



International Association for Ecology

The Analysis of a Population Model Demonstrating the Importance of Dispersal in a Heterogeneous Environment

Author(s): D. A. Roff

Source: *Oecologia*, Vol. 15, No. 3 (1974), pp. 259-275

Published by: Springer in cooperation with International Association for Ecology

Stable URL: <http://www.jstor.org/stable/4214963>

Accessed: 08/02/2009 01:56

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=springer>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.



Springer and International Association for Ecology are collaborating with JSTOR to digitize, preserve and extend access to *Oecologia*.

<http://www.jstor.org>

The Analysis of a Population Model Demonstrating the Importance of Dispersal in a Heterogeneous Environment

D. A. Roff

School of Biological Sciences, University of Sydney

Received June 10, 1973

Summary. In a previous paper (Roff, 1974) a simulation model was presented demonstrating the importance of dispersal in a spatially heterogeneous environment. In the present paper this model is analysed in detail. It is shown that the qualitative properties of the model can be understood within the framework of a more general mathematical model. The effect of dispersal in a heterogeneous environment is to reduce the variance in the environmental fluctuations. How the subpopulations are connected with respect to dispersers may be the primary factor in determining the change in population size with changes in environmental fluctuations. Both the type of dispersal pattern and the number of subpopulations may influence the persistence of a population without affecting the mean subpopulation size. Finally, it is noted that the "value" of a dispersal pattern changes with changes in parameter values and a shift from one parameter value to another may lead to a qualitative change in the type of dispersal pattern "favoured".

1. Introduction

There has been little theoretical study of the effects of dispersal on population stability; research has centred principally on distributions resulting from dispersal and on the genetic consequences of dispersal.

Andrewartha and Birch (1954) in their "general theory of the numbers of animals in natural populations", gave a verbal argument as to why dispersal may be an important factor in maintaining populations and den Boer (1968) considered it in his "spreading of risk" concept. Reddingius and den Boer (1970) illustrated the stabilizing property of dispersal using simulation models. Their models were, however, complex and they were unable to provide a mathematical framework; "because there are so many kinds of parameters involved it is difficult to construct an ordered sequence of models" (Reddingius and den Boer, 1970). In their conclusion they suggested that "the idea that population stability in nature results from a complicated interplay between populational and environmental factors anyway cannot be mathematically proved but is an hypothesis that ought to be tested by observation".

Whilst I agree that no mathematical theorem can tell us what is happening in the real world, I think a general mathematical framework is desirable to indicate the sorts of relationships that might profitably be studied in the field.

My approach to studying the effects of complex environments has been to start with a very simple model and investigate the effects of increasing the complexity.

Some of the results of this approach have been reported in an earlier paper (Roff, 1974). The general result is that in the absence of dispersal between subpopulations, the population model is unstable and becomes extinct within a comparatively short time (less than 200 time units) but with the introduction of dispersal, the population persists for considerably longer (greater than 1000 time units).

The purpose of the present paper is to describe the relationship between the stability of the population model and the population parameters and to show how these relationships can be understood within a general mathematical analysis of population stability in a randomly fluctuating environment.

The population parameters of the simulation model are:

- a) the type of dispersal,
- b) the finite rate of increase,
- c) the carrying capacity of the habitat,
- d) the number of subpopulations.

2. The Population Model

The population is divided into a number of subpopulations (25 generally) with dispersal of animals between them. Each subpopulation is initiated with 40 animals. Population changes are generated according to the following rules:

- a) There is a "growth period" given by the equation

$$N_i(t+1) = N_i^*(t) \lambda_i(t)$$

where

$N_i(t+1)$ is the size of the i th subpopulation at time $t+1$ before either dispersal or density-dependent loss has occurred;

$\lambda_i(t)$ is the "potential finite rate of increase" which is defined as the finite rate of increase in the absence of any density effects. Various distributions of λ were used. In most cases λ is a random variable between X_1 and X_2 where X_1 and X_2 are real numbers. All distributions were tested to ensure that the observed means and variances did not differ significantly from their expected values. All λ_i s are spatially and temporally independent;

$N_i^*(t)$ is size of the i th subpopulation at time t after dispersal and any loss of animals due to density effects.

b) There is a dispersal period,

$$N_i^{**}(t+1) = N_i(t+1) - \text{Emigrants} + \text{Immigrants}$$

where

$N_i^{**}(t+1)$ is the size of the i th subpopulation at time $t+1$ after dispersal.

c) If the subpopulation exceeds the carrying capacity of its habitat, the excess is eliminated.

$$\begin{aligned} N_i^*(t+1) &= N_i^{**}(t+1) & \text{If } N_i^{**}(t+1) < K_i(t+1) \\ N_i^*(t+1) &= K_i(t+1) & \text{If } N_i^{**}(t+1) > K_i(t+1) \end{aligned}$$

where

$K_i(t+1)$ is the carrying capacity of the i th habitat at time $t+1$.

All K_i s are spatially and temporally independent. Each K_i is a random variable between X_3 and X_4 . Except where stated X_3 is zero and X_4 is 160, the mean carrying capacity therefore being 80.

As in the previous paper (Roff, 1974) the mean time to extinction of a population was used as a criterion of its stability. However, when the rate of increase, λ , was greater than 1.125 and the population persisted for longer than 1000 time units (iterations) it was impractical in terms of computer time to use the mean time to extinction and then the stability of a population was measured by the mean population size over 1000 time units. This criterion cannot be used to compare populations differing in their dispersal pattern or differing in 2 or more parameter values. In these instances a better criterion is the relative fluctuations of the populations. However, whilst mean population size does not permit us to construct an ordered sequence of models, it does permit a comparison of the behaviour of the models both between themselves and with a more general mathematical model which is the primary intent of the analysis.

In some cases, replicates of the simulations were made, but these were found to be unnecessary, the variance in the mean subpopulation size being extremely small (differences were generally within ± 3). This is not surprising as the measure is a mean of 25000 counts (25 subpopulations run for 1000 time units).

A subpopulation is considered extinct if it comprises less than two animals. In some cases, only integral changes in population size were allowed, in others changes were continuous. There is no significant difference between the results and no distinction will therefore be made.

3. The Types of Dispersal

Eight different types of dispersal patterns were studied. These may be divided into 2 categories:

a) Type I: Each subpopulation is directly connected to all other populations; all the animals are pooled after the growth period and redistributed according to one of the following rules:

(i) Type Ia. Each habitat receives the same number of animals,

$$N_i^*(t) = \frac{\sum_{j=1}^n N_j(t)}{n}$$

n is the number of habitats.

(ii) Type Ib. Animals are distributed at random throughout the habitats,

$$N_i^*(t) = \frac{p_i(t)}{\sum_{j=1}^n p_j} \sum_{j=1}^n N_j(t)$$

p is a random variable between 0 and 1.

(iii) Type Ic. Animals are distributed in a manner which takes into account the carrying capacity of each habitat, so that, for example, if the i th habitat can support twice as many animals as the j th then it receives twice as many animals as the j th,

$$N_i^*(t) = \frac{K_i(t)}{\sum_{j=1}^n K_j(t)} \sum_{j=1}^n N_j(t).$$

A consequence of this type of dispersal is that either all the subpopulations exceed the carrying capacity of their habitat, or none do.

b) Type II: Each subpopulation is connected by dispersal only to the 4 surrounding subpopulations.

(i) Type IIa. A proportion p disperse from each habitat into the four surrounding habitats each of the 4 receiving an equal number of migrants.

$$N_i^*(t) = N_i(t)(1-p) + \frac{1}{4} \sum_{j=i-2}^{j=i+2} N_j(t)p \quad (i \neq j)$$

p is proportion dispersing = 0.5.

(ii) Type IIb. The pattern of dispersal is the same as a) except that p is density dependent.

$$p_i(t) = \alpha N_i(t)$$

$$\alpha = \frac{0.4}{160}$$

(iii) Type IIc. This type differs from (i) and (ii) in that p is a function of both the density and the carrying capacity. When the carrying capacity is low the proportion dispersing will be higher than when the carrying capacity is high.

$$p_i(t) = \beta \frac{N_i(t)}{K_i(t)}$$

$$\beta = 0.1$$

(iv) Type II d. In this type of dispersal animals have the option of dispersing or not dispersing depending on whether the surrounding habitats are available. The rules for migration are:

1. Dispersal of animals from the i th subpopulation can occur if $N_i(t) > K_i(t)/2$, that is the subpopulation exceeds half the carrying capacity of its environment. However, dispersal into one of the four surrounding subpopulations is dependent upon there being one available for occupancy.

2. Dispersal into the i th subpopulation can occur if $N_i(t) < K_i(t)/2$, that is, the subpopulation is less than one half the carrying capacity of its habitat.

This model is essentially that of a territorial type of animal. Animals can easily establish territories when their numbers are low but as numbers increase ($N_i(t) > K_i(t)/2$) pressure is exerted on some to disperse. If the surrounding j th subpopulations are not very dense ($N_j(t) < K_j(t)/2$) dispersers will flow in filling them up to the point $N_j(t) = K_j(t)/2$. Thereafter territories are rigid and no more animals are allowed in. If a subpopulation is dense ($N_i(t) > K_i(t)/2$) but animals cannot disperse because there are no surrounding subpopulations available ($N_j(t) > K_j(t)/2$) then territories will contract and animals "born" in the subpopulation will be able to establish territories but dispersers coming into the area will not be able to establish territories ($N_i(t) > K_i(t)/2$). Finally, however, a point is reached when territories become rigid and no more animals, whether born in the subpopulation or not, can be accommodated ($N_i(t) > K_i(t)$). The excess is then forced completely out of the population as a whole.

(v) Type II e. This pattern is the same as (iv) except that the territorial condition is removed and animals can enter a subpopulation if it does not exceed the carrying capacity (not one half as in the previous case).

4. Results

The complexity of the simulation models prohibits a detailed analytical treatment. However, the general qualitative properties can be understood within the framework of the analyses of the exponential growth equation with random fluctuations given by Lewontin and Cohen (1969), and May (1971), and the logistic equation with random fluctuations (Levins, 1969; May, 1972).

The exponential growth equation with randomness is:

$$\frac{dN(t)}{dt} = (a + \gamma(t)) N(t) \quad (1)$$

where

a is mean growth rate,

$\gamma(t)$ is a random variable with mean zero and variance σ^2 .

If $\frac{\sigma^2}{2} > a$ then the probability for the population to become extinct tends to unity as time tends to infinity despite the fact that if a is greater than zero the mean population size tends to infinity (May, 1971). Thus

$$\text{if } \frac{\sigma^2}{2} > a \text{ and } a > 0$$

$$\text{then as } t \rightarrow \infty E(N) \rightarrow \infty \text{ but } P(N > 0) \rightarrow 0.$$

A similar stability criterion exists for the logistic equation with random fluctuations:

$$\frac{dN(t)}{dt} = N(t)\{k_0 + \gamma(t) - N(t)\} \quad (2)$$

where

k_0 is mean carrying capacity,

$\gamma(t)$ is a random variable with mean zero and variance σ^2 .

For notational convenience the time has been rescaled to absorb the conventional r/k factor (assumed to be positive).

An equilibrium probability exists provided $k_0 > \frac{1}{2}\sigma^2$ in which case the mean population size is

$$E(N) = k_0(1 - (\sigma^2/2k)) \quad (\text{May, 1972}). \quad (3)$$

The main point of the above two examples is that random fluctuations not only depress population numbers but if severe enough can cause extinction of the population. This is not obvious by an analysis of the deterministic models or by an inspection of the expectation of population growth.

The influence of the population parameters on the stability of the simulated populations was as follows.

4.1. The Effect of the Carrying Capacity; Simple Model

In addition to the growth of populations with various dispersal patterns, the growth of a population with no dispersal was also simulated. This population was composed of 25 isolated subpopulations, each of which had a carrying capacity, K (a random variable between 0 and 160). The simulated population was therefore growing according to Eq. (1) but there was a ceiling to its growth. For such a population, the criterion

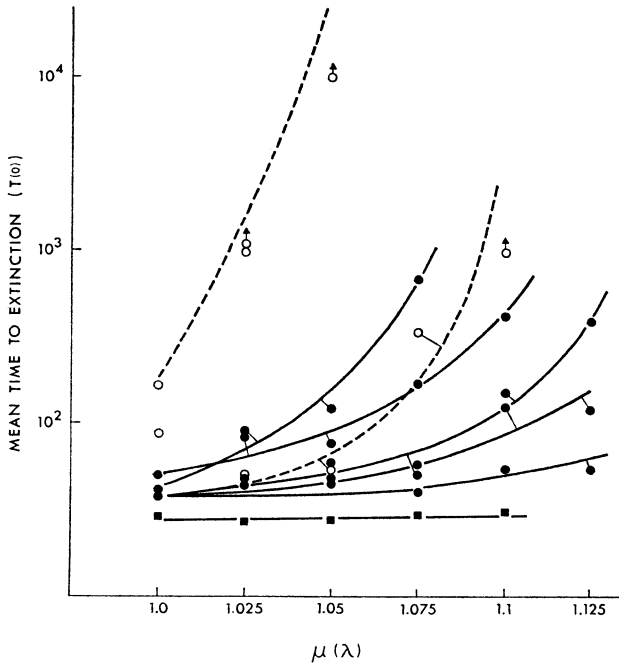


Fig. 1. The mean time to extinction, $T(0)$, as a function of the mean potential finite rate of increase $\mu(\lambda) \cdot \mu(\lambda)$ is increased by increasing the upper limit of λ . The number of subpopulations is 25. Each point represents the mean of 5 replicates. In general, the range in $T(0)$ is large. An exception is the isolated subpopulations in which the range is very small (± 10). Points with arrows indicate that at least 1 replicate did not go to extinction during the simulation. Open circles: Type I dispersal pattern. Dots: Type II dispersal pattern. Squares: Isolated subpopulations

for stability $1/2\sigma^2 > a$ no longer applies except in a qualitative sense. Under these conditions, the time to extinction will be a function of the value of the ceiling, or carrying capacity. The lowest line in Figs. 1 and 2 show the relationship between the time to extinction and the potential finite rate of increase for a population composed of 25 isolated subpopulations [increasing according to Eq. (1)]. With a mean potential finite rate of increase as high as 1.9 ($a=0.9$ $\sigma^2=1.08$) the time to extinction of the population is less than 200 time units. The expectation in the absence of a carrying capacity, i. e. $N_0\lambda^t$, is $(1.9)^{200}40$, which is a large number, and by a deterministic model the environment should be saturated within 3 time units.

4.2. The Effect of the Type of Dispersal and the Rate of Increase

Incorporation of any of the dispersal patterns into the simulation model enhances its stability by either of the two criteria used. Fig. 1

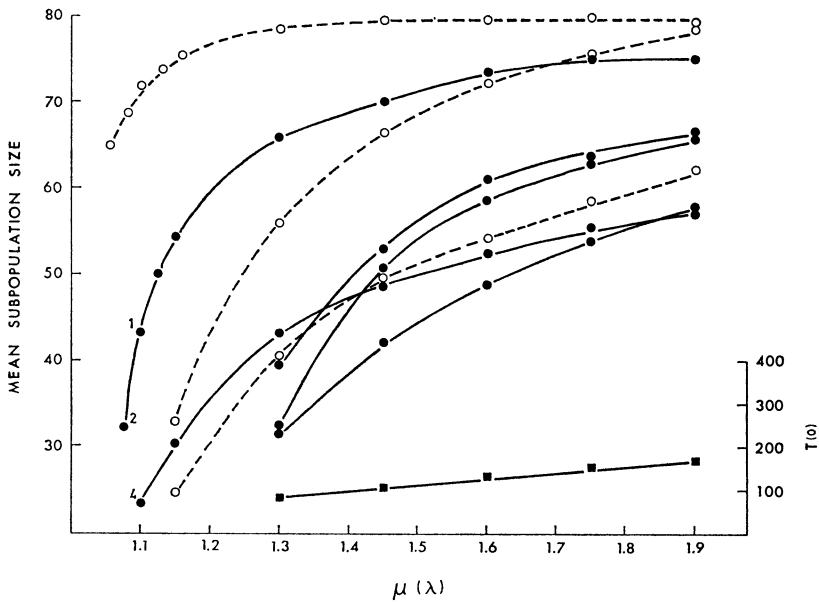


Fig. 2. The mean subpopulation size as a function of the mean potential finite rate of increase $\mu(\lambda)$. The values of the parameters and the method of increasing $\mu(\lambda)$ are the same as given in Fig. 1. Some replicates were made, but it was found that the range in the mean subpopulation size was, in general, sufficiently small (± 3) that this was unnecessary. Points below $\mu(\lambda) = 1.15$ were replicated 5 times, points after were not replicated except in some isolated cases (not shown). Figures besides some of the plots indicate the number of replicates which did go to extinction in less than 1000 time units

Symbol	Dispersal type	Symbol	Dispersal type
From top to bottom at $\mu(\lambda) = 1.9$			
○	Ic	○	Ib
○	Ia	●	IIa
●	IIe	●	IIe
●	IIc	■ ^a	Isolated subpopulations
●	IIb		

^a Read off from right-hand scale.

indicates that there is a significant increase in the time to extinction as the mean potential finite rate of increase goes from 1.0 to 1.125 and it is clear from the mean population size in Fig. 2 that the type of dispersal pattern is an important factor in determining the stability of a population. It must be remembered that population size and the time to extinction (persistence) are not related in any simple fashion. Therefore,

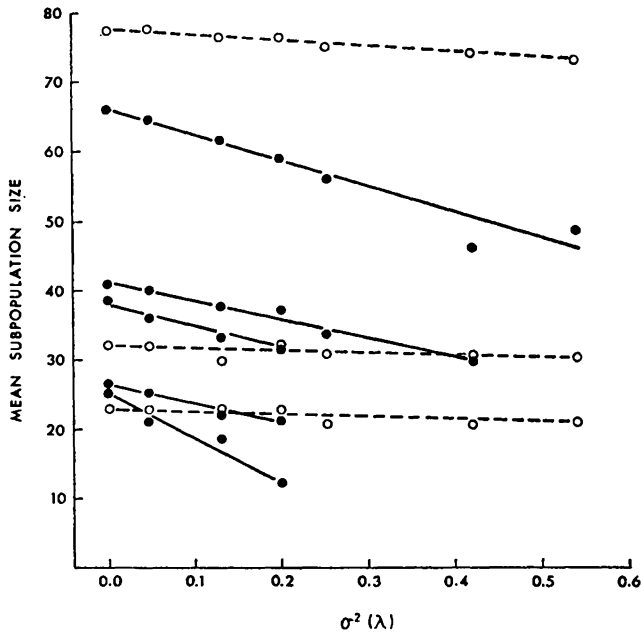


Fig. 3. Relationship between the mean subpopulation size and the variance of the potential finite rate of increase $\sigma^2(\lambda)$. $\mu(\lambda)$ is kept constant at 1.125 and the variance altered by changing the distribution of λ (see Table 1)

Symbol	Dispersal type	Symbol	Dispersal type
From top to bottom at $\sigma^2(\lambda) = 0$			
○	Ic	○	Ia
●	IIe	●	IIa
●	IIId	●	IIb
●	IIc	○	Ib

whilst we may legitimately infer that as $\mu(\lambda)$ increases and the mean subpopulation size increases then for any given dispersal pattern the stability increases we cannot say that populations differing in their dispersal patterns but with the same subpopulation size have the same mean time to extinction.

The effect of dispersal between habitats is to effectively reduce the variance of the environmental fluctuations. This is demonstrated in Fig. 3 where the mean subpopulation size is graphed as a function of the variance of the potential finite rate of increase; $\mu(\lambda)$ is kept constant at 1.125. Table 1 gives the distributions of λ used. Two points are worth noting:

Table 1. The distribution of λ used in obtaining Fig. 3 $P(x_1 < \lambda < x_2) = p$ means that with probability p λ is a random variable between x_1 and x_2

Distribution of λ	$\sigma^2(\lambda)$
$P(0 < \lambda < 1) = P(1 < \lambda < 2.5) = 0.5$	0.5417
$P(0 < \lambda < 2.25) = 1$	0.4219
$P(0 < x < 1) = 1, \lambda = 6.75x(1-x)$	0.2532
$P(0.5 < \lambda < 1) = P(1 < \lambda < 2) = 0.5$	0.2083
$P(0.5 < \lambda < 1.75) = 1$	0.1302
$P(0.75 < \lambda < 1.5) = 1$	0.0470
$P(\lambda = 1.125) = 1$	0.0000

a) The relationship between the mean subpopulation size and $\sigma^2(\lambda)$ is linear as predicted by Eq. (3). The distribution of λ is not relevant in this relationship.

b) The slopes of the lines are determined by how the habitats are connected with respect to dispersers. In the case of the Type I dispersal pattern every habitat is accessible to animals from every other habitat but the Type II dispersal pattern is limited and a habitat is accessible only to dispersers from the four surrounding subpopulations. In the latter type the resulting slopes of the lines (Fig. 3) are equal and gentle compared to the slopes resulting from Type II dispersal patterns which are also approximately equal but steep. The slope of the line is therefore determined primarily by the spatial organization of the habitat with respect to the dispersers and the position of the line on the graph is governed by the mean rate of increase and the type of dispersal (density-dependent, independent, etc.).

Point a) is illustrated more clearly by Fig. 4 in which is plotted the mean subpopulation sizes on the graph mean potential finite rate of increase against the mean/variance ratio of the potential finite rate of increase. The graph is constructed only for 1 type of dispersal pattern, Type II d, but similar graphs could be constructed for the other dispersal patterns.

To test the validity of this graph, I selected 2 combinations of $\mu(\lambda)$ and $\mu(\lambda)/\sigma^2(\lambda)$ and predicted the approximate stability of the population model under these conditions. The 2 combinations were:

a) λ varies randomly between 0.9 and 1.1. The mean is 1.0 and the mean/variance ratio is 2.0. The graph predicts that despite the very small variance the population will be highly unstable and will go to extinction in considerably less than 1000 time units. This proved to be correct, the population being extinct after 97 time units.

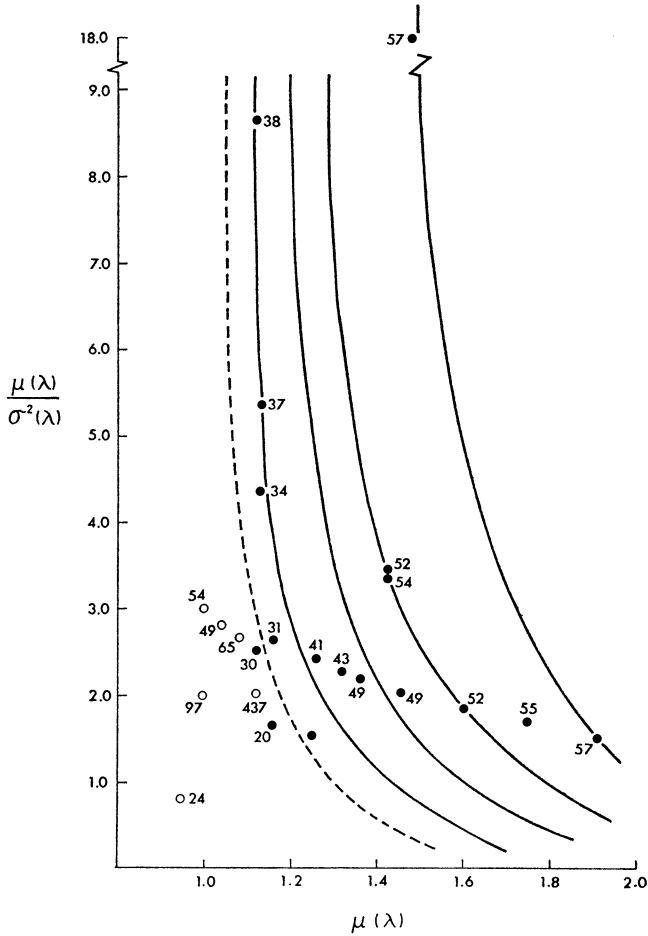


Fig. 4. A "stability" diagram for dispersal pattern II.d. The solid circles show populations still in existence after 1000 iterations, the open circles populations which become extinct during this period. The mean subpopulation size or mean time to extinction is shown beside each point

b) λ varies between 1.0 and 2.0. The mean is 1.5 and the mean-variance ratio is 18.0. In this case the potential finite rate of increase can never be less than 1.0 (though, of course, the carrying capacity can still equal 0). Nevertheless, the graph predicts that the mean subpopulation size should be significantly less than the mean carrying capacity. This prediction was also verified, the mean subpopulation size being only 57.3.

Table 2. Range and mean value of λ used in analysis of the parameters, k , the carrying capacity and n , the number of subpopulations

Dispersal type	Range of λ	Mean value of λ	Approx. population size size (Fig. 2)
Ia	0-2.6	1.3	56
Ib	0-2.6	1.3	41
Ic	0-1.1	1.05	65
IIa	0-2.8	1.4	38
IIb	0-2.8	1.4	46
IIc	0-2.8	1.4	50
IId	0-2.5	1.25	40
IIe	0-2.25	1.125	60

4.3. The Influence of the Carrying Capacity; Complex Model

To make any effect of variation in the carrying capacity or number of subpopulations obvious, I selected different values of $\mu(\lambda)$ for each dispersal pattern. The criterion used was that $\mu(\lambda)$ should not be so small that any small change would decrease the time to extinction to less than 1000 time units nor so large that any effects might be "swamped". The values of λ used are given in Table 2.

Fig. 5 shows the results of keeping the mean carrying capacity constant and reducing the variance by decreasing the range within which the carrying capacity fluctuates. The most significant point is that the mean subpopulation size is, for the most part, a linear function of the variance of the carrying capacity. Departure from linearity may occur when the variance is very large. This departure from linearity may be attributed to too few dispersers in an absolute sense. To test this idea I increased $\mu(\lambda)$ to 1.6 for the Type IIa dispersal pattern on the premise that the increase in the absolute numbers of dispersers (there is, of course, no change in the proportion) would remove the non-linearity. The line should also be shifted upwards but there should be no change in the slope. All these predictions proved correct as shown in Fig. 5.

Unlike the relationship between the mean subpopulation size and the variance of the potential finite rate of increase, the slope of the lines in Fig. 5 cannot be explained largely on the basis of the spatial organization of the subpopulations. The slope of the line appears to be a function of both the dispersal pattern and the spatial pattern with respect to dispersers.

In a series of simulations using Type IIa dispersal pattern I incorporated random catastrophes, each habitat has a certain probability that at any time it will be completely uninhabitable and all the animals are

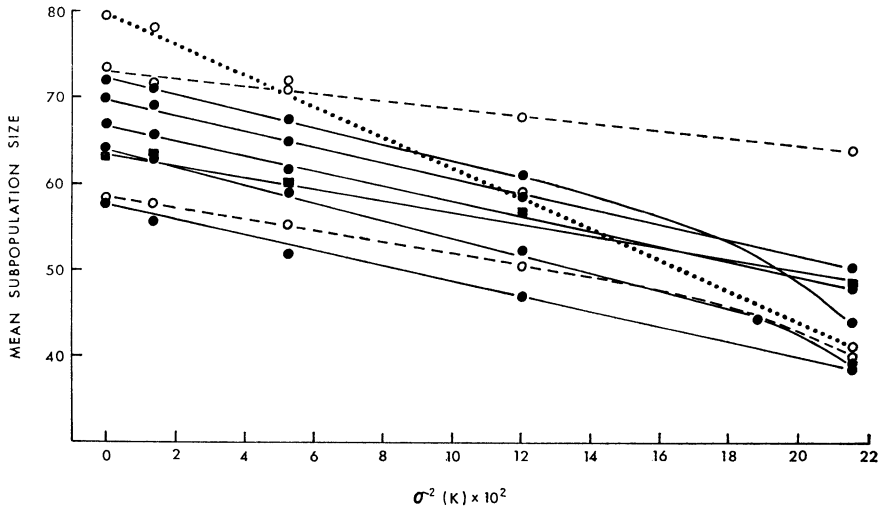


Fig. 5. The relationship between the mean subpopulation size and the variance of the carrying capacity, $\sigma^2(k)$. The mean of the carrying capacity was kept constant at 80 and its variance decreased by decreasing its range. The values of $\mu(\lambda)$ for each dispersal pattern are given in Table 2

Symbol	Dispersal type	Number of replicates
From top to bottom at $\sigma^2(k) = 0$		
○	Ia	1
○	Ic	3
●	IIb	1
● ^a	IIa	1
●	IIe	3
●	IIa	3
■	IIc	1
○	Ib	1
●	II d	3

^a $\mu(\lambda) = 1.6$

eliminated. Interestingly, the mean subpopulation size is a linear function of the mean number of catastrophes per time unit.

4.4. The Effect of the Number of Subpopulations

The final parameter to be considered is n , the number of subpopulations. From Fig. 6, it can be seen that in all but one case, when n is greater than about 15 the mean subpopulation size is approximately constant regardless of the size of n . The exception is the type Ic dispersal

Table 3. The temporal variability in mean subpopulation size for different numbers of subpopulations

Number of subpopulations	Type of dispersal			
	Ib		IIc	
	\bar{N}	$TVAR$	\bar{N}	$TVAR$
35	40.83	45.08	48.94	47.71
30	40.51	59.01	50.27	56.22
25	39.12	71.78	49.60	77.14
20	39.27	79.82	48.94	89.55
15	38.83	109.35	48.33	125.29
10	37.83	183.71	45.60	143.71
5	30.00	274.22	47.04	311.46

\bar{N} = mean subpopulation size over 1000 time units; $TVAR$ = variance in mean subpopulation size over time = $1/1000 \sum_{t=1}^{1000} (\bar{N} - \bar{N}(t))^2$ subpopulation size per time unit. Where $\bar{N}(t)$ is the mean subpopulation size per time unit.

However, although the mean subpopulation size does not increase above a certain value of n (which is dependent on the values of the other parameters) the time to extinction of the population increases as n increases. This increase is indicated by the temporal variability of the mean subpopulation size. Table 3 gives the values of the temporal variance of the mean subpopulation size for 2 dispersal patterns. The results are similar for all patterns; as n decreases, the mean subpopulation size over 1000 time units remains constant but its fluctuations per time unit become more and more severe.

5. Discussion

The present series of simulation models demonstrates the importance of dispersal as a major stabilizing factor, without which the population would quickly become extinct. Dispersal of individuals may be a humdrum irregular affair with animals leaving their homes even when density is very low and there is no population pressure to do so. Because of this, members of the population are never under the same risks and there are always individuals that by chance wander into an empty habitat and restart the subpopulation.

An important feature of population dynamics in a heterogeneous environment is that population size is maintained at a level below that of the carrying capacity. In no simulation did the mean subpopulation size exceed the mean carrying capacity. Temporal variability depresses

population numbers because if conditions are bad the population is limited and when conditions change for the better, they may not remain so sufficiently long for the population to fully utilize available resources (Levins, 1969; May, 1972). Similarly, spatial heterogeneity leads to an average population size below the average carrying capacity because all sites are not equally accessible. Thus when dispersal is limited, many sites may be unavailable to dense subpopulations far removed even though these former subpopulations may be at low densities (Levins, 1969; Gadgil, 1971).

There are a great number of different types of dispersal strategies found in nature. Undoubtedly a prime factor in this variety is the biological constraints any organism must operate within. It is, however, interesting to note that the curves for population size against $\mu(\lambda)$ for different dispersal strategies intersect (Fig. 2) and suggests that quantitative changes in parameter values may favour *qualitatively* different dispersal strategies.

The general relationship between this simulation model and the mathematical model [Eq. (1)] is clearly demonstrated in the linear relationship between the population size and the variance of the parameters, K and λ . That the distribution does not affect this slope argues for the generality of models which use only randomly varying parameters: it may be unnecessary to be overly worried about the reality of the distribution. Of course, this may not hold true for highly complex models incorporating many nonlinear relationships.

Possibly the most significant result of this analysis is that it demonstrates that the way in which we view population regulation may depend on the "level of resolution" at which we look at the problem. The simulation model was so designed that it depends on dispersal between habitats for its long-term persistence. But the dynamics of the population as a whole, or of the *average* subpopulation can be understood within a very general mathematical framework which does not include dispersal or spatial heterogeneity. This is not to say that either the model or analysis is incorrect; only that we are using 2 different levels of resolution. There are many questions we might ask of a population which do not require a knowledge of the dynamics of individual subpopulations; the *average* subpopulation suffices. This is demonstrated very clearly by the studies of Hughes and Gilbert (1968), Gilbert and Hughes (1971) and Gilbert and Gutierrez (1973) in which the dynamics of aphid populations are explored using deterministic models. But this does not imply that an analysis based on how individual subpopulations rather than the average subpopulation vary in space and time is not worthwhile. We must decide whether such a fine resolution is relevant or necessary for the sorts of questions we ask. Consider, for example, a physical chemist

trying to model some chemical reaction. How the subatomic particles interact may be superfluous information for his level of study. But how subatomic particles interact is nonetheless a worthwhile field of study.

If we ask the question, "how does temporal and spatial variability affect population numbers?" then we must look at units smaller than the population. To do so, however, involves very difficult technical problems not the least of which is the determination of the variance of biological parameters. At the present time we lack an adequate methodology to tackle this problem with much hope of success.

Acknowledgements. I would like to thank Professor R. M. May and Mr. Neil Gilbert whose help in the preparation of this paper was invaluable to me. The advice of the referee greatly aided me in improving the clarity of the paper.

References

- Andrewartha, H. G., Birch, L. C.: The distribution and abundance of animals. Chicago: Chicago University Press 1954
- Boer, P. J. den: Spreading of risk and stabilization of animal numbers. *Acta biotheor.* (Leiden) **18**, 165–194 (1968)
- Gadgil, M.: Dispersal: population consequences and evolution. *Ecology* **52**, 253–261 (1971)
- Gilbert, N., Gutierrez, A. P.: A plant-aphid-parasite relationship. *J. Anim. Ecol.* **42**, 333–338 (1973)
- Gilbert, N., Hughes, R. D.: A model of an aphid population—three adventures. *J. Anim. Ecol.* **40**, 525–534 (1971)
- Hughes, R. D., Gilbert, N.: A model of an aphid population—a general statement. *J. Anim. Ecol.* **37**, 553–563 (1968)
- Levins, R.: Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. entomol. Soc. Am.* **15**, 237–240 (1969)
- Levins, R.: The effect of random variations of different types on population growth. *Proc. nat. Acad. Sci. (Wash.)* **62**, 1061–1065 (1969)
- Lewontin, R. C., Cohen, D.: On population growth in a randomly varying environment. *Proc. nat. Acad. Sci. (Wash.)* **62**, 1056–1060 (1969)
- May, R. M.: Stability in model ecosystems. *Proc. Ecol. Soc. Aust.* **6**, 18–56 (1971)
- May, R. M.: Stability in randomly fluctuating versus deterministic environments. *In press*
- Reddingius, J., Boer, P. J. den: Simulation experiments illustrating stabilization of animal numbers by spreading of risk. *Oecologia (Berl.)* **5**, 240–284 (1970)
- Roff, D. A.: Spatial heterogeneity and the persistence of populations. *Oecologia (Berl.)* **15**, 245–258 (1974)

Mr. D. A. Roff
Institute of Animal Resource Ecology
University of British Columbia
Vancouver 8, British Columbia
Canada