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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

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have significant effects on the dynamics of resident populations, independent of the amount or quality of the habitat (reviews in Kareiva, 1990; Andrén, 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

Table 1

Parameter values held constant through all simulation experiments

Parameter	Value
Landscape size	900 cells (30 × 30)
Starting number of individuals	500
Time steps in simulation	500
Reproduction probability (RPROB)	0.5/individual/step in breeding habitat cell 0.0/individual/step in non-breeding habitat cell
Mortality probability in breeding habitat (MORT)	0.05/individual/time step
Movement probability in non-breeding habitat (NONMOVE)	1.0/individual/time step

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 2
Parameters varied in Stage II of the simulations

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

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).

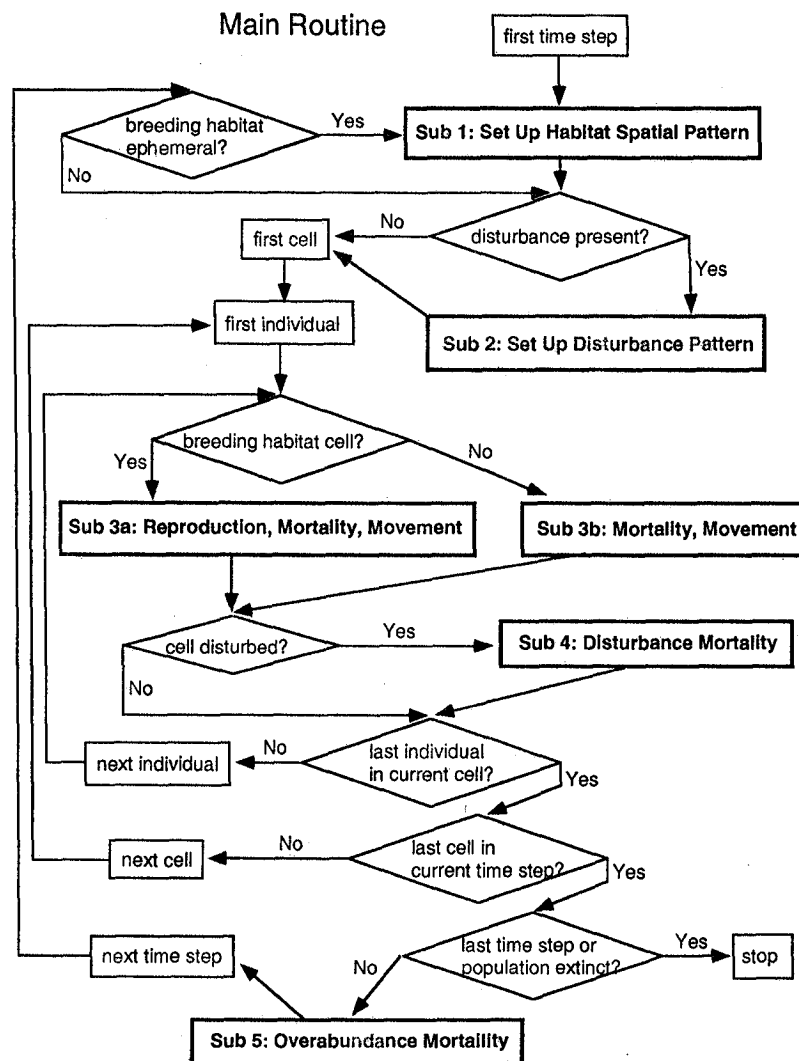


Fig. 1. Flow diagram of the simulation model: main routine.

mensional 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

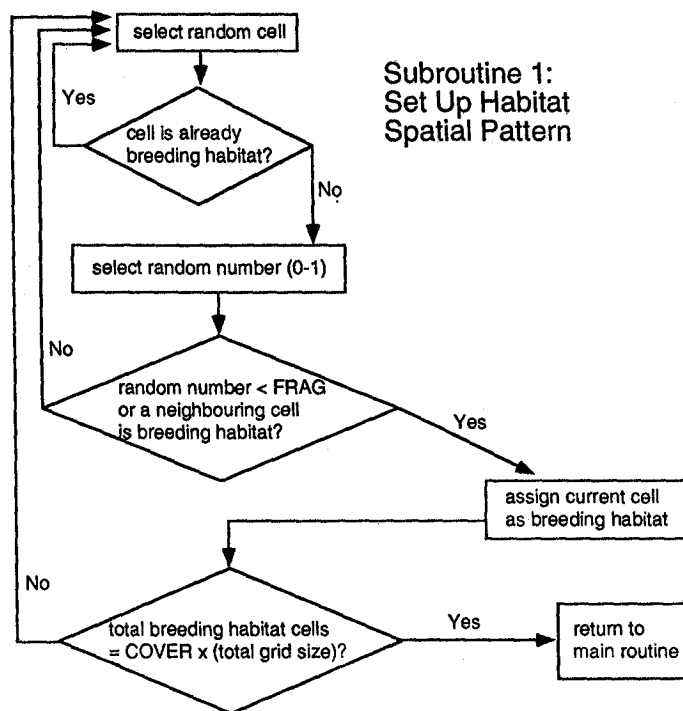


Fig. 2. Flow diagram of the subroutine in the simulation model that determines the spatial pattern (degree of fragmentation) of breeding habitat.

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.

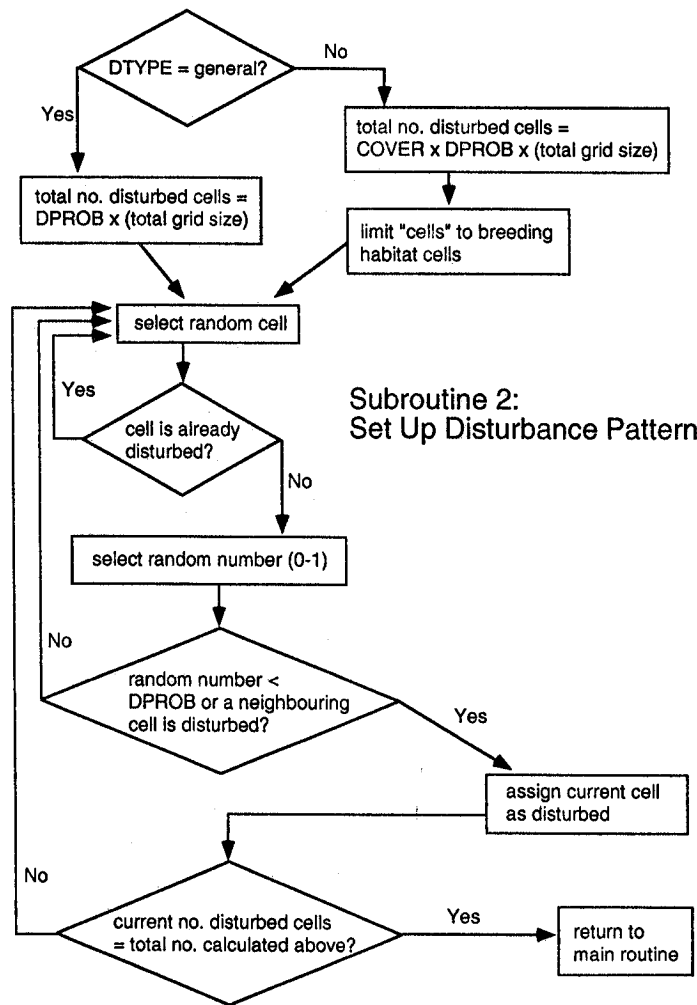


Fig. 3. Flow diagram of the subroutine in the simulation model that determines the spatial pattern (degree of contagion) of disturbances.

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

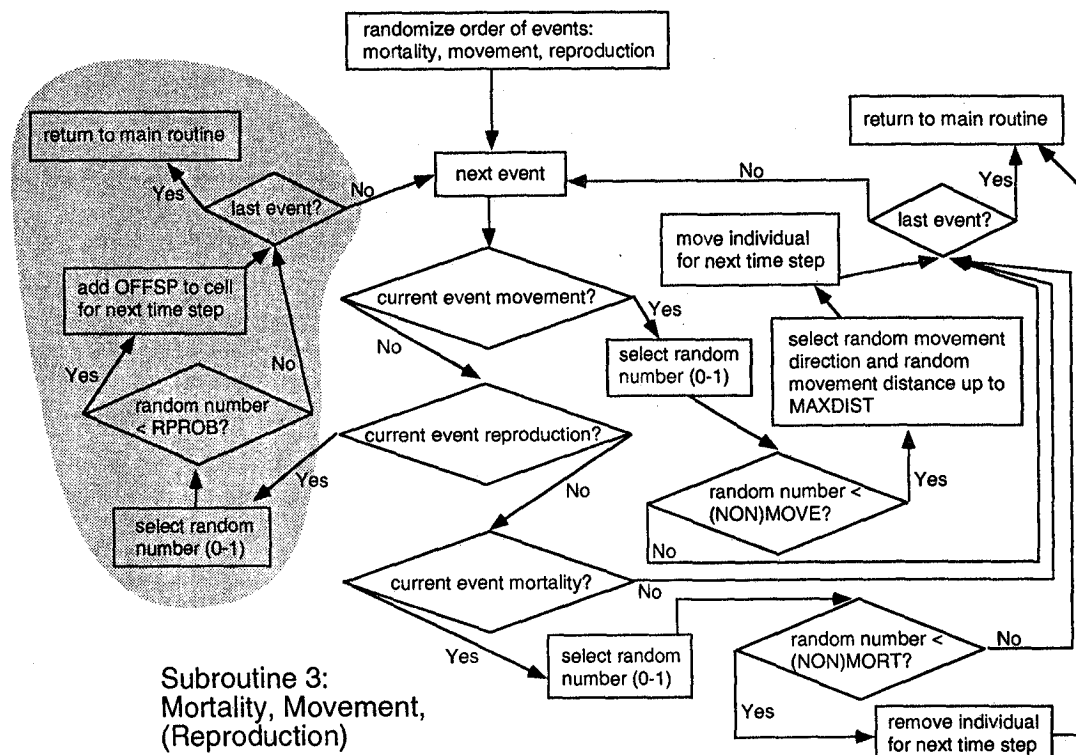


Fig. 4. Flow diagram of the subroutine in the simulation model that determines mortality, reproduction, and movement for a single individual within a time step. Note that individuals in non-breeding habitat do not enter the shaded portion of the diagram. Subroutine 3a in Fig. 1 refers to all of Fig. 4 whereas Subroutine 3b in Fig. 1 refers to the non-shaded portion of Fig. 4 only.

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 sur-

vival?', 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.

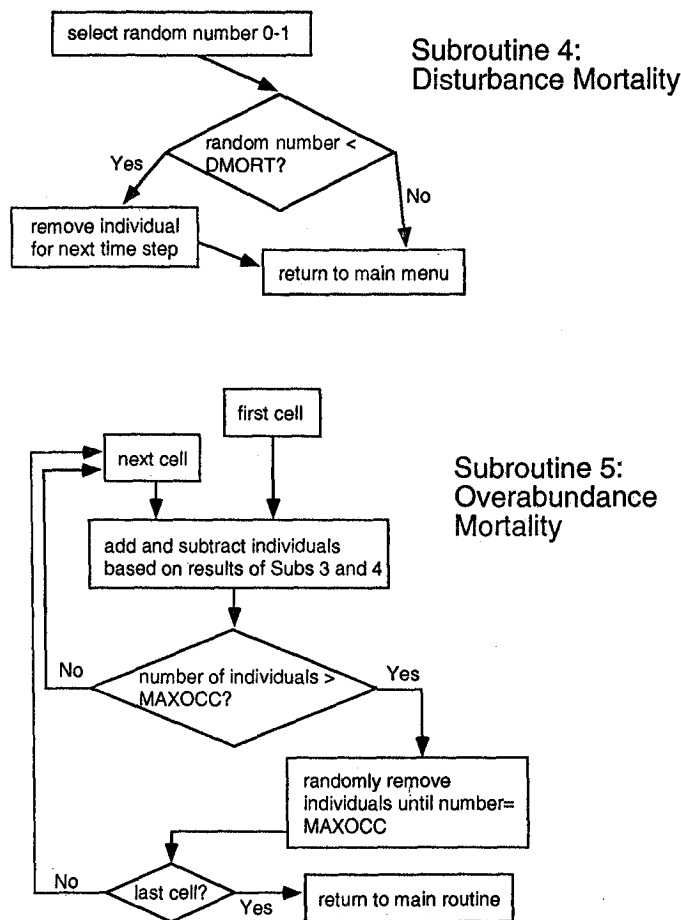


Fig. 5. Flow diagram of the subroutines in the simulation model that determine: (a) disturbance mortality for an individual within a disturbed cell; and (b) mortality due to over-abundance. Note that mortality due to overabundance is applied to all cells at the end of each time step.

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

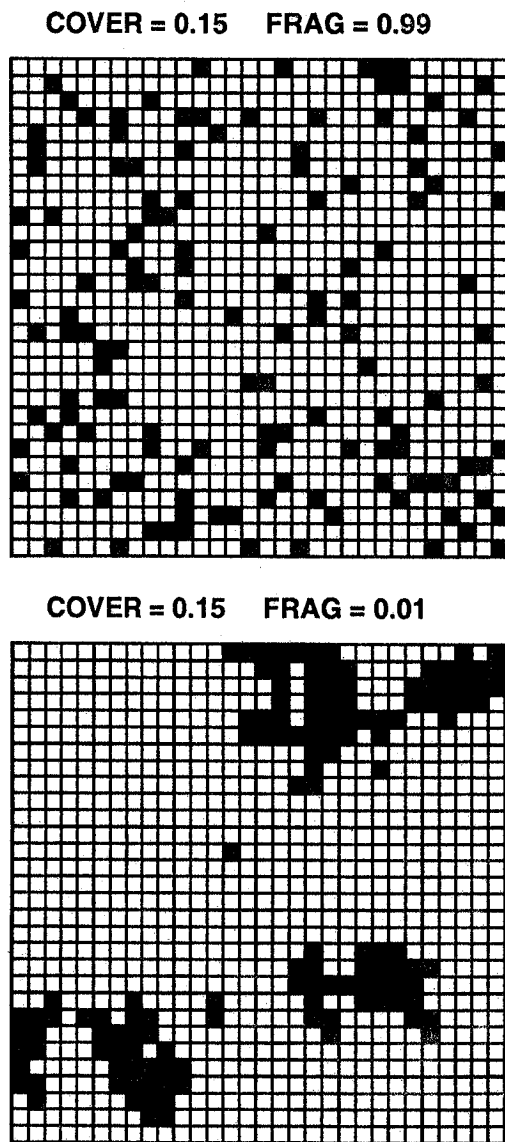


Fig. 6. Illustration of the effect of the breeding habitat fragmentation parameter (FRAG) on the spatial pattern of breeding habitat (filled cells). COVER is the proportion of the grid in breeding habitat.

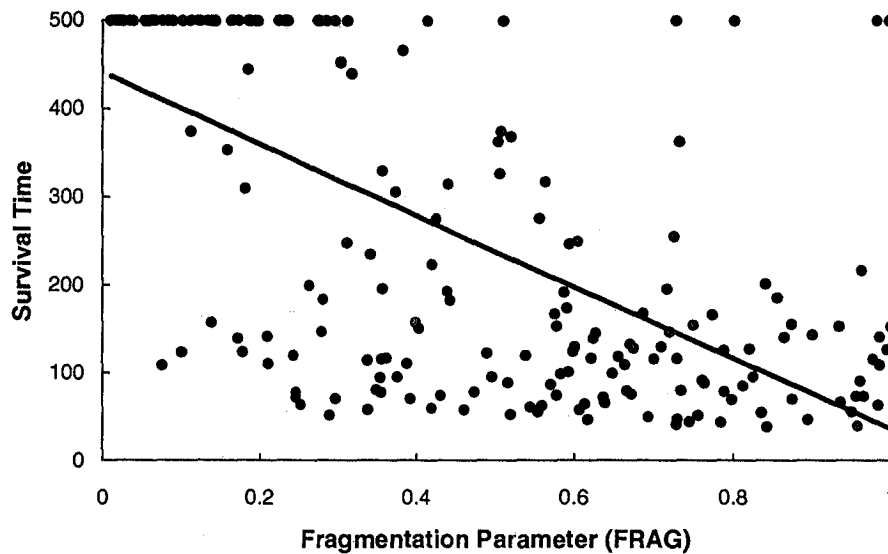


Fig. 7. Relationship between breeding habitat fragmentation and survival time based on 200 model runs using the default parameter values (Table 2).

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 reproduc-

tion (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).

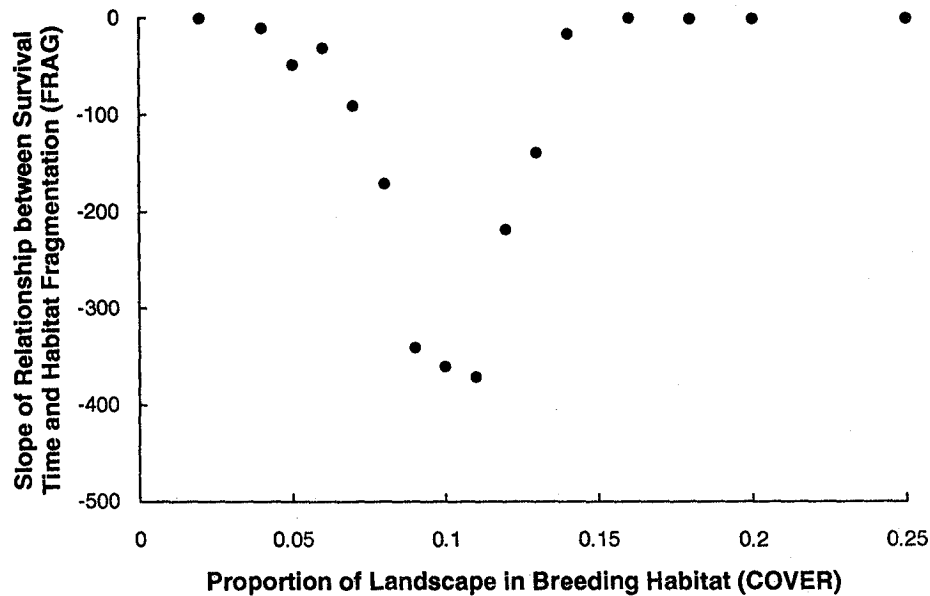


Fig. 8. Relationship between the proportion of the landscape in breeding habitat (COVER), and the slope of the relationship between population survival time and the degree of fragmentation of the breeding habitat (FRAG). Each point was constructed by running 15 replicates of the model for the given value of COVER with each of nine FRAG values, 0.1, 0.2, ..., 0.9, making a total of 135 runs for each point.

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 neces-

sarily 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.

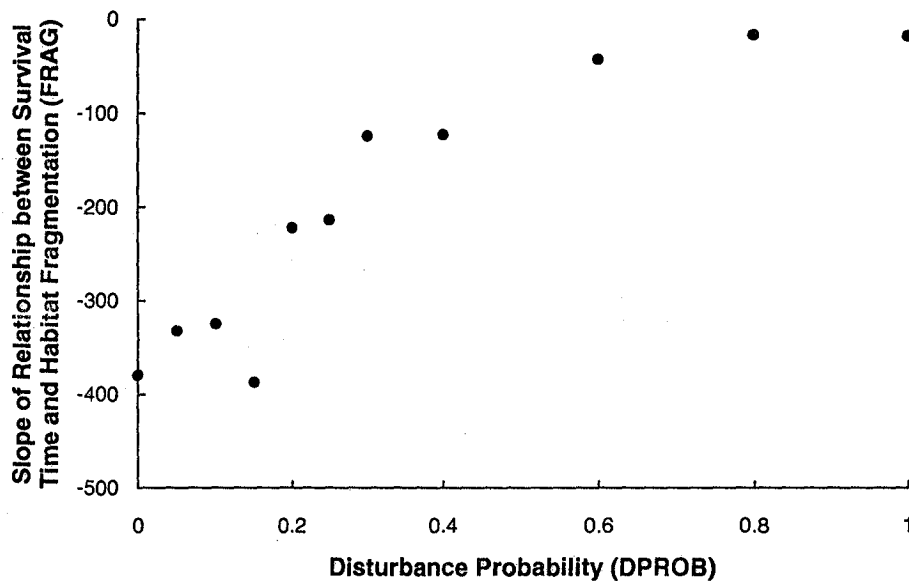


Fig. 9. Relationship between the probability of disturbance (DPROB), and the slope of the relationship between population survival time and the degree of fragmentation of the breeding habitat (FRAG). Each point was constructed by running 15 replicates of the model for the given value of DPROB with each of nine FRAG values, 0.1, 0.2, ..., 0.9, making a total of 135 runs for each point.

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 Paloheimo, 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 spe-

cies' 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.

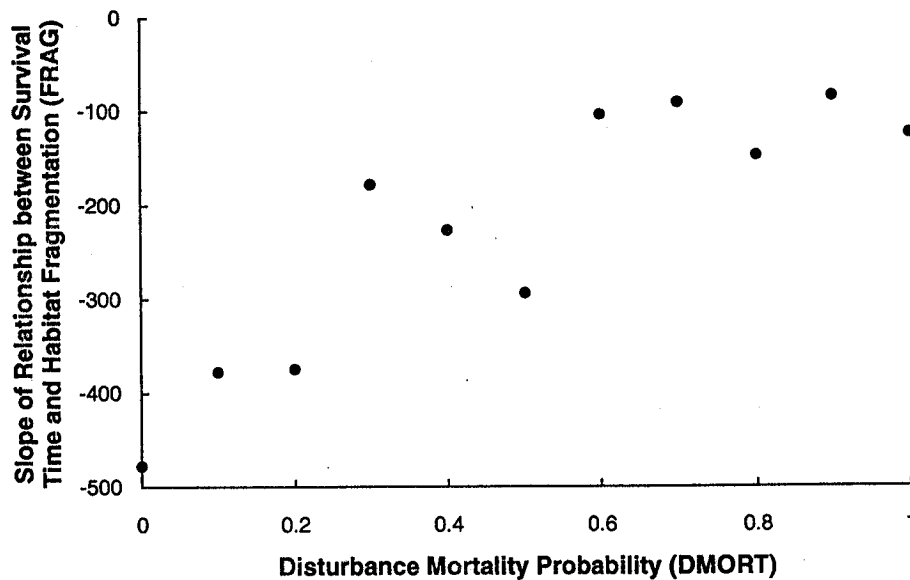


Fig. 10. Relationship between the disturbance mortality probability (DMORT), and the slope of the relationship between population survival time and the degree of fragmentation of the breeding habitat (FRAG). Each point was constructed by running 15 replicates of the model for the given value of DMORT with each of nine FRAG values, 0.1, 0.2, ..., 0.9, making a total of 135 runs for each point.

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: (i) 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-

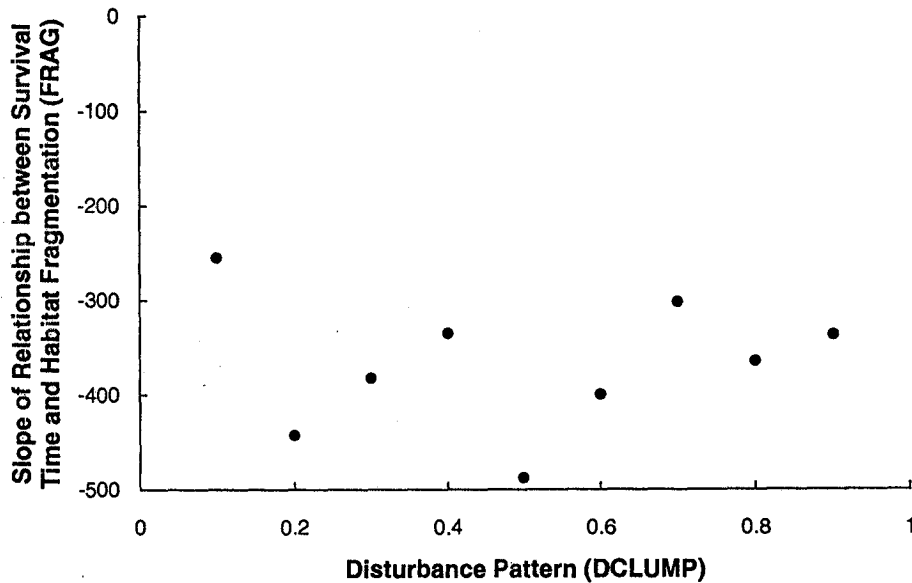


Fig. 11. Relationship between the degree of spatial contagion of disturbances (DCLUMP), and the slope of the relationship between population survival time and the degree of fragmentation of the breeding habitat (FRAG). Each point was constructed by running 15 replicates of the model for the given value of DCLUMP with each of nine FRAG values, 0.1, 0.2, ..., 0.9, making a total of 135 runs for each point.

tive to those for which spatial pattern is important. It is somewhat tempting to hypothesize that most endangered species fall within the 0.4% of parameter space (e.g. Pulliam et al., 1992; Lamberson 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 Nürnberger (1994) to decrease the probability of population survival. In Adler and Nürnberger'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

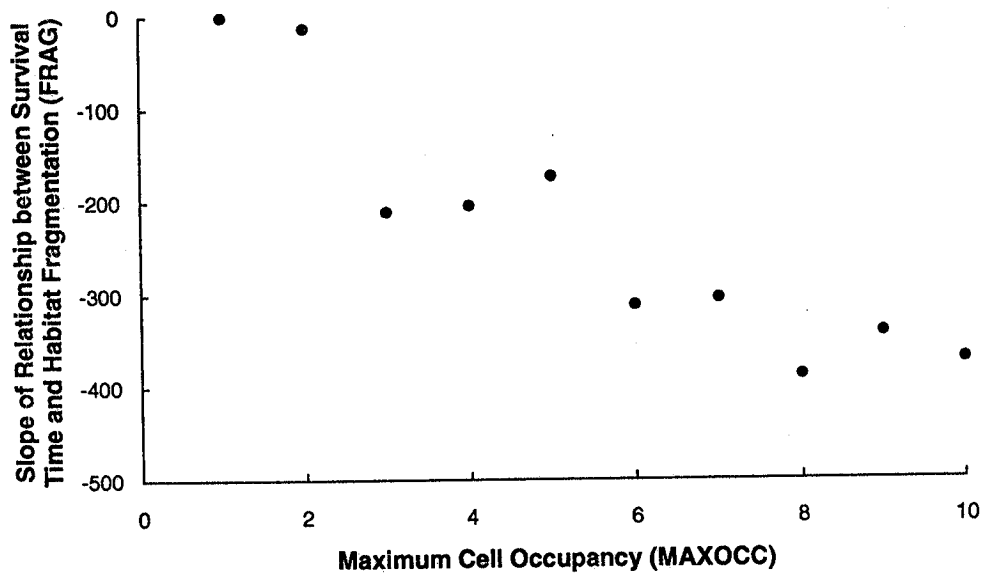


Fig. 12. Relationship between the maximum number of individuals per cell (MAXOCC), and the slope of the relationship between population survival time and the degree of fragmentation of the breeding habitat (FRAG). Each point was constructed by running 15 replicates of the model for the given value of 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

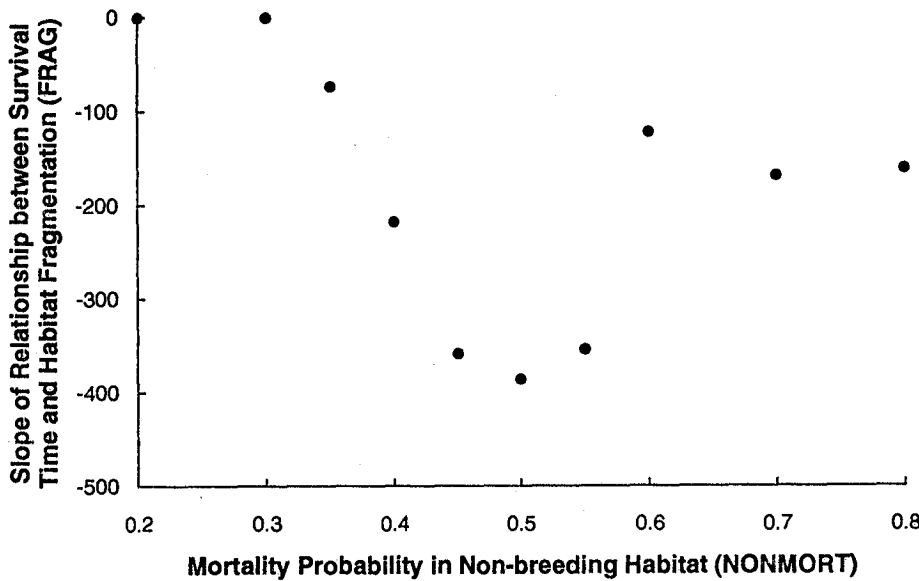


Fig. 13. Relationship between the probability of mortality in non-breeding habitat (NONMORT), and the slope of the relationship between population survival time and the degree of fragmentation of the breeding habitat (FRAG). Each point was constructed by running 15 replicates of the model for the given 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 Tellería, 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-breed-

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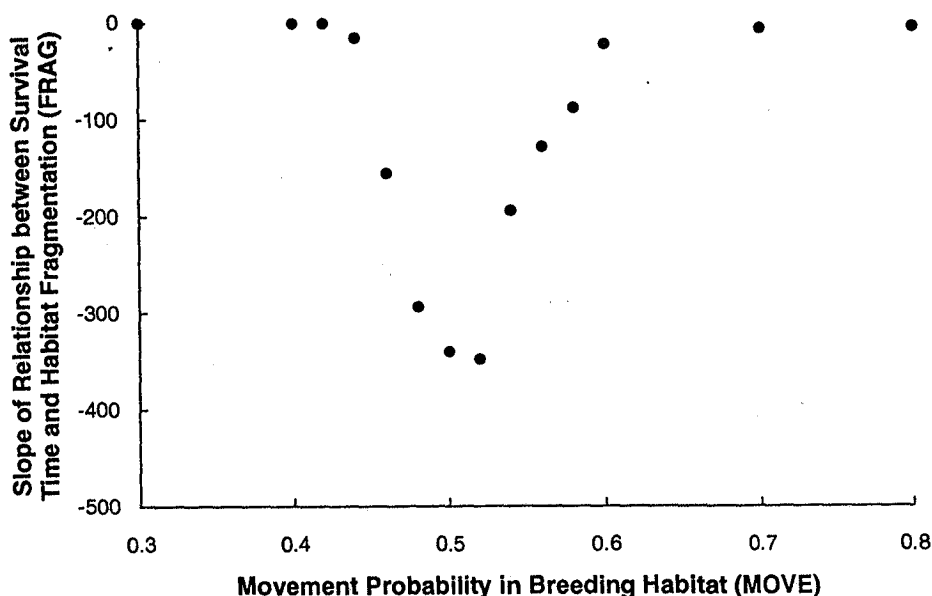


Fig. 14. Relationship between the probability of movement in breeding habitat (MOVE), and the slope of the relationship between population survival time and the degree of fragmentation of the breeding habitat (FRAG). Each point was constructed by running 15 replicates of the model for the given value of MOVE with each of nine FRAG values, 0.1, 0.2, ..., 0.9, making a total of 135 runs for each point.

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

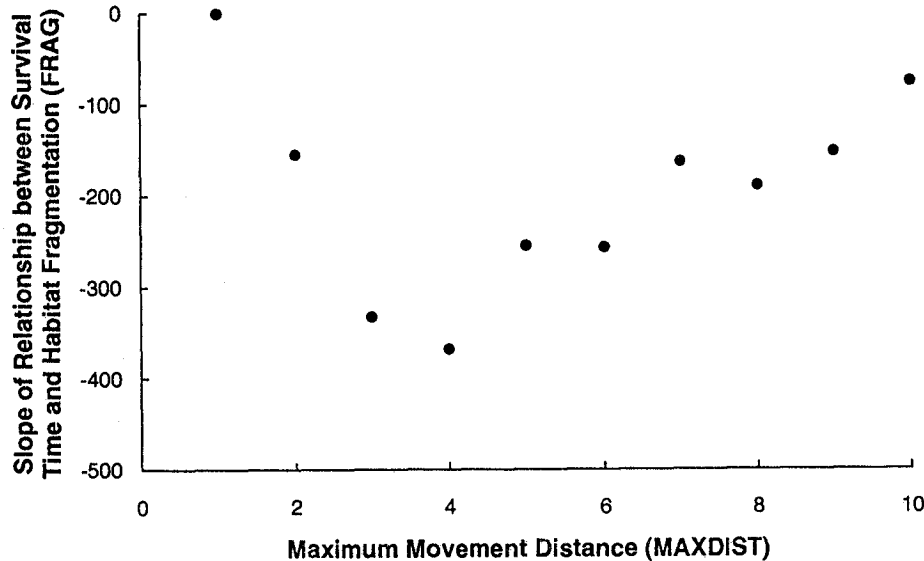


Fig. 15. Relationship between the maximum movement distance (MAXDIST), and the slope of the relationship between population survival time and the degree of fragmentation of the breeding habitat (FRAG). Each point was constructed by running 15 replicates of the model for the given value of MAXDIST with each of nine FRAG values, 0.1, 0.2, ..., 0.9, making a total of 135 runs for each point.

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 $(MAXDIST + 1)/2$ 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. $MAXDIST = 2-7$ cells).

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.

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Fig. 16. Population size after 20 time steps vs. survival time for a random selection of 200 simulation runs in which the population went extinct within 500 time steps; Spearman rank correlation = 0.804; $P < 0.0001$.

(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.

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