# Determinants of Local Population Size in Patchy Habitats

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The purpose of this study was to develop hypotheses concerning factors affecting the abundance of local populations in patchy habitats.

Our approach was to propose a model of populations in patchy habitats that includes specific spatial relationships among patches (i.e., local or subpopulations). We considered six components of population demography and dispersal: (i) intrinsic rate of population increase, (ii) patch carrying capacity, (iii) fraction of organisms dispersing from patches, (iv) mean dispersal distance away from patches, (v) distance from which dispersers are able to detect new patches, and (vi) rate of immigration from outside the areas under consideration. We then conducted simulation experiments and analysed the results to generate the hypotheses.

The following two hypotheses resulted. First, the most important determinants of average patch population size are the probability of dispersers detecting new patches (positive relationship), and the fraction of organisms dispersing from the patches (negative relationship). Second, the most important factor determining whether the exact spatial relationships among patches influence local population size is dispersal distance. If the average dispersal distance for the species is low relative to the average interpatch distance, the spatial pattern of habitat patches can have an important impact on local population size. Implications of the hypotheses are discussed.   © 1988 Academic Press, Inc.

## INTRODUCTION

The breeding habitat of most species is not uniformly distributed over space, but occurs as discrete habitat patches. Populations are therefore divided into subpopulations that are interconnected to varying degrees through dispersal among habitat patches. Theoretical studies have suggested the importance of this spatial heterogeneity for overall population survival (e.g., Roff, 1974a,b; DeAngelis *et al.*, 1979; Lomnicki, 1980; Hastings, 1982; Vance, 1984; Roughgarden and Iwasa, 1986), and abundance (e.g., Myers, 1976; Taylor and Taylor, 1977; Hanski, 1982,

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1985). Spatial heterogeneity can also determine the persistence of interacting species (e.g., Levin, 1974; Shmida and Ellner, 1984; Comins and Noble, 1985; Holt, 1985; Chesson and Murdoch, 1986).

Although habitat patchiness may enhance overall population survival, few studies have addressed the effects of the spatial relationships between a particular patch and other patches in a region (i.e., the effects of exact patch spatial arrangement) on local population dynamics. Most studies deal with regional populations. The degree to which the spatial arrangement of habitat affects population dynamics apparently depends to a large extent on the dispersal characteristics of a species. For example, if a species disperses among habitat patches using "dispersal corridors," as in white-footed mice (*Peromyscus leucopus*), then the pattern in which the patches are interconnected (i.e., their spatial arrangement) has an important effect on population dynamics (Fahrig and Merriam, 1985; Fahrig *et al.*, 1983; Lefkovitch and Fahrig, 1985). If dispersers find new patches by chance, however, as in cabbage butterflies (*Pieris rapae*) (Fahrig and Paloheimo, 1987) then the spatial arrangement of habitat has less effect on population dynamics (Fahrig, 1988; Fahrig and Paloheimo, 1988).

Consideration of the exact spatial arrangement of habitat greatly increases the complexity of a theoretical study. Equations are much simpler if spatial arrangement is excluded by assuming that all patches are equally accessible to all dispersers or that the habitat patches are evenly distributed in space. If one is considering questions concerning only the global population (all local populations combined), then such assumptions may have little effect on model predictions (e.g., Vance, 1984). However, if one is interested in understanding the dynamics of local populations, and if the actual spatial arrangement of habitat is likely to affect local population dynamics for a particular species, then such simplifying assumptions may be inappropriate. The purpose of this study is to develop hypotheses that suggest the types of species for which the spatial arrangement of habitat patches is expected to have an important impact on local population abundance.

## Methods

We approached this problem by developing a simple model of population dynamics in patchy habitats. This model includes the explicit spatial arrangement of habitat patches, and basic parameters of population growth and dispersal. We then conducted simulations using the model, to develop qualitative predictions concerning the types of species for which the spatial arrangement of habitat patches is expected to have the largest influence on local population abundance.

*The Model*

The model is a stochastic discrete-time simulation model. Both time and space in the model are in arbitrary units (time steps and spatial units). All parameters are expressed relative to these arbitrary units. There are six main parameters in the model, which determine the population sizes in each patch at each time step. These are (i) $r$, intrinsic population growth rate; (ii) $k$, patch carrying capacity; (iii) $p$, fraction of organisms that disperse from patches in each time unit; (iv) $s$, dispersal distance relative to the mean distance between patches; (v) $d$, distances from which dispersers detect new patches (detection radius) relative to the mean distance between patches; and (vi) $i$, rate of immigration into the region.

The following is a summary of the rationale of the structure of the model, also presented in Fahrig (1988). There were three general requirements that influenced our choice of model structure. First, the model had to be realistic enough that the results would be relevant for real species. Second, it had to be general enough to be applicable to a range of different species. Finally, it had to have a small number of parameters. This final requirement was important because our approach to the problem was to conduct a large number of simulation experiments, and then analyse for the relative importance of the various parameters (species characteristics) in the simulation outcomes. Since the three model requirements tended to suggest conflicting model structures, our choice was a compromise.

The model consists of two main portions: within-patch population dynamics (i.e., births and deaths) and between-patch dynamics (i.e., immigration and emigration). For within-patch processes we use a discrete approximation to the logistic model. This is a simple model requiring only two parameters ($r$ and $k$) in which population growth rate is limited by the carrying capacity of the patch. More complex and perhaps more realistic models were considered undesirable for two reasons. First, they are generally limited to a narrow range of species because they require assumptions about demographic structure. Second, more complex models usually involve many more parameters than the logistic, such as the survival probabilities of a number of age classes. We therefore chose the logistic, recognising that it is a compromise in favour of generality and simplicity, while sacrificing realism to some extent.

The particular version of the discrete form of the logistic used in this model was

$$N_{t,a} = \text{int}(.5 + N_{t-1,a}(e^{r(1 - N_{t-1,a}/k)} - 1)), \quad \text{if} \quad N_{t,a} < 0 \text{ then } N_{t,a} = 0,$$

where $N_{t,a}$ is the local population size at time $t$ in patch $a$, $r$ is the intrinsic population growth rate, and $k$ is the local carrying capacity; int is a function that truncates the quantity in the parentheses to its integer value (only whole organisms are modelled).

Choice of the approach used for modelling the dispersal behaviour was more involved. The three common methods currently found in the literature for modelling dispersal between patches were considered undesirable in this particular study. The reasons result mainly from the fact that we are concerned with local populations here, while most other studies have dealt with global (or regional) populations. A more detailed discussion of these other models follows.

First, as mentioned above, in many models of patchy populations it is assumed that all patches are equally accessible to dispersers from all patches (e.g., model I in Roff, 1974b; Vance, 1980; Roughgarden and Iwasa, 1986). Although this assumption is clearly not applicable to most species, with the possible exception of "hypothetical benthic marine invertebrates" (Vance, 1980), for certain questions these models have produced interesting insights. However, as pointed out above, models that include it cannot be used to examine the effects of the exact spatial pattern of patches on local populations, a requirement of the model used in this study.

A second common approach to including dispersal in models is to assume that patches are evenly distributed in space and that organisms disperse only to neighbouring patches (e.g., model II in Roff, 1974a,b; Reddingius and den Boer, 1970; Vance, 1984). This approach also prohibits study of various spatial arrangements on local population abundance because the model structure only allows for one spatial arrangement of patches.

A final method of modelling dispersal among patches is the explicit or implicit assumption that certain pairs of patches may be connected by corridors along which dispersers move between them. Dispersal in this type of model takes the form of a matrix of dispersal coefficients (DeAngelis *et al.*, 1979; Fahrig *et al.*, 1983; Lefkovitch and Fahrig, 1985; Urban and Shugart, 1986). If dispersal between patches is assumed to be a discrete passive diffusion process, the matrix becomes a matrix of diffusion coefficients (Hastings, 1982, 1983). This method does allow for various spatial arrangements of habitat patches, as defined by the connections between patches. This type of model is particularly suited to two sorts of species. First, it may apply to animals that disperse along a physical or behavioural dispersal corridor. For example, fish may use streams to disperse between lakes, and small mammals may use fencerows to disperse between woodlots (Fahrig and Merriam, 1985). Second, this type of model may apply to species that do not use dispersal corridors, but whose dispersers die if they disperse into the non-patch area (i.e., dispersers have only one chance to make it to a new patch). This is the case for plant seed dispersal (DeAngelis *et al.*, 1979). It would be possible to modify this type of model and apply it to the many animals, including most insects, which do not disperse along corridors and do not necessarily die when they disperse

into the non-habitat interpatch area. Such modification would likely involve division of the area under consideration into a large number of cells, and specification of the dispersal probabilities between each pair of cells. In the present study we chose not to use this approach, but to look for a simpler method of modelling the wider range of species.

In choosing the structure of the interpatch dispersal portion of the model, we did not use these previously established methods. Instead, we developed a new structure that we feel is relatively realistic and widely applicable, while still requiring only a few parameters (three). We emphasize that our model is well suited to the study undertaken here, but other models will be better suited to other situations. The following is a description of the dispersal portion of the model. Justification of the general structure with respect to the three criteria (realism, generality, and simplicity) is given at the end of this section.

The region under consideration is assumed to consist of discrete patches of breeding habitat surrounded by non-breeding habitat. The explicit spatial arrangement of breeding habitat is included; distances between all pairs of patches are required to calculate dispersal rates among the patches.

Dispersal from each patch is assumed to be, on average, equally likely in all directions, except when one patch is within detection range ($d$) of another. Dispersal is directly proportional to population size in the patches, i.e., dispersal rate ($p$) is not assumed to be density dependent. The reasons for this assumption and its possible effects on the results are taken up in the discussion.

Dispersers from patches are assumed to travel to some mean distance ($s$), expressed as a fraction of the average distance among patches. This normalisation is necessary because the absolute dispersal distance is meaningful only in the context of a particular organism and habitat. We do not assume that all dispersers move exactly the mean dispersal distance, but rather that they are spread out over space around the mean. The mean dispersal distance is taken as the mean of a normal distribution, the standard deviation of which is arbitrarily chosen as 40% of the mean. The left tail of the distribution is truncated so that a negative dispersal distance implies no dispersal. This means that, for large mean dispersal distances, dispersers are spread over a much larger area than for small dispersal distances (see Fig. 1).

The distance from which dispersers can detect a new patch (e.g., visually or by chemoreception) is called the "detection radius" ($d$). Although $d$ is a characteristic of the species, for computational ease we refer to the "detection zone" of patches. This is a circular area around the patch (radius $d$) from within which dispersers are able to detect the patch. Patches are assumed to "attract" all those dispersers that, by chance, fall within the detection zone of the patch. It is possible that the detection zone of a
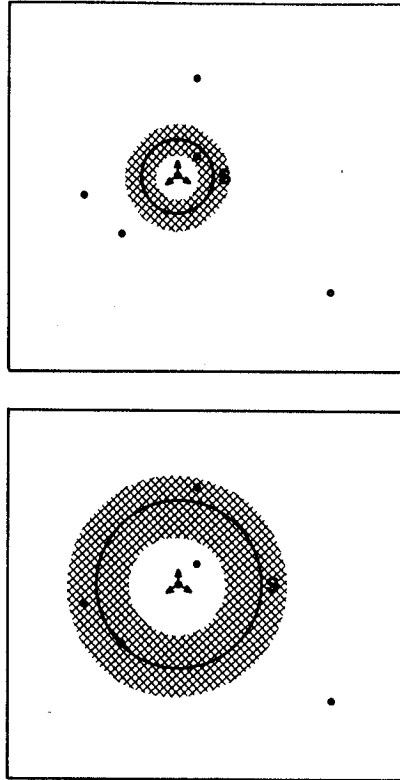
FIG. 1. Illustration of the effect of dispersal distance. Small circles, patches; $S$, mean dispersal distance as a fraction of mean interpatch distance. Above: $S = .25$. Below: $S = .60$. Shaded areas indicate one standard deviation from $S$ (i.e., 40% of $S$). Notice that, if dispersal rates (i.e., fraction of organisms dispersing from patches) are equal, then higher dispersal distances result in successful dispersal to more patches, but much lower numbers of dispersers reaching them.

recipient patch, say $a_1$, overlaps with a patch, say $a_2$, from which organisms are dispersing. This means that organisms in $a_2$ are able to detect $a_1$ from within $a_2$. In this case it is assumed that all organisms that disperse from $a_2$ to a distance less than or equal to the distance from $a_2$ to the outer edge of the detection zone of $a_1$, enter $a_1$. It is also possible that the detection zones of two patches, say $a_3$ and $a_4$, overlap. In this case, those organisms dispersing from a third patch that "land" in the overlap area are divided evenly between $a_3$ and $a_4$. It is assumed that a disperser that finds a patch enters it only if the resident population level is below the carrying capacity of the patch.

The dispersing organisms that fail to find a new patch in a particular time step may die, en igrate from the region, or detect a new patch at some future time step. The sum of mortality and emigration is arbitrarily set at 50%. The individuals that survive and remain in the region until the next time period are assumed to join a "dispersal pool," from which a fraction of organisms enters each patch in each time period. Organisms that immigrate into the region from outside it (immigration rate $= i$) are assumed to enter the dispersal pool before immigrating into the actual patches. As with dispersal from patches, it is assumed that dispersers enter patches from the dispersal pool only if the population in the patch is below the patch carrying capacity. The number of dispersers from the dispersal pool that find patches in one time step is the number of organisms in the dispersal pool times the fraction of the total area that is covered by the detection zones of all of the patches. The total number of organisms from the dispersal pool that enters each patch is proportional to the fraction of this total area that is covered by each patch.

The structure of the dispersal portion of the model is a compromise between realism, generality, and simplicity. That the dispersal assumptions are realistic has been demonstrated by their successful application to the specific case of dispersal of cabbage butterflies (Fahrig and Paloheimo, 1987; Fahrig and Paloheimo, 1988). However, the model is much more general than this sing case, since it can be made to mimic any of the other model structures described above, by modification of its parameters. If one specifies a very large dispersal distance ($s$) (e.g., twice the mean interpatch distance), the model mimics the first type described above, in which all dispersers have equal access to all patches. If one chooses an even spatial arrangement of patches, with no non-breeding area between patches and a mean dispersal distance approximately equal to the distance between the centers of the neighbouring patches, then the model becomes indistinguishable from the second type described above in which dispersal occurs only between neighbouring patches arranged on a grid. Similarly, the model can be made to mimic those which assume dispersal corridors by arranging the patches so that those between which dispersal can occur are within each other's zone of detection ($d$), and by limiting the dispersal distance to about half the mean distance between patches that are linked. The model structure therefore includes the previously suggested structures. However, it also inc des other species, such as those that have a characteristic di persal dis nce (e.g., the cabbage butterfly (Jones *et al.*, 1980; Fahrig and Paloheimo, 1988)), or those that are able to detect new patches from some distance such as dispersing birds.

The dispersal parameters in the model can capture the dispersal characteristics of a wide range of types of organisms. For example, birds inhabiting small forest fragments would have a high value of $d$ since birds

are generally able to see long distances to detect a new forest patch. They would also have high values of $p$ since all juveniles disperse, and $s$ would be low to medium depending on the distance between forest patches. Herbivorous insects in a habitat of patches of host plants would have a low value of $d$ since they have a low ability to detect host plants from a distance (Finch and Skinner, 1982); $p$ and $s$ will depend on the species of insect. For example, aphids and monarch butterflies would have high $p$ and $s$ while some other less mobile butterflies would have low $p$ and $s$ (Ehrlich, 1984). For many plants and fungi the value of $d$ would be 0. For those having wind-dispersed seeds or spores, $p$ and $s$ would generally be high, unless habitat patches are so large that most seeds or spores land within their patch of origin.

Further justification of the structure of dispersal in our model is that it is relatively simple; there are only three parameters that define dispersal between patches ($p$, $s$, and $d$). The simplicity of the model depends to some extent on the inclusion of the dispersal pool. The effects of the exact spatial locations of the patches are preserved, because the number of organisms that disperse directly between patches in each time period is calculated. However, inclusion of the dispersal pool means that it is not necessary to keep track of the exact spatial location of organisms in the non-patch matrix area in each time step. Notice that this means that the exact spatial arrangement of the habitat influences only the dispersing individuals that locate a new patch during the same time period that they emigrate from the old patch. This has the effect of decreasing the overall effect of patch spatial arrangement in the model. Depending on the species, this assumption may be a problem for producing realistic predictions (although see Fahrig and Paloheimo (1988), where this assumption produced realistic predictions for cabbage butterflies). However, for the question we are asking in this study, inclusion of a dispersal pool will not seriously affect the results because we are interested only in the relative importance of patch spatial arrangement, not the absolute importance. In fact, as explained in the discussion it turns out that the dispersal pool assumption renders the results more conservative than they would be if all organisms were explicitly tracked through the non-patch area.

### Simulation Experiments

Two thousand runs of the model were conducted. In each run there were 10 patches, and 150 time steps. A different spatial arrangement of 10 patches was used for each run. The $x$ and $y$ coordinates of each patch were chosen using a uniform random number generator, and the distances between all pairs of patches were then calculated. The initial population size in all patches and for all runs was 100 organisms. The mean values of the six parameters $r$, $k$, $p$, $s$, $d$, $i$ were chosen at random from a uniform

TABLE I

Upper Limits of Parameter Values Used in the Simulation Experiments

| Parameter | Upper limit of mean value |
|---|---|
| $r$ (Growth rate) | 0.1 |
| $k$ (Carrying capacity) | 10,000 |
| $p$ (Dispersal rate) | 1.0 |
| $s$ (Dispersal distance/mean interpatch distance) | 2.0 |
| $d$ (Detection radius/mean interpatch distance) | 0.3 |
| $i$ (Immigration rate) | 1,000 |

*Note.* Lower limit in all cases is 0, standard deviation/mean is 0.1.

distribution at the beginning of each run. The ranges of these parameters are given in Table I. Stochastic variation in the parameters was included, so that their actual values fluctuated randomly among the 10 patches (except $i$) and between the time periods. The value used for a parameter in a particular step in the simulation was drawn from a normal distribution, centered on the mean value of the parameter, and having standard deviation arbitrarily set at 10% of the mean.

The population size in each of the patches was calculated for the 150 time steps. Only the results from the final 100 time steps were included in the analyses, to allow for a "settling down" period in the dynamics. If the spatial location of patches has a large impact on local population sizes, then one would expect to find large differences among patches, due to their spatial relationships with the remaining patches. For example, one might expect the population sizes in centrally located patches to be higher than in peripheral patches, if patch spatial arrangement is important. Therefore, the type of variable that would be appropriate for measuring the effect of spatial arrangement would be one that measures the degree to which populations differ among patches. However, the variability between patches is likely to be significantly correlated with the variability within patches over time. Therefore, a variable that accurately reflects effects of spatial arrangement should measure the variability between patches, corrected for the variability within patches over time. For each run, we calculated the mean and coefficient of variation ($C.V.$) over the 100 time units for each patch, and then took the mean of these $C.V.$'s as a measure of within-patch variability over time for that run; this variable was named *tempvar* (i.e., temporal variability). The coefficient of variation ($C.V.$) among the 10 mean patch population sizes was also calculated for each run, and was labelled *patvar* (i.e., variability between patches). A significant quadratic relationship was found between ln(*tempvar*) and ln(*patvar*) (see Table II). The residuals from the regression are a measure of the variability between

TABLE II

Regression Analysis of *patvar* (Variability among Patches) on *tempvar*
(Variability within Patches over Time) for 2000 Simulations

| Source | Degrees of freedom | Sum of squares | F | Prob. > F |
|---|---|---|---|---|
| *tempvar* | 1 | 18.39 | 722.0 | 0.0001 |
| *tempvar*$^2$ | 1 | 4.00 | 157.2 | 0.0001 |
| Residual | 1997 | 50.87 | | |
| Total | 1999 | 73.26 | | |
| | | $R^2 = 0.37$ | | |

patches, corrected for the variability within patches. They are therefore a measure of the importance of patch spatial arrangement on local population size. The residuals were labelled *spatvar* (i.e., pure spatial variability).

RESULTS

The data resulting from each simulation experiment consisted of six independent variables: mean intrinsic growth rate ($r$), mean carrying capacity ($k$), mean dispersal rate ($p$), mean dispersal distance ($s$), mean detection radius ($d$), mean immigration rate ($i$). There were also two response variables: the mean of the 10 patch populations (*mnpop*), and the spatial variation among the 10 patches due to spatial arrangement (*spatvar*). Natural logarithms of *mnpop* were taken.

Although the proportion of dispersers detecting patches was not explicitly included as an input variable in the model, the fraction of dispersers from any particular patch that successfully detected any other patch was calculated as part of the simulations. As stated in the methods section, this calculation was complex because of the possible effects of overlap among patch detection zones. As well, it depended on the distance of the recipient patch from the donor patch, relative to the mean distance of dispersing organisms. For any particular run, the average probability of organisms detecting patches therefore depended in a complex manner on the dispersal distance, the detection radius, and the particular spatial arrangement chosen for the run. We felt the results of the simulations might be more easily interpreted if the average detection probability ($dp$) were included as a further independent variable in the analyses; $dp$ was therefore calculated for each run.

To gain a general understanding of the way in which the detection probability depends on the detection radius and the dispersal distance, we conducted multiple regression analyses using detection probability as the

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dependent variable, and mean detection radius ($d$), mean dispersal distance
($s$), $d^2$, $d^3$, $s^2$, $s^3$, and all other second, third, and fourth order interactions
as independent variables. The resulting regression equations are shown in
Figs. 2a and 2b. Patch detection probability is highest for intermediate dis-
persal distances (Fig. 2a). This is reasonable because for very small disper-
sal distances, the majority of dispersers do not move far enough to find
another patch. At high dispersal distances, two factors result in the
decrease in patch detection probability. First, dispersers may overshoot the
other patches in the area. Second, at high dispersal distances dispersers are
spread over much larger areas than at smaller distances, because the
standard deviation in dispersal distance is proportional to the mean (see
Fig. 1). Notice also that patch detection probability increases with
increasing detection radius (Fig. 2b). This relationship is most pronounced
for intermediate dispersal distances which, as stated above, are the distan-
ces at which detection probability is highest. Detection probability ($dp$) was
used as an additional independent variable in the remainder of the analysis.

The purpose of analysing the simulation results was to determine which
types of organisms (i.e., species characterised by which combinations of
independent variables) are expected to have low or high patch population
sizes (i.e., low or high values of $\ln(mnpop)$), and a low or high effect of
patch spatial arrangement on population abundance (i.e., low or high
values of spatvar). A standard statistical approach to problems in which
relationships between several independent variables and one dependent
variable are sought is to use the least-squares method to build the best
polynomial model relating the independent variables to the dependent
variable (Box and Draper, 1987). Although this method results in an ade-
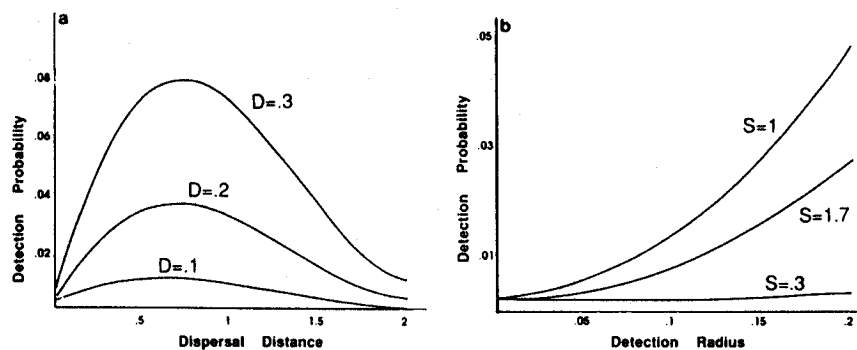quate empirical model, in our case it does not clarify our understanding of -



FIG. 2. (a) Relationship between patch detection probability and dispersal distance,
for three levels of patch detection radius ($D$). (b) Relationship between patch detection
probability and patch detection radius, for three levels of dispersal distance ($S$).

the qualitative relationships between the independent and dependent variables. In particular, it does not give us an estimate of the relative importance of each independent variable in explaining variation in the dependent variable. We therefore used the following method for analysing the simulation results. First, polynomial regression equations were calculated for each of the dependent variables (i.e., ln($mnpop$) and $spatvar$) on each of the independent variables (i.e., $r$, $k$, $p$, $s$, $d$, $i$, and $dp$). This provided us with estimates of the forms of the underlying relationships. To determine the relative importance of the independent variables, the polyno-

TABLE III

Polynomial Regression Equations

(a) Regressions of ln($mnpop$), population abundance averaged over patches

| Regression equation (i.e., ln($mnpop$) = $\cdots$) | $R^2$ | Name of polynomial variable |
|---|---|---|
| Growth rate: $2.21 + 7.21(r)$ | .0093 | $r(mn)$ |
| Carrying capacity: $1.92 + 5.24 \times 10^{-4}(k) - 1.09 \times 10^{-7}(kk^2) + 6.63 \times 10^{-12}(kk^3)$ | .0067 | $k(mn)$ |
| Dispersal rate: $7.01 - 35.3(p) + 94.6(p^2) - 107.0(p^3) + 42.3(p^4)$ | .2982 | $p(mn)$ |
| Dispersal distance: $1.36 + 11.5(s) - 19.2(s^2) + 11.5(s^3) - 2.40(s^4)$ | .1269 | $s(mn)$ |
| Detection radius: $0.535 + 13.6(d)$ | .3080 | $d(mn)$ |
| Immigration rate: $1.53 + 3.36 \times 10^{-3}(i) - 1.93 \times 10^{-6}(i^2)$ | .0421 | $i(mn)$ |
| Detection probability: $1.04 + 137.0(dp) - 1.78 \times 10^3(dp^2) + 2.40 \times 10^6(dp^3)$ | .3890 | $dp(mn)$ |

(b) Regressions of $spatvar$, variation among patch abundances due to spatial arrangement

| Regression equation (i.e., $spatvar$ = $\cdots$) | $R^2$ | Name of polynomial variable |
|---|---|---|
| Growth rate: No significant regression | | |
| Carrying capacity: No significant regression | | |
| Dispersal rate: $-9.64 \times 10^{-2} + 1.58(p) - 5.79(p^2) + 7.68(p^3) - 3.41(p^4)$ | .0253 | $p(sv)$ |
| Dispersal distance: $0.140 - 0.198(s) + 2.88 \times 10^{-2}(s^3)$ | .1404 | $s(sv)$ |
| Detection radius: $-0.056 + 0.376(d)$ | .0411 | $d(sv)$ |
| Immigration rate: $0.0368 - 7.27 \times 10^{-5}(i)$ | .0172 | $i(sv)$ |
| Detection probability: $-0.0414 + 2.61(dp) - 146(dp^3)$ | .0652 | $dp(sv)$ |

*Note.* All terms in the equations are significant at the 5% level.

mial regression equations were then used as polynomial variables in stepwise regressions of ln($mnpop$) and $spatvar$.

The polynomial regression equations giving the forms of the underlying relationships between the independent variables and the dependent variables are given in Table III. All terms in all regression equations in Table III are significant at the 5% significance level. Although there was a significant polynomial regression for almost all of the variables, there were large differences in the degree to which each of them accounted for the observed variation in the response variables (see $R^2$ values in Table III).

The results of the stepwise regressions of the dependent variables (i.e., ln($mnpop$) and $spatvar$) on the polynomial variables (Table III) are shown in Table IV. The effects of the first order interactions among the polynomial variables were also considered, but they added only slightly to the proportion of the variation explained by the polynomial variables.

The polynomial variables for mean patch detection probability ($dp$) and mean dispersal rate ($p$) were the most important factors determining average local population size, with partial $R^2$ values of .3890 and .2923, respectively. The polynomial regression equations for $dp$ and $p$ are plotted in Figs. 3a and 3b.

The polynomial variable for mean dispersal distance ($s$) was the most

TABLE IV

Stepwise Multiple Regressions of Polynomial Variables on Response Variables

| Polynomial variable | Partial $R^2$ | $F$-statistic | Probability |
|---|---|---|---|
| (a) Regression of ln(average patch population sizes), i.e., ln($mnpop$), on polynomial variables | | | |
| $dp(mn)$ | .3890 | 1272.00 | <0.0001 |
| $p(mn)$ | .2923 | 1831.19 | <0.0001 |
| $i(mn)$ | .0432 | 312.65 | <0.0001 |
| $s(mn)$ | .0297 | 269.57 | <0.0001 |
| $r(mn)$ | .0145 | 110.81 | <0.0001 |
| $d(mn)$ | .0122 | 97.78 | <0.0001 |
| $k(mn)$ | .0022 | 8.00 | <0.0001 |
| (b) Regression of spatial variation among patches due to spatial arrangement, i.e., $spatvar$, on polynomial variables | | | |
| $s(sv)$ | .1404 | 228.64 | <0.0001 |
| $dp(sv)$ | .0473 | 108.22 | <0.0001 |
| $p(sv)$ | .0256 | 43.84 | <0.0001 |
| $i(sv)$ | .0129 | 12.34 | <0.0001 |
| $d(sv)$ | .0032 | 6.00 | <0.0039 |

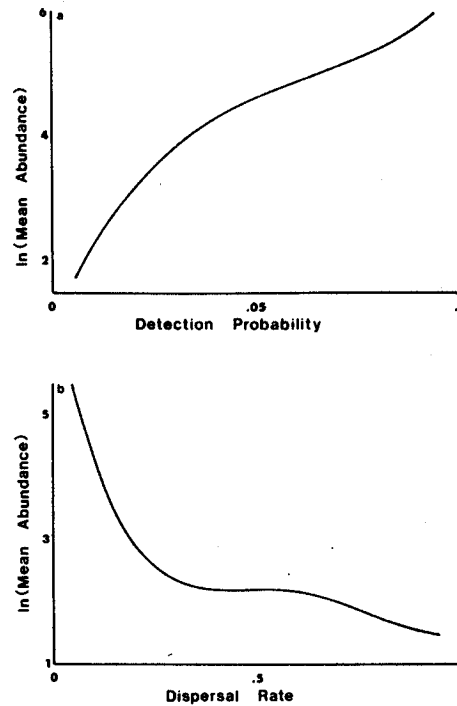*Note.* For definitions of polynomial variables see Table II.

FIG. 3. (a) Relatonship between patch detection probability and log-transformed values of average patch population abundance (averaged over 10 patches) (i.e., ln($mnpop$)). (b) Relationship between dispersal rate of organisms from patches and log-transformed values of average patch population abundance (averaged over 10 patches) (i.e., ln($mnpop$)).

important factor determining the spatial variation among local populations, with a partial $R^2$ value of .1404. The equation for this variable is shown in Fig. 4.

The results suggest the following hypotheses for populations distributed in patchy habitats. If a species' patch detection probability is high, and its dispersal rate is low, then local population abundance is expected to be high. Conversely, for high dispersal rates and low patch detection probabilities, the average patch population size is expected to be low. If a species' dispersal distance is low relative to the average distance between patches, the exact spatial location of habitat patches is expected to have a strong influence on local population dynamics (i.e., high value of spatvar). Conversely, if the dispersal distance is high, exact spatial relationships among habitat patches are not expected to significantly affect local population abundances (i.e., low value of spatvar).
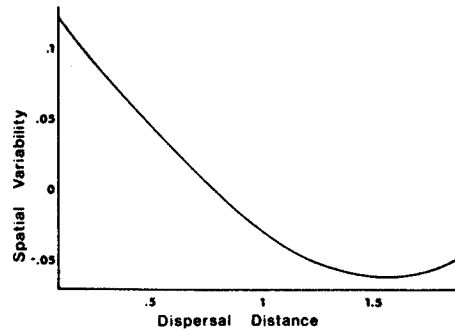
FAHRIG AND PALOHEIMO



FIG. 4. Relationship between dispersal distance and spatial variation among 10 patch population means due to patch spatial arrangement (i.e., *spatvar*); for definition see Methods section.


## DISCUSSION

Before commenting on the results of this study, we mention a difficulty that arises in any simulation study in which the relative impacts of the various model parameters on the model output is desired. In a modelling study such as this, in which analytical solutions are not possible, one is faced with the fact that it is impossible to simulate all possible combinations of parameter values. One must choose a subset of the infinite range of possibilities (Table I). The results are strictly valid only in the ranges chosen. In this study we have attempted to choose the parameter ranges that are reasonable for real populations.

The results of the analyses of average patch population size indicate the importance of dispersal on local population size. The most important factor determining size is the probability that dispersers successfully detect new patches; the higher this probability, the higher the average patch population size. This result is analogous to that of Levin *et al.* (1984) who found that, at the level of individual fitness, the optimal level of dispersal increases with an increase in the probability of a dispersing propagule successfully attaining a new site. The relative unimportance of dispersal distance ($s$) and detection radius ($d$) (Table IIIa) result from the fact that the effects of these two parameters are largely encompassed by the effect of detection probability ($dp$). The importance of the dispersal rate (fraction of local population dispersing) reflects the high risk associated with dispersal; high dispersal rates generally result in lower mean patch population sizes, unless the probability of dispersers detecting new patches is very high. A negative relationship between dispersal rate and population size has also

been found in theoretical studies in which all patches are assumed to be equally accessible to all other patches (Lomnicki. 1980), or in which patches are assumed to be evenly distributed in space (Roff, 1974a,b).

An interesting aspect of the results is that the intrinsic growth rates and carrying capacities have little effect on average population sizes in a patchy environment. Although their effects are significant and positive (see Table IIIa), each of them explains less than 1% of the explained variation in ln(*mnpop*) (see Table IVa). Their effects were almost completely swamped by the dynamics of interpatch dispersal. As stated above, this result is only valid for the range of parameter values chosen. In fact, if *r* were permitted to take on much larger values, within-patch growth might take on much more importance. However, if the ranges of values chosen for the parameters are within reasonable limits for real populations (Table I), then this result is important. It suggests that between-patch processes (i.e., dispersal) will often be more important than within-patch processes (i.e., births and deaths) in determining local population size within a habitat patch.

The residual spatial variation among patch population sizes after accounting for within-patch variability (*spatvar*) can be taken as a measure of the degree to which the particular spatial relationships between a patch and other patches in the region affect the population size within the first patch. Once again, the results indicate that the dynamics of dispersal among patches are most important in determining the level of this effect. The most important factor in this case by far is the dispersal distance. The greater the dispersal distance, the less important is the spatial arrangement of patches in causing differences among local population sizes (lower values of *spatvar*). This relationship is reasonable since, for larger distances, the same number of dispersing organisms are spread over a much larger area (Fig. 1). The result is that dispersal from a particular patch has a more general influence (i.e., affects more patches) for large dispersal distances than for small ones. Conversely, if the dispersal distance is small, then those patches that have neighbours at close distances receive many more dispersers than those that do not. In this case, the spatial relationships among patches is an important determinant of the local population size, and the spatial variation among patch sizes is high.

Inclusion of the dispersal pool in the model tends to decrease the effects of patch spatial arrangement. However, the reduction will be more pronounced for small dispersal distances than for large dispersal distances. At small dispersal distances, the dispersers that do not find patches within one time step should, in the absence of a dispersal pool, remain relatively close to their patch of origin. However, the dispersal pool effectively moves them away. Therefore, the difference in population size between patches that have close neighbours and those that do not is greater in the absence

of a dispersal pool; this difference is intensified for small dispersal distances. This means that the degree of importance of dispersal distance relative to the other parameters in affecting local population size has been under-estimated in our simulations. The finding that dispersal distance is the most important parameter is therefore conservative, and we feel confident that the inclusion of the dispersal pool did not alter the qualitative results.

Our finding that dispersal distance is much more important than other aspects of dispersal in determining the influence of patch spatial arrange-ment on local population size has not been previously suggested as far as we are aware. It was rather unexpected for two reasons. First, although other workers have not studied the problem of effects of patch spatial arrangement, previous studies of patchy populations have characteristically emphasized dispersal rate and have ignored dispersal distance. Although this has been largely a result of the previous assumptions about dispersal (i.e., equal accessibility of all patches or evenly distributed patches), the emphasis on dispersal rate gave us the preconception that its effect would be important. Second, preliminary studies using the model (Fahrig, 1988) concentrated on the effects of the detection radius because the assumption that dispersers have mechanisms for detecting new patches from their patch of origin or are led to them through dispersal corridors is implicit or explicit in many previous models. Although patch detection ability is important when considered in isolation (Fahrig, 1988), the results of this study indicate that when considered with other dispersal parameters it is almost completely outweighed by the effects of dispersal distance.

The prediction that dispersal distance largely dictates the degree to which patch spatial arrangement affects local abundance suggests some general hypotheses. It is generally believed that migratory bird species disperse shorter distances from their natal site to their reproductive site than do non-migratory birds (Whitcomb et al., 1981), mainly because the migratory phase uses up time that might otherwise be spent moving between breeding sites. If this is true then our results suggests that the spatial arrangement of bird breeding sites should be a more important determinant of local abundance of migratory species than of non-migratory species. This was in fact found in a study of birds in woodlots in Maryland (Lynch and Whigham, 1984). Also, for species that disperse long distances in the wind, such as small insects (e.g., aphids (Kennedy and Stroyan, 1959)), small plant seeds, or spores, the spatial pattern of potential breeding sites is unlikely to have much effect on local population abundance.

As in the case of total population size, the within-patch population dynamics ($r$ and $k$) are not important determinants of the effect of patch spatial arrangement on local population size. This is readily under-standable since between-patch dynamics (i.e., interpatch dispersal) are

more likely to be related to the level of importance of patch spatial arrangement.

The reasons for the lack of importance of the rate of immigration from outside the study region are less obvious. One would expect that for high rates of immigration, the effects of interpatch dispersal would be swamped, and in this case the patch spatial arrangement would have less effect on local population size. The general shape of the relationship between immigration rate and *spatvar* confirms this general expectation (see Table IIIb); *spatvar* decreases with increasing immigration rate. However, this relationship explains only a small fraction of the overall variability in *spatvar* (partial $R^2 = 0.013$; see Table IVb). The effect of dispersal distance far outweighs the effect of immigration rate. It is possible that for much higher immigration rates the swamping effect of immigration would be more pronounced. In this study, the upper limit to immigration rate was 1000 individuals per time unit. Relative to the ranges of the other parameters in the model (see Table I), we feel this represents a large immigration rate. The results indicate, therefore, that immigration from outside the study area is not expected to significantly swamp the effects of interpatch dispersal, except at extremely high immigration rates.

To conclude, we reiterate the major findings of this study that, within the context of the parameters considered here, for populations living in patchy habitats, (i) the most important determinants of mean local population size are the probability of dispersers detecting new patches (positive relationship) and the fraction of organisms dispersing from the patches (negative relationship) and (ii) the main factor that determines whether a local population will be influenced by exact spatial relationships among patches is its dispersal distance (negative relationship).

## ACKNOWLEDGMENTS

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