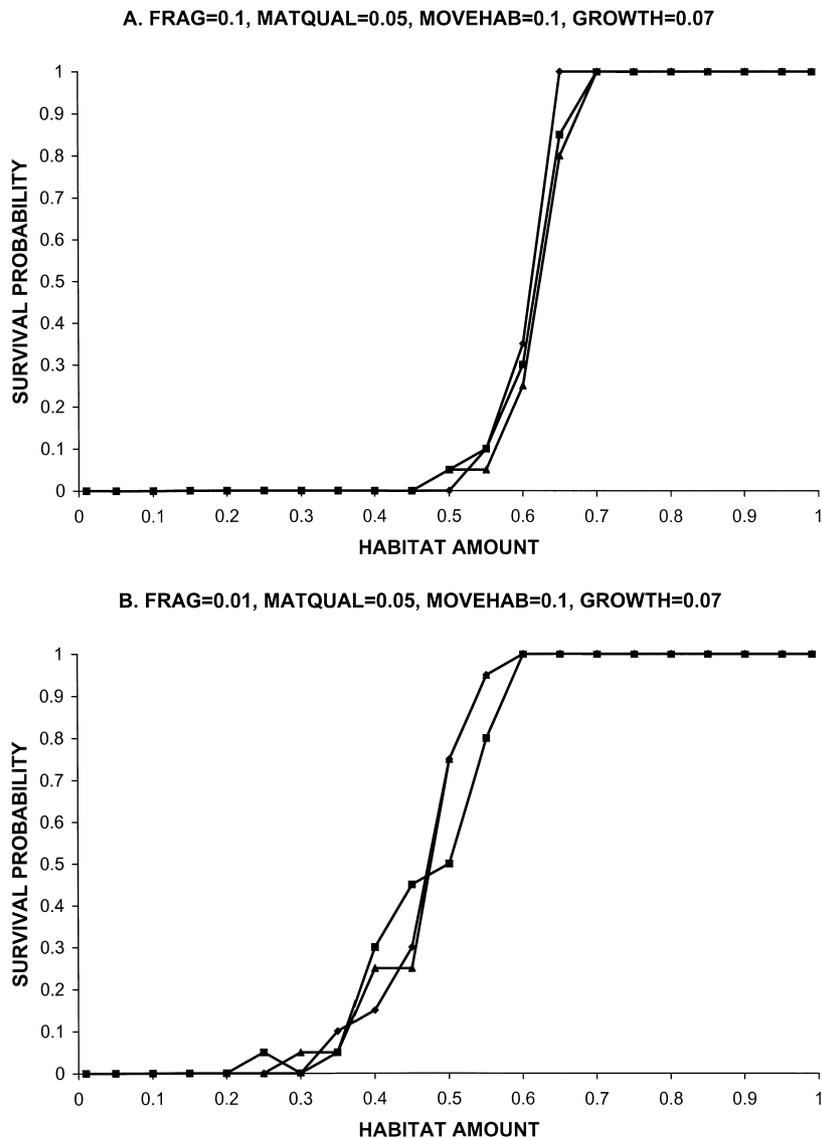


Fig. 2. Population survival probability versus habitat amount for two of the 81 parameter combinations used in the simulation experiment.

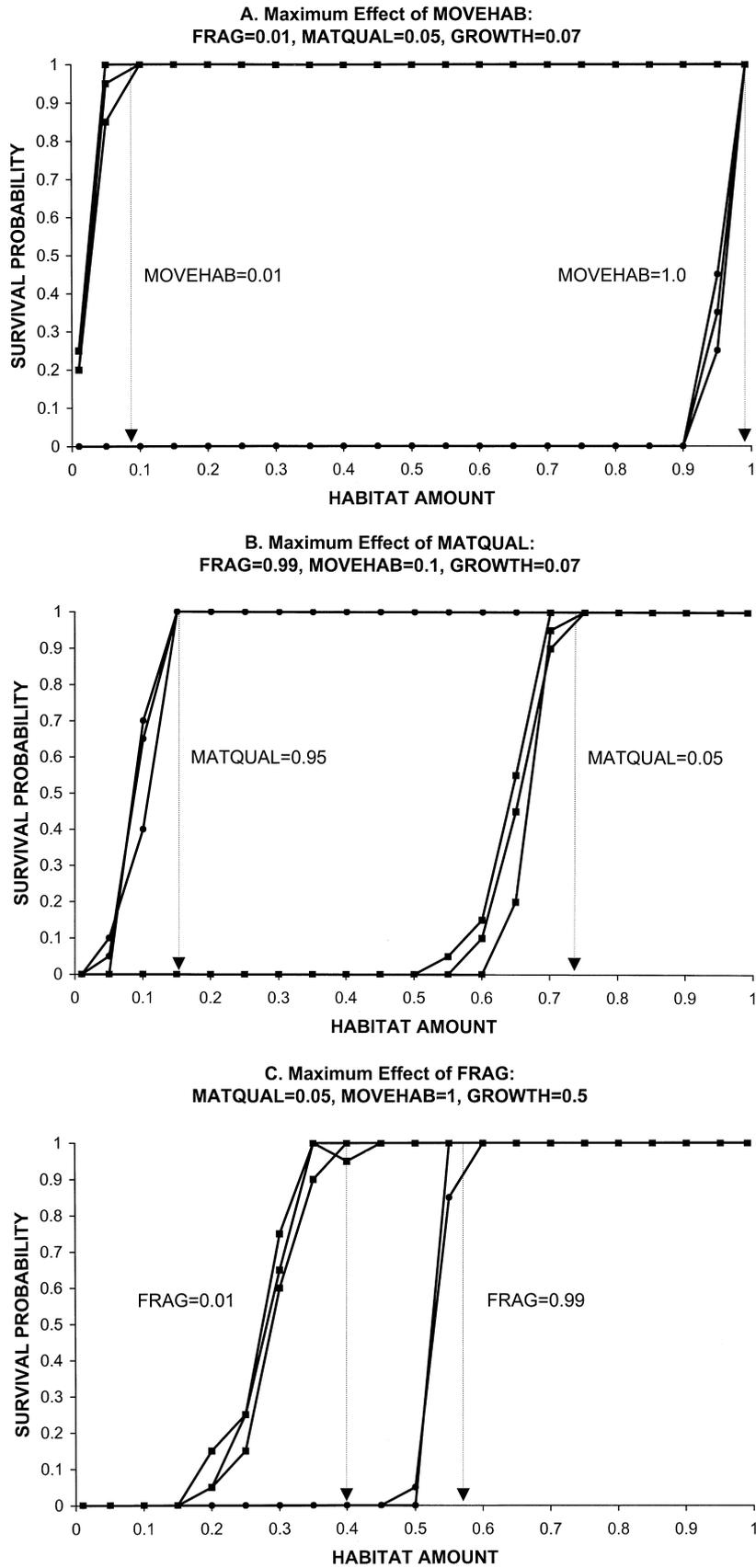


Fig. 3. Maximum effect on the extinction threshold, of shifting from highest to lowest levels of the predictor variables.

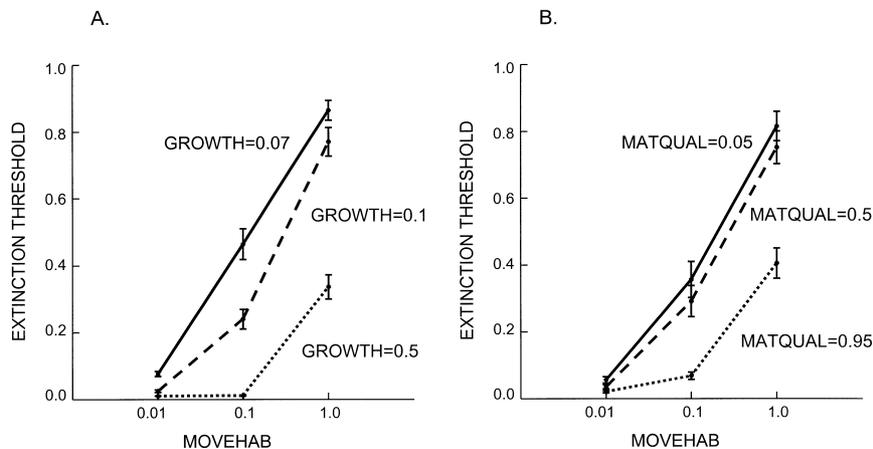


Fig. 4. Interaction effects between MOVEHAB and (A) GROWTH and (B) MATQUAL on the extinction threshold.

Table 2

Mean, minimum, and maximum shifts in the extinction threshold caused by moving from the lowest to the highest value of the predictor variables

Predictor variable	Mean shift	Minimum shift	Maximum shift
MOVEHAB	0.62	0.013	0.91
MATQUAL	0.25	0.0	0.58
FRAG	0.06	0.0	0.17

from highest to lowest levels of the predictor variables are shown in Table 2; the maximum shifts are illustrated in Fig. 3. There were significant interaction effects of MOVEHAB\*GROWTH, and MOVEHAB\*MATQUAL (see Fig. 4) and GROWTH\*MATQUAL on threshold location (Table 1).

#### 4. Discussion

An important prediction from these simulations is that there is no common threshold value across species (see also Lande, 1987; With and King, 1999). Thresholds ranged from less than 1% habitat to over 99% habitat, depending on the parameter values. Conservation activists often express frustration that scientists will not provide them with a single target for percent habitat protection (J. Langlois, Canadian Parks and Wilderness Society, pers. comm.). The results of these simulations suggest that such single targets are unrealistic. The minimum amount of habitat that needs to be preserved to allow persistence of all species in a region varies among regions, because the reproductive and dispersal attributes of the most sensitive species vary among regions. Species with low reproductive potential and a risky dispersal strategy (high emigration rate and low survival in matrix) require very large amounts of habitat for persistence. The lack of a single habitat target is generally confirmed in studies of species richness in

relation to habitat area, in which estimates of percent habitat conservation required for persistence of all species in an area range widely, from 20 to 75% (e.g. Margules and Nicholls, 1988; Soulé and Sanjayan, 1988; Noss, 1993; Saetersdal et al., 1993).

Almost all of the 243 curves of survival versus habitat amount showed a very precipitous drop in survival probability at the threshold (see also Schneider and Yodzis, 1994). This implies that predicting extinction thresholds before they are crossed is extremely important for conservation. In addition, species with long generation times will show a delayed response to habitat loss (Tilman et al., 1994; Eriksson and Kiviniemi, 1999), which will delay detection of population decline. Given this and the variability in ecological data, we are not likely to detect a problem with a population until well after we have reduced the habitat to below its threshold. Caughley (1994) suggests that conservation biologists should focus on the causes of population decline rather than the implications of small population size. I agree, but my results further suggest we need to predict extinction thresholds for species before declines are observed, in order to avoid population decline and extinction due to habitat loss.

Testing empirically for extinction thresholds is difficult. By definition, one would need to observe long-term population responses to habitat loss. However, in many cases habitat destruction has occurred only recently, and/or is still ongoing. Empirical evidence is therefore limited, and the definition of threshold used is somewhat different from that used in the modelling studies. For example, Jansson and Angelstam (1999) found thresholds in patch occupancy by the long-tailed tit (*Aegithalos caudatus*) as a function of habitat amount in the surrounding landscapes. Flather et al. (in preparation) plotted the probability that various species of forest breeding birds were found in landscapes delineated by breeding bird survey routes in the eastern US, versus the amount of forest in the landscapes. In several plots

they found a significant change in slope at a ‘threshold’ habitat amount. Above the threshold the probability of occupancy was fairly constant, while below the threshold the probability of occupancy declined precipitously with decreasing habitat amount.

The model results reported here predict the relative importance of the variables studied on the extinction threshold, but do not predict actual threshold values for specific real species. Predicting an extinction threshold for a particular species would require a model that is tailored to that species. Several factors not included in the present model could affect the location of the extinction threshold. For example, species with density-dependent dispersal or species that can detect breeding habitat from a distance should show lower extinction thresholds than species without these attributes.

Apart from reproductive rate, the results predict that the most important factor determining the location of the extinction threshold is the rate of emigration. Changing emigration rate from very low (0.01) to very high (1) resulted in a mean shift in the habitat threshold from 4 to 66% habitat (a difference of 62%). This indicates that, to predict the extinction threshold for a particular species, information on rate of emigration from habitat is critical. Emigration is unknown for most species, partly because it is difficult to separate from mortality.

The simulations predicted that the higher the emigration rate, the more habitat is required for regional population survival. This may seem counter-intuitive to many; in the metapopulation paradigm, dispersal is generally viewed as having a positive effect on population survival, through recolonization of local extinctions (e.g. Hanski, 1994). The reason for this apparent contradiction lies in the use of the term ‘dispersal ability’ in the metapopulation literature. Dispersal ability is assumed to determine the probability of colonization, and is considered to be a species trait. However, the probability of colonization does not depend simply on innate species characteristics such as the organism’s tendency to leave its current location, and its inherent movement rate. Dispersal success also depends on attributes of the landscape that may impede movement or increase dispersal mortality. Therefore, I argue that the concept of ‘dispersal ability’ is only useful when the organism is observed in its pristine environment. An organism with good dispersal ability in its pristine environment may have very poor dispersal ability in a human-altered landscape.

In fact, it is known that the optimal emigration rate increases with increasing survival rate of dispersing individuals (Comins et al., 1980; Levin et al., 1984; Klinkhamer et al., 1987). Organisms that evolved in landscapes with high habitat cover may therefore have evolved high emigration rates because of low dispersal mortality. When habitat is removed, the high emigration rate of these species greatly increases the overall

population mortality rate, by placing many organisms in perilous matrix habitat. In this case the mortality incurred during dispersal outweighs the potential positive effect of dispersal on metapopulation dynamics. This argument is supported in a study by Gibbs (1998), who compared the distributions of five woodland amphibians along a gradient of decreasing forest cover. Gibbs found that species with the highest mobility were most vulnerable to forest loss. In landscapes with low forest cover, these species presumably incur very high dispersal mortality, resulting in a situation where the total population mortality outweighs reproduction. As stated by Gibbs, these patterns are in contrast to the widely held notion that populations of the best dispersers are those most tolerant of habitat loss. Again, the apparent contradiction is due to the fact that dispersal ability changes with changing landscape structure. The interaction effect between emigration rate and matrix quality in the simulation experiment (Fig. 4B) also illustrates the large effect of dispersal mortality on population persistence. When the survival rate of dispersers is high (MATQUAL=0.95), the extinction threshold drops significantly, even for high emigration rates.

In the model, increasing habitat fragmentation causes an increase in the amount of edge in the landscape, which increases the probability of individuals leaving the breeding habitat and entering the matrix. This decreases the reproductive rate and increases the mortality rate of the population, because a smaller proportion of the population remains in the breeding habitat and a larger proportion enters matrix, where the mortality rate is higher. Although, on average, increasing FRAG resulted in an increase in the extinction threshold (more habitat needed for persistence), the magnitude of this effect was small. A shift from extremely high fragmentation to extremely low fragmentation resulted in only a 6% decrease in the mean extinction threshold. This small effect of fragmentation is most likely not a result of the particular parameter values selected in these simulations. The other predictor variables in the simulation experiment were varied over very wide ranges, and the parameters that were held constant were held at levels known a priori to maximize the effect of habitat fragmentation on population persistence (Fahrig, 1998).

The small predicted effect of fragmentation on the extinction threshold is supported by simulation studies (Fahrig, 1997, Flather and Bevers, pers. commun. [in preparation]) and empirical studies (McGarigal and McComb, 1995; Meyer et al., 1998; Trzcinski et al., 1999; Flather, pers. commun. [et al., in preparation]), which found that the effects of habitat loss far outweigh the effects of habitat pattern (fragmentation) on population density and survival. Also, in my previous simulations (Fahrig, 1998) I found that fragmentation affected population survival under only a narrow range of conditions. However, some metapopulation-type

modelling studies (Hill and Caswell, 1999; With and King, 1999) predict a much larger effect of habitat fragmentation on the extinction threshold. These models do not include dispersal mortality. Elsewhere (Fahrig, in press) I hypothesize that when dispersal mortality is incorporated in a model (current model; also Flather and Bevers, pers. commun. [in preparation]), it imposes a constraint on the potential for habitat fragmentation to mitigate effects of habitat loss.

It has been suggested (Andr n, 1994; Fahrig, 1998) that there is a threshold value of habitat amount, at about 20% habitat, below which the effects of habitat fragmentation on population persistence may become evident. It is important not to confuse this 20% fragmentation ‘threshold’ with the extinction threshold examined in this paper. The extinction threshold is the minimum amount of habitat below which the population goes extinct, whereas the habitat fragmentation threshold is the amount of habitat below which habitat fragmentation (pattern) may affect population persistence. While the former can occur at any value of habitat amount (see above), the latter appears to occur at about 20% habitat.

Although the reduction in fragmentation has only a very small effect on the extinction threshold, there does appear to be an effect of fragmentation on the steepness of the curve (compare Figs. 2A and B), where increasing fragmentation increases the steepness. This may explain why Beier (1993) predicted a more gradual shift in extinction probability with increasing habitat amount. Beier simulated population survival on a single, non-fragmented patch. If increasing fragmentation does increase the steepness of the curve then the effects of habitat loss should be more easily detected when the habitat is more fragmented.

Given the relentlessness of habitat loss, do the results suggest any practical ways in which the negative effects of habitat loss on population persistence can be ameliorated or slowed down? At first glance, the simulations appear quite hopeful in this regard. By varying the parameter values I was able to move the extinction threshold over a range of 1 to 99%. If, through conservation measures, we can change these parameters for a real species of concern, then we should be able to reduce the extinction threshold for this population, thus reducing the amount of habitat required for its persistence. However, the different factors differed greatly in the strength of their predicted effects on the threshold (Table 1). For example, the very small effect of fragmentation suggests that we cannot significantly reduce the threshold by adjusting habitat pattern (see also Fahrig, 1997). Adjustments in emigration rate could potentially produce a large effect on the threshold. However, this is not a realistic option since, in general, we can have very little effect on emigration rates of

organisms. It may be possible to improve the reproductive rates of targeted organisms by measures such as food supplementation, or provision of artificial nest sites. If the species most vulnerable to habitat loss (with the highest thresholds) can be identified and targeted with such measures, the extinction threshold for the region may be lowered.

The simulations suggest that the most promising general approach (i.e. not targeted to specific species) to reducing extinction thresholds is improvement in matrix quality, i.e. implementation of measures that improve survival rate of dispersers through matrix. This can be accomplished through maintenance of a diverse landscape structure (Halley et al., 1996; Law and Dickman, 1998), particularly by including vegetated features such as fencerows. These features increase the survival of dispersers by providing a moderated microclimate, food sources for some species, and shelter from predators (Wegner and Merriam, 1979; Fahrig and Merriam, 1985; Johnson and Adkisson, 1985; Merriam and Lanoue, 1990; Bennett et al., 1994). Dispersal mortality can also be directly reduced by the reduction of pesticide use (Halley et al., 1996; Dyer and Landis, 1997; Maurer and Holt, 1999), and reductions in road number and traffic volume (Fahrig et al., 1995; Forman and Alexander, 1998).

In summary, the simulations suggest that (i) the first priority for conservation must be habitat preservation and restoration, (ii) information on movement rates of organisms is critical for predicting extinction thresholds, and (iii) conservation strategies should consider the quality of the whole landscape, including the matrix. Habitat loss typically occurs continuously, in small increments. Intuitively, each additional hectare of forest cut, wetland drained, or beach front developed would seem to increase extinction probabilities by only a tiny amount. However, if there is a threshold in the extinction–habitat relationship, then even a small additional loss of habitat near the threshold will have a large impact on survival probability. If so, to avoid extinctions we must predict the location of the threshold, so that habitat loss can be halted before the threshold is approached.

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