When does fragmentation of breeding habitat affect population survival?

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Abstract

The goal of this study was to delineate the circumstances in which fragmentation of breeding habitat affects population survival. Fragmentation is defined (literally) as the breaking apart of habitat; note fragmentation does not imply loss of habitat. I developed a spatially explicit simulation model in which I varied the spatial pattern of breeding habitat in the landscape from contagious to fragmented, while also varying a disturbance regime, breeding habitat permanence, and the life history and movement attributes of organisms living in the landscape. The simulation results suggest that fragmentation of breeding habitat affects population survival only under the following relatively narrow set of conditions: (1) the average between-generation movement distance of the organism is about 1–3 times the expected nearest distance between breeding sites; (2) the breeding habitat of the organism covers less than 20% of the landscape; (3) the habitat is not ephemeral; (4) the organism has high breeding site fidelity; and (5) the mortality rate in the non-breeding habitat areas is much higher than the mortality rate in breeding habitat areas. Note that all of these conditions must hold for there to be an effect of breeding habitat fragmentation on population survival. These results suggest that spatially explicit simulation modelling of population dynamics is only necessary under a relatively narrow range of conditions. © 1998 Elsevier Science B.V.

Keywords: Spatially explicit modelling; Habitat fragmentation; Habitat loss

1. Introduction

Recently there has been a growing trend toward development of detailed models of species in landscapes, that can incorporate effects of landscape spatial pattern on population dynamics (Dunning et al., 1995; Holt et al., 1995). Such spatially explicit models are becoming particularly common in applied studies for predicting effects of landscape alteration on population survival (e.g. Murphy and Noon, 1992; Pulliam et al., 1992). Part of the reason for this trend is that researchers have found that fragmentation of habitat can
have significant effects on the dynamics of resident populations, independent of the amount or quality of the habitat (reviews in Kareiva, 1990; Andréén, 1994; Fahrig and Merriam, 1994). This has led to the expectation that habitat fragmentation affects population dynamics and therefore that any model that is not spatially explicit is less likely to produce realistic or meaningful results than a spatially explicit one (Wiens et al., 1993; Fahrig and Merriam, 1994). Note that fragmentation is defined here as the breaking apart of habitat and does not imply loss of habitat.

The term ‘spatially explicit population model’ (SEPM) has been used for two qualitatively different kinds of modelling. The first includes the large and burgeoning set of population-habitat models based on GIS (geographical information system) technology, in which spatially explicit habitat information is used to study the relationships between a species and a landscape (e.g. Coulson, 1992; Schulz and Joyce, 1992; Buckland and Elston, 1993). I refer to these as ‘spatially explicit habitat models’. For example, Schulz and Joyce (1992) used spatially explicit habitat information to determine the number of marten home ranges in a landscape. Hansen et al. (1993) used spatially explicit habitat information to relate bird species presence to land use and changes in land use in western Oregon. In contrast, the second type of spatially explicit population models explicitly incorporate the spatial dynamics of populations, through movement of organisms in a landscape. The relative locations of individuals and/or populations affect the probability of movement of individuals or groups of individuals between points on the landscape. The effects of this movement on the local and/or regional populations are monitored over time. In this paper, the latter type of SEPM is dealt with.

Although incorporation of spatial detail in models of population dynamics can improve prediction in some cases, it does not necessarily follow that spatially explicit modelling is required in all cases (e.g. cabbage butterflies, Fahrig and Paloheimo, 1988a). It is important to determine the circumstances under which spatially explicit modelling is not necessary, for several reasons. First, building a spatially explicit model is more time- and money-consuming than building a non-spatial model (Turner et al., 1995). Second, if landscape spatial pattern has a large effect on population dynamics, we may resort to making a different spatially explicit model for every species of interest in every landscape of interest. This approach will lead to a proliferation of detailed studies with little basis for generalization among them (Levin, 1992), at least until there is a large set of such models for comparison (Dunning et al., 1995). Finally, from a management standpoint, the circumstances under which spatially explicit modelling is not necessary are the same circumstances in which we can not influence population dynamics (e.g. of endangered species) only by adjusting the spatial pattern of habitat on the landscape.

The goal of this study was to take the first step in delineation of the circumstance in which landscape spatial pattern affects population survival. If we begin with the simplifying assumption that the only factor determining spatial pattern of a landscape is the degree of fragmentation of breeding habitat, then this problem simplifies to the question: under what conditions does breeding habitat fragmentation affect population survival? It is important to note that this is only the first step in the overall problem because other aspects of landscape pattern that may affect survival are: (1) the spatial structure of the non-breeding habitat (also termed ‘matrix’ habitat) (Fahrig and Merriam, 1994); and (2) effects of landscape spatial pattern on important interacting species such as predators (Kareiva, 1987). In the present analysis I assume homogeneity of the matrix habitat and I ignore any possible effects of landscape pattern on species interactions. The goal is then to delineate the circumstances in which fragmentation of breeding habitat affects population survival, from those in which fragmentation does not affect survival. I used a general spatially explicit model of population dynamics to delineate these circumstances.
2. Methods

2.1. Overview

I developed a spatially explicit simulation model in which the spatial pattern of the landscape can be varied from clumped to fragmented by varying a single parameter (FRAG). The model includes additional parameters that determine the spatio-temporal structure of the landscape (including a disturbance regime), as well as parameters that determine the life history and movement attributes of a hypothetical organism living in the landscape.

Because of the large number of parameters in the model, it was not possible to conduct a complete factorial experiment (Fahrig, 1991). I therefore took a two-stage approach to the experimental design. An initial set of exploratory simulations was conducted to identify a set of parameter values for which variation of breeding habitat fragmentation (FRAG) had a large effect on population survival. This set of parameter values was then used as the default for the second stage. In the second stage I conducted a separate set of simulations for each parameter of interest, in which I varied that parameter in combination with FRAG to determine how changes in the parameter of interest affect the strength of the relationship between population survival and FRAG.

2.2. The model

The model is a stochastic, individual-based simulation model. Space is represented in a two-di-

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Default Value (from Stage I)</th>
<th>Range in Stage II</th>
</tr>
</thead>
<tbody>
<tr>
<td>Breeding habitat fragmentation (FRAG)</td>
<td>NA</td>
<td>0.0–1.0</td>
</tr>
<tr>
<td>Proportion of landscape in breeding habitat (COVER)</td>
<td>0.1</td>
<td>0.02–0.9</td>
</tr>
<tr>
<td>Breeding habitat permanence (PERM)</td>
<td>Permanent</td>
<td>Permanently/ephemeral</td>
</tr>
<tr>
<td>Disturbance probability (cell/step) (DPROB)</td>
<td>0.05</td>
<td>0.0–1.0</td>
</tr>
<tr>
<td>Disturbance mortality probability (DMORT)</td>
<td>0.1</td>
<td>0.0–0.9</td>
</tr>
<tr>
<td>Disturbance pattern (DCLUMP)</td>
<td>1.0 (dispersed)</td>
<td>0.0–1.0 (clumped-dispersed)</td>
</tr>
<tr>
<td>Disturbance type (DTYPE)</td>
<td>General (occurs in both breeding and non-breeding habitat)</td>
<td>General or specific to breeding habitat</td>
</tr>
<tr>
<td>Offspring per reproduction (OFFSP)</td>
<td>1</td>
<td>1–10</td>
</tr>
<tr>
<td>Maximum cell occupancy (MAXOCC)</td>
<td>10 individuals</td>
<td>1–10 individuals</td>
</tr>
<tr>
<td>Mortality probability in non-breeding habitat (NONMORT)</td>
<td>0.5</td>
<td>0.0–0.8</td>
</tr>
<tr>
<td>Movement probability in breeding habitat (MOVE)</td>
<td>0.5</td>
<td>0.0–1.0</td>
</tr>
<tr>
<td>Maximum movement distance (MAXDIST)</td>
<td>4 cells</td>
<td>1–10 cells</td>
</tr>
</tbody>
</table>

The breeding habitat fragmentation parameter (FRAG) was varied in all simulation experiments (therefore no default value). All other parameters were varied, each in a separate set of runs, in combination with FRAG (see Section 2).
The simulation model is based on a two-dimensional rectangular grid of ‘cells’. There are two kinds of grid cells: breeding habitat and non-breeding habitat. Reproduction can occur only in breeding habitat. Individuals may die, reproduce, and/or move within each time step; the order of these events is randomized for each individual in each time step. There are four categories of parameters: (1) the parameter determining the degree of fragmentation of the breeding habitat (FRAG); (2) parameters determining other aspects of the spatio-temporal structure of the landscape (including disturbance); (3) demographic parameters determining reproduction and mortality; and (4) movement parameters (Tables 1 and 2). The model is illustrated in Figs. 1–5.

2.2.1. Spatial pattern of breeding habitat

FRAG determines the degree of spatial contagion in the distribution of breeding habitat cells. It takes on a value between (but not including) 0 and 1, where high values result in high fragmentation (Fig. 6). To set up the spatial pattern of breeding habitat (Fig. 2) at the beginning of each
simulation run, I begin with no breeding habitat and then repeat the following steps until the pre-specified number of cells (COVER; see below) is assigned as breeding habitat: (1) a grid cell is selected at random; (2) a random number between 0 and 1 is selected; and (3) if the selected cell has a neighbouring cell that has been assigned as breeding habitat or if the random number is less than FRAG, then the selected cell is assigned as breeding habitat. In simulations where the breeding habitat is assumed to be ephemeral (see below), the landscape spatial pattern is re-assigned every time step in the simulation (Fig. 1). Note that this algorithm for fragmentation (or contagion) is essentially the same as correlated or interacting percolation models (Anderson and Family, 1988; reviewed by Plotnik and Gardner, 1993).

2.2.2. Landscape spatio-temporal structure

Parameters determining the spatio-temporal structure of the landscape are: (1) the grid dimensions; (2) the fraction of grid cells in breeding habitat (COVER); (3) a parameter determining whether the habitat is ephemeral (PERM); and (4) parameters determining the disturbance pattern. Parameters determining the temporal pattern of disturbance include; (1) disturbance rate (DPROB), or the fraction of habitat disturbed per time step; and (2) disturbance mortality rate (DMORT), or the probability of mortality due to disturbance, of any individual in a cell that is disturbed. Parameters determining the spatial pattern of disturbance are: (1) disturbance clumping parameter (DCLUMP), which determines the degree of spatial contagion of the disturbances using the same algorithm as for the habitat fragmentation (above), with disturbed/undisturbed replacing breeding habitat/non-breeding habitat (Fig. 3); and (2) disturbance type (DTYPE); disturbances may either affect only breeding habitat, or breeding and non-breeding habitat alike. Note that a small value of DCLUMP results in few large disturbances whereas a large value results in a larger number of smaller disturbances.

Fig. 2. Flow diagram of the subroutine in the simulation model that determines the spatial pattern (degree of fragmentation) of breeding habitat.
2.2.3. Demographics and movement

Reproduction, mortality, and movement for a single individual are illustrated in Fig. 4. Probabilities of reproduction and movement are density-independent. Probability of mortality is density-independent as long as the population is below the maximum capacity of a cell (MAXOCC). However, if the cell population exceeds MAXOCC, individuals are killed at random to reduce the population to MAXOCC (Fig. 5B).

Reproduction occurs only in breeding habitat and is determined by the probability of reproduction per time step per individual and the number of offspring per reproduction event (OFFSP). Probability of mortality (apart from disturbance mortality) can be different in breeding habitat (MORT) and non-breeding habitat (NON-MORT).

Individuals move with some probability each time step. Movement probability can depend on whether the individual is in a breeding habitat cell (MOVE) or a non-breeding habitat cell (NON-MOVE). Movement direction is a random angle. Movement distance is also random, but is limited to a maximum (MAXDIST) per time step. From the point of view of moving individuals, the grid...
is ‘wrapped’; an individual that crosses the edge of the grid continues in the same direction on the opposite edge (Haefner et al., 1991).

2.3. Simulations

The grid size in all simulations was 900 cells (30 × 30). Each simulation began with 500 individuals distributed randomly over the grid and was conducted for 500 time steps. This was based on a series of preliminary runs using 1000 time steps, in which I found that any population that survived for the first 500 time steps survived for the full 1000 steps. The output variable used in all analyses was the survival time of the population, which was recorded as 500 if individuals were still present at the end of the 500 time steps.

To answer the question, ‘when is fragmentation of breeding habitat important to population survival?’, the ‘obvious’ approach would be to conduct a huge factorial simulation experiment in which simulations are conducted over a range of FRAG values for each of every possible combination of several levels of each of the other 11 parameters in Table 2. However, even for a simple experiment with only 3 levels for each of the 11 parameters, the computing time would be over 3 years, and there would be over 10 million observations in the output data set. I therefore chose a more feasible (although less comprehensive) two-stage approach. In the first stage, I conducted exploratory simulations to develop an intuitive understanding of the conditions under which breeding habitat fragmentation affects population survival. These were used to establish a set of ‘default’ values for the 11 parameters (Table 2). The default values were those that appeared, based on the exploratory simulations, to produce the largest effect of fragmentation on survival.
The second stage of the simulation experiments was designed to look in detail at the relationship between each parameter and the effect of fragmentation on survival. I was interested to know whether changes in the value of each parameter considered singly could remove the effect of fragmentation on survival, given that all the other parameters were held constant at the levels that should produce the largest effect of fragmentation (the default values). This two-stage approach is analogous to an empirical investigation in which initial, often informal, observations are used to produce hypotheses which are then examined in more detail in formal experimental or observational studies.

Stage II consisted of 11 independent sets of simulations, one for each of the final 11 parameters in Table 2. Each set of simulations was structured in a factorial design with 15 replicates for each combination of nine levels for FRAG (0.1, 0.2,..., 0.9) and several values for the parameter of interest covering the range indicated in Table 2. The number of levels selected for the different parameters depended on the shape of the relationship between the parameter of interest and the effect of fragmentation on survival (see Results). A typical set of simulations consisted of 9 levels of FRAG by 10 to 15 levels of the parameter of interest by 15 replicates, or about 1300–
2000 runs. For the two qualitative parameters (PERM and DTYPE) the state was chosen at random in each simulation. The ranges used for the parameters of interest were chosen using information from the preliminary (Stage I) simulations indicating the range beyond which FRAG has any effect or beyond which the population is unable to survive. In total there were 14 580 runs conducted in Stage II.

3. Results

3.1. Stage I

The purpose of the first stage was to find parameter values for which changing FRAG had a large effect on population survival. These are the ‘default’ values in Table 2. This stage was exploratory; widely different parameter combinations were used, in combination with a range of values of FRAG, to gain an overall impression of the conditions under which FRAG affected survival. Two important results emerged early in this exploratory phase. First, for most parameter combinations tried, there was no effect of FRAG on survival time. Second, in the few simulations that showed an effect of FRAG, there was a negative relationship between survival time and FRAG; the less fragmented the breeding habitat, the longer the population survived (Fig. 7).

3.2. Stage II

Although the Stage I simulations were somewhat haphazard by necessity, the Stage II simulations supported the hypotheses embodied in the Stage I simulation results, that the default parameter values represented the combination of values resulting in the largest (or close to the largest) possible effect of breeding habitat fragmentation on population survival.

The following is a summary of the Stage II results. The effect of breeding habitat fragmentation (FRAG) on survival time was highest when the proportion of the landscape in breeding habitat (COVER) was near 0.1, and decreased with both increasing and decreasing COVER (Fig. 8). At very low values of COVER all populations went extinct quickly, and at values of COVER greater than about 20%, all populations survived.

The effect of FRAG on survival was negligible when the habitat was ephemeral (PERM); the survival probability was low no matter what the spatial pattern of breeding habitat. The effect of
FRAG on survival decreased with increasing disturbance probability (DPROB), although there was still a detectable effect at fairly high disturbance probabilities (Fig. 9). Note that I could not use DPROB = 0 for the default because this would not have allowed me to explore the effects of the other disturbance parameters, DMORT, DCLUMP, and DTYPE.

The effect of FRAG on survival decreased with increasing disturbance mortality probability (DMORT), although there was still a detectable effect of FRAG at fairly high DMORT (Fig. 10). Note again that I could not use DMORT = 0 for the default because this would not have allowed me to explore the effects of the other disturbance parameters, DPROB, DCLUMP, and DTYPE.

There was no effect of the degree of the spatial pattern of disturbances (DCLUMP) on the effect of FRAG on survival time (Fig. 11). The type of disturbance (DTYPE), i.e. whether it occurred in breeding habitat only or anywhere in the grid, also had no effect on the relationship between survival time and FRAG.

When the number of offspring per reproduction (OFFSP) was increased above 1, survival was ensured; this means there was no effect of FRAG on survival time for OFFSP values other than 1. The higher the maximum cell occupancy (MAXOCC), the greater the effect of FRAG on population survival (Fig. 12).

The default mortality rate in breeding habitat (MORT) was 0.05 and in non-breeding habitat (NONMORT) was 0.5. The effect of FRAG on survival time was highest near the default value for NONMORT (0.5), and decreased with both increasing and decreasing NONMORT (Fig. 13).

The default movement probability in breeding habitat (MOVE) was 0.5 and in non-breeding habitat (NONMOVE) was 1. The effect of FRAG on survival time was highest near the default value for MOVE, and decreased with both increasing and decreasing MOVE (Fig. 14). At very high values of MOVE (> 0.7) all populations went extinct quickly, and at low values of MOVE, all populations survived. The effect of FRAG on survival time was highest at an intermediate value of maximum movement distance (MAXDIST) (4), and decreased with both increasing and decreasing MAXDIST (Fig. 15).
4. Discussion

4.1. Model assumptions

To make model analyses feasible, several simplifying assumptions were made. The model represents a simplified landscape in which habitat is divided into two sorts: breeding and non-breeding habitat. The quality of non-breeding (matrix) habitat, in terms of mortality and movement rates, is assumed to be uniform. Would the results be different under assumptions of a heterogeneous matrix? To answer this one would need to vary FRAG and the degree of matrix heterogeneity, and look for an effect of their interaction on survival time. Since the present results suggest very restricted circumstances under which fragmentation matters, one would want to know whether matrix heterogeneity can increase the negative effect of FRAG on survival. This is not simple to do because the actual pattern of heterogeneity in the matrix (e.g. linear strips resulting in corridors) would need to be considered. While the fact of a heterogeneous matrix would not necessarily increase the degree to which fragmentation affects survival, it is prudent at this time to apply the current results only to species, such as many insects and plants, for which the assumption of uniform matrix holds at least approximately.

Direction and distance of movement were assumed to be random. This is not problematic because more complicated movement assumptions would result in a reduced effect of FRAG on population survival. The random movement assumption, while realistic for many organisms such as insects and plants, is unrealistic for organisms that may actively search the landscape for breeding habitat, such as birds and mammals. However, if individuals in transit orient toward new breeding habitat from some distance, then fragmented breeding habitat is effectively joined together into non-fragmented habitat, reducing the effect of fragmentation. Therefore, although the movement assumptions are unrealistic for many organisms, they are conservative in the sense that an effect of FRAG should be apparent if there is one.
The limitation on movement distance (MAXDIST) is also a conservative assumption. Longer movement distances link together patches and reduce the effect of fragmentation. In a different spatially explicit simulation model (Fahrig and Palohéimo, 1988b), I found that variation in dispersal distance was the most important determinant of effect of landscape spatial pattern on local population size; the shorter the movement distance the greater the effect of landscape pattern on local population size.

The model is assumed to be scaled such that breeding habitat remains useable even when it is fragmented into the smallest unit (one grid cell). For any real species there is a lower limit to the size of a habitat patch that can act as breeding habitat. Therefore, in applying the results to real species it is important to scale the model landscape such that a single grid cell of breeding habitat provides enough habitat for at least one individual to breed. Patches of breeding habitat smaller than one grid cell should be defined as non-breeding habitat.

Similarly, in applying the simulation results to real species, one must correctly define the species’ habitat. For example, in the context of forest fragmentation, the same amount of forest fragmented into a large number of small pieces does not represent the same amount of breeding habitat for a forest interior species; the increase in amount of forest edge reduces the total amount of breeding habitat (Fahrig, 1997).

The model does not include species interactions. I do not know whether species interactions would affect the impact of FRAG on population survival. Note that I can not simply add more species to the current model because this would result in unmanageable complexity. Since the species would have different life history and dispersal attributes and could interact with the landscape differently, the number of parameters considered would be multiplied by the number of species included. Also, parameters would be needed to determine the type of species interactions (mutualism, predator–prey or host–parasite interaction, competition) and the strength of the interactions. Effects of species interactions on the importance of habitat fragmentation therefore remains a problem for future research.
I used survival time as the response variable because survival is the long-term goal of conservation programs. However, since in practice the data available to managers are normally in the form of population sizes or short-term trends in population sizes, I determined whether survival time was correlated with short-term population size in the simulations. The correlation was high (Fig. 16; Spearman rank correlation coefficient = 0.804; \( P < .0001 \)). This indicates that population survival time was in fact an indicator of population size on the short term.

One might suppose that the results are biased by the upper limit of 500 on population survival time. This means that any factor that increases survival rate over all would decrease the effect of spatial pattern by allowing all runs to reach the 500 time step cut-off. However, as mentioned above, in preliminary simulations 500 time steps was found to be a threshold above which population survival was assured. Therefore we are justified in concluding that a change in a parameter that assured survival to 500 time steps removes any possible effect of habitat spatial pattern on survival time.

### 4.2. Stage I simulations

For most parameter combinations tried during the exploratory phase of the simulation experiment, there was no effect of FRAG on survival time. In fact, about two months of simulation time were spent just looking for some parameter combination under which there was an effect of fragmentation. Similarly, there was no significant effect of fragmentation in about 99.6% of the parameter space examined in the stage II simulations. Note that this is not an absolute estimate of the proportion of possible conditions under which fragmentation does not matter, because: (1) for some parameters (e.g. OFFSP, MAXOCC) the total parameter space searched was arbitrary; and (ii) possible effects of higher order interactions among the parameters were not studied. However, this is an important result in itself because it suggests that there may be many circumstances in nature in which the spatial pattern of the breeding habitat is irrelevant to the survival probability of the population. Of course, I do not know how common these circumstances are in nature, rela-
Fig. 11. Relationship between the degree of spatial contagion of disturbances (DCLUMP), and the slope of the relationship between population survival time and the degree of fragmentation of the breeding habitat (FRAG). Each point was constructed by running 15 replicates of the model for the given value of DCLUMP with each of nine FRAG values, 0.1, 0.2, ..., 0.9, making a total of 135 runs for each point.

It is somewhat tempting to hypothesize that most endangered species fall within the 0.4% of parameter space (e.g. Pulliam et al., 1992; Lambersen et al., 1992), but this remains to be tested. However, there are clearly many possible scenarios that could occur for which spatially explicit population dynamics modelling would not be necessary.

In all cases where an effect of fragmentation on population survival was found, decreased fragmentation resulted in increased population survival time, i.e. the slope relating survival time to fragmentation was always negative. Habitat fragmentation (i.e. decreasing patch size with a constant total habitat amount) has also been shown by Burkey (1989), Herben et al. (1991), Adler and Nürnberg (1994) to decrease the probability of population survival. In Adler and Nürnberg’s study the size of the landscape increased with increasing fragmentation. The current study suggests that this result holds even when the landscape size is constant and when the dispersal range of the organism is quite limited. A similar result was found by Perry and Gonzalez-Andujar (1993) in a spatial model of an annual plant population. They found that metapopulation growth was faster when the pattern of heterogeneity in environmental harshness was imposed at larger than at a smaller spatial scale.

This result is in contrast to the model results of Wissel and Stöcker (1991). They compared the extinction probability of one large population to 10 subpopulations, and found that if colonization ability is large enough, the extinction rate of the several subpopulations was less than that of the one large population. This difference is probably due to the fact that Wissel and Stöcker (1991) included a single environmental noise term for the single large population, but individual (uncorrelated) environmental noise terms for each of the 10 subpopulations. This imposes a ‘spreading of risk’ (Den Boer, 1981) advantage to the subdivided populations. This is unrealistic since in a very large patch, different portions of the population will experience different environmental fluctuations. Also, in spreading of risk there is an implicit assumption that several small patches are
Fig. 12. Relationship between the maximum number of individuals per cell (MAXOCC), and the slope of the relationship between population survival time and the degree of fragmentation of the breeding habitat (FRAG). Each point was constructed by running 15 replicates of the model for the given value of MAXOCC with each of nine FRAG values, 0.1, 0.2, ..., 0.9, making a total of 135 runs for each point.

distributed over a larger region than a few large ones. This is not applicable in most real world situations where the total size of the landscape is fixed but human activities (e.g. deforestation, agriculture) alter the spatial pattern of habitat on the landscape.

4.3. Stage II simulations

To my knowledge, this study is the first to address the general question: ‘under what conditions does fragmentation of breeding habitat affect population survival?’ Most of the results are new or not generally known, and in total they can be grouped into a small number of rules that can be used to predict when fragmentation is expected to matter (see Section 5).

The effect of the amount of breeding habitat (COVER) on importance of fragmentation was very strong (Fig. 8). For COVER values greater than 20% there was no effect of FRAG on survival. There are two reasons for this. First, increasing amount of breeding habitat results in increasing survival time. Total birth rate increases and total death rate decreases because an increasing proportion of the population both reproduces and experiences the lower mortality rate in breeding habitat. At some point, enough habitat results in ensured survival, and the spatial pattern of the habitat is then unimportant. Also, the more breeding habitat there is, the smaller the distance between habitat cells, resulting in faster recolonization of local extinctions.

The value 20% is an important result in the context of current emphasis in spatial models on interfaces with GIS (geographical information systems). If a GIS indicates that over 20% of the landscape is available as breeding habitat for the species of interest, this result suggests that spatially explicit population modelling is not necessary. It is sufficient to know how much breeding habitat is available; the exact spatial locations are not important.

One must be cautious when comparing this result with others because many researchers in conservation biology use the term ‘fragmentation’ synonymously with ‘deforestation’, and include within this one concept both habitat loss and
Fig. 13. Relationship between the probability of mortality in non-breeding habitat (NONMORT), and the slope of the relationship between population survival time and the degree of fragmentation of the breeding habitat (FRAG). Each point was constructed by running 15 replicates of the model for the given value of NONMORT with each of nine FRAG values, 0.1, 0.2,..., 0.9, making a total of 135 runs for each point.

fragmentation per se (i.e. breaking apart) (e.g. McLellan et al., 1986; Santos and Telleria, 1994; Villard and Taylor, 1994). However, Andrén (1994) has reviewed both modelling and empirical studies controlling for the effects of loss (percent cover of habitat) before testing for the effects of patch size and patch isolation. He found a cut-off of about 20–30% cover above which the spatial pattern of habitat is unimportant and below which it becomes increasingly important. This provides some corroboration of my result here.

In addition, a study by Hamel et al. (1993) indirectly supports this result. They studied bird species abundances in 32 widely distributed forest patches in Tennessee. They measured patch area as well as the proportion of land with forest cover in the region in which each patch was located. They found no effects of patch area on bird abundances. However, their measured values for proportion of land with forest cover ranged from 0.26 to 0.61. The results of the present study suggest that over this range of habitat amounts, one would not expect to find any effect of habitat spatial pattern, estimated as patch size in their study.

The results for habitat permanence, disturbance probability and disturbance mortality rate indicate that the more temporally dynamic the landscape is, the less important is knowledge of the exact spatial locations of breeding habitat for predicting population survival. Similar results were found for both disturbance (Fahrig, 1991) and ephemeral habitat patches (Fahrig, 1992) using a population-based spatially-explicit simulation model. In effect, the locations from which any particular population is likely to receive immigrants change as the landscape changes, so knowledge of spatial relationships does not help predict survival time.

The negative effect of increases in the reproduction rate (OFFSP) on the relationship between habitat fragmentation and population survival time occurs because if reproduction rate is high enough, the landscape is flooded with organisms and survival is ensured. In this case changes in the spatial pattern of breeding habitat will not affect survival time.

The effects of maximum occupancy per cell (MAXOCC), mortality probability in non-breedi-
ing habitat relative to breeding habitat (NONMORT), and movement probability in breeding habitat relative to non-breeding habitat (MOVE) all have the common feature that any increase in the difference between breeding habitat and non-breeding habitat (or in the difference in the organism’s response to breeding and non-breeding habitat) increases the effect of breeding habitat fragmentation on population survival. When movement probability out of breeding patches is high and mortality rate in non-breeding habitat is low, the population becomes spread out over the landscape. This makes movement between breeding areas independent of the spatial pattern of the breeding habitat.

The importance of NONMORT is interesting from a conservation point of view. The term ‘connectivity’ has been defined as the mean probability of successful movement between all pairs of habitat patches in a landscape (Taylor et al., 1993). It depends on the spatial pattern of habitat in the landscape and the mortality rate of individuals moving between breeding habitat. The present simulations suggest that if the movement mortality rate is low enough (relative to the mortality rate in breeding habitat), making connectivity high, the spatial pattern of the habitat becomes irrelevant to the survival probability of the population. This means that survival rate outside breeding habitat in the matrix can determine whether a spatially explicit model of the population is required. This is an important result because it is often assumed that mortality in the matrix is higher than in breeding habitat, but almost no empirical studies have been conducted to test this assumption (Van Vuren and Armitage, 1994).

When movement distance is small, the effect of breeding habitat fragmentation on population survival is small because there is little or no exchange between breeding areas, no matter what their spatial pattern is. Note that this would not be true if the amount of breeding habitat on the landscape were much larger. However, we already know that this in itself would remove any effect of habitat spatial pattern on survival (see above). When movement distance is large, again the effect of spatial pattern on population survival is small.
5. Conclusion

The results suggest that fragmentation of breeding habitat affects population survival only under a relatively narrow set of conditions. For situations in which there is little spatial variation in quality (for survival and/or movement) in the non-breeding ('matrix') habitat, these conditions can be used to determine whether or not spatially explicit modelling of population dynamics is necessary. Note that all of the following conditions must hold for there to be an effect of breeding habitat fragmentation.

1. The average between-generation movement distance of the organism is about 1–3 times the expected nearest distance between breeding sites. If dispersal distance is very short, each breeding area represents an isolated population and if it is very long the whole landscape represents a single inter-mixed population; in either case spatial pattern of breeding habitat is unimportant.

because exchange of individuals between breeding areas can occur, no matter what their spatial pattern is. There is an intermediate movement distance (about 4 cells for MAXDIST in the present simulations) at which the effect of habitat spatial pattern on population survival time is maximized.

To apply this result, one must scale movement distance relative to landscape pattern. On a grid with 10% breeding habitat the expected nearest distance between breeding habitat cells is about 1.34 cells (Fahrig, 1992). Since in the model movement distances were taken from a uniform distribution (1 to MAXDIST), the mean movement distance for a run was \((\text{MAXDIST} + 1)/2\) cells. Therefore, the results suggest that the effect of FRAG is largest when average movement distances are in the range of about 1–3 times the mean nearest distance between breeding habitat cells (i.e. \(\text{MAXDIST} = 2–7\) cells).
(2) The breeding habitat of the organism covers less than 20% of the landscape.

(3) The habitat is not ephemeral. This suggests that knowledge of explicit spatial pattern of habitat is not important for predicting population dynamics of many gap-dependent species of plants, and insect species dependent on ephemeral resources such as annual plants or carcasses. Ephemeral habitats are also created for long-lived forest-dwelling species when forestry activity occurs in a patchy pattern over a large contiguous area on a short cycle of 20–80 years. For species having lifespans of several years such as trees, and some understorey perennials, mammals, and birds that specialize on forest habitat at a particular stage of the cycle (e.g. recently cut, or mature forest), the simulations predict that the spatial pattern of appropriate-aged forest is unimportant to population survival. This result was also found in a different spatially-explicit model in which I varied the ‘lifespan’ of habitat patches (Fahrig, 1992; Fahrig and Merriam, 1994).

(4) The probability of the organism moving is much lower in breeding habitat than in non-breeding habitat. In other words, the organism has high breeding site fidelity.

(5) The mortality rate in the non-breeding habitat (matrix) areas is much higher than the mortality rate in breeding habitat areas. As mentioned above, the assumption of higher mortality in the matrix is widely used but largely untested. These results suggest that spatially explicit simulation modelling of population dynamics is only necessary under a relatively narrow range of conditions.

Acknowledgements

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References


How much habitat is enough?

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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.

Keywords: Extinction threshold; Population persistence; Habitat loss; Emigration; Dispersal mortality; Matrix quality; Habitat fragmentation; Spatial model; Landscape structure

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 minimum (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 Zaschke, 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; André, 1997; Jonsen and Fahrig, 1997; Sisk et al., 1997; Pope et al., 2000). Patch context determines...
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 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 × 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: \(3(\text{GROWTH values}) \times 3(\text{MOVEHAB values}) \times 3(\text{MATQUAL values}) \times 3(\text{FRAG values}) \times 2(\text{COVER values}) \times 20(\text{replicate runs}) \times 3(\text{replicate experiments}) = 102,060\) 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

<table>
<thead>
<tr>
<th></th>
<th>d.f.</th>
<th>Type III SS</th>
<th>F</th>
<th>P</th>
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<td>FRAG</td>
<td>2</td>
<td>0.06940247</td>
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<tr>
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<td>403.61</td>
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<td>MOVEHAB</td>
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<td>FRAG*MATQUAL</td>
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<td>0.1541</td>
</tr>
<tr>
<td>FRAG*MOVEHAB</td>
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<td>1.37</td>
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</tr>
<tr>
<td>FRAG*GROWTH</td>
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<td>0.9594</td>
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<tr>
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<td>MOVEHAB*GROWTH</td>
<td>4</td>
<td>2.03723457</td>
<td>151.79</td>
<td>0.0001</td>
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</table>

*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.
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

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>Mean shift</th>
<th>Minimum shift</th>
<th>Maximum shift</th>
</tr>
</thead>
<tbody>
<tr>
<td>MOVEHAB</td>
<td>0.62</td>
<td>0.013</td>
<td>0.91</td>
</tr>
<tr>
<td>MATQUAL</td>
<td>0.25</td>
<td>0.0</td>
<td>0.58</td>
</tr>
<tr>
<td>FRAG</td>
<td>0.06</td>
<td>0.0</td>
<td>0.17</td>
</tr>
</tbody>
</table>

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; Witz 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 Sanjuyan, 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. Fither 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 (Andrén, 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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