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## Simulation Experiments Illustrating Stabilization of Animal Numbers by Spreading of Risk \*

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*Summary.* 1. This paper discusses results of simulation studies with population models that were set up to illustrate the ideas about stabilization of population fluctuations and spreading of the risk of extinction expounded by den Boer (1968). In particular, the number of factors influencing net reproduction, the heterogeneity of the habitat and the possibility of a population's containing animals of different age classes were considered as possibly contributing to stabilization and to spreading of risk.

2. The model defined by equation (3.1.2), where  $r(t)$  denotes the net reproduction from  $t$  to  $t+1$ ,  $f_i(t)$  denotes the value of the  $i$ -th environmental factor in year  $t$ , and where the other symbols denote positive constants, was simulated by choosing for the  $f_i(t)$  sequences of meteorological data from published tables. Such sequences may be serially correlated as well as correlated among themselves and using such real data was considered to be more realistic than working with sequences of independent random numbers, for example.

Increasing the number  $k$  of factors turned out to stabilize fluctuations in the density. This fact could also be mathematically proved under not very restrictive assumptions.

In a model where the logarithm of the net reproduction on the average is somewhat greater than zero, and where "crashes" may occur at high densities, the population may persist for a very long time, even if the "size" of the crashes does not depend on density, and the times at which the crashes occur are chosen at random.

3. A model formulated in terms of matrices and vectors, in which a population was supposed to consist of 9 subpopulations and of several age classes was simulated. It was assumed that after a reproduction period the animals migrate between the subpopulations or emigrate from the whole population. It turned out that increasing the number of age classes may increase stability and that models where there is exchange of individuals between subpopulations by "migration" are more stable than populations consisting of isolated subpopulations. Letting the exchange between subpopulations be "density-dependent" had some stabilizing effect too, but not very conspicuously so.

### 1. Introduction

In times of rapid economic changes an industry that produces only one specialized article will run a greater risk of failing than one manu-

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facturing a number of different articles. The latter industry has spread and thereby diminished its risk and so will have a greater chance to survive the economic changes. In a comparable way variation within natural populations and in their environments may result in a spreading, and thereby a diminution, of the risk of extinction, as is expounded by den Boer (1968). This diminution of the risk of extinction results from a relative reduction in the amplitude of the fluctuations in population size, or density.

We shall here briefly discuss some of the ways along which spreading of the risk may be brought about; for more detailed discussions of the points raised see den Boer (1968) and Reddingius (1968), Ch. 5.

In the first place, the number of factors influencing net reproduction (*i.e.* the total result of reproduction and mortality taking place over a given interval of time) is presumably very large in most instances. Imagine, *e.g.*, a population of a lepidopterous insect living in a natural habitat in the temperate region of Western Europe. Survival, encountering frequency, and mating frequency for the two sexes will be influenced by a number of weather factors like temperature, rainfall, and humidity of the air, and the influences of these factors will be different in the two sexes and in periods of activity as compared to periods of inactivity. Further, the rate of development and the number of maturing eggs (interfering with egg-resorption) within the females will also in some way be influenced by certain meteorological factors, while egg-deposition will be influenced in yet another way. The same can be said about the rate of development and survival of the embryos, about the hatching of the larvae, about survival and growth of the several successive larval instars and the moults occurring between them, about pupation, entering diapause, survival during hibernation, breaking of diapause, hatching of adults, and so on and so forth. Now when the number of factors accomplishing net reproduction is large, the influences of the various factors may tend to compensate each other more or less. The probability that the relevant factors in a given year are either all extremely favourable or all extremely unfavourable will be small as compared to the probability that the total result of all factors will not deviate much from average. Although the amplitudes of the resulting fluctuations thus will be relatively small, this will not lead to stability if a population lives in an overall very favourable or very unfavourable habitat, because in such cases the density will either increase or decrease. However, this obviously cannot go on for ever. No habitat can provide opportunities for infinite increase, and in unfavourable habitats populations will become extinct rapidly. But in many cases populations are found to persist in a given area for a long time, and in such cases if the number of factors influencing net reproduction is large this may result in a spreading

of the risk. Spreading of the risk may further be accomplished by heterogeneities within the population. The life cycles of the various individuals in a population need not be synchronous. If individuals of different ages and different stages of the life cycle are present at the same time, they will be influenced by environmental factors to a different degree. A certain temperature may be favourable for the development of eggs, but also be favourable to the activities of an insect parasite attacking first-instar larvae. High winter temperatures may increase the risk of an untimely break of diapause in pupae, but also increase the chance of survival of hibernating adults, and so on. The individuals in a population do not only differ from each other as regards their ages; in general, a population comprises different phenotypes with different sensitivities towards various environmental factors, and this will also result in spreading of risk.

In addition to the above spreading of risk in time and spreading of risk over phenotypes, heterogeneities in the habitat may result in spreading of risk in space. Animals undergo the influence of weather conditions modified by the structure of the habitat as micro-weather. As the micro-weather as well as the influences of enemies and food will vary from one place to another, this increases the number of "factors" influencing the population as a whole and may spread the risk of extinction. Moreover, the animals may move from one place to another, or even migrate from one subpopulation to another and such movements, even if they occur wholly at random, will result in leveling of the fluctuations in the size of the population as a whole as compared to the fluctuations in density that may take place in a comparatively small and homogeneous area. The varying and differing influences of a number of predators, parasites, pathogens, and other organisms, and of different conditions of several kinds of food, *etc.*, may also contribute to the spreading of risk. It is hardly surprising that only incidentally, mainly when conditions are very homogeneous, it is feasible to follow the quantitative effect of one separate factor among the many factors playing a role in the field. General population theories requiring for their verification a detailed study of the influence of separate factors in our opinion will not be very fruitful. A statistical theory starting from the ideas of heterogeneity and complexity has a better chance to provide us with an insight into population dynamics. Our purpose in the present paper is to illustrate, by means of some numerical examples, the statistical results of increasing the number of factors influencing a hypothetical population, of increasing the number of age classes that may be present at any time, and of introducing migration and/or heterogeneities in space. In Chapter 3 we shall offer some mathematical arguments to show that the results obtained with the model used there do follow from

its basic premises, and not merely from the numerical values we happen to have chosen for our parameters.

The results of increasing the number of factors, of introducing several age classes, and of assuming migration and/or heterogeneities in space will be studied separately. In nature, of course, all these and many other influences work simultaneously and interact with one another. We shall be pleased when the present paper contains some suggestions as to the construction of useful models, but this is not essential with respect to the points we wish to make.

There is one type of basic assumption that we use in all of our models and which deserves some discussion here. That is, we assume that in at least one of the model populations either net reproduction equals one on the average, or its logarithm is 0 on the average. These assumptions are not wholly equivalent, but they represent the same idea, *viz.* that population density does not show an upward or a downward trend. As was already said above, such trends cannot persist for a very long time and we are for the moment only interested in what happens later on. That is, we will restrict the present discussion to populations that are well established in their environments and that are able to persist for a long time without altering significantly, and we will demonstrate that for such populations statistical stabilization like sketched above may well play a more significant role than a possibly occurring rigid governing towards equilibrium densities.

## 2. Statistical Preliminaries

### 2.1. Notation

Capital letters  $X, Y, F$  etc. will denote *random variables*; the corresponding lower-case letters  $x, y, f$  etc. will denote *realizations* of these random variables, or values they can take on. "Ordinary" variables and constants will also be denoted by lower-case letters. Greek letters will be used wherever this is convenient. Population density at time  $t$  will be denoted by  $N(t)$  or  $n(t)$ . Net reproduction over the period  $t$  to  $t+1$  will be denoted by  $R(t)$  or  $r(t)$ , *i.e.*

$$R(t) = N(t+1)/N(t).$$

We shall further write  $Y(t) = \ln\{R(t)\}$ ,  $\ln(x)$  denoting the natural logarithm of  $x$ .

If  $A$  is a chance event, the probability that  $A$  occurs is denoted by  $P(A)$ .

$\text{Exp}(x)$  denotes the exponential function  $e^x$ , *i.e.*, if  $y = \text{exp}(x)$ , then  $x = \ln(y)$ .

### 2.2. Expectations

The mathematical expectation of  $X$  will be denoted by  $E(X)$ . For example, if  $X$  can take on one of the values  $x_1, x_2, \dots, x_k$  and no other value,  $E(X)$  is defined as

$$E(X) = \sum_{j=1}^k x_j P(X = x_j). \quad (2.2.1)$$

If  $X_1, X_2, \dots, X_k$  are random variables, and  $a_1, a_2, \dots, a_k$  and  $b$  are constants, we have

$$\mathbb{E}\left(\sum_{j=1}^k a_j X_j + b\right) = \sum_{j=1}^k a_j \mathbb{E}(X_j) + b. \quad (2.2.2)$$

### 2.3. Variances, Covariances and Correlation Coefficients

The variance of  $X$ ,  $\mathbb{E}\{X - \mathbb{E}(X)\}^2$  will be denoted by  $\text{var}(X)$ . The covariance of  $X$  and  $Y$ ,  $\mathbb{E}\{[X - \mathbb{E}(X)] \cdot [Y - \mathbb{E}(Y)]\}$  will be denoted by  $\text{cov}(X, Y)$ . From the definitions it follows that

$$\text{var}\{aX + b\} = a^2 \text{var}(X) \quad (2.3.1)$$

and that

$$\text{cov}\{aX + b, cY + d\} = ac \text{cov}\{X, Y\}. \quad (2.3.2)$$

The correlation coefficient of  $X$  and  $Y$  is defined by

$$\rho(X, Y) = \frac{\text{cov}(X, Y)}{\sqrt{\text{var}(X) \text{var}(Y)}}. \quad (2.3.3)$$

It is well-known that

$$|\rho(X, Y)| \leq 1, \quad \text{or} \quad |\text{cov}(X, Y)| \leq \sqrt{\text{var}(X) \text{var}(Y)}. \quad (2.3.4)$$

It is also well-known (and it can be easily verified using (2.2.2)) that

$$\text{var}(X + Y) = \text{var}(X) + \text{var}(Y) + 2 \text{cov}(X, Y)$$

which can be generalized to

$$\text{var}\left(\sum_{j=1}^k X_j\right) = \sum_{j=1}^k \text{var}(X_j) + 2 \sum_{j=1}^{k-1} \sum_{i=j+1}^k \text{cov}(X_j, X_i). \quad (2.3.5)$$

If  $X$  and  $Y$  are independent,  $\text{cov}(X, Y) = 0$  and then  $\text{var}(X + Y) = \text{var}(X) + \text{var}(Y)$ ; therefore, if  $X_1, X_2, \dots, X_k$  are independent, the variance of their sum is the sum of their variances.

### 2.4. Bienaymé-Chebyshev Inequality. Convergence in Probability

For any random variable  $X$  with finite expectation and variance, we have

$$\mathbb{P}\{|X - \mathbb{E}(X)| \geq \varepsilon\} \leq \frac{\text{var}(X)}{\varepsilon^2} \quad \text{for any positive } \varepsilon. \quad (2.4.1)$$

This is known as the Bienaymé-Chebyshev inequality. It implies that the smaller the variance is, the more likely  $X$  will be close to its expectation. If  $X_1, X_2, \dots, X_k, \dots$  is a sequence of random variables, this sequence will be said to converge to  $\xi$  in probability if

$$\lim_{k \rightarrow \infty} \mathbb{P}\{|X_k - \xi| > \varepsilon\} = 0 \quad \text{for any positive } \varepsilon \text{ however small.} \quad (2.4.2)$$

That is, the larger we take  $k$ , the more likely  $X_k$  is to be close to  $\xi$ .

As an example to illustrate the application of these concepts, consider the case of arithmetic averages. Let  $Y_1, Y_2, \dots$  be independent and let them all have the same expectation  $\xi$  and the same variance  $\sigma^2$ . Then let us define the arithmetic

average

$$\bar{X}_k = (Y_1 + Y_2 + \cdots + Y_k)/k.$$

It will be shown that the larger we take  $k$ , the closer  $\bar{X}_k$  will be to  $\xi$ , which implies that to estimate  $\xi$ , we can use  $\bar{X}_k$ , the estimate then being the more accurate the larger  $k$ . To prove this, note that we have

$$\text{var}(\bar{X}_k) = \text{var}\left(\frac{\sum_{j=1}^k Y_j}{k}\right).$$

From (2.3.1) it follows that  $\text{var}(Y_j/k) = \frac{1}{k^2} \text{var}(Y_j)$ , hence we have, because of the supposed independence of the  $Y$ 's:

$$\text{var}(\bar{X}_k) = \sum_{j=1}^k \text{var}(Y_j)/k^2 = k\sigma^2/k^2 = \sigma^2/k$$

and also, because of (2.2.2):

$$\mathbb{E}(\bar{X}_k) = \frac{1}{k} \sum_{j=1}^k \mathbb{E}(Y_j) = \frac{1}{k} \cdot k\xi = \xi.$$

Applying the Chebyshev inequality to  $\bar{X}_k$ , we have, then,

$$\mathbb{P}\{|\bar{X}_k - \xi| \geq \varepsilon\} \leq \frac{\sigma^2}{\varepsilon^2 k}.$$

It follows that  $\bar{X}_k$  converges to  $\xi$  in probability, since  $\sigma^2/\varepsilon^2 k \rightarrow 0$  as  $k \rightarrow \infty$ . (In fact, an even stronger statement can be shown to be true: we have  $\mathbb{P}\left[\lim_{k \rightarrow \infty} (\bar{X}_k - \xi) = 0\right] = 1$ ; but we will not use this).

### 2.5. Skewness Coefficient

The third central moment of  $X$  about its expectation,  $\mathbb{E}\{X - \mathbb{E}(X)\}^3$ , is zero when the distribution of  $X$  is symmetrical, i.e. when for all  $x$  we have  $\mathbb{P}\{X > \mathbb{E}(X) + x\} = \mathbb{P}\{X < \mathbb{E}(X) - x\}$ . Otherwise, the value of the third central moment depends on the units  $X$  is measured in; for example, if  $X$  is measured in millimetres the numerical value of this moment will be  $10^3$  as great as when  $X$  is measured in centimetres. Therefore the third central moment had better be normalized by dividing it by an appropriate power of the variance. Thus, the *skewness coefficient* of (the distribution of)  $X$  is defined as

$$\sqrt[3]{\bar{\beta}_1} = \frac{\mathbb{E}\{X - \mathbb{E}(X)\}^3}{\{\text{var}(X)\}^{\frac{3}{2}}}. \quad (2.5.1)$$

If  $x_1, x_2, \dots, x_k$  is a realization of a random sample from the distribution of  $X$ ,  $\sqrt[3]{\bar{\beta}_1}$  may be estimated by the sample skewness coefficient

$$\sqrt[3]{\bar{b}_1} = \frac{\frac{1}{k} \sum_{j=1}^k (x_j - \bar{x})^3}{\left\{ \frac{1}{k} \sum_{j=1}^k (x_j - \bar{x})^2 \right\}^{\frac{3}{2}}}, \quad \text{with } \bar{x} = \frac{1}{k} \sum_{j=1}^k x_j. \quad (2.5.2)$$

This is a realization of a random variable  $\sqrt[3]{\bar{B}_1}$ . If  $X$  is normally distributed, approximations to the distribution of  $\sqrt[3]{\bar{B}_1}$  are known, which can be used for tests of





### 2.7. Further Reading

For the reader not acquainted with mathematical statistics, the assertions above will not be easy reading. More detailed arguments, proofs *etc.* can be found in textbooks, *e.g.* Fisz (1958), Feller (1957), Mood and Graybill (1963) and others, and in the publications quoted above.

## 3. Stabilization by a Large Number of Factors

### 3.1. The Model

In this chapter we will study a model where net reproduction is determined by a varying number of weather factors. The number of factors involved will be taken to be 1, 2, *etc.*, up to 10, and it will be shown that increasing the number of factors results in stabilization of fluctuations in the density. The model is defined as follows.

Let the net reproduction  $R(t)$  be determined by factors  $F_1(t)$ ,  $F_2(t)$ , ...,  $F_k(t)$ . The  $F_i(t)$  may vary between the limits  $u_i$ ,  $b_i$ ; that is,  $u_1, u_2, \dots, u_k$  and  $b_1, b_2, \dots, b_k$  are given numbers such that

$$P\{u_i \leq F_i(t) \leq b_i\} = 1 \text{ if } b_i > u_i, \quad (3.1.1)$$

and

$$P\{u_i \geq F_i(t) \geq b_i\} = 1 \text{ if } b_i < u_i,$$

for  $i = 1, 2, \dots, k$  and  $t = 1, 2, \dots$  *ad inf.*

Then if  $f_1(t), f_2(t), \dots, f_k(t)$  are a realization of  $F_1(t), F_2(t), \dots, F_k(t)$ , the corresponding realization  $y(t)$  of  $Y(t) = \ln\{R(t)\}$  is

$$y(t) = \ln\{r(t)\} = y_{\min} + \frac{y_{\max} - y_{\min}}{\sum_{j=1}^k |b_j - u_j|} \cdot \sum_{j=1}^k |f_j(t) - u_j|. \quad (3.1.2)$$

It will be seen that as the  $f_i$  vary between  $u_i$  and  $b_i$ ,  $y$  varies between  $y_{\min}$  and  $y_{\max}$ ; in fact,  $y = y_{\min}$  if  $f_i = u_i$  for all  $i$ , and  $y = y_{\max}$  when  $f_i = b_i$  for all  $i$ . The values of  $y_{\max}$ ,  $y_{\min}$ , the  $u_i$ , and the  $b_i$  are supposed to be fixed and given in every instance. Note that if  $u_i < b_i$ , (3.1.2) means that  $y(t)$  will be the larger the larger  $f_i(t)$ , other things being equal; but if  $u_i > b_i$ ,  $y(t)$  will be the smaller the larger  $f_i(t)$ , other things being equal. We wished to use both possibilities, and that is why we used absolute values of differences rather than the differences themselves. Note also that  $|f_i(t) - u_i|$  is  $f_i(t) - u_i$  or  $u_i - f_i(t)$  according as  $u_i < b_i$  or  $u_i > b_i$  and that this does not depend on  $t$ ; in other words, for any given set of parameters the formula is always used in the same sense.

It is an essential feature of our model that the net reproduction always remains between two limits  $r_{\max} = \exp(y_{\max})$  and  $r_{\min} = \exp(y_{\min})$ . We think this a reasonable assumption. Although we may be impressed by the reproductive potential of certain animals it is evident that

reproduction is a limited faculty, and under natural conditions net reproduction is only a small portion of reproductive potential. So it is realistic to fix a maximal value of net reproduction that cannot be exceeded by the net reproduction of our hypothetical population. This does not mean, of course, that there is an upper limit to the density. In a comparable way it seems warranted to fix a minimal value of net reproduction. Admittedly net reproduction might attain the value 0 (and then its natural logarithm is minus infinity, which gives some difficulties in calculations) but we assume that if the environment is not too unfavourable, the probability that net reproduction falls below  $r_{\min}$  is negligibly small (*i.e.*, as long as a few individuals are present at least some reproduction is supposed to occur). This, again, does not mean that there is a lower limit to the density: in the course of a number of generations the population may become extinct. Strictly speaking, if the net reproduction is never zero, the density cannot become zero, but this is merely a result from the arithmetical properties of the model because net reproduction is treated as a multiplication factor. As soon as density has been calculated to become so small that it amounts to only a fraction of one individual being present, the population must be considered extinct.

For the  $f_i(t)$  we used meteorological data such as average temperature, total rainfall, *etc.* over a given month. These data were taken from published tables (for references see below) and they were used in the same temporal order in which they appear in the original tables. We did not expect that meteorological factors would be particularly well suited to prove our hypothesis, but the use of real weather data instead of some abstract random-numbers device seemed attractive because: 1. ecologists agree that weather conditions must have a profound influence on animal numbers; 2. the influence of the number of weather factors is an important point of discussion in the literature (see *e.g.* Birch, 1957; Klomp, 1962; Wilbert, 1962); 3. weather data are the only kind of environmental factors of which real values over long series of consecutive years are available; and 4. by using such data one need not suppose anything special concerning the frequency distributions of the various factors, the dependence of these on time, or the mutual correlations that might or might not occur between different factors. Instead of generating artificial values by means of some arbitrary device, one has the values dictated by nature itself, so to speak.

Of course, the special arithmetical formula (3.1.2) that we used cannot be justified by our knowledge concerning the way net reproduction is influenced by weather factors. In fact, such knowledge is lacking and therefore we feel justified to assume a model which is arithmetically as simple as is possible, the more so since we feel that our conclusions should

be valid for a more general class of models as well. Further remarks on this point will be made below, Section 3.7.2.

In all our simulation experiments with this model, we assumed  $n(0) = 500$ ,  $r_{\max} = 50$ ,  $r_{\min} = 0.02$ . From Klomp (1962, p. 86) may be derived that in many lepidopterous insects the range of  $r$  remains between the limits 0.1 and 10. To keep eruptions or crashes by a rare combination of many favourable or unfavourable factors, respectively, within the possibilities of the model, the much wider range of 0.02 to 50 was assumed. On a logarithmic scale, the limits chosen ( $y_{\max}$  and  $y_{\min}$ ) lie symmetrically with respect to zero, *i.e.*,  $y_{\min} = -y_{\max}$ . This is not very important, since the limits are only seldom, if ever, reached and the frequency distributions of the factors used may be very asymmetrical (Fig. 1; see Section 3.4).

The  $u_i$  and  $b_i$  were fixed arbitrary but in such a way that the requirement that either  $u_i \leq f_i(t) \leq b_i$  or  $b_i \leq f_i(t) \leq u_i$  was satisfied for all  $t$ , and such that with 10 factors after a given sequence of years (specified below)  $n(t)$  attains the initial value  $n(0)$  once more. This was done in order to secure that with 10 factors, density would not show an obvious upward or downward trend (see our Introduction). The calculation to determine  $u_i$  and  $b_i$  according to this requirement was rather roughly done since we saw no point in being more precise than nature itself can be supposed to be. As will be seen below, in fact our populations with 10 factors exhibited a slow upward trend and this, maybe, is not unrealistic. The values of  $n(0)$ ,  $r_{\max}$ ,  $r_{\min}$ ,  $u_1 \dots u_{10}$ ,  $b_1 \dots b_{10}$ , and the sequence of  $f_i(t)$  values for  $i = 1, 2, \dots, 10$  and  $t = 1, 2, \dots$  were stored in the memory of the computer. The computer calculated  $y(0)$ ,  $y(1)$ , ... and  $n(1)$ ,  $n(2)$ , ... for all 10 cases with 1 factor, all  $\binom{10}{2} = 45$  cases with 2 factors, all  $\binom{10}{3} = 120$  cases with 3 factors and so on up until the case with 10 factors. (As is well-known, there are  $\binom{k}{j} = \frac{k \cdot (k-1) \dots (k-j+1)}{j \cdot (j-1) \dots 3 \cdot 2 \cdot 1}$  ways of choosing  $j$  factors out of a set of  $k$  factors, see Feller, 1957, Mood and Graybill, 1963, or some other introductory text on probability theory and statistics.) The complete sequence of values of  $n(t)$  was printed out in only a few instances, but in all cases a number of statistical characteristics of the sequence obtained were calculated and printed out. As the statistics chosen differ somewhat for the two simulation experiments we performed, they will be discussed below. The computer used was the Telefunken TR4 of the Computing Centre of the University of Groningen.

### 3.2. Experiment 1

The weather factors used are defined in Table 1. The numerical data were taken from tables of the Royal Meteorological Institute (KNMI) at

De Bilt, Netherlands (Braak, 1933, 1936, 1937, 1943). Each  $r$ -value in this experiment is supposed to be determined by one or a number of meteorological conditions during a given year in the same locality (De Bilt). In factors 1, 5, 7, 8 and 9 (see Table 1) the relation between  $r$  and the value of the factor was inversed, *i.e.*, the greater the value of the factor, the smaller  $r$ . This was accomplished by taking  $u_i > b_i$  instead of  $u_i < b_i$ .

Table 1. *Definition of weather factors used in Experiment 1: 1901—1930 (30 years)*

Factor number	Definition of factor
4	number of hours of sunshine in April
6	total evaporation for April in mm
2	number of hours of sunshine during May
1 <sup>a</sup>	mean air temperature for June in °C
8 <sup>a</sup>	total evaporation for June in mm
3	mean air temperature for July in °C
7 <sup>a</sup>	total rainfall in August in mm
9 <sup>a</sup>	total rainfall in September in mm
10	mean air temperature for September in °C
5 <sup>a</sup>	mean soil temperature for December in °C

<sup>a</sup> Relation inversed.

To illustrate how such a choice of factors might be obtained, imagine a lepidopterous insect where the winged adults hatch from the soil in April (survival is favourably influenced by sunshine and evaporation, Factors 4 and 6) and move around in May to copulate and deposit eggs (number of eggs produced favourably influenced by sunshine in May, Factor 2); the larvae hatch on the plants in June (mortality increased by high temperatures and high evaporation, Factors 1 and 8) and grow up in July and August (survival favourably influenced by air temperature in July, but mortality increased by much rainfall in August, Factors 3 and 7). The fully grown larvae descend from the plants to burrow into the soil in September (rainfall unfavourable, high temperatures favourable, Factors 9 and 10) and the pupae enter diapause in December (success favourably influenced by low soil temperatures, Factor 5).

The weather data used cover a period of 30 years and so 30 generations of our imaginary insect could be calculated. The  $b_i$  and  $u_i$  were chosen so as to have  $\frac{1}{30} \ln \{n(30)/n(0)\}$  for 10 factors about 0. We shall now discuss the results on the basis of some statistical characteristics of the sequences thus obtained.

(a) The difference between the natural logarithm of the greatest density that occurred and the smallest density that occurred. This will be called the *logarithmic range*, to be abbreviated by *LR*. Of course, the greater the number of generations, the greater this *LR* will be, but with the same number of generations in each case (30 in the present instance) it can be used as a measure of stability.

It will have a comparatively large value when :

1. density shows an upward or a downward trend in time, for then in any case the density at the end of the series will differ much from initial density, and  $LR$  will be at least

$$|\ln (\text{final density}) - \ln (\text{initial density})| ;$$

2. density fluctuates heavily up and down.

It will have a comparatively low value when density fluctuates with small amplitudes about some constant value.

For each  $k$  ( $k=1, 2, 3, \dots, 10$ ) we calculated the arithmetic mean of the values of the  $LR$  obtained with all simulations with  $k$  factors working together. These averages are presented in the third column of Table 2. From 2 factors onwards, average  $LR$  steadily decreases with the number of factors. The difference between the case with 2 factors and that with 10 factors is 5.84330, which means that on the average greatest density/smallest density is nearly 1,000 times as great in cases with 2 factors as in the case with 10 factors. (*Cf.* the "orientation" at the bottom of the table.)

(*b*) *Average ln (Net Reproduction)*. For  $m$  generations, the average logarithm of net reproduction is simply  $\frac{1}{m} \{\ln [n(m)] - \ln [n(0)]\}$ . This average in its turn was averaged over all cases with  $k$  faktors, with  $k=1, 2, 3, \dots, 10$ . The resulting averages are shown in the fourth column of Table 2. The differences are not very great, and on the average the populations showed an upward trend. This is mainly a matter of the choice of our parameters, as we discussed above; the calculation of the  $u_i$  and  $b_i$  was not very precise. From 4 factors onwards, the average steadily decreases towards the final value for 10 factors. It must be noted that average  $\ln(r)$  is a statistic useful for measuring whether density shows a definite trend. If  $E\{Y(t)\}=0$ , this average will tend to zero if the length of the observational series is increased; if  $E\{Y(t)\}=\eta \neq 0$ , the average will tend to  $\eta$  as the length of the series is increased (see Section 2.4).

(*c*) *Variance of ln (Net Reproduction)*. The averaged sample variances of  $y(t)$  are shown in the fifth column of Table 2. The smaller this variance, the closer on the average net reproduction will be to its mean value, hence the less violent the fluctuations in the density will be. We see that from 1 factor onwards, the average variance steadily decreases with the number of factors. This, indeed, corroborates our conjecture: that with a large number of factors, the influences of the various factors will tend to compensate each other more or less, the probability that all factors together will have extreme values with the same sign being

much smaller than the probability that only one or a few among them will have extreme values.

(d) *Skewness of  $\ln$  (Net Reproduction)*. Average values of the sample skewness coefficients of the  $y(t)$  are given in the last column of Table 2. They are all negative, but their absolute values decrease steadily with the number of factors, and this suggests that the frequency distributions of the  $y(t)$  become more symmetrical with more factors (see Section 2.5). The results suggest that with increasing the number of factors the distribution of  $Y(t)$  might tend to normality, and this together with decreasing of  $\text{var}\{Y(t)\}$  would imply that the values  $Y(t)$  can take on become more and more centered around the expected value. If the expected value is about zero, this means stabilization.

#### Remarks

The individual results were highly variable, and it is certainly not true that by increasing the number of factors one decreases  $LR$ ,  $\text{var}\{\ln(r)\}$  and  $\sqrt{b_1}$  in *all* individual instances. Therefore in Table 2 averages are presented, in order to show the general trend apart from individual variations. These averages are not all based on the same number of items (see second column) simply because the number of combinations of  $j$  factors  $\binom{10}{j}$  is not the same for all  $j$ . If one is sceptical

Table 2. Average values of some statistics characterizing population fluctuation in Experiment 1

Number of factors ( $k$ )	Number of cases	Average $\ln$ (range) ( $LR$ )	Average $\ln$ {net repr.}	Average variance $\ln$ {net repr.}	Average skewness $\ln$ (net repr.)
1	10	15.32296	+ 0.21726	0.84199	- 0.32235
2	45	16.25782	+ 0.33397	0.79263	- 0.29222
3	120	15.22638	+ 0.35339	0.65487	- 0.20825
4	210	13.91089	+ 0.35591	0.52245	- 0.14593
5	252	12.78030	+ 0.34636	0.42594	- 0.09327
6	210	11.93802	+ 0.34474	0.35816	- 0.06235
7	120	11.34536	+ 0.34316	0.31014	- 0.03141
8	45	10.91332	+ 0.33584	0.27430	- 0.02149
9	10	10.62841	+ 0.33258	0.24649	- 0.01337
10	1	10.41452	+ 0.32988	0.22429	- 0.00700
<b>Total:</b>	<b>1023</b>				

Orientation: $\ln(1)$	= 0.00000	$\ln(10,000)$	= 9.21034
$\ln(10)$	= 2.30258	$\ln(100,000)$	= 11.51293
$\ln(100)$	= 4.60517	$\ln(1,000,000)$	= 13.81551
$\ln(1,000)$	= 6.90778	$\ln(10,000,000)$	= 16.11810

about the validity of comparisons between cases where the average is not based on the same number of items, one can still learn something from pairwise comparisons between cases with  $j$  and with  $10 - j$  factors (e.g. 1 with 9 factors, 2 with 8 factors and so on).

### 3.3. Experiment 2

The aim of our second experiment with weather factors was to try an other set of factors and a longer series of years. One might expect that the stabilizing influence of the number of factors will be the better visible the longer the series of years considered, but on the other hand the chance of including more or less continued changes in climate may also become higher in a long series of years. Such phenomena may influence the course of fluctuations. The factors used are defined in Table 3; the numerical data were taken from Labrijn (1945) and cover

Table 3. Definition of weather factors used in Experiment 2: 1735—1944 (210 years)

Factor number	Definition of factor
1	mean air temperature for January in °C
2	mean air temperature for February in °C
3	mean air temperature for March in °C
4	mean air temperature for July in °C
5	mean air temperature for August in °C
6	mean air temperature for December in °C
7	total rainfall in April in mm
8	total rainfall in May in mm
9	total rainfall in September in mm
10	total rainfall in October in mm

a period of 210 years (1735 to 1944 inclusive). This is a satisfactorily long period for most animals from the point of view of a population ecologist. The choice of the factors was determined merely by the fact that just for this set of factors such a long series of measurements is available. The construction of an imaginary animal that has to cope with these weather factors is left to the reader. Although this type of data is rather crude, methods of measurements and location where measurements are taken being not exactly the same over the whole period, the main features of climatic fluctuation should be represented by such a series.

The parameters  $u_i$ ,  $b_i$  ( $i = 1, 2, \dots, 10$ ) were chosen in such a way that with the combination of all of the 10 factors the density would be about equal to the initial density after 100 generations. Again, this

calculation was not very precise, so that  $n(100)$  was in fact somewhat above  $n(0)$  (Fig. 2), the whole sequence of 210 densities showing an upward trend with 10 factors.

When we tried to simulate the model for the first time with this set of factors, it appeared that the computer would sometimes stop halfway of the calculations because some "population density" it had to handle had become too large. Therefore the program was altered in some respects:

(a) When  $\ln\{n(t)\}$  became greater than +300, the calculation was stopped and INF was printed together with the values of the various statistics obtained thus far and the number of the generation; when  $\ln\{n(t)\}$  became smaller than -300, a similar procedure was followed, this time ZERO being printed instead of INF (in fact, the latter case did not occur).

(b) We had printed out in which generation (if ever)  $\ln\{n(t)\}$  for the first time passed the limit  $-2.302585093 = \ln(0.1)$ , or the limit  $+13.815510558 = \ln(1,000,000)$ . The choice of these limits was arbitrary.

To start with, the same statistics characterizing population fluctuation were computed as in Experiment 1. The results are presented in Table 4. In the computation of averages we excluded the cases where  $|\ln\{n(t)\}|$  increased beyond 300. In Table 4, the same trends as in Experiment 1 are apparent. Logarithmic range, variance of  $\ln(\text{net reproduction})$  and skewness of  $\ln(\text{net reproduction})$  on the average decrease with increasing number of factors. From 5 factors onwards the average  $\ln(\text{net reproduction})$  comes closer to 0 towards the final value for 10 factors. However, the data in Table 4 are somewhat biased because those cases where the density attained very high or very low values were excluded and so the values given are too low. This bias only influences the trend in average  $\ln(\text{net reproduction})$ : as only cases with too high

Table 4. Average values of some statistics characterizing population fluctuation in Experiment 2

Number of factors	Number of cases <sup>a</sup>	Average ln-range (LR)	Average ln(net repr.)	Average variance ln(net repr.)	Average skewness ln(net repr.)
1	5	199.21519	-0.49422	1.16685	1.07616
2	30	118.97873	-0.35314	1.16217	0.73756
3	100	106.89997	-0.05873	0.81688	0.47267
4	193	103.64409	+0.07137	0.51471	0.36934
5	241	94.90829	+0.11911	0.45478	0.20948
6	204	79.57040	+0.11205	0.35433	0.15214
7	118	64.43719	+0.09852	0.28516	0.13361
8	45	53.38921	+0.09824	0.28437	0.12562
9	10	37.01648	+0.08074	0.27406	0.11933
10	1	15.08419	+0.06720	0.24420	0.10884

<sup>a</sup> Cases where  $|\ln\{n(t)\}|$  in a certain generation increased beyond 300 were excluded.



values occurred, only cases with a high positive value of average  $\ln(\text{net reproduction})$  were excluded. When relatively many of these positive values are excluded average  $\ln(\text{net reproduction})$  of the remaining cases may even be negative (this happens with 1, 2, and 3 factors).

In Table 5, fourth column, it can be seen that the percentage of all cases that had to be excluded decreased with increasing number of factors; even the absolute number of such cases decreases from 3 factors onwards, while the total number of cases increases from 1 to 5 factors.

Table 5. Number and percentage of cases where  $\ln(\text{density})$  increased beyond 300, and number and percentage of cases where density remained between 0.1 and 1,000,000

Number of factors	Number of combinations	Number of cases $ \ln(n)  > 300$	Percentage	Number of cases $0.1 < n < 1,000,000$	Percentage
1	10	5	50	0	0
2	45	15	33.3	0	0
3	120	20	16.7	0	0
4	210	17	8.1	9	4.3
5	252	11	4.4	7	2.8
6	210	6	2.9	6	2.9
7	120	2	1.7	9	7.5
8	45	0	0	7	15.6
9	10	0	0	1	11.1
10	1	0	0	0	0

This means that average  $LR$ , average  $\ln\{r(t)\}$  and average  $\text{var}[\ln\{r(t)\}]$  are more severely underrepresented the less the number of factors, and this strengthens our impression that increasing the number of factors increases stability. Moreover, the fact that the limit  $+300$  (and  $-300$ ) is less often passed by  $\ln\{n(t)\}$  the greater the number of factors, is itself significant in this respect. The number of cases where population density remains between certain positive limits for the whole period is expressed in still another way: in Table 5, last column, the percentage of all cases where  $0.1 < n(t) < 1,000,000$  for  $t = 1, 2, \dots, 210$  is given. It is seen that one of the limits 0.1 or 1,000,000 was always passed when the number of factors involved was 3 or less, but apart from this the picture is not very clear, the case with 10 factors being apparently no better in this respect than the cases with 1 factor. This can be explained as follows: as the number of factors increases, the factors that by themselves would cause  $n(t)$  to increase beyond 1,000,000 are checked by others, but their influence need not be levelled out completely: the moment of passing one of the said limits may be only delayed, and so, while the number of cases excluded because  $|\ln n(t)| > 300$  decreases the

number of cases where  $0.1 < n(t) < 1,000,000$  may in some instances increase. Table 6 shows that the number of generations it lasts before one of the limits is passed gradually increases with increasing number of factors in those cases where the limits in fact were passed within 210 generations. With 10 factors the waiting time until the first passage of 1,000,000 is much longer than in the other cases. Combining the different data and keeping in mind the various kinds of bias in the measures used, the general impression is that indeed increasing the number of factors increases stability in the sense of restricting fluctuations to narrower intervals.

Table 6. Average number of generations until  $n(t)$  passed one of the limits 0.1 or 1,000,000 for the first time ("waiting time until first passage"), for those cases where the said limits were passed within 210 generations

Number of factors	Number of cases one of the limits 0.1 or 1,000,000 was passed	Average waiting time until first passage
1	10	6.8
2	45	15.6
3	120	23.91667
4	201	27.77612
5	245	32.88571
6	204	35.24020
7	111	38.92793
8	38	37.89474
9	8	63.77778
10	1	151.0

#### 3.4. Statistical Features of the Weather Data Used in Exp. 2

With long series of data as given by Labrijn (1945), it is tempting to try and satisfy one's curiosity about randomness and mutual correlations of such factors as defined in Table 3, but a statistical analysis of data like these is not easy. We have therefore not carried out such an analysis, but some remarks concerning the type of difficulty one meets and on what might be expected may be useful. The frequency distributions of the various factors are sometimes markedly skew (Fig. 1), and therefore assuming normal distributions for them is not warranted. For example, for Factor 1 we found  $\sqrt{b_1} = 0.535$ . Assuming that the series of 210 successive mean air temperatures for January can be considered a random sample from some probability distribution, the hypothesis that this distribution is normal, having skewness coefficient zero, may be rejected at 0.02 level (Pearson and Hartley, 1962, Table 34 B).

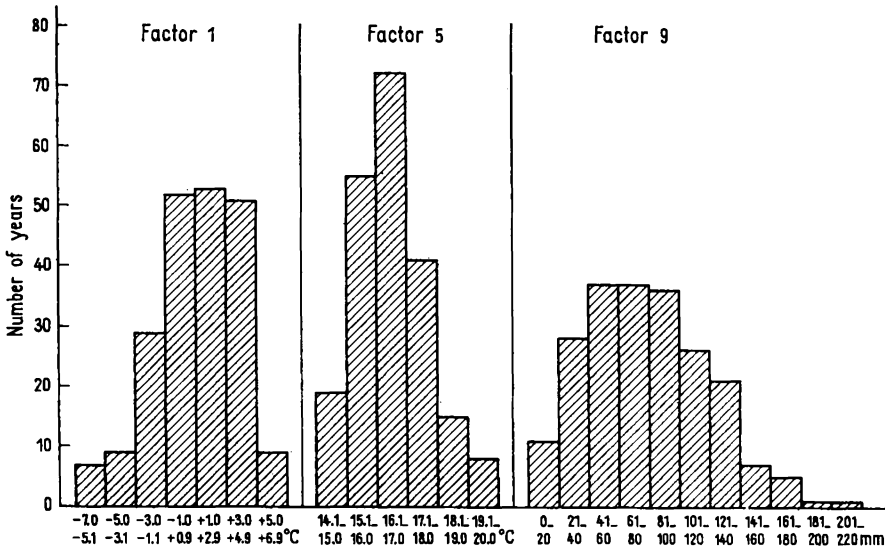


Fig. 1. Frequency distributions of three of the weather factors used in Experiment 2. For definitions see Table 3

But it is doubtful whether the assumption that the series is a random sample is justified. The circular serial correlation coefficient  $r_c$  for the series of Factor 1 is  $-0.16$ . Assuming that we have a sequence of normally distributed variates, with Anderson's formulae (cf. Section 2.5) we find  $(r_c - E(R_c))/\sqrt{\text{var}(R_c)} = -2.25$  which differs significantly from zero ( $p=0.0122$ ). But as maybe the values of Factor 1 are neither normally distributed nor serially independent, both tests of significance may be invalid; we can only say that the sequence of data is not a sequence of independent normal variates. Testing the significance of  $r_c$  by means of the distributionfree permutation test of Wald and Wolfowitz (1943) one finds the normalized test statistic to be  $-0.354$  which is not significant at 0.36 level, but as such distributionfree tests are not very powerful no definite conclusion about the serial correlation can be drawn.

We also computed the correlation coefficient between Factor 5 and Factor 9. This correlation coefficient appeared to be  $+0.158$ . The circular serial correlation coefficient for Factor 5 is  $+0.111$ , which for a series of normally distributed variates is nearly significant ( $p=0.093$ , two-sided), but for Factor 9 the circular serial correlation coefficient is  $+0.0073$  which does not significantly differ from its expectation. It seems warranted, therefore, to consider the sequence of air temperatures

for August (Factor 5) as given and to test the significance of the regression coefficient of Factor 9 on Factor 5. The regression coefficient is 5.354 which for normally distributed variates differs significantly from zero at 0.05 level ( $t = 2.307$ , 208 degrees of freedom). This test in general is sufficiently robust against moderate departures from normality of the distributions of the variates to suspect Factors 5 and 9 of being correlated.

Table 7.  $s$  = number of runs up and down in a sequence of 210 values

$$u = \frac{s - E(S)}{\sigma(S)}$$

where

$$E(S) = \frac{1}{3} (2n - 1) = 139.7$$

$$\sigma(S) = \sqrt{\frac{16n - 29}{90}} = 6.08$$

$$n = 210$$

Factor number	$s$	$u$	Factor number	$s$	$u$
1	146	1.04	6	141	0.21
2	153	2.19	7	139	-0.12
3	139	-0.12	8	152	2.02
4	138	-0.28	9	139	-0.12
5	137	-0.30	10	148	1.37

In Table 7, we present the numbers of runs up and down for the 10 sequences of 210 factors. The expected number of runs in a sequence of 210 numbers is 139.7, and the standard deviation is 6.08 (see Section 2.6). We have neglected the fact that sometimes two successive factor values are equal; this occurs so seldom that the neglect is warranted. The numbers of runs for Factors 2 and 8 differ significantly from their expectation under the hypothesis that their temporal order is random, and the cases of Factors 1 and 10 are suspect.

It appears thus that weather factors may be serially correlated in time as well as correlated among each other, and that their frequency distributions may be non-normal. The serial correlations are not very great as a rule and in short series they may well be negligible.

### 3.5. Stabilization and Regulation

The conclusion anticipated in the Introduction that stabilization by a great number of factors might play a more significant role than a rigid governing towards an equilibrium density perhaps does not yet

seem to be convincingly established by the results of Experiments 1 and 2. In Experiment 2, the population influenced by 10 factors is still very far from being stable in an ecologically realistic sense. The logarithmic range is 15.08419, which means that the greatest density was about  $3.56 \times 10^6$  times as great as the smallest one. Little is needed, however, to improve on this. In order to improve the behaviour of populations with a slow upward trend like this one, we need only assume that when density becomes very high, crashes may occur at some time. This is something very different from a precise feedback mechanism that would always force population density towards some equilibrium value like proposed by *e.g.* Wilbert (1962). Already Schwerdtfeger (1941) pointed out that populations of insect pest often build up fairly slowly until a sudden crash occurs. If one investigates into the causes of such crashes, it appears that not one single density-related factor can be held responsible for it. Rather, the crash seems to result from the interaction between a somewhat increased number of parasites, unfavourable weather, diseases and so on.

We shall now discuss results of some "crash" mechanisms that can easily be built into our model. By  $r(t)$  we shall denote net reproduction as it was in Experiment 2, *i.e.*, determined by equation (3.1.2):  $r^*(t)$  will denote net reproduction in our modified model.

(a) *Net Reproduction Negatively Density-Dependent Above a Certain Density (Experiment 2a)*. We shall put

$$\begin{aligned} r^*(t) &= \frac{r(t)}{1 + 0.002\{n(t) - 250,000\}} \quad \text{whenever } n(t) \geq 250,000 \\ &= r(t) \quad \text{whenever } n(t) < 250,000. \end{aligned} \quad (3.5.1)$$

That is,  $r^*(t)$  is negatively density-dependent when density is above 250,000 and density-independent if density is below 250,000. It will be seen that

$$\lim_{n \rightarrow \infty} \frac{r}{1 + 0.002\{n - 250,000\}} = 0.$$

The density-dependent reduction in  $r$  that can occur when density is above 250,000 may be considerable. If density is only 250,500, net reproduction is halved, and if density is 295,500, net reproduction is one tenth of what it would have been otherwise.

In Experiment 2, the values of  $n(t)$ ,  $\ln\{n(t)\}$  and  $\ln\{r(t)\}$  for  $t=0, 1, 2, \dots, 210$  were printed out by the computer for the case with 10 factors (see Fig. 2). These data can be used to simulate the present model. The value 250,000 was passed for the first time in the 139-th generation; in fact,  $n(139) = 346,945.22635$ , hence we have

$$1 + 0.002\{n(139) - 250,000\} = 194.89045,$$

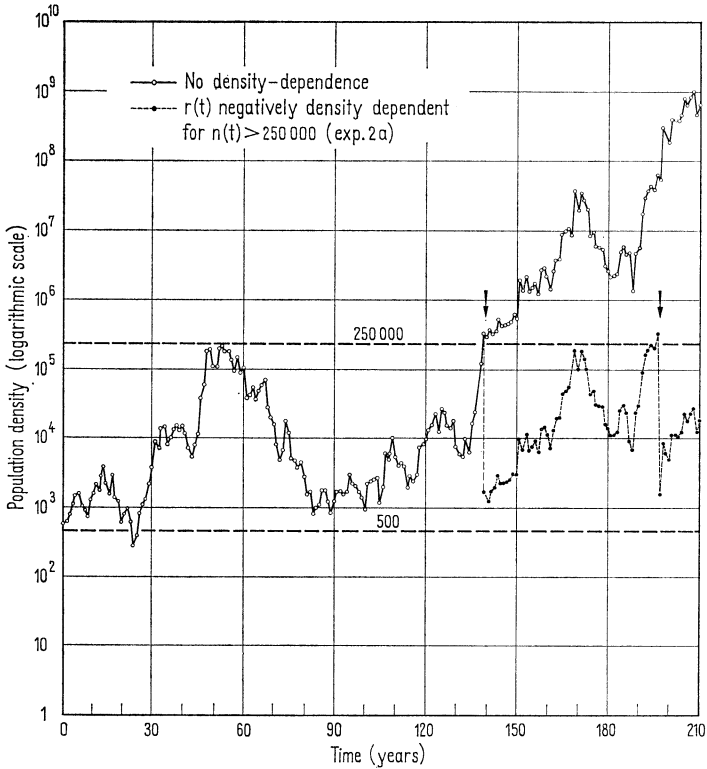


Fig. 2. Fluctuations of population density for the model population of Experiment 2 with 10 weather factors operating. Solid curve: fluctuations when no density-dependent effects occur. Interrupted curve: the same, with density-dependent reductions of net reproduction whenever density rises above 250,000 (indicated by arrows). (Experiment 2a.) For further explanation see text, Section 3.5

and so we have to subtract  $\ln(194.89045) = 5.27244$  from  $\ln(r)$  to obtain  $\ln(r^*)$ . Denoting the new densities by  $n^*(t)$ , we thus have  $\ln\{n^*(t)\} = \ln\{n(t)\} - 5.27244$  for  $t = 140, 141, \text{etc.}$  But  $n^*(t)$  again rises above 250,000 in the 196-th generation. The new correction factor is  $-5.22944$ , hence for  $t = 197, 198, \text{etc.}$  we have

$$\ln\{n^*(t)\} = \ln\{n(t)\} - 5.27244 - 5.22944 = \ln\{n(t)\} - 10.50188.$$

The resulting density fluctuations are compared to the original situation in Fig. 2, where arrows indicate the moments where a density-dependent reduction of  $r$  had to be applied.

Fig. 2 suggests that the negatively density-dependent reduction of  $r$  as defined above indeed stabilizes population fluctuation very effectively.

Table 8 shows that the logarithmic range is reduced as compared to Experiment 2, and that average  $\ln(r)$  is closer to 0. But  $\text{var}\{\ln(r)\}$  is increased; this is because of the introduction of two  $r$ 's with comparatively large absolute value. It furthermore seems that it is not essential for the stabilizing effect that the reductions in  $r$  be negatively density-dependent: density-dependent reductions were applied only two times, and the numerical difference between the two reductions is not important. The same effect could have been accomplished by a density-independent catastrophe of the same order of magnitude, provided only that the probability that such a catastrophe occurs is nearly zero when density is near zero, but close to 1 if density is high.

(b) *Constant Amount of Reduction of  $\ln(r)$ , Probability of Occurrence Density-Dependent (Experiment 2b)*. We now suppose that a catastrophe consists always of subtracting 3 from  $\ln(r)$ , *i.e.*  $\ln(r^*) = \ln(r) - 3$ . Furthermore, we suppose that the probability that environmental circumstances in some year are such as to permit the occurrence of a catastrophe is 0.3. Let us call years with such catastrophic circumstances  $C$ -years. Then we suppose that the probability that a catastrophe in fact occurs in a  $C$ -year depends on density in the following way: the

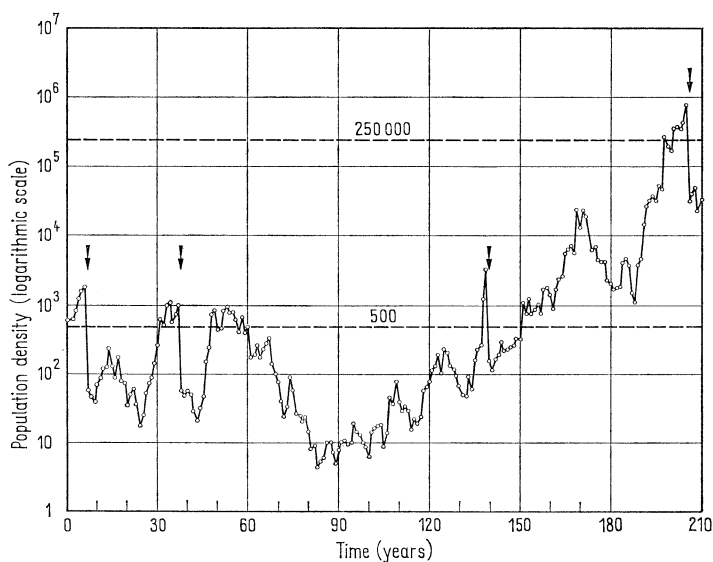


Fig. 3. Fluctuations of population density for a model population as in Experiment 2 with 10 weather factors operating when in addition catastrophes may occur with density-dependent probabilities, and the reduction in net reproduction due to the catastrophe is always the same (see arrows). (Experiment 2b.) For further explanation see text, Section 3.5

probability is 0 when  $\ln(n) < 6.21461 = \ln(500)$ , it is 0.1 when  $6.21461 < \ln(n) < 12.42922 = \ln(250,000)$  and it is 0.5 when  $\ln(n) > 12.42922$ . By these assumptions, several catastrophes could be expected to occur in a period of 210 years and this could cause extinction of the population. So we increased all logarithms of net reproductions by 0.01 to strengthen the upward trend in the density which then should be counteracted by the catastrophes, by which the situation becomes comparable with those in 2a. *C*-years were selected by choosing a sequence of 210 digits from a table of random numbers, and calling a year a *C*-year when the corresponding random digit was 3, 6, or 9 (*i.e.*, divisible by 3). If in a *C*-year density was between 500 and 250,000, a random digit was chosen from a table of random numbers and if this digit happened to be 5, a catastrophe was taken to occur, and 3 was subtracted from the logarithms of all subsequent densities. If density was above 250,000 in a *C*-year, a random digit was selected and a catastrophe was taken to occur when the digit was even. These operations were again carried out on the original data of Experiment 2 (10 factors). In all, 4 catastrophes occurred (Fig. 3). Density fluctuations were again stabilized, though to a less degree than in Experiment 2a, as will be seen by comparison of Figs. 2 and 3, and in Table 8. The variance of  $\ln(r)$  is greatly increased in this case.

(c) *Random Catastrophes in Random Years (Experiment 2c)*. In Experiment 2b, 4 catastrophes occurred, each consisting of subtraction of 3 from  $\ln(r)$ . The end result is that 12 is subtracted from density in the 210-th generation (as compared with 2a, 9.9 is subtracted in 2b; in 2a 10.5 was subtracted). The same end result can be attained by 4 catastrophes of different sizes, provided their sum is 12. From a table with random numbers, we chose the digits 7, 8, 9, 6. Their sum is 30, *i.e.* 18 more than 12. So we subtracted  $18/4 = 4.5$  from these digits and obtained 2.5, 4.5, 3.5, and 1.5. The first catastrophe then consists of subtracting 2.5 from  $\ln(r)$ , the second of subtracting 4.5 from  $\ln(r)$  and so on. The years in which these catastrophes were supposed to occur were selected at random from 210: we took a sequence of 3-digit random numbers from a table. Numbers greater than 210 were discarded and of the remaining numbers, the first four were taken to be catastrophe years. The catastrophes were then again imposed on the original sequence of 210 densities from Experiment 2 after we had added 0.01 to all  $\ln(r)$ 's (as in 2b). Thus, in this case any kind of density-dependence is avoided. Fig. 4 and Table 8 show that the amount of stabilization in this simulation is comparable to the amount of stabilization in Experiment 2b. Of course, the variance of  $\ln(r)$  is again increased due to the "randomization" of catastrophe sizes, but the logarithmic range is even



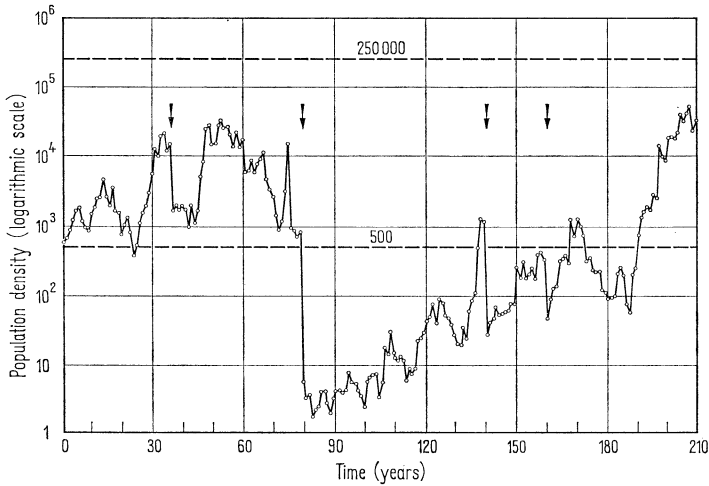


Fig. 4. Fluctuations of population density for a model population as in Experiment 2 with 10 weather factors operating when in addition random sized catastrophes may occur at random (see arrows). Further explanation is provided by the text, Section 3.5

Table 8. Comparison of fluctuation characteristics for simulation experiments with different types of “crash mechanisms” and Experiment 2 (10 factors)

	Population		
	$LR$	Av. $\ln(r)$	$\text{var}\{\ln(r)\}$
Experiment 2	15.08419	0.06720	0.24420
Experiment 2a: d.d. crashes	7.06116	0.01719	0.52285
Experiment 2b: occurrence of crash d.d.	12.07126	0.01959	2.30309
Experiment 2c: random crashes in random years	10.30400	0.01959	2.34043

better in this case. It is therefore not so essential that the probability of occurrence of catastrophes be density-dependent as might seem at first sight, although of course theoretically the probability of extinction of a population subject to catastrophes occurring at random is greater than the probability of extinction of a population where catastrophes have a small probability to occur when density is low.

One can go on inventing models and envisaging different possibilities this way. But we think to have demonstrated by now that rigorous density-dependent regulation mechanisms need not be as important as

has often been thought (*e.g.* by Nicholson, 1933, 1954, or Wilbert, 1962), and that stabilization by a great number of more or less randomly fluctuating factors on the other hand can be effective (possibly supplemented by an incidental occurrence of a limitation of the density). In addition it should be noted that in cases with a "weak" (*i.e.* only incidentally working) density-dependent device like the population shown in Fig. 2, one would need very long sequences of population counts in order to be able to infer the density-dependence from the data. In our opinion it makes little sense to theorize about quantitative relationships that cannot be measured by such data as we may obtain in practice.

N.B. From the above examples it appears that the logarithmic range is a fairly good measure of stability, but that one has to be careful about the variance of  $\ln(r)$ . This variance can be used as a comparative measure of stability only for cases where average  $\ln(r)$  has about the same value, for we have seen that by bringing average  $\ln(r)$  closer to 0 by a catastrophe mechanism one may increase the variance. In a theoretical argument where one supposes  $E\{\ln(r)\}$  to be 0, the variance can be used as well as the logarithmic range and the former then has the advantage of being more tractable mathematically than the latter (*cf.* Section 3.6).

### 3.6. *Mathematical Theory of the Number-of-Factors Model*

#### 3.6.1. Two Theorems

The numerical results obtained in the simulation experiments described in Sections 3.2 and 3.3 led us to conclude that increasing the number of factors in this model has a stabilizing influence. Whether or not this conclusion is correct was not statistically tested and sceptics might doubt whether the observed results might not be "due to chance". The problem as to how this should be tested is not well-defined, however, and anyway statistical testing would not be the proper method to handle the problem. For as we shall show in this section, our conclusion can mathematically be rigorously proved under certain assumptions that are not unreasonable and that presumably were satisfied in our simulation experiments. Instead of a simulation experiment we now carry out a conceptual experiment where we can increase the number of factors determining net reproduction by choosing factors from an infinite sequence  $F_1, F_2, \dots$  which is supposed to be at our disposal.

In Section 3.1 (formula 3.1.1) we postulated that the values of the  $i$ -th factor with probability 1 remain between two boundaries  $u_i$  and  $b_i$ . It will be necessary in what follows to state something about the whole sequence of  $F$ 's. Now if we have only a finite sequence,  $F_1, F_2, \dots, F_k$ , (say), then we could choose the smallest among the  $|b_i - u_i|$  available, call this number  $\theta_k$ , and state that

$$|b_i - u_i| \geq \theta_k \quad \text{for } i = 1, 2, \dots, k.$$

The point is, that  $\theta_k$  does not depend on  $i$ . But with an infinite sequence of  $F$ 's, we might have that  $\theta_k \rightarrow 0$  as  $k \rightarrow \infty$ : the larger we then take the number of factors, the more likely this set of factors is to contain at least one factor for which  $u_i$  and  $b_i$  differ very little. However, for factors for which  $b_i$  and  $u_i$  differ very little, we make no great error if we replace them by their expectations, such factors being nearly constant. The expectations of such nearly deterministic factors then could be incorporated into the additive constant  $y_{\min}$  in (3.1.2), since their influence on fluctuations in animal numbers is negligible. Therefore, it is reasonable to assume that the factors in the sequence we shall work with all have ranges that are not too small, and we postulate that there exists a positive number  $\theta$  such that for all  $i$

$$|b_i - u_i| \geq \theta.$$

On the other hand, it is reasonable to assume that net reproduction cannot exceed some given number (see Section 3.1). The same then must be true with respect to the influence of any one factor on  $y(t)$  in (3.1.2). We therefore postulate that there exists a number  $\sigma$  such that for all  $i$

$$|b_i - u_i| \leq \sigma.$$

The assumption that  $F_i(t)$  remains between  $b_i$  and  $u_i$  with probability 1 can now be weakened. If we only assume that

$$\text{var}\{F_i(t)\} \leq (b_i - u_i)^2 \quad \text{for all } t$$

we have

$$\text{var}\{F_i(t)\} \leq \sigma^2$$

which, together with the existence of a positive lower bound to the  $|b_i - u_i|$ , is all we shall need. We shall show that in the model defined by (3.1.2), increasing the number  $k$  of factors will bring  $\text{var}\{Y(t)\}$  closer and closer to zero. If  $E\{Y(t)\}$  then is identically zero or converges to zero fairly rapidly, this means that increasing the number of factors stabilizes numbers.

If  $F_1(t), F_2(t), \dots$  are independent, the announced theorem is very easily proved; the  $F$ 's need not even be strictly independent, as it is sufficient that they be pairwise uncorrelated.

#### Theorem 1

Let  $\{F_i(t), i = 1, 2, \dots, t = 0, 1, \dots\}$  be a stochastic process such that

$$\text{var}\{F_i(t)\} \leq \sigma^2, \quad t = 0, 1, 2, \dots \quad (3.6.1)$$

and such that for all  $t$

$$\text{cov}\{F_i(t), F_j(t)\} = 0 \quad \text{whenever } i \neq j. \quad (3.6.2)$$

Let  $\{b_i, i = 1, 2, \dots\}$  and  $\{u_i, i = 1, 2, \dots\}$  be sequences of numbers for which there exists a number  $\theta > 0$  such that

$$|b_i - u_i| \geq \theta, \quad i = 1, 2, \dots \tag{3.6.3}$$

Let  $\{Y_k(t), k = 1, 2, \dots, t = 0, 1, \dots\}$  be a stochastic process defined by

$$Y_k(t) = y_{\min} + \frac{y_{\max} - y_{\min}}{\sum_{i=1}^k |b_i - u_i|} \sum_{i=1}^k |F_i(t) - u_i| \tag{3.6.4}$$

where  $y_{\max}$  and  $y_{\min}$  are constants. Then for all  $t$ , we have

$$\lim_{k \rightarrow \infty} \text{var } Y_k(t) = 0.$$

*Proof.* For ease of writing, we put

$$y_{\max} - y_{\min} = q.$$

We have, of course,

$$\text{var}\{Y_k(t)\} \geq 0 \tag{3.6.5}$$

for all  $k$  and  $t$ . Now

$$\text{var}\{Y_k(t)\} = \frac{q^2}{\{\sum |b_i - u_i|\}^2} \sum \text{var}\{F_i(t)\}$$

according to (2.3.5) and (2.3.1), because all covariances are zero by assumption. From (3.6.1), (3.6.3) and (3.6.5) we have  $0 \leq \text{var}\{Y_k(t)\} \leq \frac{q^2 \sigma^2}{k \theta^2}$ . But  $\frac{q^2 \sigma^2}{k \theta^2} \rightarrow 0$  as  $k \rightarrow \infty$  (because  $\frac{1}{k} \rightarrow 0$ ), and this proves the theorem.

We saw in Section 3.4 that at least as far as weather factors are concerned, the assumption that all factors are pairwise uncorrelated perhaps is not realistic. In the proof of Theorem 1, we used this assumption to get rid of the covariance term in (2.3.5). Clearly it is not necessary for the validity of our proof that the covariance term be identically zero; it suffices if the covariance term in the expression for  $\text{var}\{Y_k(t)\}$  that we may write down tends to zero as  $k \rightarrow \infty$ . We shall now assume that

$$\lim_{h \rightarrow \infty} \text{cov}\{F_i(t), F_{i+h}(t)\} = 0 \quad \text{for } i = 1, 2, \dots \text{ and } t = 0, 1, \dots \tag{3.6.6}$$

This means that the sequence  $F_1(t), F_2(t), \dots$  is ordered in such a way that, starting at any place in the sequence, the covariances between the term thus chosen and subsequent terms tend to zero as we move farther to the right. Not every stochastic sequence can be ordered in this fashion. Of course, starting with  $F_1$ , we can imagine the sequence ordered so that

$$|\text{cov}(F_1, F_2)| > |\text{cov}(F_1, F_3)| > |\text{cov}(F_1, F_4)| > \dots$$

but in this ordering it is not necessarily true that also

$$|\text{cov}(F_2, F_3)| > |\text{cov}(F_2, F_4)| > |\text{cov}(F_2, F_5)| > \dots$$

and neither is it necessarily true that  $\text{cov}(F_1, F_k) \rightarrow 0$  as  $k \rightarrow \infty$ . However, imagining an infinite sequence of ecological factors, it seems reasonable to assume that any factor will be significantly correlated with only a finite number of other factors and in our opinion the condition (3.6.6) is not very restrictive. Moreover, one might state other conditions having the same effect. A theorem like the following one must be considered as a line of thought rather than as a unique truth.

*Theorem 2*

Let  $\{F_i(t)\}$  and  $\{Y_k(t)\}$  be as in Theorem 1, except that instead of (3.6.2) we have (3.6.6).

Then  $\lim_{k \rightarrow \infty} \text{var}\{Y_k(t)\} = 0$  for  $t = 0, 1, \dots$

*Proof.* From (2.3.5), (2.3.1), and (2.3.2) we have

$$\text{var}\{Y_k(t)\} = \frac{q^2}{\{\sum |b_i - u_i|\}^2} \left[ \sum_{i=1}^k \text{var}\{F_i(t)\} + 2 \sum_{i=1}^{k-1} \sum_{j=i+1}^k \text{cov}\{F_i(t), F_j(t)\} \right].$$

From (2.3.4) and (3.6.1) it follows that for all  $i$ ,  $|\text{cov}\{F_i(t), F_j(t)\}| \leq \sigma^2$  but we have to deal with  $2 \cdot \frac{1}{2} k(k-1)$  covariance terms whose sum therefore can be of the order of  $k^2$ , whereas the sum of the variances is of the order  $k$ , a fact which we used in the proof of Theorem 1. We shall now use the fact that if  $k$  is large, a great number among the  $k(k-1)$  covariances is vanishingly small by assumption. According to (3.6.6) corresponding to any positive  $\epsilon$ , however small, we can find an integer  $g$  (which may be large) such that  $|\text{cov}\{F_i(t), F_j(t)\}| < \epsilon$  whenever  $j - i > g$ . Having found such a  $g$ , let us assume that  $k > g$  and let us write for convenience

$$\text{cov}\{F_i(t), F_j(t)\} = c_{ij}.$$

For  $1 < g < k$  we may split the sum of covariances thus:

$$\sum_{i=1}^{k-1} \sum_{j=i+1}^k c_{ij} = \sum_{i=1}^{k-g-1} \sum_{j=i+1}^{i+g} c_{ij} + \sum_{i=1}^{k-g-1} \sum_{j=i+g+1}^k c_{ij} + \sum_{i=k-g}^{k-1} \sum_{j=i+1}^k c_{ij}$$

where for the  $c_{ij}$  in the first term and in the last term,  $j - i \leq g$ , whereas in the middle term we have  $j - i > g$ . We are not sure that the  $c_{ij}$  in the first and last term are  $< \epsilon$  in absolute value, but we know them to be less than  $\sigma^2$  in absolute value. In the middle term, because  $j - i > g$ , all  $c_{ij}$  are less than  $\epsilon$  in absolute value. We now wish to know how many  $c_{ij}$  this term contains. We have

$$\begin{aligned} \sum_{i=1}^{k-g-1} \sum_{j=i+g+1}^k c_{ij} &= c_{1,g+2} + c_{1,g+3} + \dots + c_{1,k} && (k-g-1 \text{ terms}) \\ &+ c_{2,g+3} + \dots + c_{2,k} && (k-g-2 \text{ terms}) \\ &+ \dots + c_{k-g-1,k} && (1 \text{ term}) \end{aligned}$$

hence this sum contains  $1 + 2 + \dots + (k - g - 1)$  terms  $= \frac{1}{2}(k - g - 1)(k - g)$  terms. As there are in all  $k(k - 1)$  covariances, it follows that  $2 \cdot \frac{1}{2}(k - g - 1)(k - g)$  among these are less than  $\varepsilon$  in absolute value and the remaining  $k(k - 1) - (k - g - 1)(k - g)$  terms  $= g(2k - g - 1)$  terms are less than  $\sigma^2$  in absolute value, but not necessarily less than  $\varepsilon$ .

We have, then,

$$0 \leq \text{var}\{Y_k(t)\} \leq \frac{q^2}{k^2 \theta^2} [k\sigma^2 + g(2k - g - 1)\sigma^2 + (k - g - 1)(k - g)\varepsilon] \\ = \frac{q^2}{\theta^2} \left[ \left( \frac{1 + 2g}{k} - \frac{g(g + 1)}{k^2} \right) \sigma^2 + \left( 1 - \frac{g + 1}{k} \right) \left( 1 - \frac{g}{k} \right) \varepsilon \right].$$

We can make this as small as we please by taking  $g$  and  $k$  large enough. Indeed, if  $k > g$ , then  $\left| 1 - \frac{g + 1}{k} \right| < 1$  and  $\left| 1 - \frac{g}{k} \right| < 1$ , hence  $\left| \left( 1 - \frac{g + 1}{k} \right) \left( 1 - \frac{g}{k} \right) \varepsilon \right| < \varepsilon$ . Suppose we wish  $\text{var}\{Y_k(t)\} \leq \delta$ . First, we choose  $g$  so large that  $|\text{cov}\{F_i(t), F_j(t)\}| < \theta^2 \delta / 2q^2$  if  $j - i > g$ . According to the above argument, this can always be done. Then we keep  $g$  fixed and choose  $k$  so large (*i.e.* larger still than  $g$ ) that

$$\left\{ \frac{1 + 2g}{k} - \frac{g(g + 1)}{k^2} \right\} \sigma^2 < \theta^2 \delta / 2q^2.$$

With such a  $k$ , we have  $\left| \left( 1 - \frac{g + 1}{k} \right) \left( 1 - \frac{g}{k} \right) \right| < 1$ , hence according to the above inequality, with  $\varepsilon = \theta^2 \delta / 2q^2$ :

$$0 \leq \text{var}\{Y_k(t)\} < \frac{q^2}{\theta^2} \left[ \frac{\theta^2 \delta}{2q^2} + \frac{\theta^2 \delta}{2q^2} \right] = \delta.$$

This proves the theorem.

What these theorems amount to is that under the conditions assumed, the greater the number of factors determining net reproduction in our model, the more “deterministically” the model behaves, since the Bienaymé-Chebyshev inequality (see Section 2.4) implies that the smaller the variance of  $Y = \ln(R)$ , the closer  $Y$  may be expected to be to its expectation. If this expectation is zero or nearly so, population density then in most cases will not change by more than a small amount from one generation to the next. In fact, it suffices to require that  $E\{Y_k(t)\} \rightarrow 0$  when  $k \rightarrow \infty$ : *i.e.* that whereas trends may occur when only a few factors influence net reproduction, when the number of factors increases they will more and more tend to compensate each other so that their total result on  $\ln\{R(t)\}$  is about zero on the average.

### 3.6.2. Additional Remarks

The model defined by (3.1.2) and (3.6.4) is, of course, rather a special one. The theorems stated, however, apply to this model only. It is a mere conjecture that similar results will hold for other types of model as

well. It should nevertheless be noted that the model perhaps is not so restrictive as may appear when the factors  $F$  are taken to be environmental factors such as they are actually observed, like air temperature, evaporation and so on. It might be that the additive linear relationship (3.6.4) holds when the factor values have been transformed in some way. In general, if  $R(t)$  is influenced by measurable factors  $G_1, G_2, \dots, G_k$ , we might have a relationship of the form

$$Y(t) = \ln\{R(t)\} = y_{\min} + \varphi\{G_1(t), G_2(t), \dots, G_k(t)\}$$

where  $\varphi(\cdot)$  is some function, *i.e.*, the regression function of  $Y(t)$  on  $G_1(t), G_2(t), \dots, G_k(t)$ . In all cases where this relationship can be put in the form

$$\varphi(G_1, G_2, \dots, G_k) = q \cdot \frac{\sum_{i=1}^k |\varphi_i(G_i) - u_i|}{\sum_{i=1}^k |b_i - u_i|}$$

we can put  $\varphi_i(G_i) = F_i$ ,  $q = y_{\max} - y_{\min}$ , and apply the above theory. The  $G_i$  (or  $F_i$ ) may even depend on population density  $N$ , although it should be noted that if  $Y(t)$  depends on  $N(t)$ , the  $Y$ 's will be serially correlated and this may have some bearing on the stability of the fluctuations in the density which for simplicity of the argument we have not gone into here (*cf.* Reddingius, 1968, Part 2). The model breaks down, of course, if the influences of the various factors on the logarithm of net reproduction are not additive and if the factors cannot be transformed in some way to become additive.

#### 4. Stabilization by Migration and by Age Differences

##### 4.1. The Model

It is assumed that the population consists of 9 subpopulations. Each subpopulation consists of animals in  $m+1$  age classes numbered 0, 1, 2, ...,  $m$ . Let  $n_{\alpha j}(t)$  ( $\alpha=0, 1, \dots, m$ ;  $j=1, 2, \dots, 9$ ) denote the number (or density) of animals in the  $\alpha$ -th age class in the  $j$ -th subpopulation present at time  $t$ . Let the time unit be denoted by "a year". A year consists of  $r$  "seasons". In any of these "seasons" we may have:

- (1) a reproduction period;
- (2) an emigration period, and
- (3) an immigration period.

We consider only the case with 1 season; results of a simulation experiment with 3 seasons and no migration are briefly discussed in Reddingius (1968), Section 5.3. It is assumed that during the repro-

ductive period the animals stay in the subpopulations where they are, and that individuals do not reproduce during migration.

It is assumed that during the reproduction period:

(a) an animal in age class  $a$  in subpopulation  $j$  will produce  $f_{aj}$  offspring (which at the beginning of the next unit of time will be in age class 0). The total number of offspring in the  $j$ -th subpopulation will be

$$\sum_{a=0}^m n_{aj}(t) f_{aj}.$$

Of course, some of the  $f_{aj}$  may be zero, e.g.  $f_{0j}$  or  $f_{mj}$ .

(b) of all animals of age class  $a$ ,  $j$ -th subpopulation, a fraction  $s_{aj}$  will survive until the end of the reproduction period; where

(aa)  $f_{aj}$  is a realization of a random variable  $F_{aj}$  such that  $E(F_{aj}) = \varphi_{aj}$ ,  $\text{var}(F_{aj}) = \theta_{aj}^2$ , and  $\ln(F_{aj})$  is normally distributed;

(bb)  $s_{aj}$  is a realization of a random variable  $S_{aj}$  with  $E(S_{aj}) = \sigma_{aj}$ ,  $\text{var}(S_{aj}) = \psi_{aj}^2$ , and  $\ln(S_{aj})$  is normally distributed.

This part of the model is a stochastic version of the model proposed by Leslie (1945). It is postulated that  $S_{mj} = 0$  with probability 1 for all  $j$ , i.e. no animal can grow older than  $m$  years.

During the emigration period:

(c) an animal of age  $a$  in subpopulation  $j$  has a probability  $p_{aj}$  of emigrating. To determine the numbers in the different age classes in the different subpopulations that do and do not emigrate, the normal approximation is used, i.e. the number emigrating is assumed to be normally distributed with expectation  $s_{aj} n_{aj}(t) p_{aj}$  and variance  $s_{aj} n_{aj}(t) p_{aj}(1 - p_{aj})$ . Let  $L_{aj}$  denote the fraction of all animals in age class  $a$  and subpopulation  $j$  that emigrate. These emigrating animals together form an "emigration pool". The total number of animals of age class  $a$  in this pool is

$$K_a = \sum_{j=1}^9 L_{aj} S_{aj} N_{aj}(t)$$

if  $a > 0$ , and

$$K_0 = \sum_{j=1}^9 L_{0j} \sum_{a=0}^m F_{aj} N_{aj}(t).$$

From this pool, a part immigrates into each of the 9 subpopulations. This is accomplished as follows: first, the number  $k_a$  in the pool is divided into 9 portions, the  $i$ -th portion receiving  $g_{ai} k_a$  animals, with  $\sum_{i=1}^9 g_{ai} = 1$  for all  $a$ . An animal in the  $i$ -th portion may immigrate into the  $i$ -th subpopulation only, with probability  $q_{ai}$ , i.e. the probability



that it immigrates into the  $j$ -th subpopulation is 0 if  $j \neq i$ , and the probability that it disappears without immigrating is  $1 - g_{ai}$ . The effects of migration are thus that a certain "mortality" is added to the mortality already occurring during the reproduction period, and that part of the animals is redistributed over the subpopulations.

The  $g_{ai}$  are deterministic constants that are determined in a way to be described below. Let  $I_{aj}$  denote the fraction from the  $j$ -th portion of the emigration pool that immigrates into the  $j$ -th subpopulation. In computing realizations of this fraction, again the normal approximation is used.

After the immigration period, the year is over, and all animals in age class  $a$  pass to age class  $a + 1$  ( $a = 0, 1, \dots, m - 1$ ). The newly born ones form the age class 0. We have, then,

$$\begin{aligned} N_{0j}(t+1) &= \sum_{a=0}^m N_{aj}(t) F_{aj}(1 - L_{0j}) + g_{0j} I_{0j} K_0 \\ &= \sum_{a=0}^m (1 - L_{0j} + g_{0j} L_{0j} I_{0j}) F_{aj} N_{aj}(t) \\ &\quad + \sum_{i \neq j} g_{0j} I_{0j} \sum_{a=1}^m L_{ai} F_{ai} N_{ai}(t). \end{aligned} \quad (4.1.1)$$

$$\begin{aligned} N_{a+1,j}(t+1) &= S_{aj}(1 - L_{aj}) N_{aj}(t) + g_{aj} I_{aj} K_a \\ &= S_{aj}(1 - L_{aj} + g_{aj} I_{aj} L_{aj}) N_{aj}(t) \\ &\quad + g_{aj} I_{aj} \sum_{i \neq j} S_{ai} N_{ai}(t) \quad \text{for } a = 0, 1, \dots, m - 1. \end{aligned} \quad (4.1.2)$$

The whole sequence of events is illustrated in Fig. 5.

We worked with two versions of the model. In the first version, migration was supposed to be density-independent. The  $p_{aj}$ ,  $g_{aj}$  and  $q_{aj}$  are given constants. The  $g_{aj}$  in fact were computed from given weighing factors  $w_{aj}$  as follows:

$$g_{aj} = \frac{w_{aj}}{\sum_{j=1}^m w_{aj}}.$$

In the second version, migration was supposed to be density-dependent. If  $n_{aj}$  denoted the number of age class  $a$  in the  $j$ -th subpopulation before emigration, the emigration probabilities  $p_{aj}$  depend on  $n_{aj}$  according to the formula

$$p_{aj} = \frac{\pi_{aj} n_{aj}}{n_{aj} + \tau_{aj} + \chi_j}$$

where  $\pi_{aj}$ ,  $\tau_{aj}$  and  $\chi_j$  are given constants. These  $p_{aj}$  are increasing functions of  $n_{aj}$ ; we have  $p_{aj} = 0$  if  $n_{aj} = 0$  and as  $n_{aj}$  increases,  $p_{aj}$  ap-

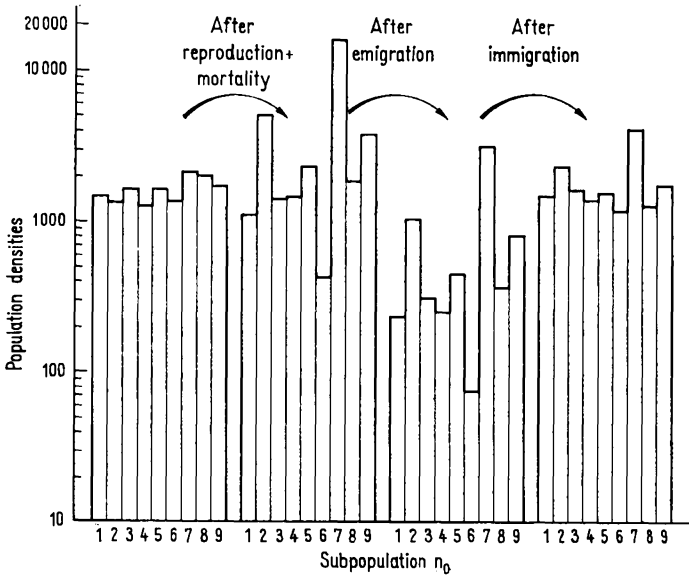


Fig. 5. Illustrating the dynamics of a model population consisting of 9 subpopulations where migration between subpopulations occurs after the reproductive season. The model is described in the text, Section 4.1

proaches the limit  $\pi_{aj}$ . As during migration some animals disappear, this amounts to introducing some density-dependent mortality. Moreover, the largest subpopulations will contribute most to the "emigration pool". Immigration is made density-dependent by varying the  $g_{aj}$ ; the  $g_{aj}$  are taken to be given constants as before.

The  $g_{aj}$  are determined by the formula

$$g_{aj} = \frac{w_{aj}/(n_{aj} + 1)}{\sum_{j=1}^9 w_{aj}/(n_{aj} + 1)}$$

where  $n_{aj}$  now denotes the number present in age class  $a$  in subpopulation  $j$  after emigration, but before immigration. The fraction a given subpopulation will receive from the emigration pool is inversely proportional to its relative density. Note that in the density-dependent version both emigration *and* immigration are density-dependent, by which arrangement the subpopulations are prevented to deviate much from each other in density.

This model was simulated on the Electrologica X1 computer of the Central Computing Institute of the University of Leiden.

#### 4.2. Types of Experiments

The computer program provided for a great many possible variations in number and values of the parameters. Only a few comparatively simple cases were finally used. We shall denote the different experiments here by means of a short-hand code.

##### *NMSP (No Migration Similar Populations)*

Subpopulations consist of 1 age class only. The minimum number of age classes the computer program presupposed was 2, but we provided for this by putting

$$\varphi_{1j} = 0.00001, \quad \theta_{1j} = 0.00001, \quad \sigma_{1j} = 0.00001, \quad \psi_{1j} = 0.00001.$$

The contribution of the second age class (1) then is negligible. The 9 subpopulations were isolated: no migration occurred. All subpopulations had the same parameters which were as follows:

$$\varphi_{0j} = 1, \quad \theta_{0j} = 0.677, \quad j = 1, 2, \dots, 9.$$

Simulations of this model serve as a kind of "control experiment": in this case there is no spreading of risk by heterogeneity and dispersal in space or by differing in age.

##### *DIMSP (Density Independent Migration Similar Populations)*

Again, subpopulations consist of 1 age class only, but now density-independent migration occurs. The subpopulations are otherwise wholly similar to those in *NMSP*. We put

$$\begin{aligned} \varphi_{0j} &= 2, & \theta_{0j} &= 1.354 \\ p_{0j} &= 0.8, & w_{0j} &= 1, & q_{0j} &= 0.375 \end{aligned}$$

for  $j = 1, 2, \dots, 9$ .

##### *DIMDP (Density Independent Migration Different Populations)*

If a population consists of several subpopulations, circumstances will not be exactly similar in all subpopulations. In the present model, all subpopulations consist of 1 age class as before, but there are 3 groups of subpopulations with different parameters.

For  $j = 1, 2, 3$ , we put

$$\varphi_{0j} = 1.5, \quad \theta_{0j} = 1.0155, \quad p_{0j} = 0.8, \quad w_{0j} = 1.5, \quad q_{0j} = 0.583.$$

For  $j = 4, 5, 6$  we put

$$\varphi_{0j} = 2.0, \quad \theta_{0j} = 1.354, \quad p_{0j} = 0.8, \quad w_{0j} = 2.0, \quad q_{0j} = 0.376$$

and for  $j = 7, 8, 9$  we put

$$\varphi_{0j} = 2.5, \quad \theta_{0j} = 1.6925, \quad p_{0j} = 0.8, \quad w_{0j} = 2.5, \quad q_{0j} = 0.2505.$$

The parameters were in general chosen in such a way that the population could be supposed to remain approximately constant on the average, and such that the ratio of standard deviation to expectation for  $F_{a,j}$  is about constant.

To illustrate the first idea mentioned, let us compute with expectations and probabilities as if they were exact values and fractions. Suppose all subpopulations contain  $n$  animals. Then in subpopulations 1, 2, and 3 there are produced  $1.5n$  new individuals in each of them;  $0.8 \times 1.5n = 1.2n$  are emigrating, so there are  $0.3n$  individuals left. In each of the subpopulations 4, 5, and 6 there are produced  $2n$  individuals of which  $1.6n$  are emigrating, leaving  $0.4n$ . In subpopulations 7, 8, and 9,  $2.5n$  new individuals are produced,  $2n$  emigrate, and  $0.5n$  are left.

In total, there are  $(1.2 + 1.6 + 2) \times 3n = 14.4n$  emigrating individuals from 9 subpopulations.

$$\begin{aligned} g_{0j} &= \frac{1.5}{18} = 0.083, & j = 1, 2, 3 \\ &= \frac{2}{18} = 0.1111, & j = 4, 5, 6 \\ &= \frac{2.5}{18} = 0.1389, & j = 7, 8, 9 \end{aligned}$$

and

$$\begin{aligned} g_{0j} \times 14.4n &= 1.2n, & j = 1, 2, 3 \\ g_{0j} \times 14.4n &= 1.6n, & j = 4, 5, 6 \\ g_{0j} \times 14.4n &= 2.0n, & j = 7, 8, 9. \end{aligned}$$

There are immigrating

$$\begin{aligned} 0.583 \times 1.2n &= 0.70n \text{ in each of subpopulations 1, 2, 3;} \\ 0.376 \times 1.6n &= 0.60n \text{ in each of subpopulations 4, 5, 6 and} \\ 0.2505 \times 2n &= 0.50n \text{ in each of subpopulations 7, 8, 9} \end{aligned}$$

and all subpopulations will contain  $n$  individuals as before.

#### *DDMDP (Density Dependent Migration Different Populations)*

The parameters  $\varphi_{0j}$ , and  $\theta_{0j}$  are the same as in *DIMDP*, but the "migration parameters" are as follows:

$$\begin{aligned} \pi_{0j} &= 0.95 \\ \tau_{0j} &= 28.00 \\ \chi_j &= 1.25 \end{aligned}$$

for  $j = 1, 2, \dots, 9$ , and the  $q_{0j}$  and  $w_{0j}$  were the same as in *DIMDP*. In this case, the  $p_{0j}$  are 0.8 when  $n_{0j} = 1,500$ , so if the density in the subpopulations is about 1,500, the population is expected to remain approximately constant. We shall refer to 1,500 as the "equilibrium density".  $p_{0j}$  will be 0.9 when  $n_{0j} = 5,062.5$  and 0.10 when  $n_{0j} = 33.08$ .

*NMHP (No Migration Heterogeneous Populations)*

The subpopulations have 3 age classes; there is no migration and all subpopulations have the same parameters:

$$\begin{aligned} \varphi_{0j} &= 0.11 & \theta_{0j} &= 0.067 \\ \varphi_{1j} &= 4.0 & \theta_{1j} &= 2.708 \\ \varphi_{2j} &= 5.0 & \theta_{2j} &= 3.0 \\ \sigma_{0j} &= 0.21 & \psi_{0j} &= 0.05 \\ \sigma_{1j} &= 0.10 & \psi_{1j} &= 0.05. \end{aligned}$$

The greatest characteristic root of the expectation matrix

$$\begin{pmatrix} \varphi_{0j} & \varphi_{1j} & \varphi_{2j} \\ \sigma_{0j} & 0 & 0 \\ 0 & \sigma_{1j} & 0 \end{pmatrix} = \begin{pmatrix} 0.11 & 4.0 & 5.0 \\ 0.21 & 0 & 0 \\ 0 & 0.10 & 0 \end{pmatrix}$$

is  $\lambda = 1.02723$ , a corresponding characteristic vector being

$$\begin{pmatrix} n_0 \\ n_1 \\ n_2 \end{pmatrix} = \begin{pmatrix} 0.8168 \\ 0.1670 \\ 0.0162 \end{pmatrix}.$$

That is, if the subpopulations were deterministic, and if the age distribution were stable, 81.68% of the animals would be in age class 0, 16.7% in age class 1 and 1.62% in age class 2, and the population size would be multiplied by a factor 1.02723 each year (*cf.* Leslie, 1945; in stochastic simulation experiments such as these, the populations as a rule subsist for a longer time when the "expected multiplication factor" is somewhat larger than 1).

*DIMHP (Density Independent Migration Heterogeneous Populations)*

Again, there are 3 age classes; in other respects, the model is similar to *DIMDP*.

$$\left. \begin{aligned} \varphi_{0j} &= 0.088 & \theta_{0j} &= 0.0536 \\ \varphi_{1j} &= 3.2 & \theta_{1j} &= 2.1664 \\ \varphi_{2j} &= 4.0 & \theta_{2j} &= 2.4 \\ \sigma_{0j} &= 0.168 & \psi_{0j} &= 0.05 \\ \sigma_{1j} &= 0.08 & \psi_{1j} &= 0.05 \end{aligned} \right\} j = 1, 2, 3$$

$$\left. \begin{aligned} \varphi_{0j} &= 0.11 & \theta_{0j} &= 0.067 \\ \varphi_{1j} &= 4.0 & \theta_{1j} &= 2.708 \\ \varphi_{2j} &= 5.0 & \theta_{2j} &= 3.0 \\ \sigma_{0j} &= 0.21 & \psi_{0j} &= 0.05 \\ \sigma_{1j} &= 0.10 & \psi_{1j} &= 0.05 \end{aligned} \right\} \begin{array}{l} j = 4, 5, 6 \\ \text{(same as in } NMHP) \end{array}$$

$$\left. \begin{aligned} \varphi_{0j} &= 0.1375 & \theta_{0j} &= 0.08375 \\ \varphi_{1j} &= 5.0 & \theta_{1j} &= 3.385 \\ \varphi_{2j} &= 6.25 & \theta_{2j} &= 3.75 \\ \sigma_{0j} &= 0.2625 & \psi_{0j} &= 0.05 \\ \sigma_{1j} &= 0.125 & \psi_{1j} &= 0.05 \end{aligned} \right\} j = 7, 8, 9$$

$$\begin{aligned} p_{aj} &= 0.8; & a &= 0, 1, 2; & j &= 1, 2, \dots, 9 \\ w_{aj} &= 1; & a &= 0, 1, 2; & j &= 1, 2, \dots, 9 \\ q_{aj} &= 0.93; & a &= 0, 1, 2; & j &= 1, 2, \dots, 9. \end{aligned}$$

*DDMHP (Density Dependent Migration Heterogeneous Populations)*

The parameters are similar as those in *DIMHP*, except that

$$\begin{aligned} \pi_{aj} &= 0.8; & a &= 0, 1, 2; & j &= 1, 2, \dots, 9 \\ \tau_{aj} &= 400; & a &= 0, 1, 2; & j &= 1, 2, \dots, 9 \\ \chi_{aj} &= 100; & a &= 0, 1, 2; & j &= 1, 2, \dots, 9 \\ w_{aj} &= 1; & a &= 0, 1, 2; & j &= 1, 2, \dots, 9. \end{aligned}$$

The subpopulations all started at time  $t=0$  with 1,500 animals. For *NMHP*, *DIMHP* and *DDMHP* the numbers in age classes 0, 1, and 2 were 1,220, 255, and 25, which up to rounding-off differences is a stable age distribution for the populations in *NMHP*.

4.3. Results

In what follows, the “total population density” will be the average of the densities of the 9 subpopulations. That is, we shall suppose each subpopulation to occupy an area of unit size, so that the total population occupies an area of 9 units. Note that the net reproduction of the total population is *not* the average of the net reproductions of the 9 subpopulations:

$$R(t) = \frac{\sum_{j=1}^9 \sum_{a=1}^m N_{aj}(t+1)}{\sum_{j=1}^9 \sum_{a=1}^m N_{aj}(t)} \neq \frac{1}{9} \sum_{j=1}^9 \frac{\sum_{a=1}^m N_{aj}(t+1)}{\sum_{a=1}^m N_{aj}(t)} \neq \frac{1}{9} \sum_{j=1}^9 \frac{1}{m} \sum_{a=1}^m \frac{N_{aj}(t+1)}{N_{aj}(t)}.$$

The simplest model considered is *NMSP*. It can therefore be used as a basis for comparison: it symbolizes a population without any means of spreading the risk of becoming extinct (Den Boer, 1968).

In Fig. 6 fluctuations over the first 60 years in the total population densities are shown for *NMSP*, *DIMSP*, *DIMDP*, and *DDMDP*, *i.e.*

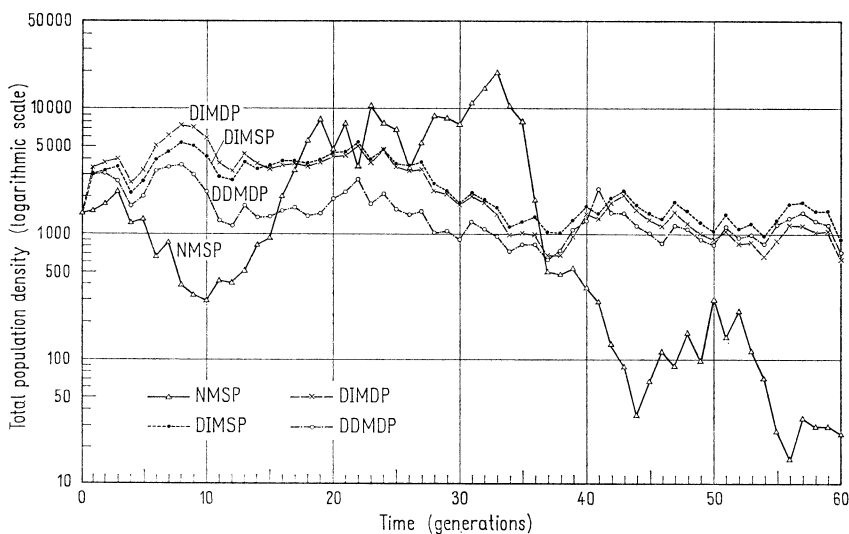


Fig. 6. Fluctuations in the density of 4 model populations consisting of one age class. See Section 4.3

the populations with only one age class. It is obvious that *NMSP* is “less stable” than the other populations. The figure furthermore suggests that *DIMSP*, *DIMDP* and *DDMDP* do not differ very much (*DDMDP* might be somewhat more stable than the other two migration

Table 9. *Logarithmic range (LR) = natural logarithm of quotient of highest density/smallest density for years 0—75 inclusive*

Sub-population	Model						
	<i>NMSP</i>	<i>DIMSP</i>	<i>DIMDP</i>	<i>DDMDP</i>	<i>NMHP</i>	<i>DIMHP</i>	<i>DDMHP</i>
1	∞	3.82625	4.58395	3.43721	2.96156	2.76481	3.78338
2	∞	4.35028	5.10169	3.46574	2.98523	2.59197	3.23301
3	∞	3.80333	4.37827	2.86790	4.22018	2.50300	3.10513
4	∞	3.45632	4.00369	2.75366	2.62886	2.08105	2.94270
5	7.64683	3.99212	4.65014	3.86493	4.42184	3.07865	2.57938
6	∞	3.74029	4.56851	3.58906	4.79062	2.37422	3.40842
7	∞	4.82268	5.62618	3.54385	3.63401	2.49428	2.85023
8	∞	3.80677	4.36055	2.93916	4.73771	2.44746	3.03356
9	4.52526	6.82785	5.18178	3.71113	4.73989	2.89232	2.46720
Total pop.	5.31812	2.36555	3.60321	1.76130	2.11182	1.52141	1.76689
Av. 1—9	∞	4.29177	4.71720	3.35252	3.90211	2.58087	3.04478

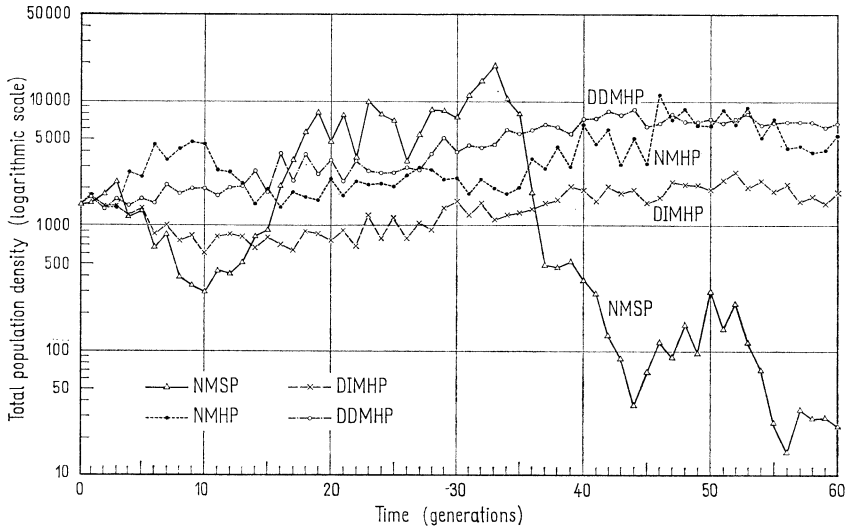


Fig. 7. Fluctuations in the density of 4 model populations, one of which consisting of one age class and three consisting of 3 age classes. See Section 4.3

models: Table 9 and 10, but see also Table 11). In Fig. 7 *NMSP* is compared to the models with 3 age classes: *NMHP*, *DIMHP* and *DDMHP*. Fluctuations in *NMSP* are far more violent than those in even *NMHP*. A difference between *DIMHP* and *DDMHP* is not very obvious from Fig. 7 just as there did not appear to be much difference between *DIMDP* and *DDMDP* from Fig. 6 (in this case *DIMHP* might

Table 10. Average  $\ln(\text{net reproduction})$  for total population, years 0–75 inclusive

	Model						
	<i>NMSP</i>	<i>DIMSP</i>	<i>DIMDP</i>	<i>DDMDP</i>	<i>NMHP</i>	<i>DIMHP</i>	<i>DDMHP</i>
Av. $\ln(r)$	-0.06721	-0.01443	-0.02420	-0.00498	+0.00432	-0.00553	+0.01945

Table 11. Mean square deviation of  $\ln(\text{net reproduction})$  from 0, and variance of  $\ln(\text{net reproduction})$  for total population, years 0–75 inclusive

	Model						
	<i>NMSP</i>	<i>DIMSP</i>	<i>DIMDP</i>	<i>DDMDP</i>	<i>NMHP</i>	<i>DIMHP</i>	<i>DDMHP</i>
av. $\{\ln(r)\}^2$	0.42149	0.06218	0.06832	0.07782	0.11283	0.05383	0.04000
var $\{\ln(r)\}$	0.41698	0.06197	0.06773	0.07776	0.11273	0.05367	0.03962



be somewhat more stable than *DDMHP*: Table 9 and 10, but see also Table 11).

Table 9 shows the different values obtained for the logarithmic range. The differences between columns are fairly well represented by the data for the total population, and they are more conspicuous than the differences within columns. Table 10 shows average  $\ln$  (net reproduction) for the total populations. This is very close to 0 for *DDMDP*, *NMHP* and *DIMHP*. The value of *DDMHP* is too large in comparison to the others. This might be the result of the "density-dependence" because the initial density 1,500 is still below the "equilibrium density", hence the "emigration mortality" has been on the average "too small" in comparison to the other models. This resulted in some upward trend. The variances of  $\ln$  (net reproduction) for the total populations are given in Table 11 together with the time averages of the squares of  $\ln$  (net reproduction), being the mean square deviation of  $\ln$  (net reproduction) from zero. The differences between these two statistics are small in all cases. *DIMSP*, *DIMDP* and *DDMDP* do not differ much from each other as regards the variances, but have much smaller variances than *NMSP*, *DIMHP* and *DDMHP* have smaller variances than *NMHP*. Finally, *NMHP* has a smaller variance than *NMSP*. This suggests that both heterogeneity within the population and migration — whether density-dependent or not — between different parts of a heterogeneous area increase stability of the fluctuations in the density of the total population. *DDMHP* according to this variance criterion does somewhat better than all the others, but not so according to the criteria in

Table 12. Number of generations before population density crossed one of the limits 4,500 ( $3 \times$  initial density) or 500 ( $\frac{1}{3} \times$  initial density) for the first time. If 4,500 was passed, this is marked with a +; if 500 was passed, this is marked with a -

Sub-population	Model						
	<i>NMSP</i>	<i>DIMSP</i>	<i>DIMDP</i>	<i>DDMDP</i>	<i>NMHP</i>	<i>DIMHP</i>	<i>DDMHP</i>
1	5-	12+	12+	14-	4-	10-	18+
2	2-	2+	2+	2+	17+	10-	33+
3	2-	10+	10+	22+	23-	9-	31+
4	3-	5+	5+	12-	22-	15-	22+
5	8-	6+	6+	6+	11-	7-	35+
6	2-	2-	2-	2-	28+	19-	16+
7	3+	1+	1+	1+	4+	9-	16+
8	4-	1+	1+	1+	20-	47-	16+
9	8-	3+	3+	6+	5-	8-	14-
Total pop.	8-	7+	6+	> 75	9+	> 75	29+
Av. 1-9	4.3	4.7	4.7	7.3	14.9	14.9	22.8

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Table 10 and 11. Finally, in Table 12 first passage times for either 4,500 ( $3 \times$  initial density) or 500 ( $\frac{1}{3} \times$  initial density) are given. The longest passage times (no passage) for total populations occur in *DDMDP* and *DIMHP*. The differences between *NMSP*, *DIMSP*, *DIMDP* and *NMHP* are less obvious than with the preceding criteria. With wider limits the differences might have been more obvious.

From Tables 9—11 it will be evident that the spreading of risk brought about by exchange between subpopulations and by heterogeneity according to age within populations may contribute to an important degree to a stabilization of fluctuations in animal numbers. Moreover, a density-dependent exchange under specified conditions will hardly do better than a density-independent exchange. An improvement by density-dependent exchange may especially occur when mortality during migration is also density-dependent. This may happen *e.g.* when individuals grown up in a dense population have a decreased viability. Note that the type of “density-dependence” that we have used in this model is not a “governing” one, *i.e.* it does not operate as a negative feedback forcing population density towards its equilibrium value.

#### 4.4. Remarks on the Migration-and-Age Classes-Model

The model used in this chapter, crudely simple as it may be from a biological point of view, does not lend itself as easily to a general mathematical treatment as the model discussed in Chapter 3. Only a few sketchy remarks will be made here. We think that the numerical results presented in the preceding section provide a nice illustration of the theoretical ideas set forth by Den Boer (1968), but we are aware of the fact that this illustration has resulted from an appropriate choice of the values of the parameters, which was, in fact, attained after some trial and error. Because there are so many kinds of parameters involved, it is difficult to construct an ordered sequence of models. If one increases the number of age classes, or the number of subpopulations, one increases the degree of complexity of the model. A new age class is not simply added to the age classes already present; one has to do something about the expectations and variances of the *F*'s and *S*-es of all “new” age classes. Increasing the number of age classes, or the number of subpopulations, is therefore not fully comparable to increasing the number of “factors” in the model of Chapter 3.

From (4.1.1) and (4.1.2) it is apparent that both addition and multiplication are involved in determining population density at time  $t + 1$  from population density at time  $t$ . The present model is therefore not easily “linearized” by taking logarithms. The best way to handle this model would perhaps be to consider the population as a vector whose com-

ponents represent the density of the various age classes and subpopulations. For example,  $N_{aj}(t)$  could be conceived as the  $(jm + a)$ -th element of the population vector  $N(t)$ . According to (4.1.1) and (4.1.2), the  $N_{aj}(t+1)$  are linear combinations of the  $N_{aj}(t)$ , and therefore (4.1.1) and (4.1.2) could be written as

$$N(t+1) = R(t) N(t)$$

where  $R(t)$  is a matrix whose elements are random variables  $R_{11}$ ,  $R_{12}$ , ...,  $R_{ij}$ , ...,  $R_{mh}$ ,  $R_{mh}$  if there are  $h$  subpopulations. The  $R_{ij}$  could be defined in terms of the  $F_{aj}$ ,  $S_{aj}$ ,  $L_{aj}$ ,  $g_{aj}$  and  $I_{aj}$ . We would thus obtain a generalized stochastic version of the matrix model that is often used in population mathematics (Leslie, 1945, 1948; Skellam, 1966). Age and variation in time and space are represented here by discrete variables, whereas in reality they can vary continuously. Similar models in terms of continuously varying quantities might be set up, but by taking the number of classes large enough and the time unit small enough, the discrete model could provide as close an approximation to the continuous one as is desired. With using digital computers, such approximations are nearly always necessary. A further biomathematical investigation of this sort of complex models might yield interesting results (see also *e.g.* Holgate, 1967), but we think we have sufficiently well shown that complex models in principle may show a greater stability than less complex ones.

The idea that population stability in nature results from a complicated interplay between populational and environmental factors anyway cannot be mathematically proved, but is a hypothesis that ought to be tested by observation. This testing does not require as sophisticated mathematics as a complete theoretical survey of a certain class of models would employ.

## 5. Discussion

We should like to generalize a remark that we made earlier with respect to a mathematical theorem: the results obtained are to be seen as a line of thought rather than as a set of unique truths. We have illustrated the hypothesis put forward by Den Boer (1968) stating that the complexity of a natural situation can bring about a stabilization of animal numbers. By the very nature of such a hypothesis, its truth can never be rigorously proved, for of course one could construct a model of a complex situation in which animal numbers were not stable. However, we are convinced that our examples show that things like number of factors influencing animal numbers, heterogeneity of habitats and heterogeneity within a population may well contribute to the relative stability of the population's density. Further research on this matter,

both empirical and theoretical, is needed before our hypothesis can be more precisely stated and its consequences quantitatively analyzed.

As we announced in Section 1, in all of our models we have chosen the values of the relevant parameters in such a way 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 (*i.e.* the version with the largest number of factors, or with the greatest amount of exchange between subpopulations). We have stated that we did so because we simply wished to restrict the discussion to persisting populations. Yet to a convinced "regulationist" our argument will appear more or less circular, since persistence of populations will in his view provide evidence for the operation of density governing mechanisms, and maybe he will feel that we have presupposed something that could not have evolved in nature without strong density-dependent restrictions on population increase or decrease. A detailed discussion of this matter falls outside the scope of this paper and we refer the reader to Reddingius (1968), Chapter 5; but we will make some short remarks here.

Clearly there may exist populations the density of which goes down until extinction follows. The study of such populations is, of course, highly interesting but we are not talking about such a study at this moment. The case of a population showing an upward trend is more relevant. Such an upward trend will sooner or later either be restricted and brought to a halt, or result in a catastrophe. Such a catastrophe may result in extinction, but this need not always be the case. Catastrophes may even return more or less periodically (*cf.* Baltensweiler, 1968). The incidental occurrence of a crash or of a limitation of the density may keep the population "persisting" in the sense considered above, until less "favourable" circumstances prevail. We have shown how this might work in Section 3.5 above; for a detailed discussion, see Den Boer (1968), Sections III.4 and III.5. We do not deny that populations may become extinct. Furthermore, our point is not that restriction of density fluctuations does not occur in nature, but rather that such restriction must be seen as part of a very complex pattern of environmental and "populational" influences on net reproduction so that the role of density-dependent "factors" cannot be easily singled out, and that even if such restriction does play an important role, it does not follow that the density is regulated toward some kind of an equilibrium value<sup>1</sup>.

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<sup>1</sup> Some population ecologists turn out to attach much significance to the phenomenon that for many natural populations net reproduction on the average is close to 1. It must be noted that in any case the longer a population is observed to persist, the closer the average value of the net reproduction, computed over the whole observation period, has to be to 1. This is a statistical truism that has in itself nothing to do with "regulation".

In theorizing about persistence or non-persistence of animal populations it must be kept in mind that our information about animal populations is highly biased, because for technical and economic reasons mainly very dense populations are investigated, although it might be much worth while to consider the question as to how a sparse population could persist, since most animal populations in most environments seem to be relatively sparse (Williams, 1964). Further, there is an important difference between "populations" in models and natural populations in that in the field the distinction between "persisting populations" and "populations showing a prolonged trend" can be safely made *afterwards*, whereas in a model population we incorporate a high chance of persistence by our choice of parameters. That is, on the basis of theory we can distinguish between persisting and non-persisting populations; but we can hardly predict to which of these two categories some given natural population will turn out to belong.

So we feel justified in having proceeded as we described in this paper, studying the stabilizing influence of the number of factors, of heterogeneity of the population and of "life history" on density fluctuations under the assumption of absence of important trend.

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