Landscape Ecology vol. 4 nos. 2/3 pp 157-170 (1990)
SPB Academic Publishing bv, The Hague

The elements of connectivity where corridor quality is variable

Kringen Henein and Gray Merriam
The Ottawa-Carleton Institute of Biology, Department of Biology, Carleton University, Ottawa, Canada KIS 5B6

Keywords: connectivity, corridor, landscape, model

Abstract

Small mammals in heterogeneous environments have been found to disperse along corridors connecting habitat patches. Corridors may have different survivability values depending on their size and the degree of cover they provide.

This deterministic model tests the effects of varying corridor quality on the demographics of a metapopulation of *Peromyscus leucopus*. Two types of corridors are defined based on the probability of survival during a dispersal event.

Results indicate that mortality during movement through corridors influences metapopulation demographics. We found that:

1. Any connection between two isolated patches is better than no connection at all in terms of persistence and population size at equilibrium.
2. Metapopulations with exclusively high quality corridors between patches have a larger population size at equilibrium than do those with one or more low quality corridors.
3. Increasing the number of high quality corridors between patches has a positive effect on the size of the metapopulation while increasing the number of low quality corridors has a negative effect.
4. The addition to a metapopulation of a patch connected by low quality corridors has a negative effect on the metapopulation size. This suggest the need for caution in planning corridors in a managed landscape.
5. There is no relationship between the number of corridors and the metapopulation size at equilibrium when the number of connected patches is held constant.
6. Geometrically isolated patches connected by low quality corridors are most vulnerable to local extinctions.

We conclude that corridor quality is an important element of connectivity. It contributes substantially to the effects of fragmentation and should be carefully considered by landscape planners.

Introduction

Natural landscapes are never homogeneous. Variations in soil, topography, and vegetation result in mosaics in which some areas are suitable animal habitat and some are not (Wilcove *et al.* 1986). Agricultural practices accentuate this by further fragmenting the landscape into pasture and cropland, with scattered remnants of the natural community retained as woodlots and fencerows (Henderson et *al.* 1985).

Small mammals in such heterogeneous environments aggregate in suitable patches that may be isolated from each other to varying degrees by an inhospitable matrix. Interconnected populations make up a functional unit that Levins (1970) has called a metapopulation. Local extinctions are a common occurrence in fragmented landscapes (den Boer 1981). Population sizes fluctuate due to variations in weather, resources, and predation. The persistence of a metapopulation depends on the ability of the populations in the patches to exchange individuals by dispersal (Fahrig and Merriam 1985).

In the past, the effects of dispersal were not stressed by population ecologists, as dispersers were assumed to be individuals with low survivability and poor reproductive potential (Lidicker 1975). However, many studies have shown the importance of dispersal to the dynamics of metapopulations in heterogeneous landscapes (Reddingius and den Boer 1981; Roff 1974a, b; Lidicker 1975; Hamilton and May 1977; Comins *et al.* 1980; Gaines and McClenaghan 1980; Lomnicki 1980; Fahrig and Merriam 1985).

Dispersal is difficult to measure in nature due to the large scale (i.e., tens of hectares) at which it sometimes takes place, the problem of separating emigration from mortality (Fairbairn 1977), and the difficulty of identifying dispersers (Gaines and McClenaghan' 1980). Models have been developed to estimate dispersal rates based on patch geometry (Stamps *et al.* 1987), dispersal success based on distance moved (Waser 1985; Buechner 1987) and dispersal effects on connected patches (Roff 1974a, b; Reddingius and den Boer 1970; Hamilton and May 1977; Fahrig 1983).

Reddingius and den Boer (1970) developed a model for insects that showed the importance of dispersal between patches to the persistence of the population. They found that migration damped the effect of environmental fluctuations. As long as populations did not fluctuate in synchrony, recolonization could offset local extinction. Roff (1974a, b) extended this work to show that such spreading of risk among patches was essential for overall population stability. Hamilton and May (1977) designed an evolutionarily stable strategy that showed dispersal to be adaptive for a species even in stable environments where fluctuations are small and empty habitats may be unavailable.

Field studies have shown that some small mammals in patchy environments tend to disperse along corridors connecting habitat patches (Wegner and Merriam 1979; Henderson *et al.* 1985). Fahrig (1983) designed a stochastic model to test the importance of such corridors to the recolonization of local extinctions and the persistence and stability of a metapopulation of *Peromyscus leucopus* in woodlots in an agricultural mosaic in the Ottawa area. Fahrig and Merriam (1985) found that populations in isolated (i.e. unconnected) woodlots became extinct within four model years, while connected patches were able to persist for much longer periods. They concluded that for a particular species, there is a minimum number of patches to which a population group must have access to ensure its survival. In an extension of this work, Lefkovitch and Fahrig (1985) showed that the elements of connectivity affecting the metapopulation were 1) whether or not patches were connected, and 2) the size of the largest geometric figure of which a patch was a part.

In those studies, variation in corridor quality was not considered. Patches were either connected or they were not. What constitutes a corridor for a particular species depends on such factors as the physical aspects of the landscape (cover, type of vegetation, moisture, elevation, etc.), the distance between patches, and the behaviour of the animals themselves. These components describe the connectivity of a habitat (Merriam 1984), and imply that not all corridors are created equal. For example, a species may show a reluctance to travel in certain types of agricultural areas while moving freely through others. Ongoing studies in this laboratory show that corn and small grain fields, as well as fencerows, are used by *P. leucopus,* but hayfields present a barrier (Wegner and Merriam, submitted). Yahner (1983) found that *P. leucopus* in shelterbelts in Minnesota showed poor dispersal tendencies across non-wooded areas such as roadsides. Savidge (1973) reported homing of *P. leuco-*

pus across a stream to be less successful than homing without such a barrier. Ogilvie and Furman (1959) studied *Microtus montanus* in fencerows and found that bare or shrubby corridors were less well used than weedy ones. Merriam and Lanoue (in press) have found both resident and translocated, telemetrically tracked *P. leucopus* to move along fencerows in preference to fields, and to clearly prefer structurally complex over simpler fencerows.

Given the amount of evidence that the quality of corridors affects their role in connectivity, we wanted to reassess the elements of connectivity when corridor quality was allowed to vary. Using the work of Fahrig (1983) as a starting point, we developed a deterministic model to simulate a *P. leucopus* metapopulation in which habitat patches are connected by corridors of either high or low quality. Quality was defined by the survival rate of the animals using the corridors, since this factor has the most fundamental effect on demography.

The model was designed to show how quality and quantity of connectivity in a heterogeneous landscape affect the size and persistence of fragmented populations. It addresses the following questions:

1. Does the quality of connections among patches affect the size of a metapopulation?
2. Does the number of corridors in a metapopulation affect the overall metapopulation size?
3. Do extinctions occur more frequently in patches with low quality connections?
4. Is the proportion of low to high quality corridors a factor in metapopulation size and persistence?

The null hypothesis states that there is no significant effect on size and survival of metapopulations when quality of connections is varied.

Methods

The model is designed to simulate the population dynamics of *P. leucopus* within and between patches for a number of breeding seasons. Model functions are based on the connectivity of the patches and demographic parameters from the literature. Population sizes are calculated for each patch, for each of thirty-three weeks, in each year. By changing the pattern and quality of connections between patches for each simulation run, comparisons of population size and patch persistence can be made between landscape arrangements. The model was written in Microsoft Fortran 77 V3.30 and can be run on IBM compatible personal computers. A simplified logic diagram is provided in Fig. 1 and a program listing may be obtained from the authors.

A) Model parameters

The simulation uses a number of structural parameters to control run cycling and landscape pattern. Metapopulations are set up with from two to five patches. All patches are assumed to be equal in size, appeal, and viability. Since dispersal has been found to be density-independent (Krohne *et al.* 1984; Krohne and Miner 1985), patch size is not a contributing factor to the dynamics of the model, although in reality it may contribute to the carrying capacity of a population through resource availability (Fahrig and Merriam 1985). Pairs of patches are designated as unconnected, connected by high quality corridors, or connected by low quality corridors.

Each run follows a metapopulation for ten years. This was sufficient time for all 45 patterns studied to reach equilibrium. (*i.e.,* for each pattern there exists a population size such that the number of mice in the last week of year n reduces over winter to a population in week 1 of year n + 1 that recapitulates the previous year. Week 33 of year n + 1 = week 33 of year n. Because of the deterministic nature of the model, this cycle continues to repeat thereafter). The 33 weeks for which the population size is calculated each year include a breeding season of 28 weeks, typical of *P. leucopus* in northern latitudes (Rintamaa *et al.* 1976; Hansen and Batzli 1978; Millar *et al.* 1979; Millar 1984; Wolff 1985). The breeding season begins in the second week of the simulation (corresponding to the first week in March), and there are four additional weeks at the end of the season, taking the population to the last week in October. The remaining 19 weeks represent winter and are modelled by applying an overwinter

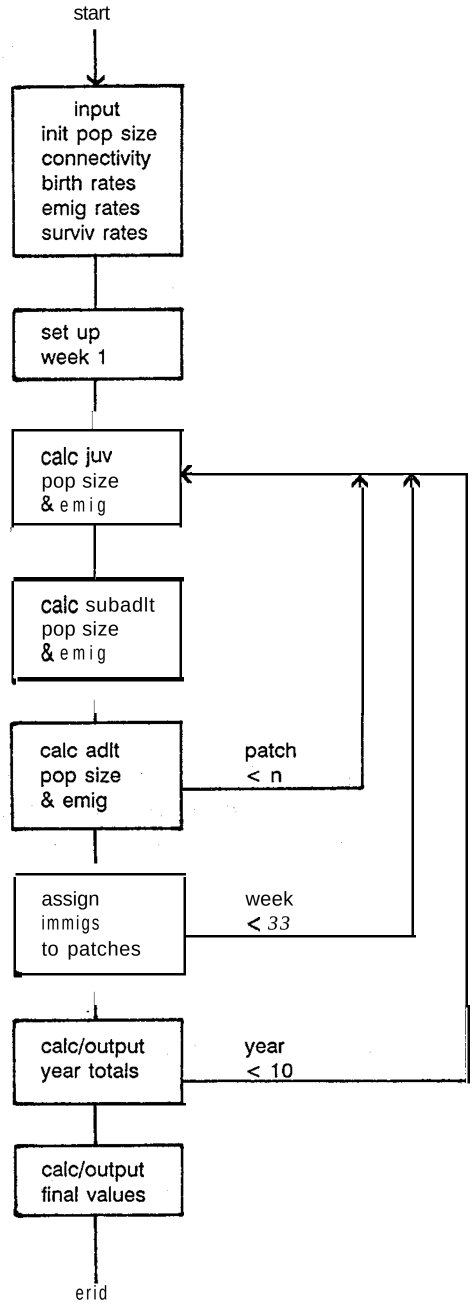

Fig. 1. Logic diagram.

survival rate to the previous October's population at the beginning of each new year.

There are four age classes of mice in the model: nestlings (under three weeks old), juveniles (3 to 6 weeks of age), sub-adults (6 to 8 weeks old), and adults (over 8 weeks) (Harland *et al.* 1979). The last three classes represent mice of trappable age capable of dispersing among patches. As in Fahrig's (1983) model, nestlings, defined by Sheppe (1965) as unweaned babies less than 3 weeks old, do not move from patch to patch and are not included in weekly totals.

Demographic parameters were estimated from *P. leucopus* studies in the literature. They are used for all runs and have no variance associated with them. This means that population dynamics are deterministic in these simulations. Although not realistic, this enables conclusions to be drawn from the comparison of different patch and corridor arrangements that would otherwise be difficult to do with confidence. Demographic parameters include birth rate, age-specific emigration rate, average litter size, nestling survival, resident survival by age group, overwinter survival, and corridor survival for the two corridor types. Table 1 shows the values used and the literature sources for their calculation.

Breeding in *P. leucopus* is bimodal, especially in northern populations (Sheppe 1965; Rintamaa *et al.* 1976; Wolff 1985) with peaks in the spring and fall, and a hiatus over midsummer. Therefore the birth rate is high in April and May, and again in August and September, but lower in the intervening periods.

Emigration rates are difficult to obtain from the literature because emigration and immigration are not usually separated from gross mortality and recruitment. We have used the work of Krohne *et al.* (1984) to calculate three dispersal rates based on age and season (Table 1). Juveniles had low dispersal in the spring (weeks 1 – 13) and high dispersal in autumn (weeks 27–33), with moderate dispersal in between. Sub-adults had high dispersal in spring and summer (weeks 1–26), and moderate dispersal in autumn (weeks 27-33). Adults had low dispersal in spring and autumn, and moderate dispersal in summer.

Movement between patches occurs only through corridors in this simulation. To test the hypothesis that differences in corridor quality affect population dynamics, it was necessary to find a method of modelling the variability in the patch connections. Two approaches were possible: 1) Divide emigrants among outgoing routes based on corridor differ-

Table 1. Demographic parameters for *Peromyscus leucopus* used in the simulation runs.

Parameter			Reference
Weekly birth rate:	low	.30	Millar *et al.* 1979, Sheppe 1965,
	moderate	.60	Rintamaa et *al.* 1976,
	high	.90	Wolff 1985
Average litter size		4.9	Morris 1986, Millar *et al. 1979,* Millar 1984
Nestling survival rate		.75	Harland *et al.* 1979, Wolff 1985
Weekly emigration:	low	.15	Krohne *et al. 1984*
	moderate	.23	
	high	.30	
Weekly resident survival rate:	juvenile	.90	Fairbairn 1977, Millar 1984
	subadult	.93	Adler and Tamarin 1984,
	adult	.96	Wolff 1985
Weekly corridor survival rate:	low quality	.73	see text
	high quality	.81	
Overwinter survival rate		.25	Snyder 1955, Fairbairn 1977, Harland *et al.* 1979

ences (mice actively choose one corridor over another, with the bias toward the higher quality route). 2) Assign different survival rates to the corridors so there is a higher success rate in high quality routes than in low quality ones (mice do not discriminate among corridors). We chose the second approach.

Since we are not aware of any studies that measure corridor mortality directly, corridor survival rates had to be estimated indirectly. Several trial runs were made to establish values that would not only fall within reasonable bounds, but would also produce stable results when combined with other demographic parameters in the model. Increased mortality during dispersal is expected (Krohne and Burgin 1987), so survival rates in the corridors had to be set lower than those in the patches, but how much lower? Using data gathered by Lanoue (1988) on mouse mortality per trapping night as a guide, we initially set a lower limit of 66% for survival during a dispersal event. Since Metzgar (1967) showed a higher mortality rate in unfamiliar areas such as corridors than in home territory, the survival rate in high quality corridors had to fall below 90%, the patch survival rate for juveniles. In the end, we chose the corridor survival rates shown in Table 1. These rates lay within this range, and allowed the various patch arrangements under comparison to reach equilibrium by year ten.

B) Model description

The model inputs all required parameters at the beginning of the run, including the initial population values. Each week then builds on the previous week until thirty-three weeks have been calculated. Subsequent years apply the overwinter survival rate to the values in the last week of the previous year to begin a new season.

There are two aspects of the population dynamics that must be handled: 1) The within-patch interactions involving 'births' of new juveniles, 'graduation' from juvenile to sub-adult and from sub-adult to adult, and deaths of individuals of all ages based on the resident survival rates. 2) The between-patch population dynamics, including emigration from each patch along corridors with high or low survival rates, and immigration into patches by surviving emigrants from a variety of starting points. Dispersing mice only move one patch per week, but may move again any number of times over the season.

For the first seven weeks of each year, only adults surviving from the previous autumn are present. The first births occur in week five, and the first juveniles are added to the population in week eight. For the remaining weeks, three age classes are calculated as follows:

1) Juveniles: New additions each week are based on the number of births to females present three weeks previously, linearly averaged over three weeks to allow for asynchronous pregnancies.

$$J_{nt} = \frac{\frac{(A_{t-3})}{2} \times b_{t-3} \times L}{3}$$

J_n = new juveniles
A = adults
b = birth rate
L = litter size
t = time in weeks

A proportion of juveniles present three weeks previously will graduate to the sub-adult class. A graduation factor sets this proportion. If the number of juveniles in week t-4 was zero, then all juveniles from week t-3 will be ready to achieve sub-adult status and the factor will be 1. If juveniles were present in week t-4 but not in week t-5, then half the juveniles in week t-3 will be ready to become sub-adults (factor = 2). Otherwise one third will move up to sub-adult status **(factor = 3).** The graduation rate is calculated from the resident class survival rate and the emigration rates, and represents the per cent of juveniles available for graduation in a particular week.

$$SA_{nt} = \frac{J_{t-3} \times g_{jt}}{k}$$

SA_n = new sub-adults
J = juveniles
g_j = juvenile graduation rate
k = graduation factor **(1,2,3)**

After new additions and graduates have been accounted for, the proportion of juveniles emigrating is calculated based on the juvenile emigration rate for the week.

$$E_{jt} = (J_{t-1} + J_{nt} - SA_{nt}) \times e_{jt}$$

E_j = juvenile emigrants
e_j = juvenile emigration rate

Then the size of the juvenile population (before immigration) is calculated as: the previous week's population size plus new juveniles, minus graduates to the sub-adult class, minus emigrants. The resident survival rate is applied to this result.

$$J_t = (J_{t-1} + J_{nt} - SA_{nt} - E_{jt}) \times S_j$$

J = juvenile population size before immigration
S_j = resident survival rate for juveniles

Finally, the emigrants are assigned to various destinations according to corridors leading out of the patch.

$$I_j = \sum_{i=1}^{n} \left(\frac{E_i}{c_i} \times r_{ij} \right)$$

I_j = immigration at patch i
E_i = no. of emigrants at patch i
c_i = no. of corridors out of patch i
r_{ij} = survival rate in corridor i
n = no. of patches connected to i

Fahrig (1983) addresses the question of whether mice disperse from isolated patches (i.e. patches with no corridors). She concludes that dispersal does occur from these areas, but at a lower rate. Wegner and Merriam (1979) measured movement of *P. leucopus* between a beech-maple wood and connecting fencerows, and between the wood and surrounding fields over a breeding season. They found the frequency of travel between wood and fencerows was more than twice that between wood and fields. For a truly isolated wood, with no connecting fencerows available, less movement into the fields might be expected. Yahner (1983) found no movement of *P. leucopus* between isolated shelterbelts. Adler *et* al. (1984) live trapped 97 *P. leucopus* in woods and an adjacent field, and caught only three individuals in both areas. We applied an emigration rate to isolated patches that was 60% lower than the rate for connected patches. As in the model of Lefkovitch and Fahrig (1985), dispersers from these isolated patches were assumed lost from the system, based on a high probability of mortality in open areas.

2) Sub-adults: The procedure is similar for sub-adults. New sub-adults are added to the sub-adult population, graduates to the adult class are subtracted, emigrants are calculated and deducted, and the resident survival rate for sub-adults is applied.

$$A_{nt} = \frac{SA_{t-2} \times g_{st}}{k}$$

A, = new adults
SA = sub-adults
g_s = graduation rate for sub-adults
k = graduation factor (1,2)

$$E_{st} = (SA_{t-1} + SA_{nt} - A_{nt}) \times e_{st}$$

E_{st} = sub-adult emigrants
e_s = sub-adult emigration rate

$$SA_t = (SA_{t-1} + SA_{nt} - A_{nt} - E_{st}) \times S_{sa}$$

S_{sa} = resident sub-adult survival rate

Again, emigrants are assigned to their destinations based on connecting corridors.

3) Adults: New recruits from the sub-adult population are added, emigrants are deducted, and the adult resident survival rate is applied to obtain a new adult population.

$$E_{at} = (A_{t-1} + A_{nt}) \times e_{at}$$

E_a = adult emigrants
e_a = adult emigration rate

$$A_t = (A_{t-1} + A_{nt}) - E_{at}) \times S_a$$

A = adult population size before immigration
S_a = resident adult survival rate

When all age groups in all patches have generated emigrants, and these emigrants have all been assigned to the appropriate destinations, the total immigration to each patch can be added to the population to complete the interpatch calculations for the week.

C) Preliminary simulation runs

To ensure that results of the simulation represent true differences in connectivity rather than in the size of the initial population or the distribution of mice in the metapopulation, three preliminary runs were made.

1) Four treatments were run to test whether the size of the starting population affects the size at stability. Number of patches and type of connections were held constant, but the size of the starting population was set at 5, 10, 20, and 30 mice per patch. The initial size of individual patch populations had no effect on the size of the metapopulation at equilibrium. However, larger initial populations took longer to reach the stable point than smaller ones.

2) Five treatments were run to test whether concentrating the mice in one patch while the others are left empty affects the population size at stability. The location of the starting population in a metapopulation was varied while the number of patches, size of starting population, and type of connectivity were held constant. Concentrating the population in one patch at the start of a run made no difference to either the eventual metapopulation size or the time to equilibrium. Empty patches were colonized by week two and the distribution at the end of the first year was similar to the results of runs with the initial population equally distributed among patches.

3) Four treatments were run to test whether the number of patches alone affects the total metapopulation size at stability. The number of patches (2,3,4, or 5) was varied while holding quality of connections and total starting population constant. The number of patches in the metapopulation was positively related to the final size of the metapopulation at stability (Table 2). This implies that com-

Table 2. Effect of number of patch populations on metapopulation size in year 10, with size of initial patch populations (5 mice per patch) and quality of connections (high) held constant. For each metapopulation, a central patch is connected to 1, 2, 3, or 4 other patches, as shown in Fig. 3, patterns a, c, f, and j.

Number of patches in metapopulation	Initial size of metapopulation	Metapopulation size in year 10
2	25	36.2
3	25	54.4
4	25	61.8
5	25	83.3

parisons of metapopulation size should be restricted to metapopulations with the same number of patches.

D) Main simulation runs

1) Thirty-two simulations were run to compare size and persistence of metapopulations with different arrangements of patches and connectivity (Fig. 2). All metapopulations contained four patches. Corridors were low or high quality, or combinations of the two. Each arrangement began with five mice per patch, and was run for ten years. All simulations reached equilibrium during the ten year period.

2) Fourteen runs were made to compare population size in single patches connected to 1, 2, 3, or 4 other patches by combinations of high or low quality connections (Fig. 3).

Results

We found the persistence of a metapopulation and its size at equilibrium to depend significantly on the mortality in the corridors connecting the patches. Introduction of a single low quality corridor into a four patch metapopulation previously connected with only high quality corridors resulted in a large reduction in metapopulation size at stability. Additional low quality substitutions continued to reduce the metapopulation size (Fig. 2). This trend can also be seen at the level of the individual patch, where the largest drop in population size occurs with the addition of a single low quality corridor (Fig. 3). The results of the simulations are summarized as follows:

1) Low quality connections were better than no connections at all (compare Fig. 2: w, y, and ee with ff). Unconnected patches quickly went extinct while those connected by low quality routes persisted despite occasional local extinctions. Nevertheless, these low quality corridors constitute a drain on the metapopulation because of increased mortality associated with them. A population beginning with 20 mice in week one of the first year grew to 72 mice at equilibrium when connected by four high quality corridors (Fig. 2: b) but fell to only 9 mice when connected with four low quality corridors (Fig. 2: y).

2) Exclusively high quality connections produced the largest metapopulations at equilibrium (58-72 mice) and were always superior to those with one or more low quality connections (Fig. 5) regardless of the total number of connections involved.

3) Four high quality connections were found to be superior to three high quality connections (Fig. 2: b vs d) in terms of final metapopulation size, but four low quality connections were not as good as three low quality connections (Fig. 2: y vs s). Increasing the number of high quality corridors between patches has a positive effect on the size of the metapopulation while increasing the number of low quality connections has a negative effect.

4) The inclusion of a patch connected by low quality corridors in a metapopulation otherwise connected by high quality corridors depresses the overall metapopulation size at equilibrium. Fig. 6 compares the effect of low quality connections to unconnected patches and to high quality connections in similar four-patch metapopulations. When the central patch was connected to the other three patches using low quality connections, the metapopulation size was depressed more than when the central patch was eliminated. Although the population in the unconnected patch in Fig. 6B fell to zero, the overall metapopulation reached equilibrium at 54 mice while the metapopulation connected to the central patch by low quality connections (Fig. 6C) stabilized at only 23.

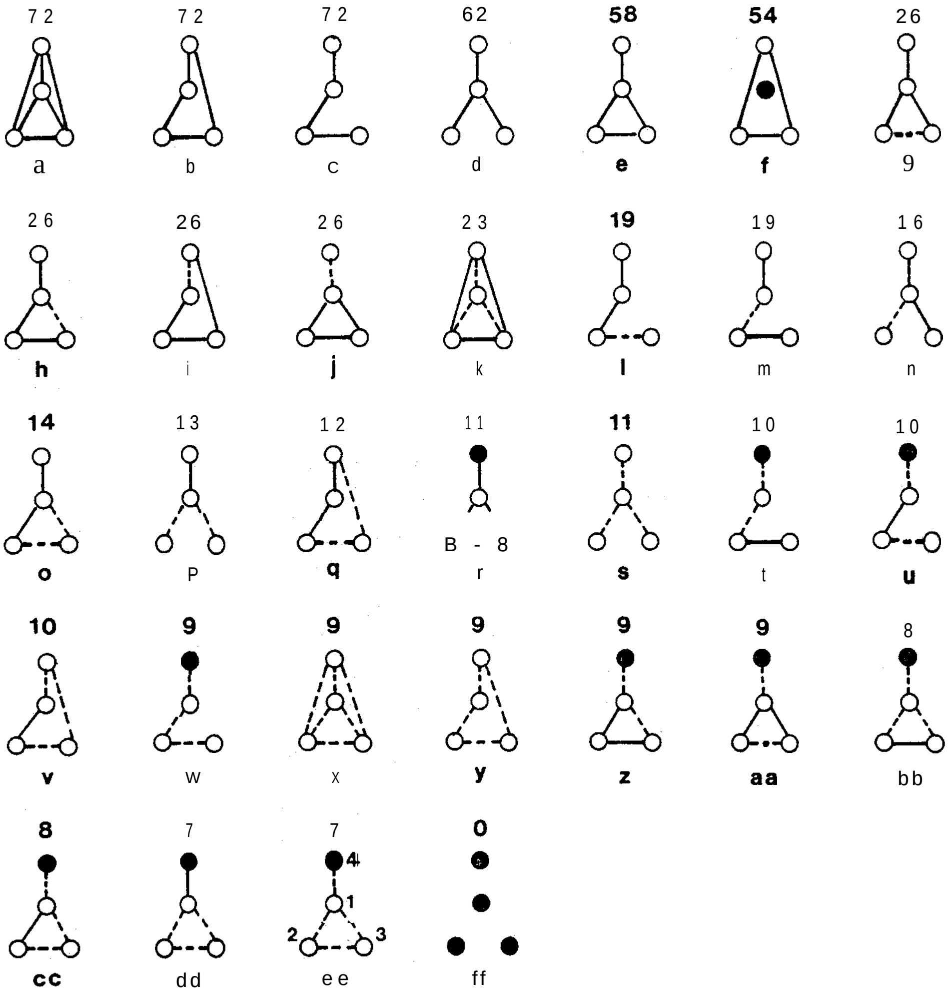

Fig. 2. Four-patch arrangements shown in order of size of metapopulation at the end of year 10. Solid lines are high quality connections and dashed lines are low quality connections. Solid circles represent patch populations suffering local extinctions during the simulation. Large numbers represent size of the metapopulation at the end of year 10. Letters are pattern identifiers. Small numbers in pattern ee are patch identifiers.

5) We found no relationship between the total number of corridors in a four-patch metapopulation and the metapopulation size at equilibrium. The Pearson correlation coefficient was only 0.165. Number of connections alone is not a predictor of population size.

6) Geometrically isolated patches connected by low quality corridors are most vulnerable to local extinctions. Patches that suffered local extinctions during the runs are shown in Fig. 2 as solid circles. Losses to emigration and death that are not offset by immigration will eventually exceed replacement by birth, and result in extinction in this deterministic model. In all cases, the geometrically most isolated patches were the ones affected. Consider pattern ee in Fig. 2. Only one third of the emigration from patch 1 goes to patch 4, and there is high mortality in the corridor. But mice from patch 4 emigrate at the same rate as from other patches so there is a relative loss at 4. Since patches 2 and 3 send only half their emigration to 1, and again there is high mortality in the corridors, the population at 1 does not increase either, and there are progressively fewer emigrants sent to 4. Patches 1, 2, and 3 even-

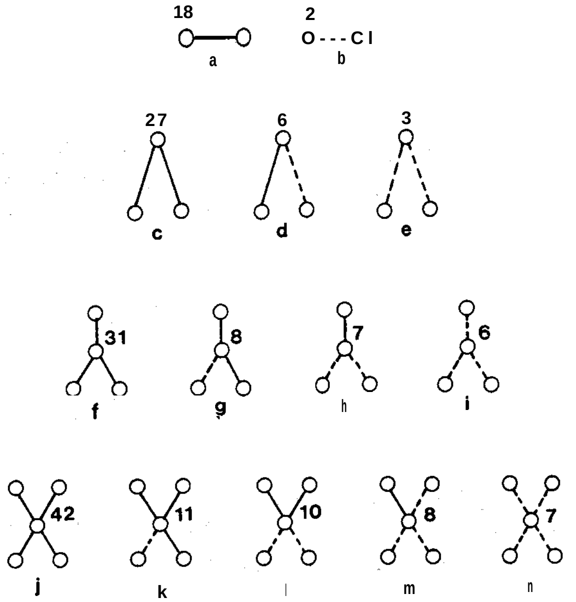

Fig. 3. Size of population in a single patch connected to 1, 2, 3, or 4 other patches by combinations of high and low quality connections. Solid lines are high quality connections. Dashed lines are low quality connections. Numbers show size of the patch population at the end of year 10. Letters are pattern identifiers.

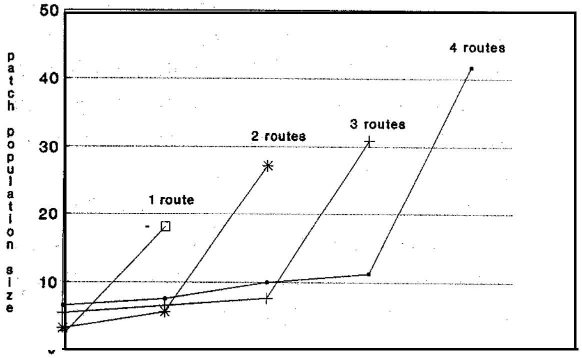

Fig. 4. Patch population size versus number of high quality connections. Patch may be connected directly to 1, 2, 3 or 4 other patches. Largest drop in population size occurs when one low quality connection is introduced.

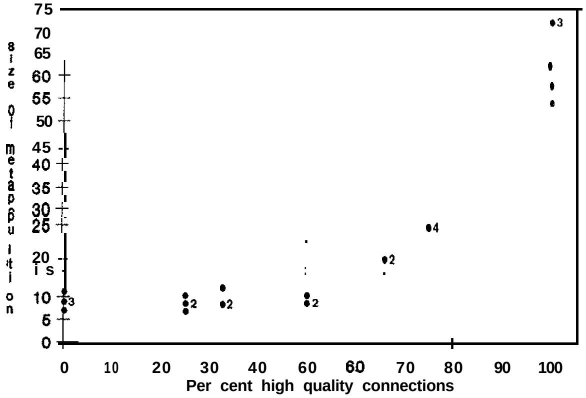

Fig. 5. Metapopulation size in year 10 versus percentage of high quality connections for all 4-patch arrangements. Numbers show number of arrangements with identical metapopulation size. Note the large drop in size associated with the addition of just one low quality corridor.

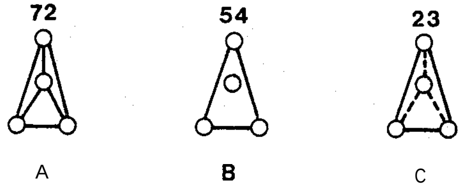

Fig. 6. Size of metapopulation for 3 arrangements showing effects of low quality connectivity on size of metapopulation in year 10. Circles are patches, solid lines are high quality connections, and dashed lines are low quality connections. Numbers represent metapopulation size in year 10. Note that the metapopulation in pattern B is larger than in pattern C even with a local extinction at the central patch.

tually stabilize at low population levels, but 4, which is more isolated, suffers local extinction over winter. Some recovery takes place when the birth and emigration rates rise in the spring, because 4 is still connected to a viable group of patches, but its population never has a chance to build up to high levels, and the extinction continues to repeat every winter thereafter. Analogous explanations apply to patterns r, t, u, w, z, aa, bb, cc, and dd in Fig. 2. Patches connected by low quality, single corridors to other groups of patches, themselves connected by mainly low quality corridors, are at risk because of the low source of immigration. Patterns f and ff in Fig. 2 are limiting cases where extinction is permanent because there is no source of colonists for the patches.

7) The size of a population at a single patch in year 10 increased with the number of other patches to which it was connected, but also with the ratio of low to high quality corridors when number of patches is held constant (Figs 3 and 4). Patches with purely high quality connections were always superior to combinations regardless of number of patches.

Discussion

The simulations confirm the findings of Fahrig and Merriam (1985) that persistence of metapopulations is enhanced by connectivity that lessens the isolation of individual patches. But the model also shows that differential survival in corridors (during dispersal events) and the qualitative pattern of connectivity have important implications for the population levels in the patches, and for the potential size and variability of the metapopulation. Although all connected arrangements survived, some stabilized at very low numbers. Very small populations are in jeopardy when fluctuations in environmental and demographic factors inevitably occur. Roff (1975) and Gilpin and Diamond (1976) found that the probability of extinction of a local patch varied inversely with the population size of the patch. This is intuitively obvious. The question really is, why is the population size so low? Of course, factors such as predator numbers and food availability may be important, but results of the simulations indicate that the pattern of connectivity in the metapopulation must also be understood to answer the question.

The number of patches in the metapopulation may be low, or the patches may be poorly connected, and this contributes to a low metapopulation size. The patch may be connected to just one other patch, with high mortality occurring in the corridor, giving it a degree of isolation not obvious without a measure of corridor quality. Thus connectivity is both qualitative and quantitative, and these characteristics make a difference, both at the patch and the metapopulation level.

Lefkovitch and Fahrig (1985) defined the elements of connectivity for a patch as: 1) the presence or absence of a connection; 2) the size of the largest geometric figure to which the patch is connected. Our results suggest that large figures increase the stability of the metapopulation only if the majority of the connections are of high quality. The elements of connectivity need revision to include this new factor.

The process of choosing corridor survival rates discussed under ‘Model Parameters’ offers insight into the interaction of pattern and demography in the system. In our model, the difference between the population size in week one and that in week thirty-three depends on the yearly net growth and the overwinter mortality. When these balance, the population stabilizes. However, if growth exceeds overwinter mortality, so that a higher population occurs in week one from year to year, then the population will grow indefinitely, as there is no stochasticity. Nor is any density dependent effect on growth included, since there is some evidence that *P. leucopus* populations at the northern limit of their range never reach carrying capacity (Middleton and Merriam 1981). For corridor survival rates below 0.73, many combinations with largely low quality connections suffered permanent extinction within 10 years. At the other extreme, patch arrangements with predominantly high quality corridors grew indefinitely when corridor survival rates were greater than 0.81. In the natural world, however, survival rates in some corridors may lie outside these limits. In this event, the carrying capacity of a metapopulation may be a critical factor, while some arrangements may not be viable. On the other hand, combinations of more extreme survival rates may be supported by arrangements of mixed corridor quality, while variations in demographic parameters such as growth and emigration may affect the level of corridor survival required for metapopulation equilibrium.

Although low quality corridors kept metapopulations from going extinct in these simulations, such connections were a drain on the overall system, resulting in stable population sizes much lower than those at the start of the simulation. High quality corridors, on the other hand, not only kept metapopulations going, but allowed them to grow and stablize at higher population levels than they began with. This is similar to Fahrig and Merriam’s (1985) findings of significantly higher growth rates with increasing connectivity. Since other checks on natural populations, such as predation, resource limitation, and crowding, will tend to control excessive growth, the minimum corridor survival rate is probably the most important of the two to know, but an understanding of both ends of the scale could help predict what results to expect from a landscape pattern.

The model assumes all patches are the same size. Urban and Shugart (1986) modelled birds in a fragmented landscape and found a curvilinear relationship between persistence and connectivity that was most pronounced for small patches. In the case of birds, connectivity was less important for large patches. Since carrying capacity was not considered a factor for *P. leucopus* in this area, and emigration was not density dependent, no size value is attached to the patches. However, the size of the fragments in a landscape can be important if choices are being made about conservation and elimination. Wilcove *et al.* (1986) argue for the preservation of a few larger fragments rather than many small ones. The model suggests, however, that at least for *P. leucopus,* the population sizes will be larger when more patches are involved in the metapopulation. In reality, separate patches will have population dynamics that are not in synchrony, and this could be an advantage during environmental fluctuations (Reddingius and den Boer 1970; den Boer 1981). Great care should be taken when choosing which fragments to maintain. Elimination of a central fragment that was actually a major source of emigrants for many others could significantly lower the size of the metapopulation (Fig. 6A and 6B). Degredation of corridors has an even greater negative effect (Fig. 6A and 6C). Connectivity and interaction among patches must be an important consideration when conservation areas are being established.

Hansson (1979) pointed out that whole landscapes must be considered in connection with species and habitat conservation or control of pests. In addition, he stressed the importance of choosing a large enough mosaic for the system to be properly understood. Each species has its dynamic range, and within this area, pattern and quality of connectivity among patches can be useful in predicting stability in a metapopulation. Additional research is required to determine this scale for *P. leucopus,* but there is evidence that, for some small mammals, it is quite large. Tegelstrom and Hansson (1987) measured dispersal distances of 3 to 5 km in the common shrew, *Sorex araneus.* Merriam and Lanoue (in press) have measured total distances moved by telemetrically marked resident and transient *P. leucopus* in farmland over two nights. Residents averaged 288.7 m, mice translocated from forest averaged 421.5 m, and those translocated from other cropland averaged 286.6 m.

The processes of model construction and evaluation can introduce a variety of problems of which modelers must beware (Loehle 1987). In this model, population parameters were chosen carefully, but there is always the chance of error, particularly as no single study can provide all the answers. Differences in design, emphasis, and locale can result in values from many contexts. We have made some assumptions to reduce complexity: for example, all patches are the same size, residents and dispersers have a 1: 1 sex ratio, population dynamics are deterministic and unaffected by carrying,capacity. The model does not describe the functioning of the real system in exact terms. Rather, it provides a tool for comparing corridors and arrangements, and making predictions about populations without the confounding influence of variations that normally occur in the field. Results are theoretical, and field work is required to extend them to the real world.

Johnson (1985) suggests that the primary use of a model is to point the way toward future research. Many additional questions arise from this work, for example:

1. What constitutes a corridor of high quality or low quality for a particular species?
2. How do animals choose among corridors when there is more than one route out of a patch? Is there a greater probability of use for a high quality corridor than a low quality one, or is the choice of corridor merely a function of proximity?
3. Does distance travelled lower the survivability of emigrants? Merriam and Lanoe (in press) found that mice travel in short bursts from cover to cover in a fencerow, which means exposure occurs more frequently in longer corridors, but may not be proportional to time or distance. Distance may be less important than type of vegetation, topography, or mouse behaviour .

As well as the answers to these questions, realistic values of corridor use are required to verify the results of the model satisfactorily. We need measurements of dispersal rates for small mammals known to be dispersing, as well as survival rates during known dispersal.

Despite the limitations imposed by the modelling techniques, we believe the results of these simulations, showing corridor quality as an additional element of connectivity, have implications for conservationists and landscape ecologists dealing with fragmented landscapes. Corridors have costs as well as benefits (Simberloff and Cox 1987). Although they facilitate movement by encouraging dispersal between patches, corridors may sometimes have a negative effect on the overall metapopulation, for example by acting as predator concentrators. Corridors in which the probability of survival is low may be less than helpful in maintaining viable populations in patchy habitat. Our results underline the importance of assessing the quality as well as the quantity of corridors when designing landscapes for conservation.

Acknowledgements

The authors wish to thank Lenore Fahrig, Richard Forman, and other anonymous reviewers for their helpful comments on an earlier draft of this paper.

References

Adler, G.H. and Tamarin, R.H. 1984. Demography and reproduction in island and mainland white-footed mice *(Peromyscus leucopus)* in southeastern Massachusetts. Can. J. Zool. 62: 58-64.

Adler, G.H., Reich, L.M. and Tamarin, R.H. 1984. Characteristics of white-footed mice in woodland and grassland in Eastern Massachusetts. Acta Theriol. 29(5): 57-62.

Comins, H.N., Hamilton, W.D. and May, R.M. 1980. Evolutionarily stable strategies. J. Theor. Biol. 82: 205–230.

Buechner, M. 1987. A geometric model of vertebrate dispersal: tests and implications. Ecology 68: 310–318.

den Boer, P.J. 1981. On the survival of populations in a heterogeneous and variable environment. Oecologia 50: 39-53.

Fahrig, L. 1983. Habitat patch connectivity and population stability: a model and case study. Master's Thesis: Carleton University.

Fahrig, L. and Merriam, G. 1985. Habitat patch connectivity and population survival. Ecology 66(6): 1762-1768.

Fairbairn, D.J. 1977. The spring decline in deer mice: death or dispersal? Can. J. Zool. 55: 84-92.

Gaines, M.S. and McClenaghan, L.R. 1980. Dispersal in small mammals. Ann. Rev. Ecol. Syst. 11: 163-196.

Gilpin, M.E. and Diamond, J.M. 1976. Calculation of immigration and extinction curves for the species-area-distance relationship. Proc. Natl. Acad. Sci., U.S.A. 73: 4130-4134.

Hamilton, W.D. and May, R.M. 1977. Dispersal in stable habitats. Nature 269: 578-581.

Hansen, L. and Batzli, G.O. 1978. The influence of food availability on the white-footed mouse: populations in isolated woodlots. Can. J. Zool. 56: 2530-2541.

Hansson, L. 1979. On the importance of landscape heterogeneity in northern regions for the breeding population densities of homeotherms: a general hypothesis. Oikos 33: 182-189.

Harland, R.M., Blancher, P. J. and Miller, J.S. 1979. Demography of a population of *Peromyscus leucopus.* Can. J. Zool. 57: 323-328.

Henderson, M.T., Merriam, G. and Wegner, J. 1985. Patchy environments and species survival: chipmunks in an agricultural mosaic. Biol. Cons. 31: 95-105.

Johnson, E.A. 1985. Fire recurrence in the subarctic and its implications for vegetation composition. Can. J. Bot. 57: 1374-1379.

Krohne, D.T. and Burgin, A.B. 1987. Relative success of residents and immigrants in *Peromyscus leucopus.* Hol. Ecol. 10: 196-200.

Krohne, D.T. and Miner, M.S. 1985. Removal trapping studies of *Peromyscus leucopus.* Can. J. Zool. 63: 71-75.

Krohne, D.T., Dubbs, B.A. and Baccus, R. 1984. An analysis of dispersal in an unmanipulated population of *Peromyscus leucopus.* Amer. Mid. Nat. 112: 146-156.

Lanoue, A. 1988. Use of corridors and scale of movement in farmland by *Peromyscus leucopus.* Master's Thesis: Carleton University.

Lefkovitch, L.P. and Fahrig, L. 1985. Spatial characteristics of habitat patches and population survival. Ecol. Modelling 30: 297–308.

Levins, R. 1970. Extinction. *In* Some Mathematical Questions in Biology. Lectures on mathematics in the life sciences. Vol. 2. pp. 77-107. Edited by M. Gerstenhaber. American Mathematical Society, Providence, R.I.

Lidicker, W.Z. 1975. The role of dispersal in the demography of small mammals. *In* Small Mammals: Their Productivity and Population Dynamics. pp. 103-128. Edited by F.B. Golley, K. Petrusewicz and L. Ryskowski. Cambridge University Press, N.Y.

Loehle, C. 1987. Errors of construction, evaluation, and inference: a classification of sources of error in ecological models. Ecol. Modelling 36: 297-314.

Lomnicki, A. 1980. Regulation of population density due to individual differences and patchy environment. Oikos 35: 185-193.

Merriam, G. 1984. Connectivity: a fundamental ecological characteristic of landscape pattern. *In* Proc. First International Seminar on Methodology in Landscape Ecological Research and Planning (Vol. 1). pp. 5-15. Edited by J. Brandt and P. Agger. Roskilde Universitetsforlag GeoRuc, Roskilde, Denmark.

Merriam, G. and Lanoue, A. (in press) Corridor use by small mammals: field measurements for three experimental types of *Peromyscus leucopus*. Landscape Ecology.

Metzgar, L.H. 1967. An experimental comparison of screech owl predation on resident and transient white-footed mice *(Peromyscus leucopus)*. J. Mamm. **48(3):** 387-391.

Middleton, J. and Merriam, G. 1981. Woodland mice in a farmland mosaic. J. Appl. Ecol. 18: 703-710.

Millar, J.S. 1984. Reproduction and survival of *Peromyscus leucopus* in seasonal environments. *In* Winter Ecology of Small Mammals. pp. 253-266. Edited by J.F. Merritt. Carnegie Museum of Natural History, special pub. 10. Pittsburgh.

Millar, J.S., Wille, F.B. and Iverson, S.L. 1979. Breeding by *Peromyscus* in seasonal environments. Can. J. Zool. 57: 719-727.

Morris, D.W. 1986. Proximate and ultimate control on life history variation: the evolution of litter size in white-footed mice *(Peromyscus leucopus)*. Evolution **40(1):** 169-181.

Ogilvie, R.T. and Furman, T. 1959. Effect of vegetational cover of fence rows on small mammal populations. Ecology 40: 140-141.

Reddingius, J. and den Boer, P.J. 1970. Simulation experiments illustrating stabilization of animal numbers by spreading of risk. Oecologia 5: 240-284.

Rintamaa, D.L., Mazur, P.A. and Vessey, S.H. 1976. Reproduction during two annual cycles in a population of *Peromyscus leucopus noveboracencis*. J. Mamm. **57(3):** 593-595.

Roff, D.A. 1974a. Spatial heterogeneity and the persistence of populations. Oecologia 15: 245-258.

Roff, D.A. 1974b. The analysis of a population model demonstrating the importance of dispersal in a heterogeneous environment. Oecologia 15: 259-275.

Roff, D.A. 1975. Population stability and the evolution of dispersal in a heterogeneous environment. Oecologia 19: 217-237.

Savidge, I.R. 1973. A stream as a barrier to homing in *Peromyscus leucopus*. J. Mamm. **54(4):** 982-984.

Sheppe, W.A. 1965. Unseasonal breeding in artificial colonies of *Peromyscus leucopus*. J. of Mamm. **46(4):** 641-646.

Simberloff, D. and Cox, J. 1987. Consequences and costs of conservation corridors. Cons. Biol. 1(1): 63-71.

Snyder, D.P. 1956. Survival rates, longevity, and population fluctuations in the white-footed mouse, *Peromyscus leucopus*, in southeastern Michigan. Misc. Pub. Museum Zool. Univ. Michigan. 95: 1-33.

Stamps, J.A., Buechner, M. and Krishnan, V.V. 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. Amer. Nat. **129(4):** 533-552.

Tegelstrom, H. and **Hansson,** L. 1987. Evidence of long distance dispersal in the common shrew (*Sorex araneus*). Z. **Sau**getierkunde 52: 52-54.

Urban, D.L. and Shugart, H.H. 1986. Avian demography in mosaic landscapes: modeling paradigm and preliminary results. *In* Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates. pp. 273-279. Edited by J. Verner, M. Morrison and C.J. Ralph. University of Wisconsin Press, Madison.

Waser, P.M. 1985. Does competition drive dispersal? Ecology **66(4):** 1170-1175.

Wegner, J. and Merriam, G. 1979. Movement by birds and small mammals between a wood and adjoining farmland habitats. J. Appl. Ecol. 16: 349-357.

Wegner, J. and Merriam, G. Use of spatial elements in a farmland mosaic by a woodland rodent. Biol. Conserv. in press.

Wilcove, D.S., **McLellan,** C.H. and Dobson, A.P. 1986. Habitat fragmentation. *In* Conservation Biology: The Science of Scarcity and Diversity. pp. 237-256. Edited by M.E. Soule. Sinauer Associates, Inc. Sunderland, Mass.

Wolff, J.O. 1985. Comparative population ecology of *Peromyscus leucopus* and *Peromyscus maniculatus*. Can. J. Zool. 63: 1548-1555.

Yahner, R.H. 1983. Population dynamics of small mammals in farmstead shelterbelts. J. Mamm. **64(3):** 380-386.