

RELATIVE EFFECTS OF HABITAT LOSS AND FRAGMENTATION ON POPULATION EXTINCTION

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Abstract: In their review of the recent "explosion of spatially explicit theory" in ecology, Kareiva and Wennergren (1995) suggest a number of emerging principles for species conservation. One of these principles is that how habitats are arranged in space can mitigate the risks of species extinctions from habitat loss. I tested this by estimating the relative importance of habitat loss and habitat spatial pattern (fragmentation) on population extinction, using a simple, spatially explicit simulation model. Results indicate that the effects of habitat loss far outweigh the effects of habitat fragmentation. I therefore suggest that, in fact, details of how habitats are arranged cannot usually mitigate the risks of habitat loss. Conservation efforts should be aimed foremost at stopping habitat loss and at habitat restoration.

J. WILDL. MANAGE. 61(3):603-610

Key words: conservation biology, extinction, fragmentation, habitat ecology, habitat fragmentation, habitat loss, habitat restoration, simulation, spatial model, species conservation.

Destruction and fragmentation (literally "breaking apart") of natural habitats are the 2 most important factors in the current species extinction event (Groombridge 1992). Loss and fragmentation of habitat result in reduced population sizes, which increases the probability of extinction by demographic and/or environmental stochasticity (Burkey 1995). However, effects of habitat amount and fragmentation are confounded in many studies that claim to show an effect of fragmentation. This arises through frequent use of the term "fragmentation" to mean simultaneously both loss and fragmentation of habitats (Diffendorfer et al. 1995, Holt et al. 1995, Robinson et al. 1995, Schumaker 1996).

Furthermore, negative effects of decreasing size and increasing isolation of habitat patches often are interpreted as fragmentation effects (Dodd 1990, Robinson et al. 1992, van Apeldoorn et al. 1992, Celada et al. 1994, Hunter et al. 1995), when in fact they may be interpreted more correctly as negative effects of large-scale habitat loss. If habitat loss results in a constant number of smaller patches, then patch size effects are due to habitat loss alone. If whole patches are removed from the landscape, then isolation of remaining patches increases but fragmentation per se is actually decreased because there are fewer patches (Ripple et al. 1991); in this case isolation effects are due to habitat loss alone. Only when the number of patches increases by the breaking apart of habitats do we find that both habitat loss and fragmentation per se are involved in the decreasing

size and increasing isolation of habitat patches (Fig. 1).

When habitat amount is held constant or controlled for, fragmentation generally has either no effect (Middleton and Merriam 1983, Hamel et al. 1993) or a negative effect on population survival (Burkey 1989, 1995; Atmar and Patterson 1993, Adler and Nuernberger 1994, Andr n 1994, Irlandi 1994, Dytham 1995). However, because habitat loss and fragmentation typically occur together, it is not clear which process has the larger effect on extinction. If fragmentation is important, then within some limits it should be possible to mitigate effects of habitat loss by ensuring that remaining habitat is not fragmented. On the other hand, if the effects of fragmentation are trivial in comparison to the effects of loss, then the assumption that loss can be mitigated by reduced fragmentation (Kareiva and Wennergren 1996) has potentially dangerous consequences for conservation (Danielson 1994). The goal of this study therefore was to assess the relative importance of habitat loss and fragmentation on population extinction.

This work was supported by a Natural Sciences and Engineering Research Council of Canada grant to the author. C. Cui assisted with computer programming. I am grateful to J. Faaborg and J. Meyer for reviews of the manuscript.

METHODS

I constructed a spatially-explicit simulation model (Figs. 2-5), in which parameters deter-

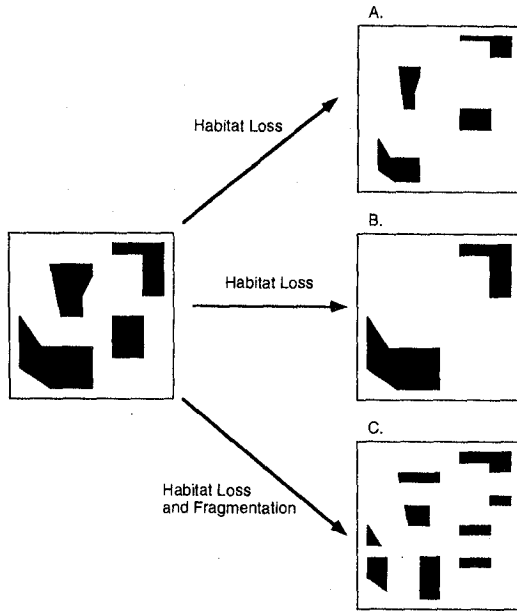


Fig. 1. Effects of habitat loss and fragmentation on patch size and isolation. A. If habitat loss results in a constant number of smaller patches, then patch size effects are due to habitat loss alone. B. If whole patches are removed from the landscape, then isolation of remaining patches increases but fragmentation per se is actually decreased since there are fewer patches; in this case isolation effects are due to habitat loss alone. C. When the number of patches increases by the breaking apart of habitat, both habitat loss and fragmentation per se are involved in decreasing size and increasing isolation of habitat patches.

mining amount of breeding habitat (COVER), and fragmentation of breeding habitat (FRAG) can be varied independently. The model includes additional parameters that determine the life history and movement attributes of a hypothetical organism living in the simulated landscape. The model is stochastic and individual-based. Space is represented in a 2-dimensional rectangular landscape of "cells"; the landscape size in the simulations is 900 cells (30 x 30). There are 2 kinds of cells: breeding habitat and nonbreeding habitat; reproduction can occur only in breeding habitat.

Fragmentation of breeding habitat takes on a value between (but not including) 0 and 1, where low values result in low fragmentation and high values result in high fragmentation. To initialize the spatial pattern of breeding habitat on the landscape at the beginning of a simulation run (Fig. 3), I begin with no breeding habitat and then repeat the following steps until the proportion of the grid in breeding habitat has reached COVER: (1) a cell is selected at ran-

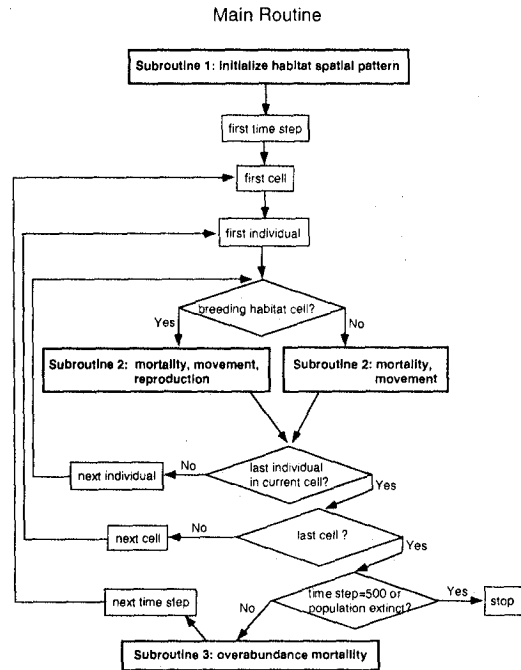


Fig. 2. Flow diagram of the main routine in the simulation model.

dom; (2) a random number between 0 and 1 is selected; (3) if the selected cell has a neighboring cell that has been assigned as breeding habitat or if the random number is less than FRAG,

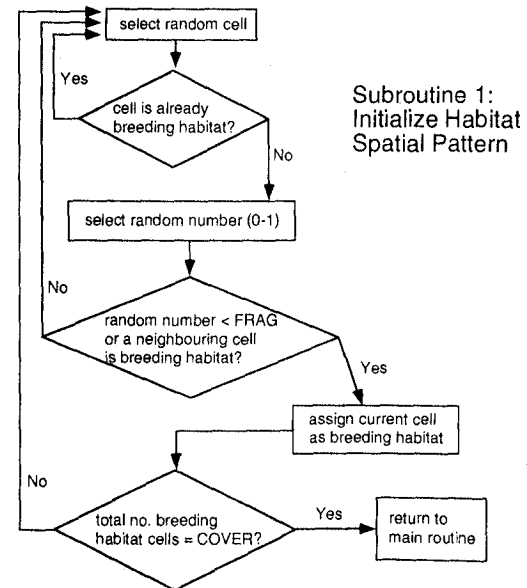


Fig. 3. Flow diagram of the model subroutine for initialization of the spatial pattern of breeding habitat.

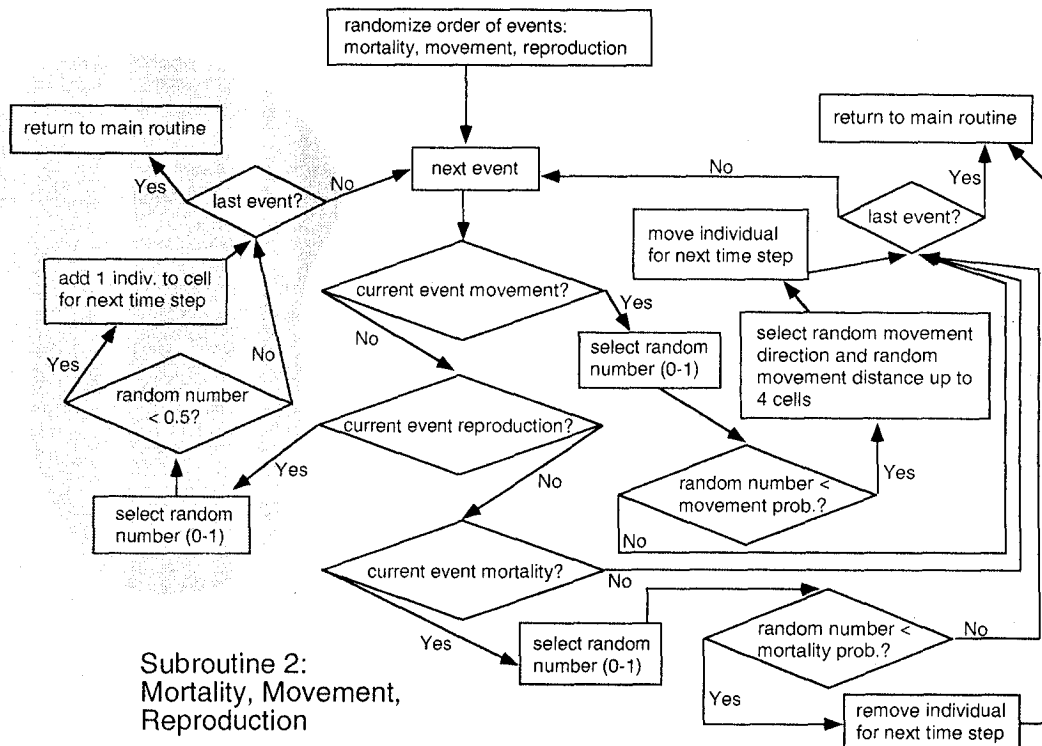


Fig. 4. Flow diagram of the model subroutine for individual mortality, movement, and reproduction. The shaded portion (reproduction) is implemented only if the individual is in breeding habitat. Movement probabilities per time step are 0.5 and 1.0 in breeding and nonbreeding habitat. Mortality probabilities per time step are 0.05 and 0.5 in breeding and nonbreeding habitat.

then the selected cell is assigned as breeding habitat. This algorithm for fragmentation is essentially the same as correlated or interacting percolation models (Anderson and Family 1988, Plotnik and Gardner 1993). The spatial pattern

of breeding habitat is then constant throughout the simulation run.

For the current simulations, life history and movement parameters were set at values resulting in the largest possible effect of FRAG on extinction time, as determined in preliminary runs (Fig. 6). Therefore, the results of this study give the maximum importance of FRAG relative to COVER. In retrospect, this produced the most conservative possible results because FRAG was found to be much less important than COVER in affecting extinction probability and extinction time.

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 (Fig. 4). Probabilities of reproduction and movement are density-independent. Probability of death is density-independent as long as the population is below the maximum capacity of a cell (10 in the current simulations). However, if the cell population exceeds the maximum, individuals are killed at random to reduce the population to the maximum capacity (Fig. 5).

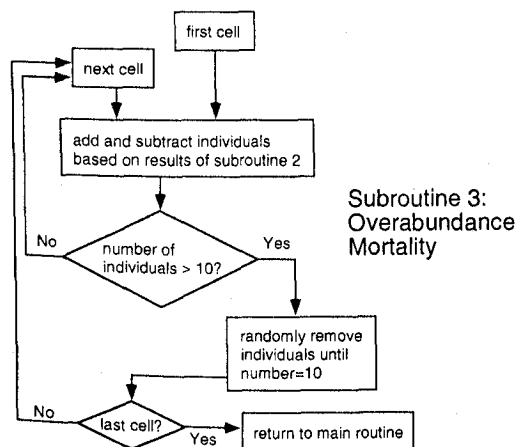


Fig. 5. Flow diagram of the model subroutine for overabundance mortality.

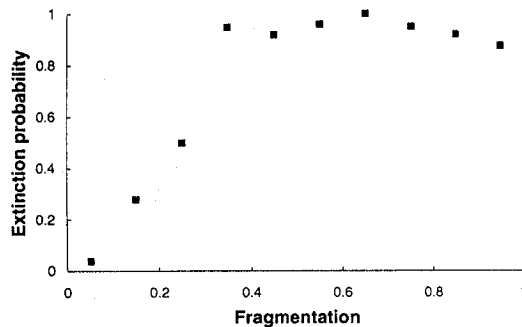


Fig. 6. Illustration of maximum effect of breeding habitat fragmentation (FRAG) on extinction probability, based on 200 simulation runs. All model parameter values (except FRAG) were held constant among runs, at values that maximize the effect of FRAG; all simulated landscapes contained 10% breeding habitat. Extinction probabilities were estimated as the fraction of runs extinct, calculated within FRAG ranges of 0.1; probabilities are plotted at range midpoints. Increasing fragmentation of breeding habitat significantly increases the probability of extinction because it increases the ratio of habitat edge to interior. This increases the probability that individuals move into nonbreeding habitat, where survival rate is lower. Population growth is therefore lowered by a reduction in both reproductive and survival rates.

Reproduction occurs only in breeding habitat and is determined by the probability of reproduction per time step per individual (0.5 in the current runs) and the number of offspring per reproduction event (1 in the current runs). Probability of mortality is much lower in breeding habitat than in nonbreeding habitat (0.05 and 0.5/time step in the current simulations).

Individuals move with some probability each time step. Movement probability is lower if the individual is in a breeding habitat cell than a nonbreeding cell, on the assumption that individuals in nonbreeding habitat "want" to move to breeding habitat; movement probabilities in the current simulations were 0.5 and 1.0 for breeding and nonbreeding habitat. Movement direction is taken as a random angle. Movement distance is also random, but is limited to a maximum of 4 cells per time step in the current simulations. From the point of view of moving individuals, the landscape is "wrapped": an individual that crosses the edge of the landscape continues in the same direction on the opposite edge (Haefner et al. 1991). Note that the rate of emigration from patches increases with decreasing patch size in this model because individuals in smaller patches have a higher probability of crossing the patch edge, than do individuals in larger patches, for a given movement distance.

Two thousand simulation runs were conduct-

ed. For each run, values were randomly selected for FRAG (range 0–1) and COVER (range 0–1). Each simulation began with 500 individuals distributed randomly over the landscape and was conducted for 500 time steps or until the population went extinct, whichever came first. The 500 time step limit was based on a series of preliminary runs using a maximum run period of 2,000 time steps, in which I found that any population that survived for the initial 500 time steps survived for the full 2,000 steps. For each run I recorded whether or not the population went extinct, and the extinction time for those that went extinct. The results were analyzed with multiple logistic regression analysis and multiple regression analysis (SAS Inst. Inc. 1990).

RESULTS

Amount of breeding habitat had a much greater effect than FRAG on extinction probability (Table 1A; Figs. 7A, 8A). In fact, in all simulation runs with COVER >0.2, the population survived for the full 500 time steps (Fig. 7A). Fragmentation effects are expected only when amount of habitat is less than about 10–30% of the landscape (Andrén 1994). When I limited the dataset to the 417 runs with COVER less than 0.2, the results were almost identical to the results when all 2,000 runs were included: the effect of COVER far outweighed the effect of FRAG on extinction probability (Table 1B, Figs. 7B, 8B). Note that the shape of the relation in Fig. 8B reflects the relation shown in Fig. 6 (where COVER = 0.1). However, in Fig. 8B, extinction probability never reaches 1 because at all levels of FRAG there are some runs with relatively high COVER values (near 0.2); these populations are highly likely to persist.

I also conducted multiple regression analysis of extinction time on COVER and FRAG, using the 210 runs that went extinct within 500 time steps (Table 1C; Figs. 7C, 8C). Again, COVER has a large effect on extinction time; no effect of FRAG was detected.

DISCUSSION

A possible criticism of the model is the relatively simplistic algorithm for simulation of movement behavior. However, the movement algorithm also produces a conservative result because more complicated movement assumptions are likely to reduce the effect of fragmen-

Table 1. Analyses of simulation results.

A. Multiple logistic regression analysis based on all 2,000 simulation runs. Response variable is 0/1 for extinct/not extinct within 500 simulation time steps.

Source	Deviance	Prob. Type I error	Parameter
Intercept	59.5	0.0001	3.7
Amount of breeding habitat	119.5	0.0001	-48.7
Fragmentation of breeding habitat	18.7	0.0001	2.4

B. Multiple logistic regression analysis based on the 417 simulation runs with amount of breeding habitat < 0.2. Response variable is 0/1 for extinct/not extinct within 500 simulation time steps.

Source	Deviance	Prob. Type I error	Parameter
Intercept	55.6	0.0001	3.6
Amount of breeding habitat	109.4	0.0001	-47.8
Fragmentation of breeding habitat	18.7	0.0001	2.4

C. Multiple regression analysis based on the 210 simulation runs in which the populations went extinct within 500 simulation time steps. Response variable is survival time.

Source	t for H ₀ : par. = 0	Prob. Type I error	Estimate
Intercept	0.7	0.49	6.7
Amount of breeding habitat	12.2	0.0001	1,191.8
Fragmentation of breeding habitat	-0.7	0.51	-9.4

tation. If individuals follow movement corridors (Beier 1993, Bennett et al. 1994) or orient toward new breeding habitats from some distance (Fahrig and Paloheimo 1988), then fragmented breeding habitats are joined effectively into non-fragmented habitats, reducing the effect of fragmentation. Therefore, although the movement assumptions are unrealistic for many organisms, they are conservative in the sense that they increase the likelihood of observing an effect of fragmentation on extinction.

Several theoretical studies have examined the effects of either habitat loss (Lande 1987, Lawton et al. 1994, Tilman et al. 1994, Dytham 1995, Hanski et al. 1996, Venier and Fahrig 1996) or fragmentation (Adler and Nuernberger 1994; others reviewed in Durrett and Levin 1994). Bascompte and Solé (1996) included both habitat loss and fragmentation in a theoretical study of factors determining extinction thresholds. However, to my knowledge this is the first theoretical investigation of the relative importance of habitat loss and fragmentation. An explicitly spatial approach was taken in order to separate these 2 effects (Bascompte and Solé 1996).

The simulation results suggest that habitat loss has a much larger effect than habitat fragmentation per se on population extinction. While several empirical studies have examined effects of fragmentation under constant habitat amount (Middleton and Merriam 1983, McLellan et al. 1986, Hamel et al. 1993, Atmar and Patterson 1993, Irlandi 1994, Burkey 1995), I

know of only one study that examined the independent effects of both habitat loss and fragmentation. McGarigal and McComb (1995) sampled vegetation and birds in 30 landscapes in Oregon, and developed measures of forest configuration (fragmentation) that were statistically independent from forest amount. When they examined the independent effects of habitat area and configuration on bird abundance, they found that "with the exception of a few 'edge' species, variation in abundance among landscapes was more strongly related to changes in habitat area; habitat configuration was of secondary importance."

To apply the simulation results to real species, it is important to correctly define the species' habitat. For example, in the context of forest loss and fragmentation, loss of habitat is greater than the loss of forest for forest interior species, and loss of habitat is less than the loss of forest for forest edge species (there even may be an increase in habitat amount for edge species; Fig. 9). In addition, some edge species, such as the brown-headed cowbird (*Molothrus ater*) have negative effects on habitat quality for other species (e.g., neotropical migrants) thus reducing or eliminating their reproductive success in forest edge (Robinson et al. 1995). This can be viewed as a loss of suitable habitats for those species. To identify the independent effects of loss and fragmentation for edge or interior species, the landscape must be mapped in terms of the actual habitat of the species, and not simply as forest/nonforest.

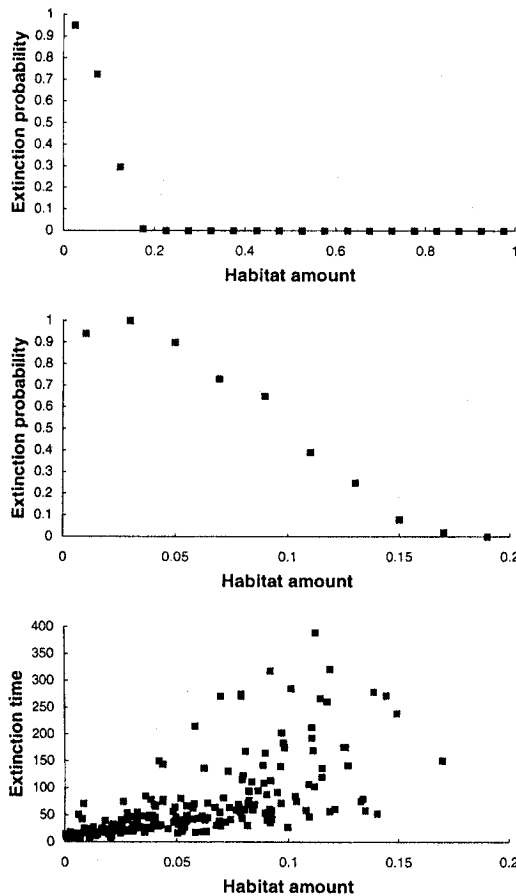


Fig. 7. Relation between proportion of landscape in breeding habitat (COVER) and A. extinction probabilities based on all 2,000 runs, B. extinction probabilities based on only the 417 runs with amount of breeding habitat < 0.2 , and C. extinction time based on only the 210 runs that went extinct within the 500 time step limit of the simulations. Extinction probabilities are estimated as the fraction of runs extinct, calculated within COVER ranges of 0.05 for plot A and 0.02 for plot B; probabilities are plotted at range midpoints.

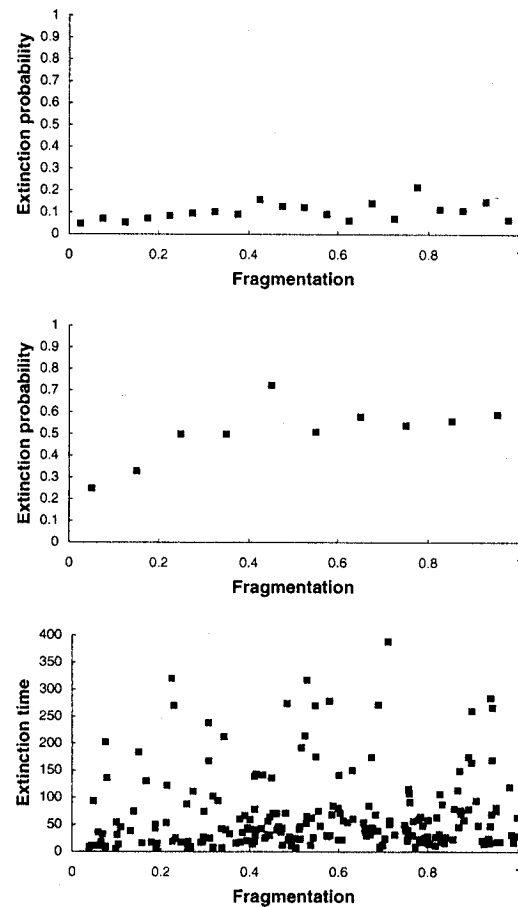


Fig. 8. Relation between fragmentation of breeding habitat (FRAG) and A. extinction probabilities based on all 2,000 runs, B. extinction probabilities based on only the 417 runs with amount of breeding habitat < 0.2 , and C. extinction time based on only the 210 runs that went extinct within the 500 time step limit of the simulations. Extinction probabilities are estimated as the fraction of runs extinct, calculated within FRAG ranges of 0.05 for plot A and 0.01 for plot B; probabilities are plotted at range midpoints.

Also, for any species there is a lower limit to the size of a patch that can act as breeding habitat. As an extreme example, a single old-growth tree in the center of a large clearcut does not represent habitat for a bird requiring old-growth forest as breeding habitat. In the simulations here, the smallest spatial unit (1 cell) had a maximum capacity of 10 individuals. Therefore, the simulations were scaled such that the smallest possible unit represents useable breeding habitat. In applying the results to real species one should omit from the map patches of habitat that are smaller than the minimum for that species.

The results suggest that when breeding hab-

itat covers more than 20% of the landscape, survival is virtually ensured no matter how fragmented the habitat is. The prediction of a threshold in habitat cover is consistent with others (Lande 1987, Lawton et al. 1994, Schneider and Yodzis 1994, Hanski et al. 1996). The exact value of the threshold will depend to some extent on the demographic potential of the organism and the absolute scale of the landscape. However, for large landscapes, the 20% rule is probably realistic. A 20% habitat threshold also has been predicted for survival of the northern spotted owl (*Strix occidentalis caurina*; Lamberson et al. 1992). Of course many organisms, particularly habitat specialists, depend on hab-

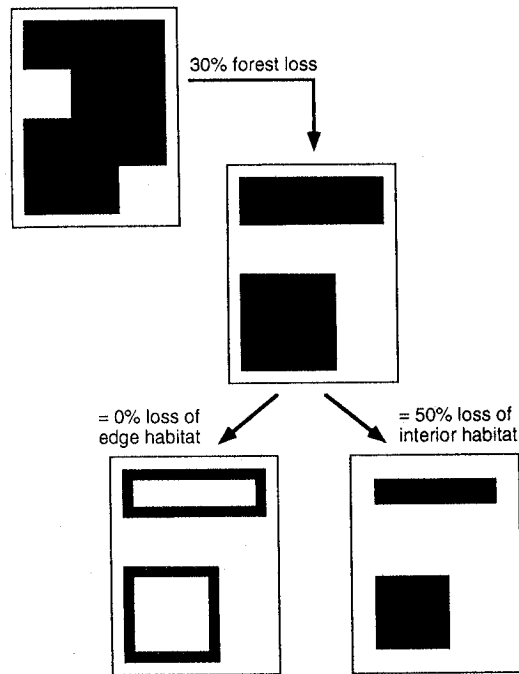


Fig. 9. Effect of forest loss on habitat amount for forest edge vs. forest interior species. In this hypothetical example, loss of 30% forest represents no loss of habitat for a forest edge species, but about 50% loss of habitat for a forest interior species.

itat types that make up less than 20% of the pristine landscape before alterations by human activities. These organisms are likely to be particularly vulnerable to habitat loss.

This study suggests that in fact "details of how habitats are arranged" (Kareiva and Wennergren 1995) are unlikely to mitigate the risks of habitat loss. This result is robust because the default assumptions in the simulation model were selected to maximize the possible effect of habitat fragmentation. To significantly improve survival prospects of endangered species we must therefore stop habitat loss and increase efforts in habitat restoration. Current emphasis in conservation biology on habitat spatial pattern (e.g., Fahrig and Merriam 1994) may be misplaced.

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Received 17 October 1996.

Accepted 17 March 1997.