Relative Importance of Spatial and Temporal Scales in a Patchy Environment

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The purpose of this study was to examine the relative importance of temporal and spatial scales of habitat heterogeneity on regional abundance of populations in patchy environments. Temporal scale is habitat lifespan relative to the generation time of the organism, and spatial scale is the distance between habitat patches relative to the dispersal distance of the organism. A spatially explicit simulation model of population growth and dispersal was constructed for a population that is distributed on a grid. The grid contains two sorts of habitat, useable and non-useable habitat; useable habitat occurs in habitat patches. Habitat patches are transient; they are "born" at random with a specified probability, and they exist for a specified length of time, the patch "lifespan." Distance between patches is directly related to habitat patch size when the fraction of the grid in useable habitat is held constant. A factorial simulation experiment was conducted in which the fraction of the grid in useable habitat was held constant and patch lifespan, patch size, and species dispersal distance were varied. The relative importance of temporal scale (patch lifespan) and spatial scale (patch size, a surrogate for inter-patch distance per species dispersal distance) on regional population size was tested by analysis of variance. Population size increased with increasing temporal scale and decreased with increasing spatial scale. The effect of temporal scale far outweighed the effect of spatial scale. Implications for design of ecological research programmes are discussed.   © 1992 Academic Press, Inc.

INTRODUCTION

Recently there has been growing emphasis in ecology on the "scale problem" which, in most cases, boils down to the question: what is the appropriate scale for study of a particular ecological problem? (Morris, 1987; Hastings, 1988; Smith and Urban, 1988; Brown, 1989; Jessop and Anderson, 1989; Wiens, 1989; Taggart and Frank, 1990; Rose and Leggett, 1990). To understand the relationship of an organism to its environment, one must understand the interactions between the intrinsic scales of heterogeneity within the environment and the scales at which the organism can respond to this heterogeneity. Environmental heterogeneity falls

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into two broad categories: spatial and temporal heterogeneity. Spatial heterogeneity is habitat patchiness. Temporal heterogeneity is variability over time in the extent and quality of habitat, or ecological disturbance ((Rykiel, 1985; Fahrig, 1990a). Environments are heterogeneous on many spatial and temporal scales, while organisms have particular scales on which they can respond to environmental heterogeneity (Fahrig and Paloheimo, 1988a; Kareiva, 1987). For example, an organism's ability to respond to spatial heterogeneity may depend on the distance over which it can disperse, while its ability to respond to temporal heterogeneity may depend on its generation time.

Effects of spatial and temporal scales are almost never included in the same ecological study. For example, two common spatial and temporal habitat scales considered in ecology are habitat patch size and habitat lifespan, respectively. Patch size is central to the debate over nature reserve design (Diamond, 1975; Margules *et al.*, 1982; Burkey, 1989), but in these studies it is assumed that all patches are of infinite lifespan (i.e., they remain indefinitely). Habitat lifespan, on the other hand, is important in studies of ephemeral and disturbed habitats (McKee and Mackie, 1981; Agur and Deneubourg, 1985; Hobbs and Hobbs, 1987; Hastings and Wolin, 1989), but here patch size is ignored. In many ecological systems both patch size and patch lifespan may vary over the range of a species.

The purpose of the present study was to examine the relative impacts of temporal and spatial habitat scales, and the interactions of these scales, on population abundance. Temporal scale in this study is habitat lifespan relative to species generation time, and spatial scale is distance between habitat patches relative to species dispersal distance. The problem was approached using a simulation model of population dynamics in an environment of transient habitat patches.

THE MODEL

The model is of the dynamics of a population in an environment composed of two sorts of habitat: "useable" habitat is habitat in which the organism can survive and reproduce, and "non-useable" habitat is inhospitable to the organism. The useable habitat occurs as discrete patches termed "habitat patches." The habitat patches are transient; they exist for a limited time only, and new habitat patches appear at random. I refer to the appearance and disappearance of habitat patches as patch "births" and "deaths" and the whole process as "habitat dynamics." The model is a simulation model in which time and space are discrete. Time is divided into time "steps" and space is divided into a grid of spatial "cells." The numbers of cells and steps are specified at the start of a simulation.

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TABLE 1

Parameters Used in the Simulation Experiment

(a) Parameters remaining constant among simulations	
Fraction of grid composed of useable cells, H	0.10
Per capita birth rate per step	4.0
Death rate per step	0.75
Age at maturity	1 step
Maximum population per useable cell	100
Fraction of population dispersing per step	0.20

(b) Parameters taking on different values	
Lifespan of patches, L	1, 7, 13, 19, 25 steps
Size of patches, S	1, 6, 11, 16, 21 cells
Mean dispersal distance, Z	1, 3, 5, 7, 9 cells
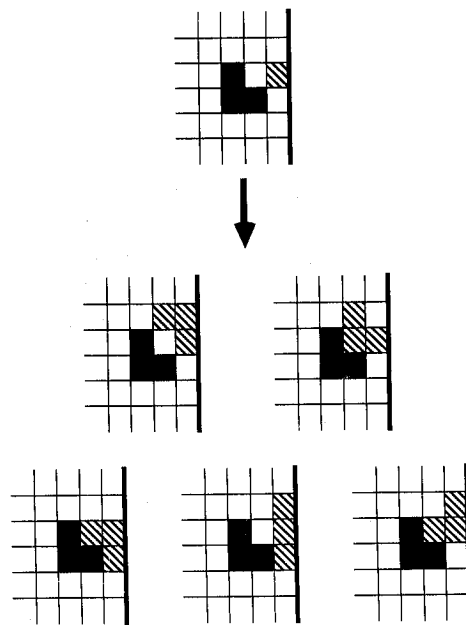
Fig. 1. Illustration of patch "birth." The patch size is 3 cells. The solid patch is "left over" from the previous time step, i.e., has not "died" yet. In the first frame the shaded cell has been identified (procedure described in text) as the centre of a new patch. The following 5 frames are the 5 possible configurations for the new patch; the one actually used in the simulation is chosen at random. Note that the patch does not overlap with the existing patch, and the patch is constrained by its proximity to the edge of the grid.

Within a time step, the sequence of events is (i) patch births, (ii) survival and reproduction of organisms, (iii) dispersal of organisms, and (iv) patch deaths. The parameter values used in the simulations are in Table I.

Habitat Dynamics

In any time step, each spatial cell is either useable or non-useable habitat. The useable cells are grouped to form the habitat patches. The size of the grid in cells (G), the fraction of the grid that is made up of useable habitat (H), the size of habitat patches in number of cells (S), and the lifespan of patches (L) are set at the start of a simulation. The probability of patch birth per cell per time step (B) is calculated from these as described below. The following method is then used to simulate the habitat dynamics. A counter moves sequentially to each cell on the grid. If the cell is not already part of a habitat patch, a random number is drawn from a uniform distribution (0 to 1). If the number is less than B the cell forms the centre of a new habitat patch, i.e., there is a patch birth. The patch is then enlarged to the prescribed size S by adding cells concentrically around the initial cell (see Fig. 1). When there are more than one equivalent possibilities for the location(s) of the additional cell(s), the choice is made randomly. Patches may be contiguous but they do not overlap.

Probability of patch birth (B). The simulation is divided into two phases: the set-up period and the simulation proper. The purpose of the set-up period is to avoid synchrony in patch births and deaths. The idea is to stagger the births of patches over time so that at the start of the simulation proper the prespecified fraction H of the space is filled with habitat patches, but these patches range in age. The number of time steps in the set-up period is equal to L, the patch lifespan. By the end of the setup period there are approximately GH cells in habitat patches, where G is the size of the grid in cells. The number of patches is GH/S. To stagger the patch births over the set-up period, the patch birth rate per time step is divided by the length of the set-up period, L. The probability per cell per time step of patch birth in the set-up period is then H/SL.

During the simulation proper, patches "die" when they have existed for L time steps. When a patch dies it is converted to non-useable habitat, and any organisms that are there die. If the fraction of the grid remaining in useable habitat after patch deaths in time step t is F_t, then the fraction of the grid remaining in non-useable habitat is $1 - F_t$, the fraction of the grid that remains to be converted to useable habitat is $H - F_t$, and the probability of a non-useable cell becoming the centre of a new habitat patch is

$$B_t = \frac{H - F_t}{S(1 - F_t)}. \tag{1}$$

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The probability B is therefore adjusted each time step to account for the areas that remain in habitat patches from the previous time step. This procedure ensures that at all times the proportion of the grid in useable habitat is close to H, but the patches are located randomly on the grid and they are of a range of ages.

Demographics and Dispersal

At the start of the simulation proper there is a number of individuals in each useable habitat cell. The model then keeps track of the population size within each cell. Each time step new individuals are born and some fraction of the population dies. Population growth rate is density-independent, but there is a ceiling to the population size in each cell,

$$N_{t+1,i} = PN_{t,i}(1+R), \quad \text{if} \quad N_{t+1,i} > K \quad \text{then} \quad N_{t+1,i} = K, \quad (2)$$

where $N_{t,i}$ is the population size in time step t and cell i, P is the survival rate, R is the per capita birth rate per time step, and K is the per cell population ceiling.

Dispersal between cells is density-independent. The shape of the dispersal curve away from a point of dispersal (cell a) follows a negative exponential function as in DeAngelis *et al.* (1985), but in two dimensions. The number of dispersers reaching the distance r from a (i.e., landing on the circle with radius r from a) is

$$D_a(r) = 2\pi r\, D_{a,0} e^{-kr}, \quad (3)$$

where k is a parameter that determines the rate of decay of the negative exponential curve, and thereby determines the mean dispersal distance. To find the number dispersing to an annulus around a (delineated by distances r_1 and r_2) we take the difference of the integral of (3) from a to r_2 and a to r_1. The number dispersing to a single cell (b) in this annulus is proportional to the size of the cell relative to the size of the annulus. The immigration rate is

$$D_{a,b} = [2D_{a,0}/(kr_1 + kr_2)][e^{-kr_2}(-r_2 - 1/k) + e^{-kr_1}(r_1 + 1/k)]. \quad (4)$$

If we know (or can assume) the total number of dispersers leaving a (i.e., $D_{a,\text{all}}$), we can substitute $D_{a,0}$ in (4) with $D_{a,\text{all}}k^2/(2\pi)$, obtained by integrating (3) over r from 0 to ∞. The mean dispersal distance is $2/k$. Only dispersers that land on habitat patches survive.

In a spatially explicit model it is necessary to make a decision about what happens to organisms that move beyond the borders of the grid. I calculate the total number of immigrants to each cell using Eq. (4). The sum of these over all cells is the total number of dispersers less the number

that move beyond the borders of the grid. To return these "lost" dispersers to the grid, I redistribute them among the cells in proportion to the calculated immigration. In this way the dispersers all remain on the grid, and the spatial relationships among patches are maintained. This method results in the same bias as for absorbing borders: population abundances are lower at the edge than the middle of the grid.

SIMULATION EXPERIMENT

Scales

The overall goal of the simulation experiment was to compare the relative effects of temporal scale (patch lifespan relative to organism generation time) and spatial scale (interpatch distance relative to organism dispersal distance) on regional population abundance. In the simulations organism generation time is held constant, so temporal scale is the patch lifespan, L.

Spatial scale is more difficult to define. Distance between patches was not explicitly modelled because as new patches are born they are located randomly on the grid. Distance between patches could be varied by varying the amount of space on the grid in useable habitat. However, this would mean that as interpatch distance increased the regional population size would decrease. The effect of inter-patch distance on colonization rate would then be confounded with the effect of regional population abundance on colonization rate. I therefore decided instead to vary dis-
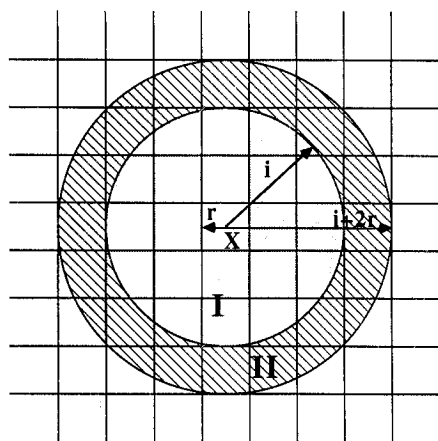

FIG. 2. Illustration for calculation of mean nearest neighbour distance between patches (see text). The case illustrated is for patches of size (S) 1 cell.

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Experimental Design

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tance between patches by holding the amount of space occupied by useable habitat constant and varying patch size. Distance between patches then increases with increasing patch size. The mean nearest neighbour distance between patches can be calculated approximately. Referring to Fig. 2, to calculate the probability that the nearest patch to patch X is in region II:

p (there is no patch in region I) $= (1 - H/S)^{(\pi i^2/S) - 1}$;

p (there is no patch in region II) $= (1 - H/S)^{\pi(i + 2r)^2/S - \pi i^2/S}$, where r is the radius of a patch;

therefore,

p (the nearest patch to X is in region II) $= (1 - H/S)^{(\pi i^2/S) - 1}$ $[1 - (1 - H/S)^{\pi(i + 2r)^2/S - \pi i^2/S}])$.

The mean distance to the nearest patch from X is then

$$NN = \sum_{i=r}^{\infty, \text{by } 2r} i(1 - H/S)^{(\pi i^2/S) - 1} [1 - (1 - H/S)^{\pi(i + 2r)^2/S - \pi i^2/S}]. \quad (5)$$

Note that this is an approximation because the patches are not circular. Equation (5) implies a direct relationship between patch size (S) and distance between patches (NN). Since the spatial scale (M) is defined as the distance between patches relative to the dispersal distance (i. e., $M = NN/Z$), in the simulations it can be approximated by $M = S/Z$.

Experimental Design

The simulation experiment was in a standard factorial design (e.g., Hicks, 1982). Five levels were chosen for each of three parameters: patch lifespan L, patch size S, and species dispersal distance Z. Although the parameter values in the model were constant, the creation of patches was stochastic in space and time as described above. Therefore, 6 replicate runs of each of the 125 combinations were conducted. This allowed detection of any possible two-way interaction effects. The size of the grid was 400 cells (20 by 20), and the starting population size in each habitat cell was 100 individuals. Each simulation ran for 50 time steps, and the average population size per useable cell was computed for the final 20 time steps.

Choice of Parameter Levels

A limitation of simulation experiments (relative to analytical modelling) is that, as in a "real" experiment, each run in the simulation experiment can only give results for one of an infinite number of possible combinations of parameter values. The challenge is to choose meaningful levels for the parameters.

Patch lifespan (*L*).   A population is unable to survive in any environment in which individual patches exist for less than the minimum time required for the organism to reach reproductive age. Also, if new patches are continually being created, as long as patches exist for much longer than the lifespan of the organism, local populations will overlap extensively in time. Colonization of new patches will then be virtually certain; regionally, the habitat will be essentially permanent. The levels of patch lifespan for the simulations were chosen to bracket these extremes. Since the age at reproduction was 1 step, this is the minimum patch lifespan used. With a survival rate of 0.25 per time step, the lifespan of the organism is about 3 time steps. Therefore a maximum patch lifespan of 25 steps should be long enough to approach habitat permanence.

Patch size (*S*).   The smallest patch size used was 1 cell and the largest was 21 cells. The amount of the grid made up of habitat was held constant at 10% for all simulations, so for those simulations in which the patch size was 21 there were, on average, only 2 habitat patches on the grid. This is a minimum reasonable number of patches since, for population survival, it is necessary that when one patch is "born," there is some other patch on the grid from which it can obtain immigrants.

Species dispersal distance (*Z*).   The patch sizes used in the simulation experiment were, 1, 6, 11, 16, and 21 cells. For these patch sizes NN is approximately 1.2, 9.1, 16.5, 24.4, and 31.8 cells, respectively. Because of the relatively small size of the grid used in the present simulations, these

TABLE II

Analysis of Variance of Simulation Results: Dependent Variable Is Mean Population
Size Averaged over Useable Cells

Source	D.F.	Type III S.S.	F-value
(a)			
Temporal scale, *L*	4	23725841	4636
Spatial scale, *M*	24	1825530	60
L × *M*	96	2153228	18
Error	590	739466	
(b)			
Patch lifespan, *L*	4	23349052	3764
Patch size, *S*	4	910222	147
Mean dispersal distance, *Z*	4	803781	130
L × *S*	16	848760	34
L × *Z*	16	1015571	41
S × *Z*	16	104119	4
Error	654	1412560	
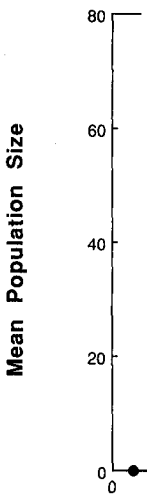
Fig. 3.   Mean populati
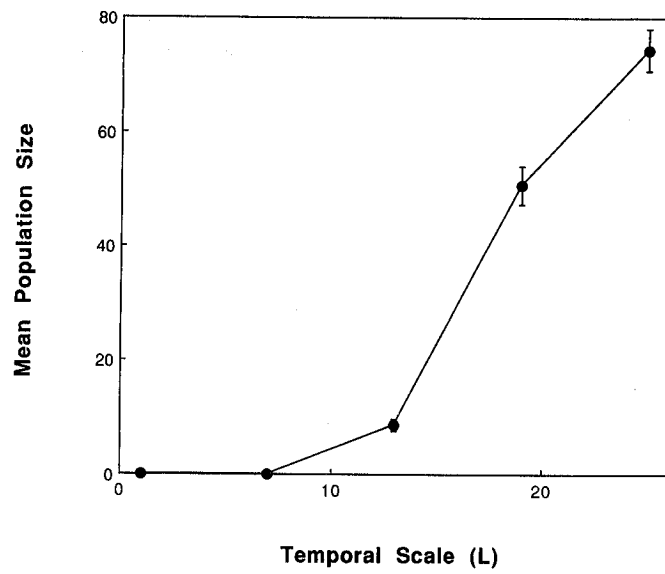intervals.
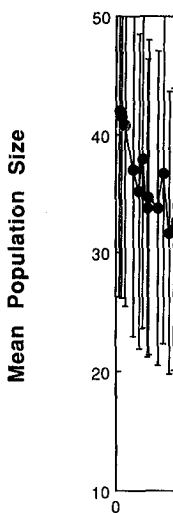
Fig. 4.   Mean populati
intervals.

FIG. 3. Mean population size per useable cell vs. temporal scale, L, with 95% confidence intervals.

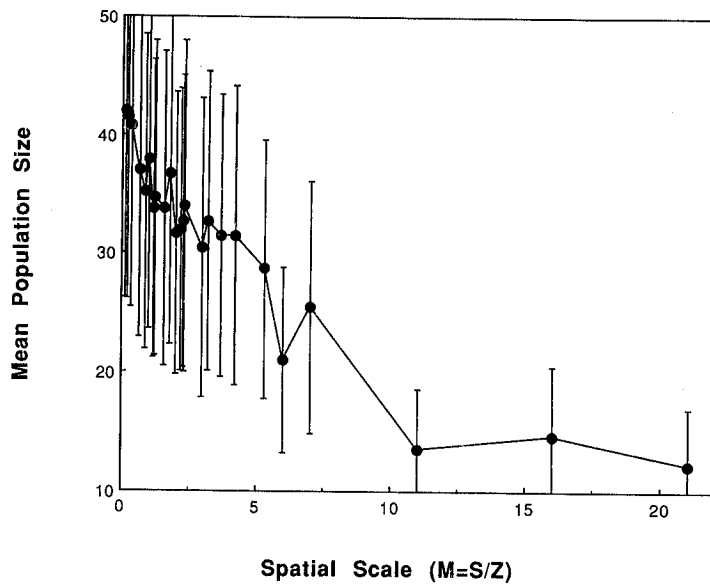
FIG. 4. Mean population size per useable cell vs. spatial scale, M, with 95% confidence intervals.

values of NN are over-estimates for the largest patch sizes. Mean dispersal distances were chosen such that the smallest mean dispersal distance (1 cell) would restrict colonization when inter-patch distances are large, and the largest mean dispersal distance (9 cells) would allow colonization even for the largest inter-patch distances.

Simulation Results

As described in the "The Model" section, each simulation began with a set-up period in which the initialization of patches was distributed over time. There was therefore a small chance in any simulation that at the end of the set-up period (i.e., when population dynamics are initiated) there would be no habitat patches on the grid. In this case the population would go extinct immediately. These amounted to 35 of the 750 simulations, and were omitted from the analyses.

Since the simulation experiment was set up as a factorial experiment, it was appropriate to analyse the output using analysis of variance. The analyses of variance were conducted using the procedure GLM in SAS (1989). Table II(a) gives the analysis of variance for the effects of temporal scale (L) and spatial scale $(M = S/Z)$ and their interaction. L, M, and $L \times M$ all had significant effects on regional population size but L, the temporal scale, was by far the most important, explaining over 85% of the variability. The curves are shown in Fig. 3, 4, and 5. Table II(b) gives the analysis of variance when the components of spatial scale, patch size (S), and dispersal distance (Z) are examined separately. The curves for S and Z are shown in Fig. 6 and 7.
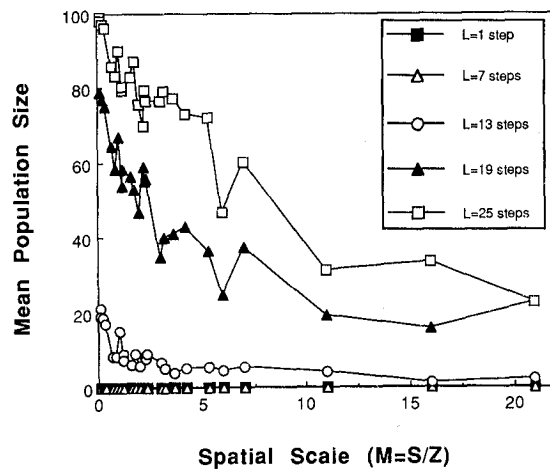

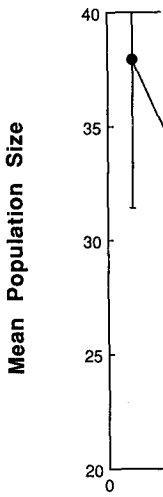FIG. 5. Mean population size per useable cell vs. interaction between L and M.

FIG. 6. Mean population intervals.
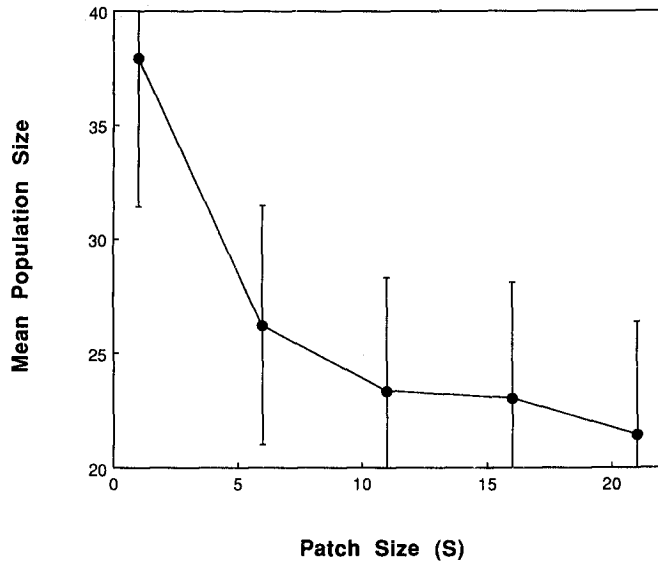

FIG. 7. Mean population confidence intervals.

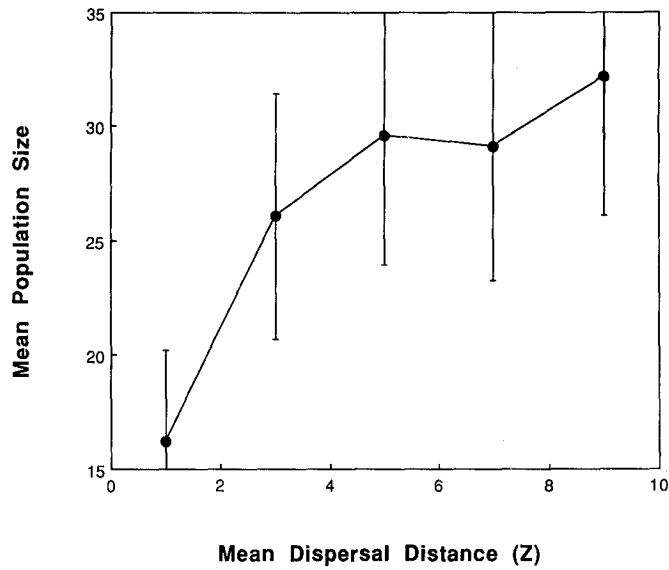FIG. 6. Mean population size per useable cell vs. patch size, S, with 95% confidence intervals.

FIG. 7. Mean population size per useable cell vs. dispersal distance, Z, with 95% confidence intervals.

Regional extinctions were closely tied to temporal scale. All of the simulations with $L = 1$ and $L = 7$ and 15% of the runs with $L = 13$ were regionally extinct before the 50-step time limit. There were no regional extinctions for runs with $L = 19$ or $L = 25$.

DISCUSSION

The overwhelming importance of the temporal scale over the spatial scale was not intuitively obvious, and has interesting implications. This result complements another result (Fahrig, 1990b) in which a simulation experiment suggested that the temporal scale of dispersal (dispersal frequency) far outweighed the spatial scale (dispersal distance) in affecting population recovery from disturbance. This and the present study are the only single-species studies in which the relative importance of temporal and spatial scales are examined (Chesson (1985) compared the effects of spatial, temporal, and spatio-temporal variability on two-species coexistence). Of course, the proviso must be made here that, in the case of a simulation experiment, it can always be argued that the results might be different for different ranges of the parameters than those chosen. The parameter levels in this simulation experiment were deliberately chosen to cover a wide range (Table Ib and "Choice of Parameter Levels" section above).

This result is important in light of recent emphasis on spatial heterogeneity in ecological systems (e.g., Baker, 1989; Barmuta, 1989; Folse et al., 1989; Hansson, 1989; Jessop and Anderson, 1989; Turner et al., 1989). It suggests that in studies of population stability (by any definition), it is critical to determine the degree of temporal variability in the spatial pattern of habitat, relative to the generation time of the organism. In other words, do patches of habitat remain in the same locations for many generations, or do patches disappear and others appear frequently? For example, the population abundance of a herbivore that depends on ephemeral patches of plants should be greatly influenced by whether or not the patches occur predictably in the same places every year. If the habitat of a particular species is essentially permanent relative to the generation time of the species, the result indicates that the spatial scale can be important. However, it appears that such constancy would need to be on the order of habitat lifespan of at least 25 times the generation time of the organism, since in the present simulations this was the maximum used, and even at this level increases in patch lifespan cause an increase in population size (Fig. 3).

The question of the best design of nature reserves has so far been focussed on the trade-off between size and number of reserve fragments (Burkey, 1989). However, the present result suggests that if one is

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attempting to ensure survival of a particular species, the size of reserve fragments may be less important than their persistence over time. Since habitat continually undergoes modification due to processes such as disturbance (natural or man-made), more attention should be placed on the duration of reserve fragments as habitat for the particular species of interest. Of course, the situation is much more complex if the goal is to conserve assemblages of species or entire ecosystems (Baker, 1989).

Experimental studies in ecology tend to be conducted over short time periods, usually between 1 (or less) and a few generations of the species (Tilman, 1989), and over small spatial areas relative to the area that the population covers (Kareiva and Andersen, 1989). Studies such as this one suggest that to make meaningful statements about population size and survival, larger areas and longer timespans must be considered. This is normally an unrealistic expectation of most experimental programs. Therefore, renewed emphasis should be placed on observational (as opposed to experimental) studies. For example, the populations in several patches of different ages could be observed and compared. To design such observational programs, one must first determine the relevant scales for the study. An appropriate way to do this is to use whatever estimates (guesses) are available for the species scales (generation time, dispersal frequency, dispersal distance) and the habitat scales (habitat lifespan, interpatch distances). If habitat is very ephemeral, particulars about spatial parameters such as dispersal distance and inter-patch distance may be ignored. Instead, one may need to study local populations in several habitats of different ages to understand the dynamics of the population as a whole. On the other hand, if habitat is virtually permanent, dispersal and related spatial problems must be considered. In both cases, larger scales than are normally used in ecology are required. Along with renewed emphasis on observational studies, modelling studies will also be important to support and extend the short-term small-scale studies (e.g., Lefkovitch and Fahrig, 1985; Kareiva and Odell, 1987).

A primary goal of studies such as this one is to answer the fundamental scale question: can we identify environments that because of their intrinsic scales of heterogeneity, should favour the population survival of particular species? This question is very difficult, because it implies that to understand the relationship between an organism and its environment the organism must be studied in all possible environments (having different scales of heterogeneity). In other words, the "right" scale for a study is not necessarily intrinsic to the species but depends on the particular location of the study. If the habitat–species relationships were to be determined solely through empirical study, the organism must be studied everywhere in its range to be understood. To overcome this problem we need to develop general hypotheses about the relationships between environmental and

organism scales. Such hypotheses should allow one to focus on the most relevant components of heterogeneity in particular situations. They can be developed either from analytical models (e.g., Gurney and Nisbet, 1978; Hastings and Wolin, 1988; Chesson and Huntly, 1988), or if the problem cannot be solved analytically, from relatively simple simulation models (e.g., Lefkovitch and Fahrig, 1985; Fahrig, 1988; Fahrig and Paloheimo, 1988b; Turner *et al.*, 1989; this paper).

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REFERENCES

AGUR, Z., AND DENEUBOURG, J. L. 1985. The effect of environmental disturbances on the dynamics of marine intertidal populations, *Theor. Pop. Biol.* **27**, 75–90.

BAKER, W. L. 1989. Landscape ecology and nature reserve design in the boundary waters canoe area, Minnesota, *Ecology* **70**, 23–35.

BARMUTA, L. A. 1989. Habitat patchiness and macrobenthic community structure in an upland stream in temperate Victoria, Australia, *Freshwater Biol.* **21**, 223–236.

BROWN, M. W. 1989. Density dependence in insect host–parasitoid systems: A comment, *Ecology* **70**, 776–779.

BURKEY, T. G. 1989. Extinction in nature reserves: The effect of fragmentation and the importance of migration between reserve fragments, *Oikos* **55**, 75–81.

CHESSON, P. L. 1985. Coexistence of competitors in spatially and temporally varying environments: A look at the combined effects of different sorts of variability, *Theor. Pop. Biol.* **28**, 263–287.

CHESSON, P., AND HUNTLY, N. 1988. Community consequences of life-history traits in a variable environment, *Ann. Zool. Fenn.* **25**, 5–16.

DEANGELIS, D. L., WATERHOUSE, J. C., POST, W. M., AND O'NEILL, R. V. 1985. Ecological modelling and disturbance evaluation, *Ecol. Modell.* **29**, 399–419.

DIAMOND, J. M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of nature reserves, *Biol. Conserv.* **7**, 129–145.

FAHRIG, L. 1988. A general model of populations in patchy habitats, *Appl. Math. Comput.* **27**, 53–66.

FAHRIG, L. 1990a. Interacting effects of disturbance and dispersal on individual selection and population stability, *Comments Theor. Biol.* **1**, 275–297.

FAHRIG, L. 1990b. Simulation methods for developing general landscape-level hypotheses of single-species dynamics, *in* "Quantitative Methods in Landscape Ecology" (M. G. Turner, and R. H. Gardner, Eds.), Springer-Verlag, New York (in press).

FAHRIG, L., AND PALOHEIMO, J. 1988a. Effect of spatial arrangement of habitat patches on local population size, *Ecology* **69**, 468–475.

FAHRIG, L. AND PALOHEI... habitats, *Theor. Pop. Bi...*

FOLSE, L. J., PACKARD, J. ... in a heterogeneous habi...

GURNEY, W. S. C., AND N... environments, *Am. Nat...*

HANSSON, L. 1989. Predat... *Oikos* **54**, 117–119.

HASTINGS, A. 1988. Food ...

HASTINGS, A. AND WOLIN, ... **70**, 1261–1266.

HICKS, C. R. 1982. "Funda... Winston, New York.

HOBBS, R. J., AND HOBBS, ... to patchy soil disturban...

JESSOP, B. M., AND ANDI... temporal pattern of j... (*A. aestivalis*) density or... 1564–1574.

KAREIVA, P. 1987. Habita... *Nature* **326**, 388–390.

KAREIVA, P., AND ANDERSI... models and experiment... New York.

KAREIVA, P., AND ODELL, ... predators use area restr...

LEFKOVITCH, L. P., AND ... population survival, *Ec...*

MARGULES, C., HIGGS, A.... any lessons for nature r...

MCKEE, P. M., AND MAC... *Sphaerium occidentale* ... 2219–2229.

MORRIS, D. W. 1987. Ecol...

ROSE, G. A., AND LEGGET... correlations: An exampl...

RYKIEL, E. J., JR. 1985. T... *Ecology* **10**, 361–365.

SAS INSTITUTE INC. 1989. ... Institute Inc., Cary, NC

SMITH, T. M., AND URBA... *Vegetatio* **74**, 143–150.

TAGGERT, C. T., AND FRAM... processes: probing the s... Marine Ecosystems" (K... AAAS, Washington, DC

TURNER, M. G., GARDNER... spread of disturbance a...

TILMAN, D. 1989. Ecologic... Term Studies in Ecolog...

WIENS, J. A. 1989. Spatial

FAHRIG, L. AND PALOHEIMO, J. 1988b. Determinants of local population size in patchy habitats, *Theor. Pop. Biol.* **34**, 194–213.

FOLSE, L. J., PACKARD, J. M., AND GRANT, W. E. 1989. AI modelling of animal movements in a heterogeneous habitat, *Ecol. Modell.* **46**, 57–72.

GURNEY, W. S. C., AND NISBET, R. M. 1978. Single-species population fluctuations in patchy environments, *Am. Nat.* **112**, 1075–1090.

HANSSON, L. 1989. Predation in heterogeneous landscapes: how to evaluate total impact? *Oikos* **54**, 117–119.

HASTINGS, A. 1988. Food web theory and stability, *Ecology* **69**, 1665–1668.

HASTINGS, A. AND WOLIN, C. L. 1989. Within-patch dynamics in a metapopulation, *Ecology* **70**, 1261–1266.

HICKS, C. R. 1982. "Fundamental Concepts in the Design of Experiments," Holt, Rinehart & Winston, New York.

HOBBS, R. J., AND HOBBS, V. J. 1987. Gophers and grassland: A model of vegetation response to patchy soil disturbance, *Vegetatio* **69**, 141–146.

JESSOP, B. M., AND ANDERSON, W. E. 1989. Effects of heterogeneity in the spatial and temporal pattern of juvenile alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*) density on estimation of an index of abundance, *Can. J. Fish. Aquat. Sci.* **46**, 1564–1574.

KAREIVA, P. 1987. Habitat fragmentation and the stability of predator–prey interactions, *Nature* **326**, 388–390.

KAREIVA, P., AND ANDERSEN, M. 1988. Spatial aspects of species interactions: The wedding of models and experiments, *in*, "Community Ecology" (A. Hastings, Ed.), Springer-Verlag, New York.

KAREIVA, P., AND ODELL, G. M. 1987. Swarms of predators exhibit "preytaxis" if individual predators use area restricted search, *Am. Nat.* **130**, 233–270.

LEFKOVITCH, L. P., AND FAHRIG, L. 1985. Spatial characteristics of habitat patches and population survival, *Ecol. Modell.* **30**, 297–308.

MARGULES, C., HIGGS, A. J., AND RAFE, R. W. 1982. Modern biogeographic theory: are there any lessons for nature reserve design? *Biol. Conserv.* **24**, 115–128.

MCKEE, P. M., AND MACKIE, G. L. 1981. Life history adaptations of the fingernail clams *Sphaerium occidentale* and *Musculium securis* to ephemeral habitats, *Can. J. Zool.* **59**, 2219–2229.

MORRIS, D. W. 1987. Ecological scale and habitat use, *Ecology* **68**, 362–369.

ROSE, G. A., AND LEGGETT, W. C. 1990. The importance of scale to predator–prey spatial correlations: An example of Atlantic fishes, *Ecology*, in press.

RYKIEL, E. J., JR. 1985. Towards a definition of ecological disturbance, *Australian Journal of Ecology* **10**, 361–365.

SAS INSTITUTE INC. 1989. SAS/STAT user's guide, version 6, fourth edition, Volume 2. SAS Institute Inc., Cary, NC.

SMITH, T. M., AND URBAN, D. L. 1988. Scale and resolution of forest structural pattern, *Vegetatio* **74**, 143–150.

TAGGERT, C. T., AND FRANK, K. T. 1990. Perspectives on larval fish ecology and recruitment processes: probing the scales of relationships, *in*, "Patterns, Processes, and Yields of Large Marine Ecosystems" (K. Sherman and L. M. Alexander, Eds.), AAAS Selected Symposium, AAAS, Washington, DC.

TURNER, M. G., GARDNER, R. H., DALE, V. H., AND O'NEILL, R. V. 1989. Predicting the spread of disturbance across heterogeneous landscapes, *Oikos* **55**, 121–129.

TILMAN, D. 1989. Ecological experimentation: Strengths and conceptual problems, *in*, "Long-Term Studies in Ecology" (G. E. Likens, Ed.), Springer-Verlag, New York.

WIENS, J. A. 1989. Spatial scaling in ecology, *Funct. Ecol.* **3**, 385–397.