Spatial Heterogeneity and the Persistence of Populations

D. A. Roff

School of Biological Sciences, University of Sydney

Summary. The hypothesis that dispersal in a heterogeneous environment can be an important factor in population stability is examined. It is shown that dispersal may increase the persistence time of a population by several orders of magnitude.

1. Introduction

Andrewartha and Birch (1954) in their "general theory of the numbers of animals in natural populations" maintain that animal numbers are determined by a multitude of factors, many of which are independent of population density. They suggest that a population is best considered as a set of local populations each subject to different environmental conditions. At any one time some areas will be unoccupied, some will have a few animals and some will contain relatively dense populations. Dispersal between subpopulations causes fluctuations in population size to be damped. It is the central theme of the theory of Andrewartha and Birch that fluctuations in population numbers can only be understood when environmental and genetical heterogeneity are taken into account.

Den Boer's (1968) concept of "spreading of risk" is essentially the same idea; "heterogeneity and instability must not be considered as just a drawback of field data to be neglected ... heterogeneity and/or instability must be recognized as fundamental features of a natural situation. The chance of survival of a population may even be increased, because the variation within the population makes it possible to cope with the variation in space and time of the habitat".

In discussing the "spreading of risk in space" den Boer notes "the fluctuations of animal numbers in the population as a whole will be the resultant of the numerical fluctuations in the different places (subpopulations). ... Migration between subpopulations will generally contribute to the stabilizing tendency of spatial heterogeneity, since in this way extreme effects of some places will be levelled out more thoroughly. Hence, migration will improve the outcome of spreading of the risk in space".

Reddingius and den Boer (1970) demonstrated the stabilizing in-
fluence of migration and age classes in a series of simulation experiments.
However, their model is rather complex and the demonstration of the
stabilizing influence of spatial heterogeneity and age classes results
"from an appropriate choice of the values of the parameters, which was,
in fact, attained after some trial and error" (Reddingius and den Boer,
1970). The choice of parameters was made using the criterion that "the
population density would not be expected to show a strong tendency to
increase or to decrease in the most complex version of the model".
This choice was made because they "wished to restrict the discussion to
persisting populations". Because of this restriction and because of the
complexity of their models "it is diffcult to construct an ordered se-
quence of models" (Reddingius and den Boer, 1970).

The purpose of the present study was to begin with a simple po-
pulation model with few parameters and explore the effect of intro-
ducing other parameters such as migration. Using this procedure, it is
possible to investigate the relative importance of each parameter.

In the simplest model, a full analytical treatment of its stability is
possible (Lewontin and Cohen, 1969; Levins, 1969; May, 1971). In the
more complex model, incorporating migration, a theoretical analysis is
extremely difficult and therefore a numerical analysis using computer
simulated populations was adopted.

There are numerous definitions of stability (Lewontin, 1969). I will
use the word "stability" in the sense of "persistence". Population A is
said to be more stable than population B if its mean time to extinction
is longer. This criterion permits us to construct an ordered sequence of
models.

2. The Population Models

The basic population model is

$$N(t+1) = i = \sum_1^n N_i(t+1) = \sum_{i=1}^n N_i(t)\lambda_i(t)$$

where

$N(t+1)$ is the size of the population at time $t+1$,

$N_i(t)$ is the size of the ith subpopulation at time t,

$\lambda_i(t)$ is the "potential finite rate of increase", that is the rate of
increase in the absence of any density limiting factors. Various distri-
butions of $\lambda_i(t)$ were used, the details of which are given in section 3.

The population is divided into 25 subpopulations. Each subpopulation
begins initially with 40 animals. Four types of populations were studied.
These 4 population types constitute a "set". Within any set the same
sequence of random numbers was used for each population run. Thus

each population within a set is subjected to exactly the same environmental fluctuations. Eleven replicates were made. As all replicates were qualitatively identical the results of only one set will be given.

A subpopulation is considered extinct if there are less than 2 animals in it. Subpopulations were allowed to change only by integer steps.

2.1 Population Model 1

In this model there is no dispersal between subpopulations and no limit to the number of animals that can exist in any subpopulation.

2.2 Population Model 2

In this model the subpopulations are still isolated (no dispersal) but an upper limit to the size of a subpopulation is introduced. The upper bound for the ith subpopulation at time t, K_i (t), is a random variable between 0 and 160. $K_i(t)$ may be considered as the carrying capacity of the habitat of the ith subpopulation at time t. If a subpopulation exceeds its upper bound the excess animals are eliminated. Biologically this is equivalent to the death of the excess or their migration out of the population. In reality the correlation between the carrying capacities of adjacent habitats will depend upon the distance between habitats and the number of factors which determine the carrying capacity: increasing either of these will, in general, decrease the correlation. For simplicity I have assumed the extreme case of no correlation between habitats either in space or time.

The size of the ith subpopulation at time t is therefore given by

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

where

$$N_i^*(t) = N_i(t) \qquad \text{If } N_i(t) \leq K_i(t)$$
$$N_i^*(t) = K_i(t) \qquad \text{If } N_i(t) \geq K_i(t)$$

2.3 Population Model 3

This model comprises a population divided into 25 subpopulations connected by dispersal. As in population model 1 no limit is set to the number of animals that can exist in a subpopulation; a subpopulation is allowed to exceed K_i. In this instance K is viewed as an environmental factor causing dispersal rather than limiting numbers.

Each subpopulation is connected by dispersal to its 4 nearest neighbours. The rules for dispersal are as follows:

a) Dispersal of animals from the ith subpopulation can occur if $N_i(t) > \dfrac{K_i(t)}{2}$. However, dispersal into one of the 4 surrounding sub-

populations is dependent upon there being one available for occupancy.

b) Dispersal into the ith subpopulation can occur if $N_i(t) < \dfrac{K_i(t)}{2}$.
The size of the ith subpopulation at time $t+1$ is therefore given by

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

where

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

2.4 Population Model 4

This model incorporates both dispersal and an upper limit to the size of a subpopulation.

The size of the ith subpopulation at time $t+1$ is given by the set of equations

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

where

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

and

$$N_i^{*}(t) = N_i^{**}(t) \qquad \text{If } N_i^{**}(t) < K_i(t)$$
$$N_i^{*}(t) = K_i(t) \qquad \text{If } N_i^{**}(t) > K_i(t).$$

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

3. The Potential Finite Rate of Increase (λ)

In models 1 and 3 the potential finite rate of increase is also the actual finite rate of increase. In models 2 and 4, however, the actual finite rate of increase will be something less than the potential since the size of any subpopulation is limited. The actual finite rate of increase will

be a function of the number of subpopulations that exceed the upper limit per unit time.

A number of distributions of λ were used. Each such distribution will be described in the following way:

Given that $X_1\lambda < \lambda < X_2$ denotes that λ is a random variable between X_1 and X_2 the statement that $P(X_1 < \lambda < X_2) = p$ will mean that the probability that λ takes some value between X_1 and X_2 is p.
The distributions of λ may be divided into two classes:
   a) density—dependent;
   b) density—independent.

All distributions were tested to ensure that the observed means and variances were not significantly different from their expected values.

3.1 Density-Dependent

The potential finite rate of increase is distributed in the following manner

If $K_i(t)/20 < N_i(t) < K_i(t)/4$, then $P(0 < \lambda < 1) = P(1 < \lambda < 4) = 0.5$, and if $N_i(t) < K_i(t)/20$ or $N_i(t) > K_i(t)/4$, then $P(0 < \lambda < 1) = P(1 < \lambda < 2) = 0.5$.

At any given time a subpopulation is equally likely to increase or decrease but when a subpopulation is not too sparse $(N_i(t) > K_i(t)/20)$ nor too dense $(N_i(t) < K_i(t)/4)$ its potential finite rate of increase is high, having a mean value of 1.5.

3.2 Density-Independent

Three different distributions of λ were studied. All have the same mean but the variances are different. The mean value of λ equals 1.125. Therefore the subpopulations are biased towards increasing.

The distributions studied were as follows:
   a) $P(0 < \lambda < 1.0) = P(1.0 < \lambda < 2.5) = 0.5$;
   b) $P(0 < \lambda < 2.25) = 1$;
   c) $P(0.5 < \lambda < 1.0) = P(1.0 < \lambda < 2.0) = 0.5$.

Distribution a) represents an environment which is highly variable. At any one time the population is equally likely to increase or decrease but the amount by which a population may increase is such that the mean potential rate of increase exceeds 1.0.

Concerning b) a subpopulation is more likely to increase than decrease. This, therefore, represents an environment in which there are more "good" seasons than "bad" ones. "Bad" seasons when they do occur may be very severe (λ close to 0).

Distribution c) represents an environment which has only small fluctuations. A subpopulation is equally likely to increase or decrease but bad seasons are never very severe (λ is never less than 0.5).

Mathematically the decreasing "severity" of environments a), b), c) is given by their variances which are 0.5417, 0.4219 and 0.2083 respectively.

4. Analysis and Results

4.1 Population Model 1: No Migration, No Upper Bound

Lewontin and Cohen (1969) analysed the stability of a population following the growth equation

$$N(t+1) = N(t)\lambda(t).$$

This equation is the same as that for the subpopulations of population model 1, the whole population simply consisting of 25 replicates. Lewontin and Cohen (1969) concluded that "if a population is growing in a randomly varying environment such that the finite rate of increase per generation is a random variable with no serial autocorrelation ... even though the expectation of population size may grow indefinitely large with time, the probability of extinction may approach unity,"

i.e. as $t \to \infty \, E(N) \to \infty$ but $P(N > 0) \to 0$.

May (1971) analysed the equivalent differential equation

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

where

a   is the mean growth rate,

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

The mean population size, $\mu(N)$ is

$$\mu(N) = N_0 \, e^{at}$$

where

N_0 = initial population size, t = time.

Clearly as time goes on the expectation of N when the growth rate is positive, $a > 0$, increases without bound. However, the root-mean square relative fluctuations about the population mean are

$$\frac{\text{Variance}}{\text{Mean}} = (e^{\sigma^2 t} - 1)^{1/2}$$

and as time goes on the population fluctuations become relatively more and more severe. Finally if $\sigma^2 > 2a$ "then the probability for the system to become extinct tends to unity as the time tends to infinity" (May, 1971).

"The basic message from this discussion of the growth of a population in a randomly varying environment is that such fluctuations do not

Table 1. Population model 1

Distribution of λ	$\mu\,(\lambda)$	$\sigma^2(\lambda)$	$T(o)$	$N(200)$	$n(o)$
3.1	1.144[a]	0.6765	38	—	—
3.2 a	1.125	0.5417	43	—	—
3.2 b	1.125	0.4219	101	—	—
3.2 c	1.125	0.2083	—	10^9+	11

The stability of a population composed of 25 isolated subpopulations allowed to increase without bound.

λ = Potential finite rate of increase; $\mu(\lambda)$ = mean λ; $\sigma^2(\lambda)$ = variance of λ; $T(o)$ = time to extinction; $N(200)$ = mean subpopulation size over 200 iterations; $n(o)$ = mean number of subpopulations extinct per iteration.

[a] The mean and variance of 3.1 are estimated from the simulation data, no theoretical method for calculating it being available.

merely enhance the possibility of extinction (which is intuitively obvious), but if large enough, as measured by the (above) criterion, will produce extinction even in a population whose expectation value is increasing exponentially" (May, 1971).

The above phenomenum of an infinite expectation but a zero probability of persisting, is clearly demonstrated by the simulation experiment. The results of these are shown in Table 1 and Figs. 1 and 2. In all but 1 case, the population becomes extinct in considerably less than 200 time units (one time unit being one iteration), despite the fact that their expectations increase with time. The population that does persist for 200 time units has a mean subpopulation size after 200 time units in excess of 10^9. However, 11 subpopulations are extinct after this time.

4.2. Population Model 2: No Dispersal, Upper Bound

It is clearly unrealistic to allow a subpopulation to reach sizes in excess of 10^9 animals. The effect of imposing a limit to the size of a subpopulation is to reduce its stability and the population previously showing unlimited growth (Fig. 2) now becomes extinct within 100 time units (Fig. 2).

4.3. Population Model 3: Dispersal, No Upper Bound

The effect of introducing dispersal into population model 1 is to stabilize the population. The results of the simulations are shown in Figs. 1 and 3. In the 3 populations which previously became extinct
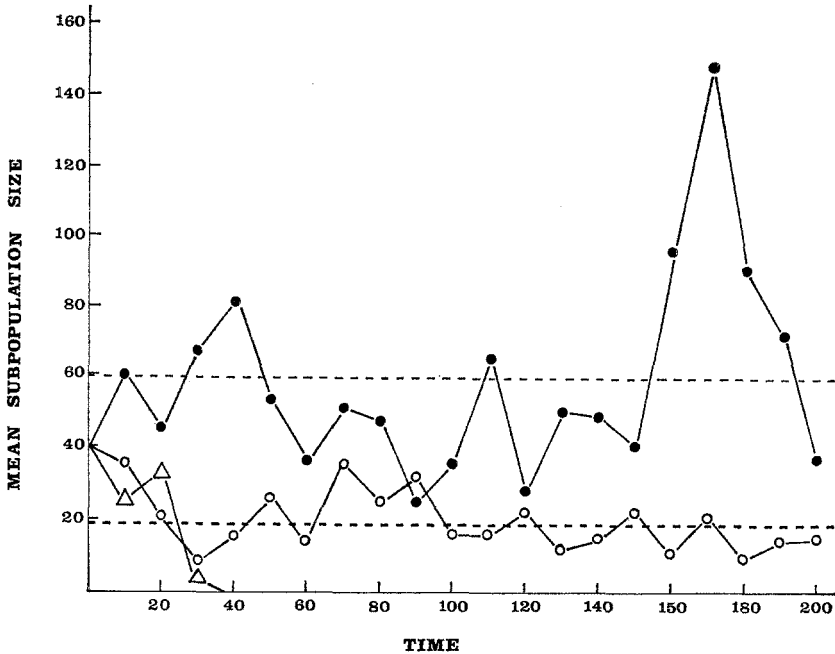
D. A. Roff

Fig. 1. Size changes of the simulated population with a density-dependent potential
finite rate of increase (3.1)

Symbol	Migration	Size limit to subpopulation
△	No	No
●	Yes	No
○	Yes	Yes

there is now no trend over 200 time units for the populations to go to
zero or to increase indefinitely. Individual subpopulations may, however,
show large increases in size; in the density-dependent case (Fig. 1) a
subpopulation size of about 550 occurs and in the density-independent
(Fig. 3) subpopulation sizes of about 10^7 are reached in 1 or 2 of the sub-
populations. It is the increase in a few subpopulations which is responsible
for the very large increase in mean subpopulation size around $t = 170$
in Fig. 1 and $t = 200$ and $t = 250$ in Fig. 3.

The population which previously, in the absence of dispersal and an
upper limit to subpopulation size, showed unlimited growth again grows
indefinitely as is to be expected (Fig. 3). However, now no subpopulations
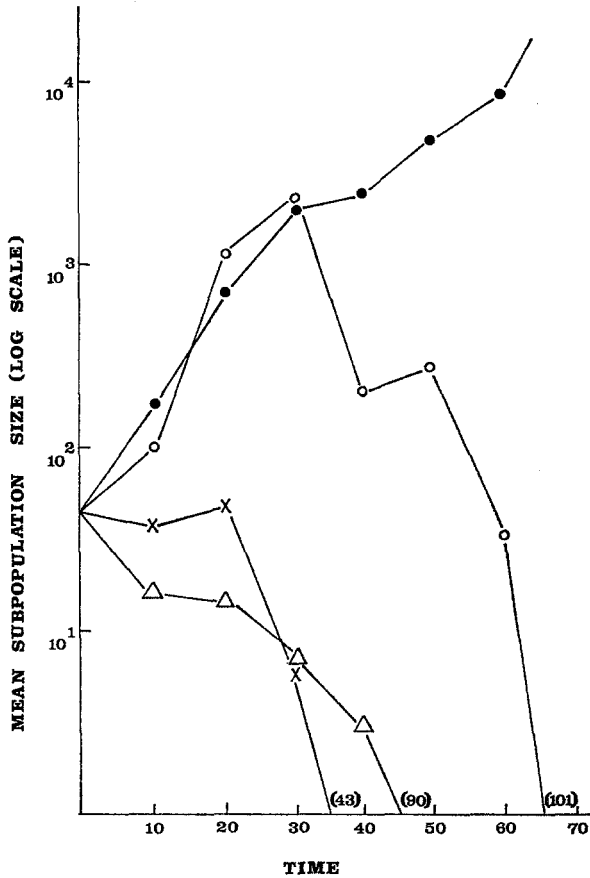are extinct.

Fig. 2. Size changes of the simulated populations with isolated subpopulations and density-independent potential finite rates of increase. Figures in brackets show time at which all subpopulations are extinct ($N = 0$)

Symbol	Migration	Size limit to subpopulation	Varience of λ
×	No	No	0.5417
○	No	No	0.4219
●	No	No	0.2083
△	No	Yes	0.2083

4.4. Population Model 4: Dispersal, Upper Bound

The incorporation of an upper bound into population model 3 has a significant effect though this is not obvious from the mean number of
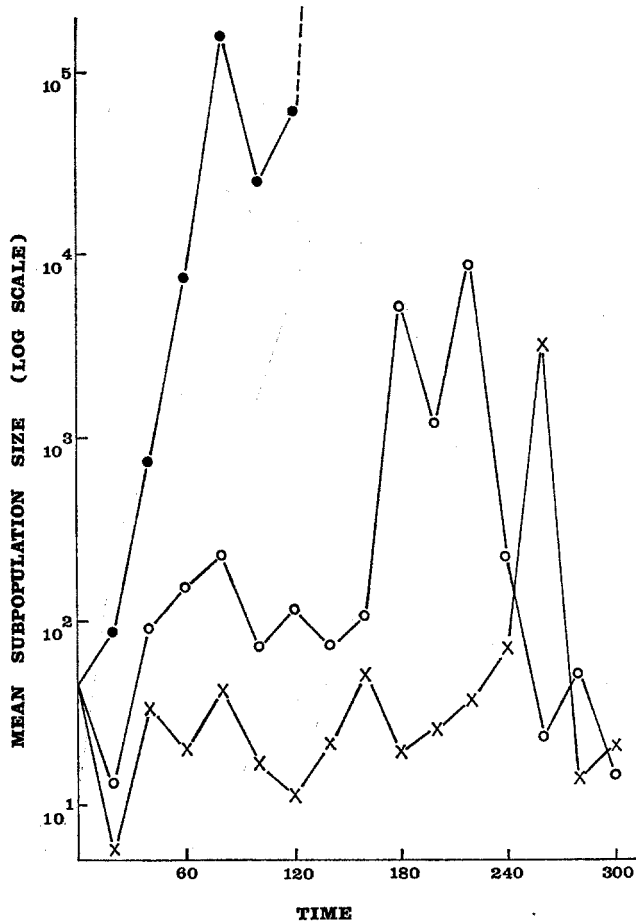
Fig. 3. Size changes of the simulated populations incorporating migration between
subpopulations and density-independent potential finite rates of increase
(Population model 3)

Symbol	Migration	Size limit to subpopulation	Variance of λ
×	Yes	No	0.5417
○	Yes	No	0.4219
●	Yes	No	0.2083

subpopulations which exceed this limit per unit time (Table 2). The
population with a density-dependent potential finite rate of increase
now has a mean subpopulation size only 1/3 that of the same population

Table 2. Population model 4

Distribution of λ	$T(o)$	$N(1000)$	N	$n(K)$	$n(o)$
3.1	—	19.24	20.3	0.95	7.15
3.2 a	437	—	—	—	—
3.2 b	—	29.4	30.9	1.95	3.40
3.2 c	—	40.68	36.0	2.90	0.30

The stability of a population composed of 25 subpopulations connected by dispersal and with an upper bound to size.
λ = potential finite rate of increase; $T(o)$ = time to extinction; $N(1000)$ = mean subpopulation size at time $t = 1000$; N = Mean subpopulation size over 1000 iterations; $n(K)$ = mean number of subpopulations that exceed their upper bound per iteration; $n(o)$ = mean number of subpopulations that are extinct per iteration.
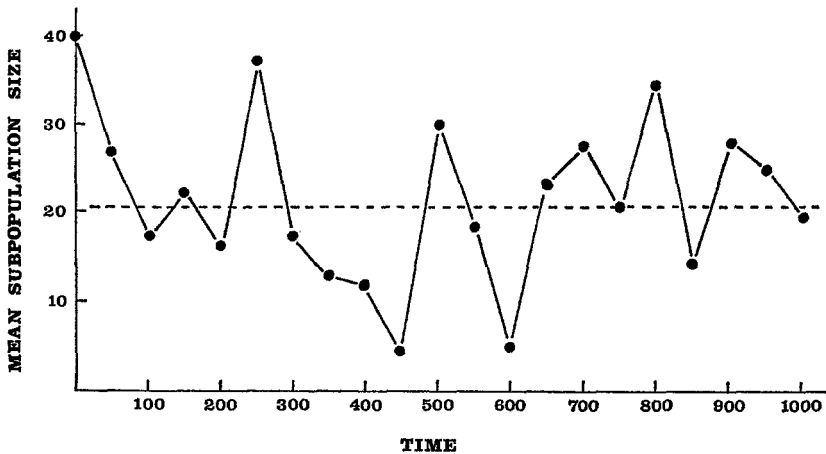

Fig. 4. Size changes of the simulated population model 4 with a density-dependent potential finite rate of increase (see also Fig. 1 showing size changes over 200 time units)

without limitations on subpopulation size (Fig. 1). The mean number of subpopulations that are extinct per unit time is over 5 times (7.15) that of the unbounded population (1.4). But the mean number of subpopulations which exceed the upper bound is less than one per time unit (0.95). The stability of this population can be gauged from the fact that it is still in existence after 1000 time units and shows no trend to increase or decrease (Fig. 4).
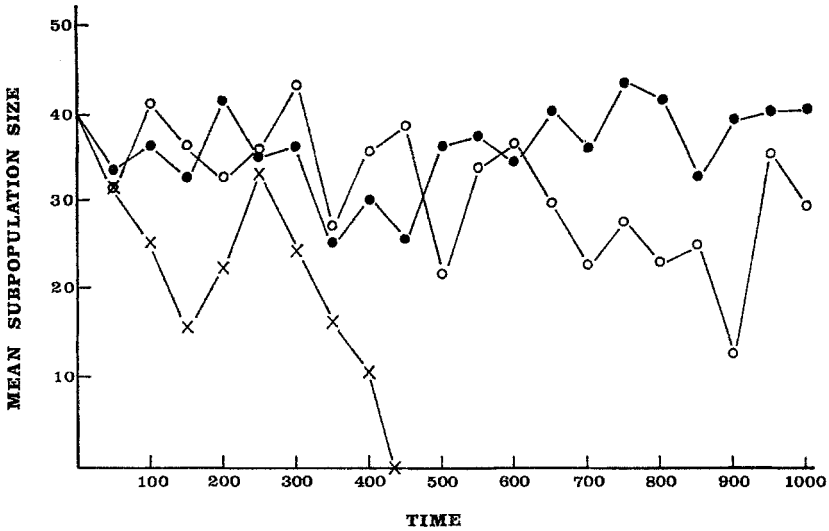
17*

Fig. 5. Size changes of the simulated population model 4 with a density-independent
potential finite rate of increase

Symbol	Migration	Size limit to subpopulation	Variance of λ
×	Yes	Yes	0.5417
O	Yes	Yes	0.4219
●	Yes	Yes	0.2083

The populations with a density-independent potential finite rate of
increase show a similar pattern to the above (Fig. 5). The population in
the most unstable environment (in the sense of large fluctuations) is
"destabilized" to the extent that it persists for only 437 time units. The
other 2 populations, however, are still in existence after 1000 time units
and show no tendency to increase or decrease. The mean number of
subpopulations that are extinct per unit time is less than for the "den-
sity-dependent" population but the mean number of subpopulations
which exceed the upper limit is higher (Table 2), though they are still
relatively small.

5. Discussion

With respect to the population models 1 and 2 in which the "po-
tential" finite rate of increase, λ, is density-independent (though the
actual rate of increase in model 2 is density-dependent) we may note that

the stability is related to the variance of λ. Thus in terms of stability 3.2a is less stable than 3.2b which is less stable than 3.2c and the variance of 3.2a is greater than 3.2b which is greater than 3.2c (Table 1).

We cannot, however, use persistence as a criterion of stability for population models 3 and 4 because the populations persist throughout the simulation. Another criterion of stability is that population A is more stable than population B if its fluctuations are relatively less, or its numbers approach zero less often than B. Using this criterion an ordered sequence can be constructed for population models 3 and 4 and is the same as that for population models 1 and 2 (see Table 2). Whilst these 2 criteria of stability seem complementary in the simple case considered here it does not necessarily follow that this will always be the case.

By analogy with the stability criteria for population model 1 ($\sigma^2 > 2a$) we may suggest that the stability of all the populations considered in this study is related to the mean potential finite rate of increase and the mean/variance ratio. A more detailed discussion of this relationship will be given in a later paper (Roff, 1974).

It has now been demonstrated both analytically and numerically for populations with a stochastic exponential growth rate, that increasing environmental variability greatly reduces the probability of persistence of a population. If the environment is spatially and temporarily variable but no movement of animals occurs then, as is intuitively obvious, the persistence time of a population is not significantly changed. However, if movement between subpopulations is allowed the persistence time may be increased by several orders of magnitude or more. This increase is sufficient to make it a plausible hypothesis that dispersal is an important factor in the persistence of populations in the real world.

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 biotheoret. (Leiden) 18, 165–194 (1968)

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.: The meaning of stability. In: Diversity and stability in ecological systems. Brookhaven Symposium in Biology No 22, p. 13–24. Springfield, Va.: National Bureau of Standards, U.S. Department of Commera 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)
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.: The analysis of a population model demonstrating the importance of dispersal in a heterogeneous environment. Oecologia (Berl.) 15, 259–275 (1974)

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