The Study of Population Growth in Organisms Grouped by Stages

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SUMMARY

In this extension to the use of matrices in population mathematics (Lewis [1942] and Leslie [1945]), the division of a population into equal age groups is replaced by one of unequal stage groups, no assumptions being made about the variation of the duration of the stage that different individuals may show. This extension has application in ecological studies where the age of an individual is rarely known. The model is briefly applied to three experimental situations.

INTRODUCTION

A parameter which many of the theories of population growth define in some way is known as the innate capacity for increase or intrinsic rate of increase (Lotka [1925]). In essence, this purports to state the rate of increase of a population having a stable age structure, constant temperature, moisture etc., and unlimited space, and in which no inter- or intraspecific density effects occur (except, of course, those which ensure that each female becomes fertilised as soon as and when necessary). Such conditions for a species cannot occur in nature but some environments can approximate to them; for example, the storage by man of large quantities of a homogeneous foodstuff creates an enormous and more or less uniform environment for insects.

All the published models which consider the point at all, treat a population of a species as being divisible into age groups. In trying to visualise an experiment which would test the various hypotheses, it was soon obvious that it would be impossible to look at individuals and estimate their age. Their *stage* can be recognised, and if one has other knowledge of the biology of the species, an individual's age may be approximately specified by this means. But the variation in developmental rate shown by even the sibs from inbred parents is sufficient to introduce considerable errors.

The model presented in this paper, which may be regarded as a generalisation of one proposed independently by Lewis [1942] and Leslie [1945], avoids this problem by using stage groupings instead of age groupings. In the hypothetical case of the distinct stages occupy-

1

ing equal periods of time, with no variation between individuals, a stage grouping model would be identical with the corresponding age grouping model using that unit of time.

MODEL

In a species in which there are s distinct stages recognisable (sex may be taken into account) and where there are $n_{i,t}$ individuals in stage i ($i = 1, 2, \cdots, s$) at time t, the number N_t of the total population at time t may be expressed as

$$n_{1,t} + n_{2,t} + \cdots + n_{s,t} = N_t . \qquad (1)$$

The numbers of each stage at time $t + 1$ are a function of the numbers at time t and the performances of the different stages (including interactions such as cannibalism, and also immigration and emigration) during the time interval $(t, t + 1)$.

Emigration may, of course, depend on the population size and structure; and so far as population growth is concerned, the emigrating individuals may be regarded as deaths. Immigration can be incorporated into models by considering the individuals concerned as being new births into their physiological age group in the population. However, unless there is some attraction to the population which depends upon its size and structure, it is difficult to see how immigration can be considered as depending upon the population itself. If, however, the population is isolated (e.g. on an oceanic island or in a jam jar) or forms a segment of a larger uniform population we can neglect both emigration and immigration. Some discussion of the effects of these two factors is presented by Lopez [1960]; they will be assumed absent for the purposes of the present paper.

As a first approximation, we can describe deterministically the relation of the numbers in stage p at time $t + 1$ to those in all other stages at time t by postulating the linear first order relationship

$$n_{1,t}m_{p,1,t} + n_{2,t}m_{p,2,t} + \cdots + n_{p,t}m_{p,p,t} + \cdots + n_{s,t}m_{p,s,t} = n_{p,t+1}$$

$$(2)$$

the constants $m_{p,j,t}$ ($j = 1, 2, \cdots, s$) numerically representing the biological dependence of the pth stage at time $t + 1$ upon the jth stage at time t. Some of these constants may be zero; none can be negative since this could imply a negative number of individuals (see also p. 6).

The series of equations obtained in this way for all s stages at

times t and $t + 1$ can be expressed in matrix notation as

$$\begin{bmatrix} m_{1,1} & m_{1,2} & \cdot\cdot & m_{1,s} \\ m_{2,1} & m_{2,2} & \cdot\cdot\cdot & m_{2,s} \\ \cdot & \cdot & & \cdot \\ \cdot & \cdot & & \cdot \\ \cdot & \cdot & & \cdot \\ m_{s,1} & m_{s,2} & \cdot\cdot\cdot & m_{s,s} \end{bmatrix}_t \begin{bmatrix} n_1 \\ n_2 \\ \cdot \\ \cdot \\ \cdot \\ n_s \end{bmatrix}_t = \begin{bmatrix} n_1 \\ n_2 \\ \cdot \\ \cdot \\ \cdot \\ n_s \end{bmatrix}_{t+1}$$

or

$$\mathbf{M}_t \mathbf{n}_t = \mathbf{n}_{t+1} \tag{3}$$

where $\mathbf{n}_t$ and $\mathbf{n}_{t+1}$ are vectors representing the stage composition of the populations N_t and N_{t+1} and $\mathbf{M}_t$ is a matrix of the coefficients $m_{p,j,t}$. The square matrix $\mathbf{M}_t$ is of order s and thus at most has s latent roots λ_i, each with its appropriate stable column vector $\mathbf{v}_i$, such that

$$\mathbf{M}_t \mathbf{v}_i = \lambda_i \mathbf{v}_i \quad (i = 1, 2, \cdots, s).$$

An arbitary population structure subject to this system would approach the structure given by the vector $\mathbf{v}_1$, when each stage would increase in size λ_1 times per unit of time, where λ_1 is the latent root of largest absolute value (Sylvester's theorem; see Gantmacher [1959]).

RELATIONSHIPS WITH SOME OTHER MODELS

Infinite environment If the species is alone, has infinite food and space, other external conditions are unchanging and there are no potentially harmful interactions between stages, the dominant root of $\mathbf{M}$ will be real and positive and each element in its stable vector will be real and of the same sign. In these circumstances $\mathbf{M}$ is analogous to the matrix $\mathbf{A}$ (Lewis [1942]; Leslie [1945]) whose elements (i) on the first row, $F_x(\geq 0)$, are the number of daughters alive in the age group 0—1 at time $t + 1$ per live female aged x—$(x+1)$ at time t; (ii) on the principal sub-diagonal, P_x $(0 < P_x \leq 1)$, are the probabilities of females aged x—$(x+1)$ at time t being alive in age group $(x+1)-(x+2)$ at time $t+1$; (iii) elsewhere are zero. Lewis and Leslie show that the dominant root of $\mathbf{A}$ is the only real positive root and Leslie further shows that it is equal to e^{r_m} where r_m is the innate capacity for increase as defined by Lotka [1925] in the equation

$$N_t = N_0 e^{r_m t}. \tag{5}$$

When each life history stage of the species lasts one unit of time and the individuals show no variation, the matrix $\mathbf{M}$ will be identical with $\mathbf{A}$ (assuming the stages are taken in their temporal sequence);

A can be regarded as a special case of **M**. When the various stages have different durations, it may be possible to derive **M** from **A**, should the latter be known; it does not seem possible to derive **A** from **M**.

However, no matter in what way the population is classified, its rate of increase in the stable state is unchanged; it is therefore obvious that the dominant root of **A** is equal to that of **M**, both being equal to e^{rm}. Should the appropriate environmental conditions be simulated for a population of a species, a study of the numbers of each distinguishable stage present would therefore give an estimate of e^{rm}. This argument can be extended to population change in any circumstances. Clearly the population is the same whether we consider the change in terms of age or stage groups: thus the study of stage distributions provides an experimental realisation of Lewis' [1942] and Leslie's [1945] valuable studies on age distribution, and is especially applicable when the age of an individual cannot be determined by inspection and when distinct morphological stages exist in the life cycle.

The matrix **M** reduces to a scalar if there are no distinctly recognisable stages of the species. Similarly, the Lewis/Leslie matrix would reduce to a scalar if the unit of time for which the matrix was being constructed was considerably greater than a generation. The relation between the Lotka equation (5) and the two matrices is thus made more apparent and begins to suggest the circumstances limiting the use of equation (5).

It is of interest to compare the assumptions which are made in the derivation of Lotka's equation [1925] with those of the Lewis/Leslie and census matrices. The assumption underlying the two matrix models may be stated as *a species has stage (or age) specific properties*. Leslie's paper is a mathematical treatment of the consequences (some of which are biologically imaginary) of such properties. One of these consequences is that there is one arrangement of these properties such that the future of a population, if it could exist, would remain constant so far as its structure and its rate of increase are concerned (assuming certain things about the external environment). Lotka makes two assumptions, one explicit and one implicit. In assuming for simplicity that the birth and death rates remain constant, he implies that there is a population of the species having these properties; the case that he considers is the one in which *a species has a population structure such that certain properties of the population remain constant*. There is no doubt that this last statement is a special case of the Lewis/Leslie and census assumption.

Restricted environments   In contrast with population growth in infinite environments, a phenomenon which must be very rare indeed, a

more realistic situation would be one in which some restrictions exist.
If, for example, individuals of a species are limited to a particular
space (i.e. no immigration or emigration) and provided with a quantity
of food, the population history is very easy to imagine and has often
been described; after an initial more or less sigmoid increase in num-
bers (if the food is sufficient for an increase) there is an exponential
decay phase in which the numbers become lower until eventually
the population becomes extinct. The sigmoid phase of this kind of
population history has been investigated by several authors interested
in *Drosophila* (see e.g. Pearl [1926], Bodenheimer [1938], Chiang and
Hodson [1950], Sang [1950]) and a mathematical expression of the
growth, the logistic function, which was originally derived by Verhulst
[1839], has often been used to summarise the data.

The logistic function is usually derived from (5) in some such way
as follows:—

$$dN/dt = r_m N \qquad\qquad (6)$$

is the law operating at the beginning of population growth when the
environment may be considered to be infinite in relation to N. As
the population grows the increasing density linearly reduces r_m by ϕN
(as a first approximation only; see Rhodes [1940] para 42); i.e.

$$dN/dt = (r_m - \phi N)N \qquad\qquad (7)$$

or

$$N_t = \frac{r_m N_0 e^{r_m t}}{r_m + N_0 \phi(e^{r_m t} - 1)} \qquad\qquad (8)$$

which is the logistic

$$y = \frac{be^{ax}}{1 + ce^{ax}} \qquad\qquad (8a)$$

(Verhulst [1839]).

The assumption behind (5) and (6), from which the logistic func-
tion is derived, makes clear that (8) is strictly applicable only to those
circumstances where the population has the required structure at
time t such that the properties of the population are those defined
by (7). To apply any equation derived from (6) to population histories
when N_0 consists entirely of one age or stage group is to use it in in-
correct circumstances.

The logistic function has also been applied to population growth
when observed in a different pattern of experimentation (see especially
Gause [1934] and Park [1948]). The pattern of such experimentation

has been to renew the food completely on regular occasions, often coinciding with a census. In these circumstances, a population increases in number in a more or less sigmoid fashion and eventually tends to reach a particular size and stay at or near this level. During this second phase, sometimes known as the stationary state, the rate of increase is zero and we can assume as a first approximation, at least, that the performance of the species remains constant. It obviously cannot be assumed that the performance remains constant during the sigmoid phase. Although this is a very different experimental procedure, the logistic function has been used as a deterministic expression of population growth in these circumstances. However, the fundamental objection to the use of the logistic, which Bowley [1925], Sang [1950], Andrewartha and Birch [1954] and Southwick [1956] have pointed out, is that a linear response to density (ϕN) is an oversimplification not supported by experimental data; a simple model such as $dN/dt = (r_m - \phi N)N$ cannot be expected to adequately incorporate the effects of density.

ESTIMATION

The most relevant paper on estimation appears to be that of Quenouille [1957] to which reference should be made for the mathematical background. Quenouille showed in particular (para 6.3) that the usual multiple regression estimation procedures can be used in multiple time series.

In estimating the elements of the matrices, it is worth considering whether regression through the origin, rather than through the mean, should be used. When there are no density effects in the population studied, this method is likely to give more accurate estimates of the regression coefficients. When density effects are expected, regression through the origin will bias the results.

As has been briefly noted (p. 2) there are some limitations, determined by biological considerations, upon the values which the $m_{p,i,t}$ can take. A negative value would imply that at time $t + 1$, the numbers of stage p could be negative, a biologically meaningless statement. Negative estimates, however, can and do arise, and must be considered carefully. If the dominant root of the estimated matrix is complex, this could mean that the assumption of constant performance by each stage, during the period of time under consideration, is false. The complex roots, and the negative value for some $m_{p,i,t}$, are a consequence of this false assumption. The occurrence of complex roots could imply a regular cycle of changes in the stage specific performance (Lefkovitch and Currie [1963]). The best procedure,

if negative $m_{p,i,t}$ do occur, is to examine the dominant latent root; if it is rational and positive, it is worthwhile considering whether the *a posteriori* condition be made that

$$m_{p,i,t} \geq 0.$$

With adequate prior reason, some of the $m_{p,i,t}$ can be supposed to be and set to zero (Lefkovitch [1963]); but to preserve generality, it is probably advisable not to make this condition.

A similar argument can be used if the dominant root is rational but negative. This latter circumstance can arise if the matrix is calculated from observations over a short period, and random variation is large. Something of value may still be obtainable from such observations by making the above condition.

If the dominant root is real and positive, then a simplification of the matrix may be considered. Firstly, should there be some external information on the duration of various parts of the life cycle, it may be possible to specify that some elements are zero. Secondly, since negative elements taken alone have no meaning, these can be set to zero. Thirdly, elements not significantly different from zero may be replaced by zero. This sequence appears to be the best; obviously, as much external information as is available should be used before tests of significance are applied.

However, in going through this sequence, there is a danger that relevant information may be discarded. The simplest way in which to assess what has been discarded is by considering the dominant latent roots of the matrices. If there is little or no change in their values, what has been discarded is of little or no relevance. If the change is large, what has been discarded is of importance and should be retained. This immediately raises the problem of the reliability of the estimates of the latent roots and what is meant by a 'large' change; this problem reduces to the estimation of the standard errors of the latent roots of a matrix whose elements are the sample means of bivariate distributions. So far as I have been able to discover, there exists no published solution to this problem, nor have I been able to provide one myself.

If the dominant roots are complex, and it becomes apparent (from other considerations) that there is a cycle of stage specific performances, it would be best not to attempt to make a strictly biological interpretation of any negative $m_{p,i,t}$. Each one of these partial regression coefficients operates through a variety of biological processes; these include the rates of development and survival of several possible stages as well as fecundity rates. Any cyclic performance could be

reflected by a negative value for some $m_{p,j,t}$; the fact that any one particular development rate etc. may contribute to the values of several of the elements, which are therefore correlated, could imply that a negative value for some elements is a way that a least squares estimation procedure draws attention to false assumptions.

EXPERIMENTAL OBSERVATIONS

Methods

This account of certain experimental observations, which are recorded more fully elsewhere (Lefkovitch [1963; 1964]), is designed primarily as an example of how the model can give pertinent biological information on a species. It is not an exhaustive arithmetical study of the implications of the experiments.

There were three experiments, all using *Lasioderma serricorne* (Fabricius), the cigarette beetle, as experimental animal, at temperature and moisture conditions of 30°C, 55% R. H. and using broad wheat bran as the food substrate. In each experiment there were four replicates.

In experiment I, each culture was initiated by 100 newly emerged adults and provided with 25g (=175 cc) of the food. At intervals of three weeks, each culture was sub-divided into eight, using a sample divider (Howe [1963]). One of these parts was used, with sufficient fresh bran to make up the volume, to initiate a new culture; another part was examined and the numbers of eggs, larvae, pupae and adults, the four stages distinguished, were recorded. Thus only estimates of the numbers present at each census, and of the numbers present in the sub-culture used for further incubation, were known. There are clearly several components to the variance between replicates, one being the expected variance between a set of comparable stochastic processes, a second due to the experimental methods and a third due to any differences in the initial sex ratios. This experiment, which lasted for two years (and could have been better designed) was designed to simulate an infinite universe with infinite quantities of food.

In experiment II, the same food medium was used, but only 20 newly emerged adults were used with 5g food (=40 cc). At intervals of three weeks all the insects were removed from the food, a census made, the insects then being provided with fresh food. This experiment was continued for one year.

Experiment III was similar to Experiment II, but differed from it in that the food was not renewed. This experiment was continued for 48 weeks, at which time there were no survivors.
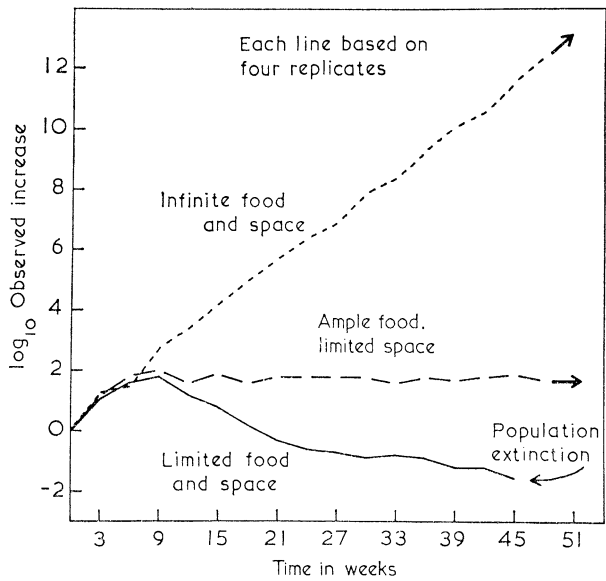
FIGURE 1.

THE HISTORIES OF THREE DIFFERENT KINDS OF POPULATION OF *Lasioderma serri-corne* (F.) AT 30C, 55%RH FED UPON WHEAT BRAN.

In Figure 1 these observations are summarised, the numbers of insects being plotted as the log increase over the original numbers against time. Detailed census observations are published elsewhere (Lefkovitch [1963; 1964]).

Estimates of the matrices **M**

In experiment I, it is assumed that from the beginning the conditions are unchanging i.e. at all times there is excess of food, ample oviposition facilities, no interactions between individuals and the environment which could produce harmful effects etc. An analysis of dispersion (Rao [1952] Ch. 7) showed that the four replicates could be treated together. These observations over the two years provided 140 values for the numbers in each stage, which were used to estimate the elements of the matrix. The estimated matrix, using classical regression methods (regression through the mean) was

$$(\mathbf{M_I}) = \begin{bmatrix} 0.250 & 1.998 & 4.734 & -0.009 \\ 1.596 & 0.173 & 25.023 & 12.021 \\ 0.152 & 0.042 & -0.110 & 1.032 \\ -0.133 & 0.854 & 1.022 & -0.231 \end{bmatrix}$$

whose dominant latent root is 4.664, with an associated normalised stable column vector of

$$[0.455 \quad 0.875 \quad 0.055 \quad 0.152]'.$$

This is interpreted as meaning that a population of this species under these conditions would eventually assume a structure indicated by the stable vector and increase in numbers at a rate of 4.664 times in every three weeks. The remaining roots are -3.252 and $0.197 \pm 0.230i$.

Regression through the origin gives an essentially similar result

$$M_I = \begin{bmatrix} 0.341 & 1.803 & 4.119 & -0.785 \\ 1.203 & 0.998 & 27.776 & 15.309 \\ 0.125 & 0.101 & 0.085 & 1.264 \\ -0.130 & 0.875 & 0.919 & -0.279 \end{bmatrix}$$

whose dominant root is 5.521, with a normalised stable column vector of

$$[0.347 \quad 0.925 \quad 0.058 \quad 0.141]'.$$

The difference between the dominant latent roots is small (Table I).

In experiments II and III, the population histories are divisible into two distinct phases. The first of these phases in both experiments appears to correspond very closely with experiment I (Figure 1) but the second phases in the two experiments differ from experiment I and from each other even though they began at the same time. In experiment II, the second phase, which will be referred to as the 'asymptotic phase', appears to indicate that the rate of increase of the population varied about zero, suggesting that the biology of the species can be taken as being constant. Similarly, in experiment III, the second phase, which will be called the 'decay phase,' it would also appear that the biology can be assumed to be constant since the numbers fell exponentially but at a faster rate than did the volume of the food; it can be inferred that there was no shortage of space but only one of food. It will be seen that these assumptions are disproved in a rather interesting way. The matrix estimated for the asymptotic phase was based on 52 observations for each row of the matrix, that of the decay phase upon 48 observations.

The matrix M_{II} of the asymptotic phase was calculated to be

$$M_{II} = \begin{bmatrix} -0.107 & -0.150 & 1.743 & -1.019 \\ 0.643 & -0.073 & 2.652 & 3.157 \\ -0.027 & 0.062 & -0.234 & 0.052 \\ -0.117 & -0.044 & 0.175 & -0.278 \end{bmatrix}$$

and the matrix $\mathbf{M}_{III}$ of the decay phase was calculated as

$$\mathbf{M}_{III} = \begin{bmatrix} -0.055 & 0.001 & 1.452 & 0.023 \\ -4.746 & 0.204 & 0.827 & 0.591 \\ -0.367 & 0.016 & 0.001 & 0.039 \\ -0.550 & 0.019 & 0.473 & 0.116 \end{bmatrix}$$

The dominant latent roots of $\mathbf{M}_{II}$ and $\mathbf{M}_{III}$ are complex which, if the 'complexity' is genuine, both disproves the assumption about a constant biology during the two phases and suggests that there is some cyclical change in the biology. In fact, all four latent roots of $\mathbf{M}_{II}$ were found to be complex: they are $0.274 \pm 1.014i$ which have modulus of 1.050 and $0.206 \pm 0.134i$ which have a modulus of 0.245. The dominant roots of $\mathbf{M}_{III}$ are $0.237 \pm 0.061i$ which has a modulus of 0.243, the remaining two roots being 0.047 and 0.005. The stable vectors associated with the complex roots are not given here but will be considered, with their biological implications elsewhere. Neither will the further computation along the lines indicated by Quenouille [1957], nor, more interestingly, the expression of the change in the biology in the species resulting from the different experimental conditions as revealed by the various matrices, be reported here.

The dominant latent roots The dominant latent root of $(\mathbf{M}_I)$, the matrix calculated by stipulating regression through the mean, is 4.664 whereas that when the matrix was calculated by stipulating regression through the origin is 5.521. Which of these values is likely to be correct? The best age specific life and fertility tables for this species that were obtained for a unit of one day (Lefkovitch [1963]) lead to the equation

$$\lambda^{45} - 0.240\lambda^{12} - 1.774\lambda^{11} - 3.917\lambda^{10} - 2.269\lambda^{9} - 2.336\lambda^{8}$$

$$- 1.663\lambda^{7} - 0.682\lambda^{6} - 0.239\lambda^{5} - 0.081\lambda^{4} - 0.012\lambda^{3}$$

$$- 0.002\lambda^{2} - 0.00003\lambda - 0.00001 = 0$$

which has a root of 1.074 with greatest modulus. Converting this from 1 day to three weeks gives a value of 4.478, a value in close agreement with that of 4.664. A further estimate can be obtained as follows:— if equation (5) is written as

$$\log_e N_t = \log_e N_0 + r_m t ,$$

and if it is assumed that this equation applies to the growth of a population when approaching the stable state as well as when it is in this

state, the slope of the linear regression of $\log_e N_t$ on t should give an estimate of r_m. The value of e^{r_m} obtained in this way is 6.082 per 3 weeks (Lefkovitch [1963]). However, it seems that the assumption is false; a population initiated by adults of *L. serricorne* should in theory show an average increase greater than that of the innate capacity at least for the first year. It must be taken, therefore, that 6.082 is an overestimate of e^{r_m}.

The decision as to which of the various estimates is likely to be nearest the true value must be left open; the value calculated from the age specific life and fertility tables uses data obtained by different experimental methods and should not be given too much weight. If the procedures used in experiment I achieved their object, namely the elimination of food and space shortages, regression through the origin is applicable and the value 5.521 is the one to be preferred. If, however, the experimental methods failed in their object and shortages did arise, this value is biased and the value obtained by using regression through the mean should be chosen. In support of the value of 5.521, it can be said that there was not the slightest evidence of food or space shortage in experiment I such as certainly occurred in experiments II and III; it is only the first of these shortages which is believed to influence population growth in *L. serricorne* as a result of high numbers (Lefkovitch and Currie [1963]).

The simplification of the matrix $\mathbf{M}_I$ was carried out in the following order: replacement of those elements which other information (Lefkovitch [1963]; Lefkovitch and Currie [1963]) suggests should be zero by that value; replacement of any remaining negative elements by zero; replacement of positive elements less than twice their standard errors by zero. At each step, the matrix was recalculated and its dominant latent root obtained; the greatest change in the value of the latter occurred as a result of the first operation (this remark is true not only of the growth phase but of the asymptotic and decay phases). There was almost no change in the value of λ_1 as a result of the second and third processes. The matrix finally obtained was

$$\mathbf{M}_{I'} = \begin{bmatrix} \cdot & 1.978 & \cdot & \cdot \\ 1.203 & 0.998 & 27.776 & 15.309 \\ 0.362 & 0.191 & \cdot & \cdot \\ \cdot & 0.835 & \cdot & \cdot \end{bmatrix}$$

whose dominant root is 5.432, a value hardly different from that of the unsimplified matrix.

The corresponding simplified matrices for experiments II and III are

$$
\mathbf{M}_{II'} = \begin{bmatrix} \cdot & \cdot & 2.516 & \cdot \\ 0.528 & \cdot & 5.294 & 3.898 \\ \cdot & 0.074 & \cdot & \cdot \\ \cdot & \cdot & 0.553 & \cdot \end{bmatrix}
$$

$$
\mathbf{M}_{III'} = \begin{bmatrix} \cdot & \cdot & 1.478 & \cdot \\ \cdot & 0.202 & \cdot & \cdot \\ \cdot & 0.016 & \cdot & \cdot \\ \cdot & 0.018 & \cdot & \cdot \end{bmatrix}
$$

Table I suggests that whereas little has been lost in going from $\mathbf{M}_{III}$ to $\mathbf{M}_{III'}$, the change from $\mathbf{M}_{II}$ to $\mathbf{M}_{II'}$ has discarded a significant part of the information; the dominant latent roots are appreciably different.

TABLE I

ESTIMATES OF DOMINANT ROOTS

Source	Unsimplified form	Simplified form
Growth phase		
a. regression through mean	4.664	----
b. regression through origin	5.521	5.432
Asymptotic phase	$0.274 \pm 1.014i$ (1.050)	0.837
Decay phase	$0.237 \pm 0.061i$ (0.245)	0.202

The dominant roots of $\mathbf{M}_{II}$, as noted above, are $0.274 \pm 1.014i$ having a modulus of 1.050. An examination of Figure 1 suggests that a value of 1 should be expected; clearly the value obtained does not differ appreciably from unity. The oscillations implied by these roots, however, suggest that some regular cycle of biological changes take place but, presumably because of inadequate estimation procedures, this has not been fully described. From other evidence (Lefkovitch and Currie [1963]), it is known that delayed density effects occur, and it is also possible that the lower pair of roots reflect a cycle of food

shortage. Thus in experiment II we can assume that the observations at the 'asymptote' show that density effects of a cyclical nature occur under these conditions. In experiment III, the complex dominant roots could be interpreted as follows: as the population is decaying because of food shortage, on occasions a few individuals manage to become adult, mate and give rise to offspring. This would be sufficient to bring about an oscillatory disturbance. The fact that the modulus of these roots is so much larger than the third root would suggest that the effect is real.

We can, then either stop at this stage, being satisfied with the complex roots, or consider whether delayed effects occur and fit a second or higher order model. But it is not the object of this paper to consider this.

A biological interpretation of the matrices, using the simplified matrices of partial regression coefficients, allows a certain number of comments upon the biology of the species. In experiment I over the period of time considered and under these particular environmental conditions, on average

a) the number of eggs found at a particular census was about equal to twice the number of larvae present at the previous census;

b) the number of larvae at a census was about equal to 1.2 times the number of eggs plus the number of larvae, 28 times the number of pupae and 15 times the number of adults at the previous census;

c) the number of pupae at a census was about a third of the number of eggs at the previous census plus a fifth of the number of larvae;

d) the number of adults at a census was about 0.8 that of the number of larvae at the previous census.

In the asymptotic phase of experiment II we find the following

a) the number of eggs at a particular census was about two and a half times the number of pupae at the previous census;

b) the number of larvae at a census was about equal to half the number of eggs plus five times the number of pupae and four times the number of adults at the previous census;

c) the number of pupae at a census was about one tenth the number of larvae at the previous census;

d) the number of adults was about half the number of pupae at the previous census.

It would seem, therefore, that there is an indication of a prolongation of the pupal, quiescent adult and/or post-emergence pre-oviposition periods. Eggs, pupae and adults affect the numbers of larvae

three weeks later to a much smaller extent than in experiment I: i.e.
there would appear to be a mortality factor operating. This is sup-
ported by the change in the dependence of pupae from eggs to larvae
together with a suggestion of increased mortality in the egg/larval
periods.

It is possible to make similar comparisons about the decay phase
of experiment III; the most striking thing about this phase is that it
indicates how much larval survival is important in these conditions.
The situation may be expressed in this way:

   a) about a fifth of the larvae survive for three weeks
   b) about 1% of the larvae pupate and become adult
   c) the adults produce as many eggs between them as there are
      adults.

The ecological implications of these observations will be discussed
elsewhere. However, the differences between the various matrices
and their biological meaning make very obvious the important point
that the elements of these matrices are cross-correlated: i.e. a real
change in the biological relationship between a pair of stages, brought
about by different conditions, will produce numerical changes through-
out the matrix without implying any biological change.

FURTHER APPLICATIONS

There are some other applications where this linear regression
method of dealing with census observations could be of use.

Equations may be built up relating the numbers of any one stage
at time $t + 1$ to all those of its own and of any other species present
at time t; any interactions between the species would be shown by
non-zero elements in the matrix. In predator-prey relationships be-
tween two species, which in certain circumstances are said to show
oscillations (Andrewartha and Birch [1954]), the dominant roots of
the matrix of regression coefficients would be complex. If in attempt-
ing to evaluate the effect of an insecticide upon a population of a
species it is considered desirable to make censuses at different times,
and if an untreated population is studied at the same time, two matrices
can be estimated from the census data and their differences examined.
These matrices would present the average of all the relationships
between stages over a unit time (including density effects etc.). It
is clear that to prevent the increase of the population, it will be neces-
sary to provide a control measure such that the increase is less than
unity i.e.

$$0 \leq \lambda_1 < 1.$$

If certain stages are inaccessible to control measures, this concept will help to allocate the kills to the remaining stages.

This procedure is applicable in circumstances in which there is a persistent or non-persistent effect; if there is no persistent effect either a complete kill must be achieved at one application or regular control measures must be applied. Since not all stages are equally controlled, this procedure would induce oscillations in the population structure. In order to estimate what percentage kill of the vulnerable stages should be attained or exceeded, one would need to arrange the kills so as to reduce the absolute value of λ_1 to less than unity. A beginning along these lines has been made by Yeo and Simpson [1960].

The model used in this paper was described as a first approximation. In a second approximation, which may be used if interactions between stages are expected which depend on the population size, structure etc. in relation to the space available, we can define the *effective numbers* present in each stage at time t by considering their biological results at time $t + 1$, and writing

$$n_{p,t,d} = n_{p,t} - \phi_{p,1,t}n_{1,t} - \phi_{p,2,t}n_{2,t} - \cdots - \phi_{p,s,t}n_{s,t} \qquad (9)$$

where $\phi_{p,j,t}$ represents an interaction of stage p with stage j at time t, or, more explicitly, the size and structure of the population at time t in the particular space available to it. No restrictions are placed upon the way $\phi_{p,j}$ can change; the relationship is almost certainly non-linearly dependent upon n_t (see e.g. Watt [1960]), the elements ϕ being, in fact the derivatives of these relationships.

Considering all stages we have

$$
\begin{bmatrix} n_{1,t} \\ n_{2,t} \\ \vdots \\ n_{s,t} \end{bmatrix}_d =
\begin{bmatrix} n_{1,t} \\ n_{2,t} \\ \vdots \\ n_{s,t} \end{bmatrix} -
\begin{bmatrix} \phi_{1,1} & \phi_{1,2} & \cdots & \phi_{1,s} \\ \phi_{2,1} & \phi_{2,2} & \cdots & \phi_{2,s} \\ \vdots & \vdots & & \vdots \\ \phi_{s,1} & \phi_{s,2} & \cdots & \phi_{s,s} \end{bmatrix}_t
\begin{bmatrix} n_{1,t} \\ n_{2,t} \\ \vdots \\ n_{s,t} \end{bmatrix} . \qquad (10)
$$

Population changes can now be described, in abbreviated notation, by

$$\mathbf{Mn}_{t,d} = \mathbf{M}(\mathbf{I}_s\mathbf{n}_t - \mathbf{\Phi}_t\mathbf{n}_t) = \mathbf{M}(\mathbf{I}_s - \mathbf{\Phi}_t)\mathbf{n}_t = \mathbf{n}_{t+1} \qquad (11)$$

where $\mathbf{M}$ is the matrix formed when there are no interactions between the stages that depend upon the number present, except those ensuring the full reproductive performance of each female, and $\mathbf{I}_s$ is the unit matrix of order s.

Putting

$$\mathbf{H}_t = \mathbf{M}(\mathbf{I}_s - \mathbf{\Phi}_t)$$

we have

$$H_t n_t = n_{t+1} \tag{12}$$

and in those circumstances in which we know that there must have been interactions between the stages, but can assume that these are unchanging over the time interval considered (e.g. the second phase of experiment II), the matrix calculated from census observations is of type H. If we know or can estimate M and H, we should be able to estimate Φ, since

$$\Phi = I - M^{-1}H \tag{13}$$

This can be done very easily with the results of the experiments recorded in this paper if the argument is accepted that the change from the growth to the second phases occurred abruptly. However the detailed interpretation of the matrices Φ is not as yet very clear and will not receive comment here.

The description of a population by a vector n_t is incomplete in the sense that this vector is not sufficient to know n_{t+1}, for which a knowledge of H_t is also required. The possibility arises that models describing population growth could use the methods of tensor calculus. This suggestion will form the subject of future studies.

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