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Habitat patch connectivity and population stability: a model and case study

University — Université

Carleton

Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée

M.Sc.

Year this degree conferred — Année d'obtention de ce grade

1983

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HABITAT PATCH CONNECTIVITY
AND POPULATION STABILITY:
A MODEL AND CASE STUDY

by

© LENORE FAHRIG, B.Sc.

A thesis submitted to the Faculty of
Graduate Studies and Research in partial fulfilment
of the requirements for the degree of
Master of Science

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ABSTRACT

I constructed a patch dynamics model which can be used to simulate the changing sizes of resident populations in a series of interconnected habitat patches. I applied the model to white-footed mice (Peromyscus leucopus) inhabiting patches of forest in an agricultural landscape. The model predicts that mouse populations in isolated woodlots are less stable (more prone to extinction) than those in connected woodlots. Field data support this prediction. I then used the model to generate long-term predictions concerning the effect of different spatial arrangements of interconnected woodlots on population stability.

ACKNOWLEDGEMENTS

Many people assisted me during this study. I would especially like to thank my supervisor, Dr. H.G. Merriam, whose comments were constructive, supportive, and always well-timed. I also thank my advisors, Dr. M.B. Fenton, for pragmatic advice during the field work and manuscript preparation, and Dr. L.P. Lefkovitch, for hours of mathematical and statistical consultation. I am also grateful to J. Wegner, for many helpful suggestions, and to D. Thomas, D. Omond and D. Tierney for technical help. Financial support was provided by graduate scholarships from Carleton University.

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INTRODUCTION

Up to 86 per cent of extinctions of birds and mammals since 1600 A.D. have been caused by man (Watt et al. 1977). Since the industrial revolution, many of these extinctions have been symptomatic of large-scale changes in the environment, caused mainly by resource exploitation and pollution. If these destructive environmental changes are allowed to continue, we threaten to destroy ourselves by destroying the habitat on which we depend for survival. It is, therefore, one of the primary aims of the ecologist to gain an understanding of the causal relationships between man's activities and species extinctions, and ultimately to be able to predict and avert the latter.

One of the most notable aspects of man's recent activity has been large-scale deforestations. In many regions, such as southern Ontario, areas which were once extensively forested are now primarily cleared. Forest now exists as small patches or 'habitat islands' surrounded by a 'sea' of nonforested land. It is clear that many large animals have suffered local and regional extinctions because the areas of remaining forest are smaller than the minimum area requirements for these animals (Matthiae and Stearns 1981). However, it is also true that woodlots often lack species whose area requirements are well met by the woodlots (Tramer and Suhrweir 1974, Matthiae and Stearns 1981). It seems, therefore, that extinctions caused by deforestation are not due entirely to the reduction in area of forests.

Probably the most widely held explanation for these extinctions is the 'isolation effect'. MacArthur and Wilson (1967) provided the impetus for a good deal of work on this idea. They suggested that the probability that a species will be found on a particular oceanic island depends on two factors: extinction rate and colonization rate. The

extinction rate on the island is determined by such factors as the size of the island, chance, predation, and competition. The colonization rate depends on the migration rate of the species and the distance between the mainland source population and the island. It is this distance factor that accounts for the isolation effect; the more isolated the island is from the mainland, the lower is its rate of colonization by mainland species. There has been much evidence supporting this idea (Crowell 1963, Hamilton et al. 1964, Simberloff and Wilson 1970, Willis 1974, Rex 1975, Diamond et al. 1976, Nilsson and Nilsson 1982, Lomolino 1982).

Workers soon realized that the isolation effect may also apply to continental situations where the 'island' is a patch of habitat such as a woodlot, surrounded by a 'sea' of other habitat such as field which isolates it from a 'mainland' or 'source' area such as a continuous forest. There is evidence for the importance of the isolation effect in this type of situation (Vuillemier 1970, Tramer and Suhrweir 1975).

Although the isolation effect, as predicted by the theory of island biogeography, appears to be important in many situations, there have been several cases of misapplication of the concept. Some workers have suggested using or have used the theory of island biogeography in situations in which no 'source' population exists (Janzen 1968, Smith 1974). This is an abuse of the model. In the situation where there are patches of habitat and no source area, it is not clear from the theory of island biogeography where the isolation effect fits in. For example, if a patch is very close to two other patches which have high extinction rates, the first patch may have a lower colonization rate than if it were a moderate distance from a patch which had a low extinction rate

(i.e. a high probability of containing the species). In this type of situation, therefore, it is important to follow the dynamics of all populations in all patches simultaneously to determine which patches, if any, will contain persistent populations. This is clearly beyond the limits of island biogeographic theory; it is a 'patch dynamics' problem.

The patch dynamics problem is probably more common than the island biogeography problem, since many organisms are naturally found in patches. For example, dung beetles live in patches of dung, leaf miners live on leaves as patches, and bark beetles use trees as patches. When deforestation is extensive, the remaining forest may be entirely in the form of patches, with no identifiable 'source' area of continuous forest. This problem is quite different from the one in which a source area exists. The persistence of forest species in the 'patch network' depends entirely on extinction rates in the patches and movements of organisms among the patches.

Although it is an important problem, the persistence of species in a patch network is not well understood at present. Although some patch dynamics models have been developed, they have been primarily proposed for theoretical investigation. The field biologist has not had access to a good framework for patch dynamics studies since the theoretical models have not been presented so that field data can be readily applied to them. Theoretical patch dynamics, therefore, has been making progress, but the study of patch dynamics in the field still relies heavily on the theory of island biogeography, which is inappropriate for this problem. I will now discuss three currently prominent patch dynamic models, and problems in their field application.

Roff (1974a,b, 1975) has developed a patch dynamics model which has resulted in the following predictions:

i) there must be some movement among patches for the overall population to be stable (i.e. to have a high probability of persisting through time).

ii) as the mortality rate of dispersers increases, the probability of a local population (i.e. the population within one patch) persisting for a given length of time declines and the rate of dispersal which maximizes population size decreases.

iii) any change in a parameter value which increases population size increases the probability of persistence (i.e. stability).

iv) if the variance associated with the population growth rate is decreased, the dispersal rate which maximizes population size decreases.

v) as the mean growth rate in patches increases or the mean carrying capacity of patches increases or the variance of the carrying capacity decreases, the rate of dispersal to maximize population size increases.

Although these predictions are interesting, they are virtually impossible to test in the field because of the difficulty in obtaining values for parameters such as the intrinsic population growth rates in different patches and the carrying capacities of the patches, not to mention the near impossibility of measuring the variances associated with these values. Another limitation of the model is that Roff applied it only to species having nonoverlapping generations.

Den Boer (1968, 1979, 1981) and Reddingius and Den Boer (1970) developed a patch dynamics model to test the notion of 'spreading of risk' of extinction. If a population in a patch has a certain risk of

becoming extinct, then the probability of the regional population (several patches) becoming extinct simultaneously will depend on rates of colonization among patches and the degree to which population fluctuations in the patches are asynchronous. As Den Boer (1981) states, "The survival time of small and isolated populations will often be relatively low, by which the survival of species living in such a way will depend on powers of dispersal sufficiently high to result in a rate of population founding that about compensates the rate of population extinctions. The survival time of composite populations uninterruptedly inhabiting large and heterogeneous areas, highly depends on the extent to which the numbers fluctuate unequally in the different subpopulations." Den Boer (1981) supports this idea with computer simulations and field data for two species of carabid beetle. Although Den Boer's work is convincing, it is unclear how this model can be applied to a different situation such as animals in isolated woodlots.

Levin (1974, 1976) produced a model which, if appropriately reformulated, may be applicable to field situations. It is a matrix model in which the population size in a patch depends on the population dynamics within the patch as well as immigration to and emigration from the patch. Two factors have kept the model out of general reach of field biologists. The first is the fact that the model is completely deterministic; variables such as growth rates and dispersal rates are not presented as random variables but as constants. Although the parameters can easily be modified to include variability, on first reading the model appears unrealistic. The second factor which makes the model unapproachable by many field biologists is the imposing nature

of the sophisticated mathematics which Levin uses to analyse properties of the model. A field biologist is not likely to consider using such a mathematically sophisticated model.

In general then, although there have been some interesting theoretical approaches to the problem of patch dynamics, field work is lacking for two main reasons. First, mathematical models often use parameters which are not estimable from field data. Secondly, the mathematics are often presented in a sophisticated way, making the models unapproachable by the field biologist.

The aims of the present study were to: i) develop a model of patch dynamics that can be applied to field data, ii) test certain predictions of the model, and iii) use results of the model and field work to answer the question 'Does population stability within a patch depend on the degree to which it is isolated from other patches?' Population stability here means the probability of persistence of the population through time; instability implies a high probability of extinction.

MODEL DESCRIPTION

The model (also presented in Fahrig et al. [1983]) is structured to follow the population sizes and age (or, more correctly, "stage") structures in a series of interconnected patches through time. A connection can imply either that the patches are sufficiently close that migration can occur among them, or that there is some physical connection that serves as a 'corridor' along which the organisms can move. There are two components to the population dynamics. They are: i) within-patch dynamics, and ii) between-patch dynamics.

Within a patch, individuals can be added to or lost from each stage class. Additions to the youngest stage class occur through births, and into the other stage classes through ageing, so that individuals 'graduate' into the next stage. Losses occur through deaths.

Between-patch dynamics consist of additions due to immigration of organisms from adjacent patches, and losses due to emigration of organisms to connected patches.

The basic operator of the model is composed of a series of transition matrices, whose elements are parameters representing population processes appropriate for a certain time interval, t . The vector of population sizes of the various stage classes in the different patches at time $t+1$ is then obtained as the product of the transition matrix for time t with the vector of population sizes at time t .

The model will be described by means of an example, namely the group of interconnected patches represented in Figure 1.

Figure 1: A suggested arrangement of four patches.

P = PATCH
C = CONNECTION

The adjacency matrix for the graph corresponding to Figure 1 is

$$A = \begin{bmatrix} 0 & 1 & 0 & 0 \\ 1 & 0 & 1 & 1 \\ 0 & 1 & 0 & 1 \\ 0 & 1 & 1 & 0 \end{bmatrix}$$

where a '1' in position $A_{i,j}$ means that there is a connection between patches i and j and a '0' means that there is no connection. If this adjacency matrix is used to multiply the vector of population sizes in the different patches, the "1's" effect the movement of all individuals in j to i . Since it is unlikely that all of the individuals in j move to i , the elements are actually numbers less than unity, each representing the probability of organisms moving from j to i . 'A' becomes, in consequence, a 'weighted-edge' graph. The probability that organisms do not move out of a patch will be represented by elements on the principal diagonal of the matrix. The transition matrix now has a typical off-diagonal element denoted by $P_{i,j}$, defined as the probability of moving from j to i , and a typical diagonal element,

$$P_{i,i} = 1 - \sum_{\substack{j=1 \\ j \neq i}}^m P_{j,i}$$

where m is the number of patches.

To include the effects of births and deaths on the patch populations, the main diagonal values in the matrix must be further modified.

Let i) the death rate in woodlot i over one time interval

$$= d_i \text{ and}$$

ii) the birth rate in woodlot i over one time interval

$$= b_i.$$

The elements of the transition matrix now differ from those just described in that the i^{th} diagonal element is

$$P_{i,i} = 1 - \sum_{\substack{j=1 \\ j \neq i}}^m P_{j,i} + b_i - d_i;$$

this matrix is denoted by X .

A further complication, which does not introduce any new principles, arises if there are several relevant stage classes in the population, say z . Each of the elements in X is replaced by a matrix Z , of dimensions $z \times z$, in which the diagonal blocks are essentially Leslie matrices as modified by Lefkovitch (1965). These matrices are further modified by the migration rates; the off-diagonal elements represent the stage-specific migration probabilities.

Since the values of p , b , and d may be functions of time, there are several transition matrices required, one for each time interval; the whole series may be repeated over a longer time period, for example, each complete breeding season. If the transition matrix for a particular time period is X_t and the vector of the number of individuals in the patches at time t is n_t , then the whole model, for one breeding season is

$$n_1 = X_0 n_0,$$

$$n_2 = X_1 n_1,$$

$$n_3 = X_2 n_2,$$

$$\begin{aligned} n_r &= X_{r-1} n_{r-1} = X_{r-1} \cdots X_1 X_0 n_0 \\ &= M n_0 \end{aligned}$$

where r is the total number of time intervals in one season.

To determine the effect of a particular arrangement of patches on the stability of one resident species, the appropriate X -matrices need to be estimated and applied repetitively to n until the population sizes in the patches stabilize.

There are many advantages to this model. First, it can be applied to any species of interest, as long as the appropriate p , b , and d values are available for the different age or stage classes (or some method of determining them is available). Second, any type of patch, and any number of them can be considered. Finally, patch size can be included in the model as a parameter in the functions determining one or all of p , b , and d .

MODEL SIMULATIONS

The Study System

To test the applicability of the model to a natural situation, and address the question of the effect of isolation on population stability as outlined in the introduction, I chose to apply it to populations of Peromyscus leucopus (the white-footed mouse) in woodlots in southeastern Ontario. There were three main reasons for selecting P. leucopus.

First, P. leucopus avoids open areas with little cover, such as grassy fields (M'Closky and Lajoie 1975, Bendell 1961, Hansen and Warnock 1978), cultivated fields (Whitaker 1967) and roadways (Qxley et al. 1974), showing a definite preference for habitats with dense cover in the form of shrubs and trees (Myton 1974, Whitaker 1967, M'Closky 1975, Van Duesen and Kaufman 1977, Hansen and Warnock 1978) and debris such as rocks and logs (Barry and Francq 1980, Bendell 1961, Miller and Getz 1977a, Madison 1977). The practice of clearing land for agriculture has, therefore, produced a very patchy P. leucopus habitat; the pieces of forest which are left to stand form habitat islands surrounded by a sea of inhospitable cleared farmland. These habitat islands are, however, not necessarily completely isolated from each other. Wegner and Merriam (1979) found that P. leucopus were readily trapped in fencerows (fencelines along which trees and shrubs are growing), which implies that they may provide corridors between woodlots along which mice will travel. Beer (1961) also observed that, instead of crossing a small meadow, mice tended to travel around it, "using the brushy edges as lanes". Finally, Sinclair et al. (1967) observed that the activities of P. leucopus in a field system were restricted to within six metres of stone walls, implying that stone fences may also act as corridors

through inhospitable fields. All of this evidence suggests that for P. leucopus in an agricultural setting, isolated woodlots are analogous to the habitat patches in the model; these are separated from each other by uninhabited fields, although sometimes linked by fencerows which are analogous to the connections in the model.

The second reason for choosing P. leucopus is that, when confined in small isolated woodlots, there is evidence that the predictions of MacArthur and Wilson's (1967) theory of island biogeography appear to hold. Gottfried (1979) found that, in 10 woodlots surrounded by cornfields, densities of P. leucopus decreased with distance of the woodlot from a large forest. Also, densities of P. leucopus in the woodlots were significantly lower than those in nearby large forests. Although there is no equivalent 'source' or 'mainland' area in the present situation, this suggests that there is a real isolation effect on P. leucopus in small woodlots and, therefore, the presence or absence of connections among woodlots may make a detectable difference to the population dynamics. Gyug (1978) also found that in small woodlots (less than three hectares in size), immigration is required for the maintenance of a P. leucopus population; without immigration, emigration from the woodlot in the fall means a very small overwintering population, which can increase the probability of extinction.

The final reason for using P. leucopus is that estimates of the appropriate parameters needed to run the model - birth rates, death rates, dispersal rates, and life history characteristics - are available in the literature.

To apply the model to P. leucopus, I made estimates of the model parameters based on information in the literature and then chose field study sites (Figure 2) representing different spatial arrangements of woodlots; two woodlots appear to be isolated and four others are interconnected by fencerows. I used the model to predict the relative population stabilities of the different field situations and collected field data to test these predictions.

Figure 2: Schematic representation of study sites.

I1, I2 = ISOLATED WOODLOTS
M1, M2, M3, M4 = CONNECTED WOODLOTS
FR = FENCEROW

Parameter Estimation

P. leucopus populations consist of three 'trappable' stage classes, namely, juveniles, subadults and adults. Infant mice are not counted until they become juveniles, because they cannot be trapped. It is, therefore, necessary to include in the model the 'modified Leslie matrices' referred to in the model description.

1) Birth Rates (b-values)

The b-values determine the number of mice which are born and which graduate from one stage class to the next during one time interval. In this model application, I have chosen one week as the time interval. An individual element, $b_{i,k}$, is actually the proportion of individuals in a stage class, k, in woodlot i which become part of the stage class k+1 in one week. There are three such stage class changes to consider; adults give 'birth' to juveniles, juveniles become subadults, and subadults become adults.

Since it takes about three weeks for a newborn P. leucopus to become a juvenile (Sheppe 1965a, Millar et al. 1979, Vestal et al. 1980), the number of juveniles added to a woodlot is approximately equal to the number born three weeks previously, minus the infant mortality over those three weeks. By combining the results of Harland et al. (1979) and Hansen and Batzli (1978), the following rates for survival from nestling to juvenile have been obtained:

mid-March - mid-June	70%
mid-June - mid-August	40%
mid-August - mid-October	20%

To determine the probability of a female giving birth during a particular week, the data of Hansen and Batzli (1978) and of Sheppe (1965a) have been used. Hansen and Batzli give proportions of females pregnant at different times in the breeding period, but since these values were obtained in Illinois, where the breeding period is longer than in southeastern Ontario, and since northern populations exhibit a more distinct bimodal breeding cycle than southern populations (Sheppe 1965a), their data have been modified to conform with Sheppes' (1965a) data of the proportions of juveniles in the population at different times during the summer. Millar et al. (1979) found that the average P. leucopus litter size was 4.9.

The weekly $b_{i,t}$ (t = week) values for juveniles over the summer are then calculated using the equation

$$b_{i,t} = \frac{\text{proportion of females pregnant at time } t-3}{3} \times 4.9 \times \text{nestling survival.}$$

The resulting $b_{i,t}$ values are given in Table 1.

Since it takes about three weeks for a juvenile to become a subadult (Synder 1956, Madison 1977), the addition of subadults through ageing of juveniles depends on the number of juveniles present three weeks previously and the probability of survival from the juvenile to the subadult age classes, as calculated from the d -values. The subadult b_i value is 0.717.

It takes about two weeks for a subadult to become an adult (Harland et al. 1979, Millar et al. 1979). The addition of adults through ageing of subadults, therefore, depends on the number present two weeks previously and the probability of survival from the subadult to the adult age

Table 1. Probability that a female present three weeks earlier gives birth to a juvenile in week "t". "t" runs from the third week in March to the second week in October.

<u>t</u>	<u>probability</u>
1	0.03
2	0.03
3	0.03
4	0.03
5	0.03
6	0.05
7	0.15
8	0.25
9	0.35
10	0.45
11	0.45
12	0.45
13	0.45
14	0.45
15	0.45
16	0.45
17	0.35
18	0.35
19	0.20
20	0.20
21	0.10
22	0.10
23	0.10
24	0.25
25	0.25
26	0.35
27	0.45
28	0.25

classes, as calculated from the d-values. The adult b_1 value is 0.801.

2) Death Rates (d-values)

The probability of P. leucopus dying during a particular week appears to be independent of the age class of the mouse and also of the population density (Miller and Getz 1977b). Miller and Getz found that the average death rate was 55.3%/60 days, which is equivalent to a weekly death rate of 8.97%. Since this "death" rate probably includes some emigration, it is likely an overestimate. Synder (1956) found a weekly death rate during the winter in Michigan of 3-8% per week. Therefore, I have estimated the mortality rate at 6% per week. This mortality rate was also used to calculate the probability of survival of juveniles to subadulthood and subadults to adulthood for the calculations of b-values for subadults and adults.

3) Dispersal Rates (p-values)

The dispersal rates are the most difficult parameters to estimate from the literature, primarily because most workers include immigration and additions due to reproduction in one value, 'recruitment'; losses due to death and emigration are also lumped. Therefore, it is difficult to distinguish between births and immigration and between deaths and emigration, creating a lack of information about P. leucopus dispersal. This is complicated by contradictions in the available data. Several questions concerning dispersal by P. leucopus had to be answered by weighing the evidence as reasonably as possible. They are as follows:

i) Is dispersal age-specific?

Madison (1977) found that the subadult dispersal rate measured as the proportion of "transient" (i.e. caught only once) individuals,

was much higher than either the juvenile or adult rates. It is possible, however, that a large number of resident individuals will be caught only once, either through trap shyness, or because they entered the trappable population near the end of the trapping period. Since these would be included in the 'transient' estimate, Madison's transience numbers can be assumed to overestimate the actual dispersal rates.

ii) Is dispersal sex-specific?

Harland et al. (1979) found that male P. leucopus migrate more than females, but Taylor (1978) and Nadeau et al. (1981) found no significant differences between male and female dispersal tendencies. Coupled with the fact that Harland et al. (1979) found that the sex ratios in the populations they studied were consistently 1:1, this suggests that sexual differences in dispersal rates are not important enough to be included as a factor in the model.

iii) Does dispersal depend on the time of year?

I found no clear evidence that dispersal rates change during the breeding season. This may be partly due to the fact that most studies do not contain a sufficient sample size of population estimates to distinguish this from the other factors affecting dispersal. Therefore, I have not included time as a factor influencing dispersal rates, realizing that this may be an erroneous decision.

iv) Is dispersal density-dependent, density-independent, or both?

Hansen and Batzli (1978) and Nadeau et al. (1981) found no significant correlation between the rate of dispersal and population

density. Middleton and Merriam (1981) suggested that in northern areas (i.e. near Ottawa), because the winter death rate is very high and the breeding season is short, P. leucopus populations may not actually "fill" the available habitat. This could mean that the populations do not reach densities that are high enough to affect the rate of dispersal. I have assumed, therefore, that in my study area, the population density does not affect dispersal rate. Density-dependent dispersal will not be included in this application of the model.

- v) Do mice disperse from a woodlot regardless of how unfavourable the surrounding environment is?

This question has implications for the relative population sizes and growth rates in isolated and nonisolated woodlots. If mice disperse from isolated woodlots and are not replaced by immigrants, the population sizes and growth rates in isolated woodlots may be lower than those in nonisolated ones.

There is some evidence that mice will disperse into inhospitable habitats such as fields (Stickel and Warbach 1960, Tardiff and Gray 1978). Gyug (1978) found that the autumn survival of P. leucopus populations in small isolated woodlots was very low because emigration was not balanced by immigration.

Although emigration occurs from isolated woodlots, P. leucopus is almost never trapped in the surrounding nonforested areas (M'Closky and Lajoie 1975, Hansen and Warnock 1978, Wegner and Merriam 1979). This implies that the rate of dispersal from isolated woodlots is not as high as that from nonisolated ones.

- vi) Does the type of fencerow (i.e. length, width, type of vegetation) affect either the tendency for mice to use it, or the survival rate of mice that do?

Ogilvie and Furman (1959) are the only workers who have studied the effect of fencerow type on mice. They assessed the relative preferences of P. maniculatus, a species closely related to P. leucopus, for three types of fencerow: weedy, shrubby, and bare. They found that the bare fencerow was slightly less well used than the other two types. The effects of length and width of fencerow on mouse movement are still unknown.

It is clear from this discussion of P. leucopus dispersal that there will be a large amount of uncertainty associated with any estimates of dispersal rates. Madison (1977) gave the following proportions of transient individuals in his populations: juveniles - 0.154, subadults - 0.571, adults - 0.111. As already stated, these are probably overestimates of actual dispersal rates, even though the relative proportions in each age group may be accurate. Therefore, I have halved the values, producing dispersal rates of

juveniles	0.077
subadults	0.286
adults	0.0555

from the nonisolated woodlots. Although mice disperse from isolated woodlots as discussed above, they may do so with a lower frequency than those in nonisolated woodlots. This is supported by the extremely low capture rate of mice in open areas mentioned earlier (page 13).

Therefore, I have again halved the above values, producing dispersal rates of

juveniles	0.0385
subadults	0.143
adults	0.0278

from the isolated woodlots.

Simulation Methods

I used the values obtained from the literature as parameter estimates, and applied the model to woodlot arrangements analogous to the actual woodlots used in the field studies (Figure 2). The computer program is given in Appendix 1.

Savidge (1973) found that a stream three to four m wide and 10-40 cm deep decreased P. leucopus dispersal by about two-thirds. Small streams separated the area sampled in M1 from that in M4, and the area sampled in M2 from that in M3. For this reason, I assumed that emigration is unevenly distributed so that 1/6 of the animals emigrate along the fencerow which involves crossing a stream, and the remaining disperse along the other fencerow.

Another factor relevant to the simulations was that the actual woodlots varied in size. Since dispersal is apparently density-independent (Hansen and Batzli 1978, Nadeau et al. 1981), it appears that the absolute population size in any woodlot is unrelated to the woodlot size. However, the proportion of mice which survive over winter in a woodlot may depend on its size, since winter resources are relatively scarce. I, therefore, assumed that spring population sizes are proportional to the areas of the woodlots in Figure 2.

Simulations of the populations in one of the two isolated woodlots and the group of four interconnected woodlots were made. The first simulation assumed that the population dynamics over the summer is a deterministic process; the parameter values had no variances associated with them. Although the parameters are actually random variables, by eliminating variance in the first simulation, I obtained results which, presumably, are equal to the average of many simulations using random

variables instead of constants (Chapman and Schaufele 1970). Although each simulation considered 28 weeks (the third week in March to the second week in October), only the data for the twelve weeks corresponding to the field studies, namely the second week in June to the first week in September, were analysed. The results of this simulation were analysed in the following way. A series of increasingly complex least squares regression models were fitted to the predicted numbers of individuals, and an analysis of variance was constructed. I then determined whether the variances estimated for factors thought relevant were significantly different from random variability. This analysis enabled predictions concerning the effect of increased habitat patch isolation on the population dynamics of P. leucopus to be inferred. These predictions were then tested by comparing them to the results of the field studies.

To determine the effects of parameter variability on the outcome of the model, further simulations, each with a different degree of variance associated with the model parameters, were made.

Simulation Results

The results of the first simulation (deterministic) are shown in Table 2.

The results of the regression analysis are given in Table 3.

The following is a summary of Table 3.

- i) Not all of the regression equations for the 5 woodlots have the same intercept ($F = 40.365$, $p < 0.01$).
- ii) Although not attaining the 5% significance level, it appears that most of this difference in intercepts is due to a difference between isolated and connected woodlots ($F = 286.017 / 42.75 = 6.690$, $0.05 < p < 0.1$).
- iii) There is a significant linear regression ($F = 552.213$, $p < 0.01$).
- iv) There is no statistical justification for the inclusion of a quadratic term ($F = 2.733$, N.S.).
- v) There is a significant difference between the slopes of the regressions for the isolated and connected woodlots ($F = 26.263$, $p < 0.01$).
- vi) There is no significant difference among slopes of regressions for different woodlots within types (i.e. isolated and connected) ($F = 0.869$, N.S.).

See Figure 3 for a summary of the resulting regression equations.

Figure 4 gives the results of the series of simulations in which stochastic variance about the model parameters was included. Figures 4ai), ii) and iii) show the results from simulations of population sizes in I1 and I2. These figures suggest that, as the parameters' variances increase, identical woodlots (I1 and I2) exhibit increasingly divergent population dynamics. This divergence was even more extreme for the interconnected woodlots (Figures 4bi), ii) and iii).

Table 2. Simulated population sizes in 5 woodlots (Figure 2) from the second week in June to the first week in September.

Week	I1 or I2 (3.75 ha)	M1 (5.3 ha)	M2 (4.5 ha)	M3 (9.8 ha)	M4 (1.5 ha)
1	9	13	13	12	7
2	10	14	14	13	8
3	10	14	14	12	9
4	11	14	14	12	10
5	10	15	15	15	12
6	11	18	18	17	14
7	12	20	20	18	15
8	13	20	20	21	18
9	17	25	25	25	23
10	18	28	28	25	24
11	16	27	27	25	23
12	16	26	26	25	23

Table 3. Analysis of variance for regressions of simulated data on time.

Source	Sum of Squares	Degrees of Freedom	Mean Square	F-statistic	Significance Level
Total	2048.183	59			
Additional due to different intercepts	414.267	4	103.567	40.365	$p < 0.01$
Due to types*	286.017	1	286.017	111.365	$p < 0.01$
Due to woodlots within types	128.250	3	128.250	16.662	$p < 0.01$
Due to linear and quadratic regression	1423.855	2	711.928	277.473	$p < 0.01$
Due to linear term alone	1416.842	1	1416.842	552.213	$p < 0.01$
Additional linear due to types	67.385	1	67.385	26.263	$p < 0.01$
Additional linear due to woodlots within types	6.691	3	2.230	0.869	N.S.
Additional due to quadratic term	7.013	1	7.013	2.733	N.S.
Residual	135.985	53	2.566		

* 'Types' refers to two types of woodlot: isolated (I1 and I2) and connected (M1, M2, M3, and M4).

Figure 3. Regressions of simulated data on time.

REGRESSION EQUATIONS

ISOLATED :

$$\text{NO. MICE} = 7.591 + .793 (\text{TIME})$$

(S.E. = .874) (S.E. = .119)

CONNECTED :

$$\text{NO. MICE} = 8.061 + 1.561 (\text{TIME})$$

(S.E. = .728) (S.E. = .099)

ISOLATED SLOPE < CONNECTED SLOPE ($F = 25.44, p < .01$)

Figure 4. Simulations using stochastic parameters.

A. 2 ISOLATED WOODLOTS (I1, I2)

i. Parameter s.d. = 1% Parameter means

ii. Parameter s.d. = 10% Parameter means

iii. Parameter s.d. = 30% Parameter means

B 4 CONNECTED WOODLOTS (M1, M2, M3, M4)

i. Parameter s.d. = 1% Parameter means

ii. Parameter s.d. = 10% Parameter means

iii. Parameter s.d. = 30 % Parameter means

Simulation Predictions

The most interesting result from the analysis of variance (Table 3) in terms of population stability is that the population growth rate (slope of regression line) in isolated woodlots is lower than in connected woodlots ($F = 26.263$, $p < 0.01$). Taylor (1978) and Middleton (1979) have shown that overwintering mortality rates of 80-90% are common in P. leucopus populations in the Ottawa area and that many woodlots may begin the spring breeding period with only a few (0 to 5) individuals. Small spring populations were also found by Harland et al. (1979). Local extinctions have been documented (Taylor 1978). It is, therefore, very important that a woodlot population be able to grow quickly during the summer. A large autumn population is necessary to ensure that some individuals will survive until the following spring.

In conclusion, the model predicts that P. leucopus populations in isolated woodlots have lower growth rates and are thus less stable than those in connected woodlots. Field studies were carried out to test this prediction. However, it was expected that the results from the field studies would be less clear-cut than the model predictions because of the effects of parameter variability on the population dynamics (Figure 4).

FIELD STUDIES

Description of the Study Sites

Seven deciduous woodlots near Ottawa were chosen for the study. Two, I1 and I2, are in the west end of Ottawa at $45^{\circ}18'55''\text{N}$ $75^{\circ}46'30''\text{W}$ and $45^{\circ}18'40''\text{N}$ $75^{\circ}46'30''\text{W}$ respectively. Their areas are 3.8 and 3.7 ha respectively. These woodlots are completely isolated; they are 350 m apart and are both completely surrounded by and separated from each other by alfalfa fields which were harvested twice during my study. The vegetation in I1 and I2 consists of sparsely distributed mature deciduous trees, primarily maple, birch, beech and poplar, and a dense understory of shrubs and saplings. Four woodlots, M1, M2, M3 and M4, are south of Ottawa near Manotick at $45^{\circ}12'50''\text{N}$ $75^{\circ}41'30''\text{W}$, $45^{\circ}12'40''\text{N}$ $75^{\circ}41'40''\text{W}$, $45^{\circ}12'50''\text{N}$ $75^{\circ}41'20''\text{W}$, and $45^{\circ}12'10''\text{N}$ $75^{\circ}41'10''\text{W}$ respectively. Their areas are 5.3, 4.5, 9.8 and 1.5 ha respectively. There is a series of fencerows connecting the four fencerows in a ring, and a narrow stream flows through the area (see Figure 2). The seventh woodlot, FF, is also located near Manotick at $45^{\circ}14'45''\text{N}$ $75^{\circ}40'50''\text{W}$ and is 1.7 ha in area. M1, M2, M3, M4 and FF are mature deciduous woods, with dense canopies and relatively little understory vegetation. In the areas studied within each of these woodlots, the dominant tree is maple.

Field Methods

The seven woodlots - I1, I2, M1, M2, M3, M4, and FF - were studied during the summer of 1982. There were two phases of sampling: trapping and tracking.

During September and October, three of the woodlots - FF, I1, M4 - were live-trapped using Sherman-type live traps. The traps were placed on grids covering the entire woodlots, with 25 m between traps. FF was trapped every day from 4 to 9 September and from 15 to 25 September, I1 was trapped each day from 26 September to 7 October, and M4 was trapped every day from 15 September to 1 October. All animals were removed and taken to woodlots at least 5 km away.

Once a week, from the first week of June to the first week of September, the populations in six of the woodlots - I1, I2, M2, M3 and M4 - were assessed using smoked paper tracking (Sheppe 1965b). Thirty cm lengths of 3.75 cm (inside diameter) plastic water pipe were lined with glossy paper coated with black smoke produced by a flame burning naphtha gas (80% by volume) and benzene (20%). One hundred tubes were arranged in a 100 x 100 m grid (tubes 10 m apart) in each woodlot. All tubes were checked weekly for P. leucopus tracks. The smoked paper was replaced if a track was found or if the paper was smudged for some other reason. The data were recorded as either 'presence' or 'absence' of P. leucopus tracks, irrespective of the number of times an animal, or possibly several animals, went through the tube. During 5 weeks - June week 2, July week 2, July week 3, August week 1, and September week 1 - two sunflower seeds were placed at one end of each tube.

The following data analyses were performed.

- 1) Analysis of trapping success and recruitment rate.

The trapping results were analysed using a nonlinear regression model in order to obtain estimates of the trapping success (proportion of population trapped per day) and population recruitment (number of individuals added to the population per day). The model is as follows:

If $n_{t,i}$ = number of individuals present in woodlot i on day t , and

p_i = proportion of individuals in i not trapped each day, and

$q_i = 1 - p_i$ = trapping success, and

$y_{t,i}$ = number of individuals in i trapped on day t , then

$$y_{t,i} = (1 - p_i)n_{t,i}$$

Also, if a_i = number of recruitments, i.e. additions of trappable mice due to immigration and young mice per day, then

$$n_{t+1,i} = p_i n_{t,i} + a_i$$

$$\begin{aligned} y_{t+1,i} &= (1 - p_i)n_{t+1,i} \\ &= (1 - p_i)(p_i n_{t,i} + a_i) \\ &= p_i y_{t,i} + a_i(1 - p_i) \end{aligned} \quad (1)$$

Because equation 1 is nonlinear with respect to the parameters a_i and p_i , a nonlinear regression analysis was performed. The model parameters were estimated by maximizing the 'log likelihood' of the data, on the assumption that deviations follow a Poisson distribution. A series of increasingly complex models was fitted to the data. At each step the decrease in deviance of the more complex model from the less complex one was compared with the appropriate Chi^2 distribution to determine whether any new parameters were necessary. This analysis allowed estimates of trapping success ($1 - p_i$) and population recruitment rate (a_i) to be made.

2) Relationship between trapping and tracking.

Smoked paper tracking has never before been used in the same way that I used it in this study. Therefore, I felt it was necessary to demonstrate a correlation between the tracking data and the number of mice trapped, a more common method of population estimation. Correlations of the number of tracks with the number of mice trapped and of the number of tracks with the number of mice trapped per unit area were compared, to see whether tracking was a better measure of population size or population density.

3) Baited and nonbaited tracking data.

To include the data from the baited and nonbaited weeks in the same analyses, a relationship between the two was necessary. For this purpose, I compared the baited tracking data to the nonbaited data from the nearest week in the same woodlot. All of these comparisons were combined in one data set to obtain a general relationship between baited and nonbaited tracking data. The relationship was estimated as the linear least squares regression equation of the number of tracks in baited weeks on the number of tracks in nonbaited weeks. To obtain estimates of nonbaited values corresponding to observed baited values, the actual baited values were entered in this equation.

This method was slightly biased because there was an error term associated with the prediction variable (number of tracks in baited weeks). However, this bias was probably very small.

4) Regression analysis of tracking data.

The same method was used to analyse the tracking data for the six woodlots - I1, I2, M1, M2, M3 and M4 - as was used in analysing the simulated data.

Sheppe (1965b) has shown that P. leucopus demonstrate a strong neophilia (attraction to new objects). He found that tracking records fell from 2.29 per mouse on the first night of tracking to 0.05 on the eighth night. For this reason I have not included the first week of tracking data (June week 1) in the analysis. This leaves 12 weeks of tracking data, corresponding to the 12 weeks of simulated data.

Field Results

- 1) The trapping data for FF, I1 and M4 are given in Appendix 2.

The results of the analysis of trapping success and recruitment rate are given in Table 4.

The following is a summary of Table 4.

- i) There is a significant recruitment of individuals into the woodlots through immigration and/or reproduction ($\chi^2 = 8.367$, $p < 0.005$).
- ii) The three woodlots do not have significantly different recruitment rates ($\chi^2 = 0.548$, N.S.).
- iii) The three woodlots do not have significantly different trapping successes ($\chi^2 = 0.845$, N.S.).
- iv) The overall recruitment rate is 2.018 mice/day/woodlot.
- v) The overall trapping success is 43.1% of the mice present in a woodlot per day.

See Figure 5 for a summary of the resulting regression equation.

- 2) The correlations between tracking and trapping data are given in Figure 6a and 6b. A higher correlation was found between the number of tracks and number of mice trapped (73.80%) than between number of tracks and the number of mice trapped per unit area (59.59%). This indicates that the tracking data are a better measure of absolute population size than population density.

- 3) The relationship between the tracking data for the baited and nonbaited weeks is given in Figure 7. The resulting equation was

$$\log\left(\frac{\text{bait. \# tracks}}{\text{area}} + 1\right) = .87341 + .80199 \log\left(\frac{\text{nonbait. \# tracks}}{\text{area}} + 1\right)$$

Table 4. Nonlinear regression analysis of trapping data.

Parameter Estimates	Model			
	1	2	3	4
Combined (all 3 woodlots) trapping success	0.247	0.431	0.437	
Combined recruitment rate (no. mice per day)		2.018		
FF recruitment rate			1.787	1.707
I1 recruitment rate			1.637	1.583
M4 recruitment rate			2.526	2.526
FF trapping success				0.542
I1 trapping success				0.353
M4 trapping success				0.432
Deviance (-2 x log likelihood of regression)	63.581	55.213	54.666	53.821
Difference in deviance from previous model (= χ^2)		8.367	0.548	0.845
Degrees of freedom		1	2	2
Significance level		$p \leq 0.005$	N.S.	N.S.

Figure 5. Regression of trapping results on time.

REGRESSION EQUATION :

$$y_{t+1} = .569 y_t + .870$$

(S.E. = .799) (S.E. = .550)

Figure 6. Correlations between trapping and tracking data.

CORRELATION = 73.80 % , $p < 0.01$

CORRELATION = 59.59 % , $p < 0.05$

Figure 7. Comparison of tracking data from baited and nonbaited weeks.

$$Y = \log \left(\frac{\text{tracks} / 7 \text{ days} + 1}{\text{woodlot area}} \right) : \text{baited weeks}$$

$$X = \log \left(\frac{\text{tracks} / 7 \text{ days} + 1}{\text{woodlot area}} \right) : \text{nonbaited weeks}$$

REGRESSION EQUATION : $Y = .873 + .802 X$

CORRELATION = 61.41 % , $p < 0.01$

This was used to obtain estimates of nonbaited values corresponding to observed baited values. The resulting 12 weeks' tracking results for the 6 woodlots - I1, I2, M1, M2, M3, and M4 - are given in Table 5.

4) The results of the regression analysis of the tracking data (Table 5) are given in Table 6. Note that the dependent variable was transformed to $(\text{tracks})^{.5}$ which stabilized the variance, i.e. the variance became approximately constant over the times and woodlots.

The following is a summary of Table 6.

- i) Not all of the regression equations for the 6 woodlots have the same intercept ($F = 3.190$, $p < 0.05$).
- ii) Most of this difference in intercepts is due to a difference between isolated and connected woodlots ($F = 6.407$, $p < 0.05$).
- iii) Different woodlots within the same type did not have significantly different intercepts ($F = 2.385$, N.S.)
- iv) There is a significant linear regression ($F = 61.14$, $p < 0.01$).
- v) There is statistical justification for the inclusion of a quadratic term ($F = 11.805$, $p < 0.01$).
- vi) There is a significant difference between the slopes (linear term) of the regressions for the isolated and connected woodlots ($F = 4.795$, $p < 0.05$).
- vii) There is no significant difference among slopes of different woodlots within types ($F = 2.394$, N.S.).
- viii) There are no significant differences in the quadratic terms for isolated and connected woodlots ($F = 0.0363$, N.S.) or for woodlots within types ($F = 0.6794$, N.S.). This implies that the woodlots reach their maximum population sizes at approximately the same time; this occurs in the second week of August.

See Figure 8 for a summary of the resulting regression equations.

Table 5. Weekly tracking data. Number of tracks in 6 woodlots
(Figure 2) from the second week in June to the first week in
September.

Week	I1 (3.8 ha)	I2 (3.7 ha)	M1 (5.3 ha)	M2 (4.5 ha)	M3 (9.8 ha)	M4 (1.5 ha)
1	0	0	0	0	0	1
2	3	1	1	1	2	18
3	6	0	1	2	2	1
4	2	2	1	0	1	2
5	0	5	1	9	5	26
6	4	8	4	19	5	21
7	10	14	5	19	9	8
8	12	15	19	18	10	19
9	2	13	16	14	27	13
10	2	6	5	3	6	2
11	9	6	15	3	8	9
12	8	5	11	20	7	14

Table 6. Analysis of variance for regressions of tracking data on time.

Source	Sum of Squares	Degrees of Freedom	Mean Square	F-statistic	Significance Level
Total	163.592	71			
Additional due to different intercepts	16.307	5	3.262	3.190	$p < 0.05$
Due to types	6.551	1	6.551	6.407	$p < 0.05$
Additional due to woodlots within types	9.756	4	2.439	2.385	N.S.
Due to linear and quadratic regression	74.583	2	37.291	36.472	$p < 0.01$
Due to linear term	62.513	1	62.513	61.140	$p < 0.01$
Additional due to quadratic term	12.070	1	12.070	11.805	$p < 0.01$
Additional due to separate linear and quadratic regressions for types	4.939	2	2.470	2.416	N.S.
Due to linear term	4.903	1	4.903	4.795	$p < 0.05$
Additional due to quadratic term	0.0371	1	0.0371	0.0363	N.S.
Additional due to regression on woodlots within types	12.551	8	1.569	1.535	N.S.
Due to linear term	9.793	4	2.448	2.394	N.S.
Additional due to quadratic term	2.779	4	0.6947	0.6794	N.S.
Residual	55.212	54	1.022		

Figure 8. Regressions of tracking data on time.

REGRESSION EQUATIONS

ISOLATED :
 $\sqrt{\text{NO. TRACKS}} = - .574 + .746(\text{TIME}) - .041(\text{TIME})^2$
 (S.E.=.663) (S.E.=.234) (S.E.=.018)

CONNECTED :
 $\sqrt{\text{NO. TRACKS}} = - .427 + .818(\text{TIME}) - .044(\text{TIME})^2$
 (S.E.=.591) (S.E.=.209) (S.E.=.016)

ISOLATED SLOPE < CONNECTED SLOPE (F= 4.80, p < .05)

DISCUSSION

The main prediction generated by the model, that P. leucopus populations in isolated woodlots have lower growth rates than those in connected woodlots, is supported by the field results ($F = 4.795$, $p < 0.05$). As stated earlier, this has important implications for the population stability (i.e. survival) of P. leucopus in fragmented habitat. If isolated populations have lower growth rates, they will begin the winter with fewer individuals. This means they will likely have higher probabilities of becoming extinct before the following spring. Re-establishment of extinct local populations will take longer in isolated patches than in connected ones. In a whole region, therefore, the probability that P. leucopus populations will persist depends on the degree to which individual patches are isolated from one another.

EXTENSION OF THE MODEL

The model appears to be a good predictor of differences between woodlots' P. leucopus population dynamics over the short term (one season). Therefore, it is of interest to use the model for long-term predictions of the effects of varying degrees of isolation on woodlot population size.

Suppose each of four woodlots of equal areas may or may not be 'connected' to each of the other three. Suppose also that the stability of a population depends directly on the degree to which it is connected to other woodlots (or the degree to which it is not isolated). Figure 9 gives the eleven possible arrangements of the four woodlots in the predicted order of increasing overall population stability.

I have performed eleven simulation experiments (Fahrig et al. 1983), corresponding to the eleven hypothetical arrangements. Stochastic variability (s.d. = 10% of parameter means) was included. In each experiment, the four woodlots each begin the first season with nine adult mice. Population sizes are calculated for each week, for each age class in each woodlot from the third week in March until the second week in October. Each simulation was run for 100 'years', and it was assumed that the adult population in each woodlot in the spring was 15% of the population in the previous fall (Taylor 1978, Middleton 1979). The mean yearly final sizes (in the second week of October) of the total populations in the four woodlots over 100 years were calculated.

The means and survival data are presented in Table 7. A number of results are of interest.

i) The P. leucopus populations in completely isolated woodlots became extinct within three to four years.

Figure 9. Groups of four woodlots arranged in suggested order of increasing overall population stability.

Table 7. Average yearly final population sizes (A.Y.F.'s) and survival in years. Numbering of woodlots is the same as in Figure 9.

		Woodlot	A.Y.F.	Survival (years)
a		1	0.03	3
		2	0.06	3
		3	0.06	4
		4	0.05	3
b		1	30.30	87
		2	29.40	88
		3	0.07	3
		4	0.31	4
c		1	8.50	22
		2	7.90	23
		3	30.60	96
		4	30.20	96
d		1	30.60	100
		2	31.70	100
		3	32.30	100
		4	0.08	3
e		1	0.25	4
		2	34.20	100
		3	32.90	100
		4	35.00	100
f		1	31.90	100
		2	32.30	100
		3	32.40	100
		4	31.90	100
g		1	32.00	100
		2	33.10	100
		3	32.00	100
		4	32.80	100
h		1	4.30	35
		2	12.20	37
		3	8.30	38
		4	8.70	37
i		1	34.00	100
		2	33.30	100
		3	35.10	100
		4	34.00	100
j		1	30.50	100
		2	32.10	100
		3	31.40	100
		4	32.00	100
k		1	30.60	100
		2	32.60	100
		3	31.50	100
		4	31.60	100

ii) If two woodlots were connected to each other, but to no other woodlots, their populations became extinct within the 100 years. The length of time required for this extinction was quite variable. The populations in a linkage of two woodlots were quite unstable, but less so than a completely isolated one.

iii) In almost every arrangement containing three or more interconnected woodlots, the P. leucopus populations survived for 100 years, although those in individual woodlots sometimes became extinct. There was one exception to this result; the entire population in 'h' died out. The reasons for this are not apparent, but it perhaps can be explained by regarding the triangle as forming one unit of a pair, and so 'h' approximates 'b'.

iv) The prediction of Diamond (1975) that woodlots arranged in a triangle or circle have more stable populations than those arranged linearly was not supported in this experiment. This is evident from two comparisons. First, the three woodlots in the triangle in 'e' had similar average final populations to those of the three linearly arranged woodlots in 'd'. Second, the four woodlots in the circle 'i' had similar average final populations to those arranged linearly in 'f'.

v) Although one might predict on the basis of intuition that, within a particular arrangement of woodlots, the one having the highest number of connections should be the most stable, since it has the highest number of possible sources for population replenishment in the case of extinction, this is not supported by the simulations. Woodlots having higher numbers of connections had approximately equivalent average final population sizes to other woodlots in the same interconnected group (see results for arrangements 'd', 'f', 'g', and 'j').

vi) The population means of those populations that survived 100 years were all very similar (between 30 and 35 mice).

The results of the simulation experiments indicate that the spatial connectivity of habitat patches is important for several reasons. First, it is evident that links among habitat patches can increase the probability of survival of resident populations. Second, it appears that, for a particular species which inhabits a certain type of patch, there is a minimum number of patches which need to be connected in order to ensure the survival of the species in that area. It does not seem to make much difference how these patches are interconnected, as long as the minimum number of patches is involved.

From these simulations it is apparent that the spatial arrangement of interconnected habitat patches associated with a stable and abundant population depends on the species under consideration and, in particular, on the interplay between the intrinsic growth and movement rates. For example, a species having a higher growth rate/movement rate ratio than P. leucopus would probably require a smaller minimum number of interconnected patches for population stability than the minimum number required by P. leucopus (i.e. 3), since movement would have less effect on the population than reproduction. If the growth rate/movement rate ratio were lower than that for P. leucopus, the minimum number of interconnected patches required would need to be higher than that for P. leucopus.

The results indicate that nature reserve planners may need to consider the question of the connectivity of reserves in terms of one or a few critical species, especially those considered most likely to be deleteriously affected by decreased patch size and increased patch

isolation. The model can then be used to provide guidance on the most suitable spatial arrangement of interconnected patches, both in terms of their number and also of their sizes, to ensure long-term stability of the populations of concern.

CONCLUSION

In conclusion, three lines of evidence supported the hypothesis that P. leucopus populations in isolated woodlots are less stable than those in nonisolated woodlots: i) short-term (one season) model simulations predicted that population growth rates in isolated woodlots are lower than those in nonisolated woodlots, ii) field data from one season supported this prediction, and iii) long-term model simulation experiments predicted extinctions of isolated populations and persistence of nonisolated ones.

Forest habitat fragmentation in the Ottawa area has not yet led to a measurable increase in the extinction rate of local populations of woodland organisms (Middleton 1982). However, my study suggests that further isolation of woodlots will probably cause local or even regional extinctions; the decrease in population growth rate which I have documented for P. leucopus in isolated woodlots may be an early symptom of problems to come.

Finally, although the model described here has been applied to P. leucopus in woodlots, it may be a useful tool for predicting changes in the population dynamics of any of the many organisms that are found living in habitat patches.

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Appendix 1. Computer program for the simulation of *Peromyscus leucopus* population dynamics in 4 woodlots

11:32 MAR 24 '83 MICE.F61WEGNS

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1 - C THIS PROGRAM IS A SIMULATION OF THE POPULATION DYNAMICS
2 - C OF PEROMYSCUS LEUCOPUS IN 4 WOODLOTS. THE WOODLOTS ARE
3 - C DENOTED BY 'I' OR 'J'. MICE CAN MOVE FROM ONE WOODLOT
4 - C (EG: I) TO ANOTHER (EG: J) ONLY IF THERE IS A CONNECTION
5 - C (EG: FENCEROW) BETWEEN THEM. THE PROGRAM CALCULATES THE
6 - C POPULATION SIZES IN THE FOUR WOODLOTS EACH WEEK FROM THE
7 - C SECOND WEEK OF MARCH TO THE SECOND WEEK IN OCTOBER FOR
8 - C 100 CONSECUTIVE YEARS.
9 - C
10 - C 'NRUN' IS A COUNTER WHICH DENOTES THE YEAR OF THE SIMULATION.
11 - C 'MIN' IS AN ARRAY CONTAINING THE MINIMUM POPULATION SIZES
12 - C IN EACH WOODLOT IN EACH YEAR. 'AV' IS AN ARRAY CONTAINING
13 - C THE AVERAGES, CALCULATED OVER 100 YEARS, OF THE FINAL
14 - C POPULATION SIZES FOR THE YEAR (IN THE SECOND WEEK OF
15 - C OCTOBER) IN EACH WOODLOT. 'VARAV' IS AN ARRAY CONTAINING
16 - C THE VARIANCES OF THE 'AV' VALUES AND THE COVARIANCES
17 - C BETWEEN PAIRS OF THEM. 'CORR' IS AN ARRAY CONTAINING THE
18 - C CORRELATION COEFFICIENTS OF PAIRS OF 'AV' VALUES.
19 - C 'N' IS AN ARRAY CONTAINING THE POPULATION SIZES OF EACH OF THE
20 - C THREE AGE CLASSES - JUVENILE, SUBADULT, AND ADULT - IN EACH
21 - C WOODLOT IN EACH WEEK FOR EACH YEAR. AGE CLASS IS DENOTED BY
22 - C 'K' OR 'L'.
23 - C 'Q' IS AN ARRAY CONTAINING THE PROBABILITIES OF ADULT
24 - C FEMALES 'GIVING BIRTH' TO A JUVENILE DURING A PARTICULAR
25 - C YEAR. THE FEMALES WILL HAVE ACTUALLY GIVEN BIRTH THREE
26 - C WEEKS PREVIOUSLY; IT TAKES THREE WEEKS FOR A BABY MOUSE
27 - C TO BECOME A JUVENILE. JUVENILES ARE COUNTED INSTEAD OF
28 - C BABIES BECAUSE POPULATION ESTIMATES OF BABIES IN THE
29 - C FIELD ARE VERY DIFFICULT TO OBTAIN; BABIES ARE NOT
30 - C 'TRAPPABLE'.
31 - C 'W' IS AN ARRAY CONTAINING THE PROBABILITY THAT JUVENILE
32 - C MICE SURVIVE AND GRADUATE INTO THE SUBADULT AGE CLASS.
33 - C 'S' IS AN ARRAY CONTAINING THE PROBABILITY THAT SUBADULT
34 - C MICE SURVIVE AND GRADUATE INTO THE ADULT AGE CLASS.
35 - C 'E' IS AN ARRAY CONTAINING THE PROPORTION OF EACH AGE CLASS
36 - C WHICH EMIGRATES FROM A WOODLOT (I) TO ANOTHER WOODLOT (J) IN
37 - C A WEEK.
38 - C 'D' IS AN ARRAY CONTAINING THE PROPORTION OF EACH AGE CLASS
39 - C WHICH DIES EACH WEEK.
40 - C 'Z' IS AN ARRAY CONTAINING VALUES WHICH DETERMINE THE RATE OF
41 - C IMMIGRATION INTO A WOODLOT (I). THE VALUES IN Z ARE THE
42 - C PROPORTIONS OF THE THREE AGE CLASSES IN EACH OF THE WOODLOTS
43 - C CONNECTED TO I (EG: J) WHICH IMMIGRATE TO I IN A WEEK.
44 - C 'X' IS AN ARRAY CONTAINING THE COMBINED EFFECTS OF DEATH (D)
45 - C EMIGRATION (E) AND IMMIGRATION (Z). X IS CALCULATED LATER IN
46 - C THE PROGRAM.
47 - C 'NT' IS AN ARRAY CONTAINING THE TOTAL POPULATION SIZES
48 - C (JUVENILES + SUBADULTS + ADULTS) IN THE FOUR WOODLOTS EACH
49 - C WEEK FOR 100 YEARS.
50 - C 'T' IS A COUNTER DENOTING THE WEEK.
51 - C 'I' AND 'J' ARE COUNTERS DENOTING WOODLOTS.
52 - C 'K' AND 'L' ARE COUNTERS DENOTING AGE CLASSES.
53 - C
54 - C INTEGER NRUN
55 - C REAL MIN(4), AV(4), VARAV(4,4), CORR(4,4)
56 - C DO 1 I=1,4
57 - C AV(I)=0.0
58 - C DO 1 J=1,4

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59 - 1  VARAV(J,I)=0.0
60 -    DO 8010 NRUN=1,100
61 -    WRITE(6,16)NRUN
62 - 16  FORMAT(/3X,'SIMULATION FOR YEAR',I3/)
63 -    REAL N(3,4,33,100),Q(3,4,5,32),W(3,4),S(3,4)
64 -    REAL E(3,4,3,4),D(3,4,3,4),Z(3,4,3,4),X(3,4,3,4)
65 -    REAL NT(4,29,100)
66 -    INTEGER T,I,J,K,L
67 - C
68 - C    IN THE FOLLOWING SECTION THE VALUES OF N FOR THE FIRST FIVE
69 - C    WEEKS OF YEAR 1 ARE READ FROM A FILE (7).
70 - C
71 -    REAL RNOM
72 -    DO 100 T=1,5
73 -    DO 100 I=1,4
74 -    DO 100 K=1,3
75 - 100  N(K,I,T,NRUN)=0.
76 -    IF(NRUN.EQ.1)THEN
77 - 200  READ(7,15)T,I,K,VALN
78 -    IF(T.NE.0)THEN
79 -    N(K,I,T,1)=VALN
80 -    GO TO 200
81 -    ENDIF
82 -    ENDIF
83 - C
84 - C    IN THE FOLLOWING SECTION VALUES OF N FOR THE FIRST FIVE WEEKS
85 - C    OF ALL YEARS BUT THE FIRST ARE CALCULATED.  THESE VALUES
86 - C    DEPEND ON THE FINAL VALUES OF N (IN THE SECOND WEEK OF
87 - C    OCTOBER) IN THE PREVIOUS YEAR (NRUN-1).
88 - C
89 -    IF(NRUN.NE.1)THEN
90 -    DO 203 I=1,4
91 -    N(3,I,1,NRUN)=NT(I,33,NRUN-1)/4.
92 - 203  CONTINUE
93 -    DO 204 T=2,5
94 -    DO 204 I=1,4
95 -    N(3,I,T,NRUN)=0.9355*N(3,I,T-1,NRUN)
96 - 204  CONTINUE
97 -    DO 205 T=1,5
98 -    DO 205 I=1,4
99 -    N(3,I,T,NRUN)=INT(N(3,I,T,NRUN)+0.5)
100 - 205  CONTINUE
101 -    ENDIF
102 - 15  FORMAT(3I5,F10.6)
103 - C
104 - C    IN THE FOLLOWING SECTION THE Q ARRAY IS READ FROM A FILE (8).
105 - C    A RANDOM NUMBER GENERATOR IS USED TO OBTAIN APPROXIMATIONS OF
106 - C    THESE VALUES; IN EACH YEAR THE Q VALUES WILL BE SLIGHTLY
107 - C    DIFFERENT.
108 - C
109 -    DO 300 T=5,32
110 -    DO 300 I=1,4
111 -    DO 300 K=1,3
112 - 300  Q(K,I,T)=0.
113 - 400  READ (8,25)T,I,K,VALQ
114 -    IF(T.NE.0)THEN
115 -    Q(K,I,T)=VALQ
116 -    NN=1
117 -    VQ=0.0
118 -    DO 450 NN=1,100

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119 - CALL RANDOM(RNOM)
120 - IF(RNOM.LE.Q(K,I,T))THEN
121 - VQ=VQ+0.01
122 - ENDIF
123 - 450 CONTINUE
124 - Q(K,I,T)=VQ
125 - GO TO 400
126 - ENDIF
127 - C
128 - C IN THE FOLLOWING SECTION THE W ARRAY IS READ FROM A FILE (8).
129 - C AGAIN, RANDOM APPROXIMATIONS OF THESE VALUES ARE CALCULATED
130 - C EACH YEAR.
131 - C
132 - DO 500 I=1,4
133 - DO 500 K=1,3
134 - 500 W(K,I)=0.
135 - 600 READ(8,35)I,K,VALW
136 - IF(I.NE.0)THEN
137 - W(K,I)=VALW
138 - NN=1
139 - VW=0.0
140 - DO 650 NN=1,100
141 - CALL RANDOM(RNOM)
142 - IF(RNOM.LE.W(K,I))THEN
143 - VW=VW+0.01
144 - ENDIF
145 - 650 CONTINUE
146 - W(K,I)=VW
147 - GO TO 600
148 - ENDIF
149 - 25 FORMAT(3I5,F10.4)
150 - 35 FORMAT(2I5,F10.4)
151 - C
152 - C IN THE FOLLOWING SECTION THE S ARRAY IS READ FROM A FILE (8).
153 - C RANDOM APPROXIMATIONS ARE CALCULATED EACH YEAR.
154 - C
155 - DO 700 I=1,4
156 - DO 700 K=1,3
157 - 700 S(K,I)=0.
158 - 800 READ(8,35)I,K,VALS
159 - IF(I.NE.0)THEN
160 - S(K,I)=VALS
161 - NN=1
162 - VS=0.0
163 - DO 850 NN=1,100
164 - CALL RANDOM(RNOM)
165 - IF(RNOM.LE.S(K,I))THEN
166 - VS=VS+0.01
167 - ENDIF
168 - 850 CONTINUE
169 - S(K,I)=VS
170 - GO TO 800
171 - ENDIF
172 - 55 FORMAT(4I5,F10.4)
173 - C
174 - C IN THE FOLLOWING SECTION THE D ARRAY IS READ FROM A FILE (8).
175 - C RANDOM APPROXIMATIONS ARE CALCULATED FOR EACH YEAR.
176 - C
177 - DO 900 I=1,4
178 - DO 900 K=1,3

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179 -      DO 900 J=1,4
180 -      DO 900 L=1,3
181 -      900 D(L,J,K,I)=0.
182 -      1000 READ(8,55)I,K,J,L,VALD
183 -      IF(I.NE.0)THEN
184 -      D(L,J,K,I)=VALD
185 -      NN=1
186 -      VD=0.0
187 -      DO 1050 NN=1,100
188 -      CALL RANDOM(RNOM)
189 -      IF(RNOM.LE.D(L,J,K,I))THEN
190 -      VD=VD+0.01
191 -      ENDIF
192 -      1050 CONTINUE
193 -      D(L,J,K,I)=VD
194 -      GO TO 1000
195 -      ENDIF
196 - C
197 - C      IN THE FOLLOWING SECTION THE E ARRAY IS READ FROM A FILE (8).
198 - C      RANDOM APPROXIMATIONS ARE TAKEN EACH YEAR.
199 - C
200 -      DO 1100 I=1,4
201 -      DO 1100 K=1,3
202 -      DO 1100 J=1,4
203 -      DO 1100 L=1,3
204 -      1100 E(L,J,K,I)=0.
205 -      1200 READ(8,55)I,K,J,L,VALE
206 -      IF(I.NE.0)THEN
207 -      E(L,J,K,I)=VALE
208 -      NN=1
209 -      VE=0.0
210 -      DO 1250 NN=1,100
211 -      CALL RANDOM(RNOM)
212 -      IF(RNOM.LE.E(L,J,K,I))THEN
213 -      VE=VE+0.01
214 -      ENDIF
215 -      1250 CONTINUE
216 -      E(L,J,K,I)=VE
217 -      GO TO 1200
218 -      ENDIF
219 - C
220 - C      IN THE FOLLOWING SECTION THE Z ARRAY IS READ FROM A FILE (5).
221 - C      RANDOM APPROXIMATIONS ARE TAKEN EACH YEAR.
222 - C
223 -      DO 1300 I=1,4
224 -      DO 1300 K=1,3
225 -      DO 1300 J=1,4
226 -      DO 1300 L=1,3
227 -      1300 Z(L,J,K,I)=0.
228 -      1400 READ(5,55)I,K,J,L,VALZ
229 -      IF(I.NE.0)THEN
230 -      Z(L,J,K,I)=VALZ
231 -      NN=1
232 -      VZ=0.0
233 -      DO 1450 NN=1,100
234 -      CALL RANDOM(RNOM)
235 -      IF(RNOM.LE.Z(L,J,K,I))THEN
236 -      VZ=VZ+0.01
237 -      ENDIF
238 -      1450 CONTINUE

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239 -      Z(L,J,K,I)=VZ
240 -      GO TO 1400
241 -      ENDIF
242 -      REWIND (5)
243 -      REWIND (8)
244 - C      CALCULATION OF THE X ARRAY.
245 -      DO 5000 I=1,4
246 -      DO 5000 K=1,3
247 -      DO 5000 J=1,4
248 -      DO 5000 L=1,3
249 -      X(L,J,K,I)=-D(L,J,K,I)-E(L,J,K,I)+Z(L,J,K,I)
250 - 5000 CONTINUE
251 -      DO 8000 T=5,32
252 - C
253 - C      IN THE FOLLOWING SECTION THE X ARRAY IS MULTIPLIED BY THE
254 - C      VALUES OF N IN WEEK T TO GIVE NEW VALUES OF N. THESE NEW
255 - C      VALUES GIVE THE AGE CLASS POPULATION SIZES AFTER THE EFFECTS OF
256 - C      DEATH, IMMIGRATION, AND EMIGRATION FOR A WEEK. CHANGES IN N
257 - C      DUE TO BIRTHS AND 'GRADUATIONS' INTO THE NEXT AGE CLASS WILL
258 - C      BE ACCOUNTED FOR LATER.
259 - C
260 -      DO 7000 I=1,4
261 -      DO 7000 K=1,3
262 -      N(K,I,T+1,NRUN)=0.0
263 -      DO 6000 J=1,4
264 -      DO 6000 L=1,3
265 -      N(K,I,T+1,NRUN)=(N(K,I,T+1,NRUN))+(X(L,J,K,I)*N(L,J,T,NRUN))
266 - 6000 CONTINUE
267 - C
268 - C      CHANGES IN N DUE TO BIRTHS AND 'GRADUATIONS' INTO NEXT AGE CLASS
269 - C
270 - C      IN THE FOLLOWING EQUATION, ADDITIONS TO THE JUVENILE AGE
271 - C      CLASSES IN THE FOUR WOODLOTS FROM WEEK T TO WEEK T+1 ARE
272 - C      CALCULATED. THE CHANGE IN THE NUMBER OF JUVENILES DEPENDS
273 - C      ON THE NUMBER OF ADULT FEMALES PRESENT THREE WEEKS PREVIOUSLY
274 - C      (IT TAKES THREE WEEKS FOR A BABY TO BECOME A JUVENILE), THE
275 - C      VALUE OF Q FOR WEEK T, AND THE NUMBER OF JUVENILES THAT
276 - C      GRADUATE TO THE SUBADULT CLASS DURING THE WEEK.
277 - C
278 -      IF(K.EQ.1)THEN
279 -      N(K,I,T+1,NRUN)=N(K,I,T+1,NRUN)+((0.5)*Q(K,I,T)*N(3,I,T-3,NRUN))+N
280 -      1(K,I,T,NRUN)-(W(2,I)*N(1,I,T-3,NRUN))
281 -      ENDIF
282 - C
283 - C      IN THE FOLLOWING EQUATION, ADDITIONS TO THE SUBADULT AGE
284 - C      CLASSES IN THE FOUR WOODLOTS FROM WEEK T TO WEEK T+1 ARE
285 - C      CALCULATED. THE CHANGE IN THE NUMBER OF SUBADULTS DEPENDS
286 - C      ON THE NUMBER OF JUVENILES PRESENT THREE WEEKS PREVIOUSLY
287 - C      (IT TAKES THREE WEEKS FOR A JUVENILE TO BECOME ASUBADULT),
288 - C      THE VALUE OF W FOR WEEK T, AND THE NUMBER OF SUBADULTS THAT
289 - C      GRADUATE TO THE ADULT CLASS DURING THE WEEK.
290 - C
291 -      IF(K.EQ.2)THEN
292 -      N(K,I,T+1,NRUN)=N(K,I,T+1,NRUN)+(W(K,I)*N(1,I,T-3,NRUN))+N(K,I,T,N
293 -      1RUN)-(S(3,I)*N(2,I,T-2,NRUN))
294 -      ENDIF
295 - C
296 - C      IN THE FOLLOWING EQUATION, ADDITIONS TO THE ADULT AGE
297 - C      CLASSES IN THE FOUR WOODLOTS FROM WEEK T TO WEEK T+1 ARE
298 - C      CALCULATED. THE CHANGE IN THE NUMBER OF ADULTS DEPENDS

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299 - C      ON THE NUMBER OF SUBADULTS PRESENT TWO WEEKS PREVIOUSLY
300 - C      (IT TAKES TWO WEEKS FOR A SUBADULT TO BECOME AN ADULT) AND
301 - C      THE VALUE OF S FOR WEEK T.
302 - C
303 -      IF(K.EQ.3)THEN
304 -          N(K,I,T+1,NRUN)=N(K,I,T+1,NRUN)+(S(K,I)*N(2,I,T-2,NRUN))+N(K,I,T,N
305 -          1RUN)
306 -      ENDIF
307 - C
308 - C      NOW THE VALUES CALCULATED FOR N IN WEEK T+1 ARE CONVERTED TO
309 - C      WHOLE NUMBERS.
310 - C
311 -      N(K,I,T+1,NRUN)=INT(N(K,I,T+1,NRUN)+0.5)
312 -      IF(N(K,I,T+1,NRUN).LT.0.)THEN
313 -          N(K,I,T+1,NRUN)=0.
314 -      ENDIF
315 -      7000 CONTINUE
316 -      8000 CONTINUE
317 - C
318 - C      CALCULATION OF NT FOR YEAR NRUN.
319 - C
320 -      DO 13 T=5,33
321 -          DO 13 I=1,4
322 -              NT(I,T,NRUN)=0.0
323 -              DO 12 K=1,3
324 -                  NT(I,T,NRUN)=NT(I,T,NRUN)+N(K,I,T,NRUN)
325 -              12 CONTINUE
326 -          13 CONTINUE
327 -          IF(NRUN.EQ.1.OR.NRUN.EQ.2.OR.NRUN.EQ.5.OR.NRUN.EQ.10.OR.NRUN.EQ.20
328 -          1.OR.NRUN.EQ.30.OR.NRUN.EQ.40.OR.NRUN.EQ.50.OR.NRUN.EQ.70.OR.NRUN.E
329 -          20.100.)THEN
330 -              WRITE(6,45)((NT(I,T,NRUN),I=1,4),T=5,33)
331 -          45 FORMAT(3X,'NUMBER OF MICE IN 4 WOODLOTS DURING A SUMMER'///7X,'WEE
332 -          1K',8X,'WOODLOT 1',3X,'WOODLOT 2',3X,'WOODLOT 3',3X,'WOODLOT 4'//3X
333 -          2,'MAR-WEEK 2',4F12.0/3X,'MAR-WEEK 3',4F12.0/3X,'MAR-WEEK 4',4F12.0
334 -          3/3X,'APR-WEEK 1',4F12.0/3X,'APR-WEEK 2',4F12.0/3X,'APR-WEEK 3',4F1
335 -          42.0/3X,'APR-WEEK 4',4F12.0/3X,'MAY-WEEK 1',4F12.0/3X,'MAY-WEEK 2',
336 -          54F12.0/3X,'MAY-WEEK 3',4F12.0/3X,'MAY-WEEK 4',4F12.0/3X,'JUN-WEEK
337 -          61',4F12.0/3X,'JUN-WEEK 2',4F12.0/3X,'JUN-WEEK 3',4F12.0/3X,'JUN-WE
338 -          7EK 4',4F12.0/3X,'JUL-WEEK 1',4F12.0/3X,'JUL-WEEK 2',4F12.0/3X,'JUL
339 -          8-WEEK 3',4F12.0/3X,'JUL-WEEK 4',4F12.0/3X,'AUG-WEEK 1',4F12.0/3X,'
340 -          9AUG-WEEK 2',4F12.0/3X,'AUG-WEEK 3',4F12.0/3X,'AUG-WEEK 4',4F12.0/3
341 -          1X,'SEP-WEEK 1',4F12.0/3X,'SEP-WEEK 2',4F12.0/3X,'SEP-WEEK 3',4F12.
342 -          20/3X,'SEP-WEEK 4',4F12.0/3X,'OCT-WEEK 1',4F12.0/3X,'OCT-WEEK 2',4F
343 -          312.0)
344 -      ENDIF
345 - C
346 - C      CALCULATION OF MIN FOR YEAR NRUN.
347 - C
348 -      DO 102 I=1,4
349 -          MIN(I)=1.E10
350 -      102 CONTINUE
351 -          DO 103 T=5,33
352 -              DO 103 I=1,4
353 -                  IF(NT(I,T,NRUN).LT.MIN(I))THEN
354 -                      MIN(I)=NT(I,T,NRUN)
355 -                  ENDIF
356 -              103 CONTINUE
357 -              WRITE(6,17)MIN
358 -      17 FORMAT(/1X,'MINIMUM VALUES FOR THE YEAR'//1X,'WOODLOT',9X,'1',9X,'

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359 -      12',9X,'3',9X,'4'/F19.0,3F10.0)
360 - C
361 - C      CALCULATION OF AV AND VARAV.
362 - C
363 -      DO 104 I=1,4
364 -      AV(I)=AV(I)+NT(I,33,NRUN)
365 -      DO 104 J=1,4
366 -      VARAV(J,I)=VARAV(J,I)+NT(I,33,NRUN)*NT(J,33,NRUN)
367 -      104 CONTINUE
368 -      8010 CONTINUE
369 -      DO 8011 I=1,4
370 -      DO 8011 J=1,4
371 -      VARAV(J,I)=(VARAV(J,I)-(AV(I)*AV(J))/100.)/99.
372 -      8011 CONTINUE
373 -      DO 8012 I=1,4
374 -      AV(I)=AV(I)/50
375 -      8012 CONTINUE
376 -      WRITE(6,18)AV,VARAV
377 -      18 FORMAT(////1X,'AVERAGES OF YEARLY FINALS (AYF)'/1X,'WOODLOT',10X,
378 -      1'1',10X,'2',10X,'3',10X,'4'//F24.5,3F11.5////1X,'VARIANCES AND COV
379 -      2ARIANCES OF AYF'/1X,'WOODLOT',10X,'1',10X,'2',10X,'3',10X,'4'//4X
380 -      3,'1',2X,E17.4,2X,E9.4,2X,E9.4,2X,E9.4//4X,'2',2X,E17.4,2X,
381 -      4E9.4,2X,E9.4,2X,E9.4//4X,'3',2X,E17.4,2X,E9.4,2X,E9.4,2X,E
382 -      59.4//4X,'4',2X,E17.4,2X,E9.4,2X,E9.4,2X,E9.4)
383 - C
384 - C      CALCULATION OF CORR.
385 - C
386 -      DO 8014 I=2,4
387 -      I1=I-1
388 -      DO 8013 J=1,I1
389 -      CORR(J,I)=VARAV(J,I)/SQRT(VARAV(I,I)*VARAV(J,J))
390 -      CORR(I,J)=CORR(J,I)
391 -      8013 CONTINUE
392 -      CORR(I,I)=1.0
393 -      8014 CONTINUE
394 -      CORR(1,1)=1.0
395 -      WRITE(6,19)CORR
396 -      19 FORMAT(////1X,'CORRELATIONS BETWEEN PAIRS OF AYF'/1X,'WOODLOT',10
397 -      1X,'1',10X,'2',10X,'3',10X,'4'//4X,'1',2X,F17.5,2X,F9.5,2X,F9.5,2X,
398 -      2F9.5//4X,'2',2X,F17.5,2X,F9.5,2X,F9.5,2X,F9.5//4X,'3',2X,F17.5,2X,
399 -      3F9.5,2X,F9.5,2X,F9.5//4X,'4',2X,F17.5,2X,F9.5,2X,F9.5,2X,F9.5)
400 -      STOP
401 -      END

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Appendix 2. Trapping data: number of mice removed from woodlots FF, I1, and M4. No traps set where blank entries occur.

Date	FF	I1	M4
September 4	9		
5	7		
6	9		
7	4		
8	3		
9	1		
10			
11			
12			
13			
14			
15	4		22
16	3		15
17	2		12
18	1		10
19	2		5
20	1		2
21	1		2
22	1		4
23	0		3
24	3		1
25	0		3
26		11	2
27		13	1
28		8	4
29		4	3
30		2	0
October 1		6	1
2		1	
3		1	
4		0	
5		1	
6		0	
7		0	

END

1 0 0 9 8 4

FIN