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P. H. Leslie

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ON THE USE OF MATRICES IN CERTAIN POPULATION MATHEMATICS

BY P. H. LESLIE, *Bureau of Animal Population, Oxford University*

CONTENTS

1. INTRODUCTION

If we are given the age distribution of a population on a certain date, we may require to know the age distribution of the survivors and descendants of the original population at successive intervals of time, supposing that these individuals are subject to some given age-specific rates of fertility and mortality. In order to simplify the problem as much as possible, it will be assumed that the age-specific rates remain constant over a period of time, and the female population alone will be considered. The initial age distribution may be entirely arbitrary; thus, for instance, it might consist of a group of females confined to only one of the age classes.

The method of computing the female population in one unit's time, given any arbitrary age distribution at time t, may be expressed in the form of $m+1$ linear equations, where m to $m+1$ is the last age group considered in the complete life table distribution, and when the same unit of age is adopted as that of time. If

n_{xt} = the number of females alive in the age group x to $x+1$ at time t,

P_x = the probability that a female aged x to $x+1$ at time t will be alive in the age group $x+1$ to $x+2$ at time $t+1$,

F_x = the number of daughters born in the interval t to $t+1$ per female alive aged x to $x+1$ at time t, who will be alive in the age group 0–1 at time $t+1$,

then, working from an origin of time, the age distribution at the end of one unit's interval will be given by

$$\begin{aligned} \sum_{x=0}^{m} F_x n_{x0} &= n_{01} \\ P_0 n_{00} &= n_{11} \\ P_1 n_{10} &= n_{21} \\ P_2 n_{20} &= n_{31} \\ \vdots &\quad \vdots \\ P_{m-1} n_{m-1,0} &= n_{m1} \end{aligned}$$

or, employing matrix notation, $Mn_0 = n_1$, where n_0 and n_1 are column vectors giving the age distribution at $t = 0$ and 1 respectively, and the matrix

$$M = \begin{bmatrix} F_0 & F_1 & F_2 & \dots & . & F_k & F_{k+1} & \dots & F_{m-1} & F_m \\ P_0 & . & . & \dots & . & . & . & \dots & . & . \\ . & P_1 & . & \dots & . & . & . & \dots & . & . \\ . & . & P_2 & \dots & . & . & . & \dots & . & . \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ . & . & . & \dots & P_{k-1} & . & . & \dots & . & . \\ . & . & . & \dots & . & P_k & . & \dots & . & . \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ . & . & . & \dots & . & . & . & \dots & P_{m-1} & . \end{bmatrix} \quad 0 < P_x < 1;\ F_x \geqq 0.$$

This matrix is square and consists of $m+1$ rows and $m+1$ columns. All the elements are zero, except those in the first row and in the subdiagonal immediately below the principal diagonal. The P_x figures all lie between 0 and 1, while the F_x figures are by definition necessarily positive quantities. Some of the latter, however, may be zero, their number and position depending on the reproductive biology of the species we happen to be considering in any particular case, and on the relative span of the pre- and post-reproductive ages. If $F_m = 0$, the matrix M is singular, since the determinant $|M| = 0$.

Since $Mn_0 = n_1$, and $Mn_1 = M^2_{n_0} = n_2$, etc., the age distribution at time t may be found by pre-multiplying the column vector $\{n_{00}\, n_{10}\, n_{20} \dots n_{m0}\}$, i.e. the age distribution at $t = 0$, by the matrix M^t. Moreover, it will be seen that with the help of the jth column of M^t the age distribution and number of the survivors and descendants of the $n_{j-1,0}$ individuals, who were alive at $t = 0$, can readily be calculated. Thus, $n_{j-1,0}$ times the sum of the elements in the jth column of M^t gives the number of living individuals contributed to the total population at time t by this particular age group.

2. Derivation of the matrix elements

The basic data, from which the numerical elements of this matrix may be derived, are given usually in the form of a life table and a table of age specific fertility rates. To take the P_x figures first; if at $t = 0$ there are n_{x0} females alive in the age group x to $x+1$, the survivors of these will form the $x+1$ to $x+2$ age group in one unit's time, and thus $P_x n_{x0} = n_{x+1,1}$. Then it is usually assumed (e.g. Charles, 1938, p. 79; Glass, 1940, p. 464) that

$$P_x = \frac{L_{x+1}}{L_x},$$

where

$$L_x = \int_x^{x+1} l_x\, dx,$$

or the number alive in the age group x to $x+1$ in the stationary or life table age distribution. This method of computing the survivors in one unit's time would be exact if the distribution of those alive within a particular age group was the same as in the life-table distribution.

The F_x figures are more troublesome, and in the numerical example which will be given later they were obtained from the basic maternal frequency figures (m_x = the number of live daughters born per unit of time to a female aged x to $x+1$) by an argument which ran as follows. Consider the n_{x0} females alive at $t = 0$ in the age group x to $x+1$, and let us sup-

pose that they are concentrated at the midpoint of the group, $x+\frac{1}{2}$. During the interval of time 0–1 some of these individuals are dying off, and at $t = 1$ the $n_{x+1,1}$ survivors can be regarded as concentrated at the age $x+1\frac{1}{2}$. Although these deaths are taking place continuously, we may assume them all to occur around $t = \frac{1}{2}$, so that at this latter time the number of females alive in the age group we are considering changes abruptly from n_{x0} to $n_{x+1,1} = P_x n_{x0}$. Then during the time interval 0–$\frac{1}{2}$ these n_{x0} females will have been exposed to the risk of bearing daughters, and the number of the latter they will have given birth to per female alive will be given by the maternal frequency figure for the ages $x+\frac{1}{2}$ to $x+1$. This figure may be obtained by interpolating in the integral curve of the m_x values, and thus expressing the latter in $\frac{1}{2}$ units of age throughout the reproductive span instead of in single units. The daughters born during the interval of time 0–$\frac{1}{2}$ will be aged $\frac{1}{2}$–1 at $t = 1$, the number of them surviving at this time being determined approximately by multiplying the appropriate $m_{x+\frac{1}{2}}$ figure by the factor $2\int_{\frac{1}{2}}^{1} l_x dx$ according to the given life table. Similarly, each of the $P_x n_{x0}$ females during the interval of time $\frac{1}{2}$–1 give birth to $m_{x+1-x+1\frac{1}{2}}$ daughters, the survivors of which form part of the 0–$\frac{1}{2}$ age group at $t = 1$. The survivorship factor is in this case taken to be $2\int_{0}^{\frac{1}{2}} l_x dx$.

Combining these two steps together we obtain a series of F_x figures, which may be defined as the number of daughters alive in the age group 0–1 at $t = 1$ per female alive in the age group x to $x+1$ at $t = 0$. Putting

$$k_1 = 2\int_{0}^{\frac{1}{2}} l_x dx, \quad k_2 = 2\int_{\frac{1}{2}}^{1} l_x dx,$$

then

$$F_x = (k_2 m_{x+\frac{1}{2}-x+1} + k_1 P_x m_{x+1-x+1\frac{1}{2}}),$$

and

$$\sum_{x=0}^{m} F_x n_{x0} = n_{01},$$

the total number of daughters alive aged 0–1 at $t = 1$.

3. NUMERICAL EXAMPLE

In order to see whether the P_x and F_x figures obtained in this way from the basic data give a reasonably accurate estimate of the population in one unit's time, a numerical example was worked out for an imaginary rodent population, the species chosen being the brown rat, *Rattus norvegicus*. Full details of the basic life table and fertility table which were used are given in an appendix, together with a short account of the genesis of these tables and the methods employed to estimate the rate of natural increase (r) and the stable age distribution. Compared with man, the fertility of this imaginary rat population was relatively very great; thus, the gross reproduction rate was 31·21 daughters and the net rate (R_0) 25·66, the life table used being a reasonably good one. The inherent rate of natural increase was estimated to be 0·44565 per head per month of 30 days, and the stable age distribution was so overladen with young that the proportion of females in the post-reproductive age groups was negligible. Some 74·45 % of the females were younger than 3 months, at which age breeding was assumed to commence.

By definition the Malthusian age distribution is stable; that is to say, once a population subject to the given rates of fertility and mortality achieves this form of distribution, it

continues to increase e^r times every unit of time and the proportions of the population alive in each group remain constant. Thus, in the present example, given 100,000 females distributed as to age in the stable form at $t = 0$, the number alive in each age group in 1 month's time can be immediately calculated by multiplying each element in the original distribution by 1·561505. This 'true' age distribution at $t = 1$ is compared in Table 1 with that obtained by operating on the original distribution with the P_x and F_x figures, which are given in Table 5 of the Appendix.

The agreement between the true and estimated age distributions is remarkably close. It might be expected that the principal errors would occur in the early age groups, since the

Table 1

(1) (Units of 30 days) Age group	(2) Population at $t=0$ Stable age distribution	(3) Expected population at $t=1$ Col. 2 × 1·561505	(4) Population at $t=1$ Estimated by operating on col. 2 with the matrix M
0–	37,440	58,463	58,374
1–	22,595	35,282	35,455
2–	14,417	22,512	22,519
3–	9,227	14,408	14,406
4–	5,903	9,218	9,218
5–	3,775	5,895	5,895
6–	2,413	3,768	3,768
7–	1,542	2,408	2,407
8–	984	1,537	1,537
9–	627	979	980
10–	399	623	623
11–	254	397	396
12–	161	251	251
13–	101	158	159
14–	64	100	99
15–	40	62	62
16–	25	39	39
17–	15	23	24
18–	9	14	14
19–	6	9	8
20–	3	5	5
Total	100,000	156,151	156,239

The span of the reproductive ages is from 3 to 21 months.

P_x figures are based on the stationary age distribution which is clearly very different from the stable form. However, as will be seen from Table 1, the biggest error from this cause is due to the first P_0 which overestimates the number alive in the 1–2 age group at $t = 1$ by some 0·5 %. The F_x figures underestimate the number alive in the 0–1 group by 0·2 %, and the total population is overestimated by 0·06 %. On the whole these results are satisfactory and, judging from this example, it would seem that the matrix M operating on a given age distribution should give a reasonable estimate of the population in one unit's time, provided that the unit of time and age chosen be not too coarse as compared with the life span of the species. The degree of cumulative error which is introduced by continued operation with the matrix will be considered later.

4. PROPERTIES OF THE BASIC MATRIX

The matrix M is square and of order $m+1$; it is not necessary, however, in what follows to consider this matrix as a whole. For, if $x = k$ is the last age group within which reproduction occurs, F_k is the last F_x figure which is not equal to zero. Then, if the matrix be partitioned symmetrically at this point,

$$M = \begin{bmatrix} A & . \\ B & C \end{bmatrix}.$$

The submatrix A is square; B is of order $(m-k)\times(k+1)$; C again is square consisting of $m-k$ rows and columns, the only numerical elements being in the subdiagonal immediately below the principal diagonal. The remaining submatrix is of order $(k+1)\times(m-k)$ and consists only of zero elements. Then in forming the series of matrices M^2, M^3, M^4, etc.,

$$M^t = \begin{bmatrix} A^t & . \\ f(ABC) & C^t \end{bmatrix}.$$

The submatrix C is, however, of such a type that $C^{m-k} = 0$, so that M^t, $t \geqq m-k$, will have all its last $m-k$ columns consisting of zero elements. This is merely an expression of the obvious fact that individuals alive in the post-reproductive ages contribute nothing to the population after they themselves are dead. It is the submatrix A which is principally of interest, and in the mathematical discussion which follows, attention is focused almost entirely on it and on age distributions confined to the prereproductive and reproductive age groups.

The matrix A is of order $(k+1)\times(k+1)$, where $x = k$ is the last age group in which reproduction occurs, and written in full,

$$A = \begin{bmatrix} F_0 & F_1 & F_2 & F_3 & \dots & F_{k-1} & F_k \\ P_0 & . & . & . & \dots & . & . \\ . & P_1 & . & . & \dots & . & . \\ . & . & P_2 & . & \dots & . & . \\ \multicolumn{7}{c}{\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots} \\ . & . & . & . & \dots & P_{k-1} & . \end{bmatrix}.$$

This matrix is non-singular, since the determinant $|A| = (-1)^{k+2}(P_0P_1P_2\dots P_{k-1}F_k)$. There exists, therefore, a reciprocal matrix of the form

$$A^{-1} = \begin{bmatrix} . & P_0^{-1} & . & . & \dots & . \\ . & . & P_1^{-1} & . & \dots & . \\ . & . & . & P_2^{-1} & \dots & . \\ \multicolumn{6}{c}{\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots} \\ . & . & . & . & \dots & P_{k-1}^{-1} \\ F_k^{-1} & -(P_0F_k)^{-1}F_0 & -(P_1F_k)^{-1}F_1 & -(P_2F_k)^{-1}F_2 & \dots & -(P_{k-1}F_k)^{-1}F_{k-1} \end{bmatrix}.$$

Thus, given an initial age distribution n_{x0} $(x = 0, 1, 2, 3, \dots, k)$ at $t = 0$, in addition to the forward series of operations An_0, A^2n_0, A^3n_0, ..., etc., there is also a backward series $A^{-1}n_0$, $A^{-2}n_0$, $A^{-3}n_0$, ..., etc. There is, however, a fundamental difference between these; for, whereas the forward series can be carried on for as long as we like, given any initial age distribution, the backward series can only be performed so long as n_{xt} remains $\geqq 0$, since a negative number of individuals in an age group is meaningless. Apart from this limitation, it is possible to foresee that the reciprocal matrix might be of some use in the solution of certain types of problem.

5. Transformation of the co-ordinate system

Hitherto an age distribution n_{xt} has been regarded as a matrix consisting of a single column of elements. For simplicity in notation, this column vector will now be termed the vector ξ and different ξ's will be distinguished by different subscripts (ξ_a, ξ_x, etc.). We may picture an age distribution as a vector having a certain magnitude and related to a definite direction in a vector space, the space of the ξ's. The different age distributions which may arise in the case of any particular population will be assumed to be ξ's all radiating from a common origin. The numerical elements of a ξ vector are thus taken to be the co-ordinates of a point in multi-dimensional space referred to a general Cartesian co-ordinate system, in which the reference axes may make any angles with one another. At this point in the argument another type of vector will be introduced, which in matrix notation will be written as a row vector, and which will be termed the vector η. There is an intimate relationship between this new type and the old, for, associated with each vector ξ_a, there is a uniquely determined vector η_a, and vice versa. The inner or scalar product, $\eta_a \xi_a$, is the square of the length of the vector ξ_a. Either we may picture each of these vectors as associated with a different kind of vector space, the space of the ξ's and the dual space of the η's, which are not entirely disconnected but related in a special way; or, alternatively, we may regard them as two different kinds of vector associated with the same vector space. The relationship between η and ξ is precisely the same as that between covariant and contravariant vectors in differential geometry.

If we pass from our original co-ordinate system to a new frame of reference, and the variables η and ξ undergo the non-singular linear transformations,

$$\eta = \phi H, \quad \xi = H^{-1}\psi, \quad |H| \neq 0,$$

it can be seen that since the variables are contragredient, $\eta\xi = \phi\psi$, so that the square of the length of a vector remains invariant. Moreover, since the result of operating on a vector ξ_a with the matrix A is, in general, another vector ξ_b, where ξ_a and ξ_b are both referred to the original co-ordinate system, it follows that in the new frame of reference which is defined by the linear transformations given above, the relationship

$$A\xi_a = \xi_b$$

becomes

$$HAH^{-1}\psi_a = \psi_b,$$

or

$$B\psi_a = \psi_b.$$

Thus, in the new frame of reference the matrix $B = HAH^{-1}$ operating on the vector ψ_a is equivalent to the matrix A operating on the vector ξ_a in the original frame.

It is convenient, for the purposes of studying the matrix A and of performing any numerical computations with it, to transform the variables η and ξ in the above way, choosing the matrix H so as to make $B = HAH^{-1}$ as simple as possible. For $B^t = (HAH^{-1})^t = HA^tH^{-1}$, and since A is non-singular, by the reversal law, $(HAH^{-1})^{-1} = HA^{-1}H^{-1}$. Thus, if $f(A)$ is a rational integral function of A, $f(B) = f(HAH^{-1}) = Hf(A)H^{-1}$; and the properties of matrix functions $f(A)$ can be studied by means of the simpler forms $f(B)$. Moreover, the matrices A and B have the same characteristic equation and, therefore, the same latent roots. For $B - \lambda I = H(A - \lambda I)H^{-1}$ and, forming the determinants of both sides,

$$|B - \lambda I| = |H|\,|A - \lambda I|\,|H|^{-1},$$

so that the characteristic equation is

$$|A - \lambda I| = |B - \lambda I| = 0.$$

If, in the present case, the transforming matrix is taken to be

$$H = \begin{bmatrix} (P_0P_1P_2 \dots P_{k-1}) & . & . & \dots & . & . & . \\ . & (P_1P_2P_3 \dots P_{k-1}) & . & \dots & . & . & . \\ . & . & (P_2P_3 \dots P_{k-1}) & \dots & . & . & . \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ . & . & . & \dots & (P_{k-2}P_{k-1}) & . & . \\ . & . & . & \dots & . & P_{k-1} & . \\ . & . & . & \dots & . & . & 1 \end{bmatrix}$$

in which, it is to be noted, the only numerical elements lie in the principal diagonal and are derived entirely from the life table, then

$$B = HAH^{-1} = \begin{bmatrix} F_0 & P_0F_1 & P_0P_1F_2 & P_0P_1P_2F_3 & \dots & (P_0P_1P_2 \dots P_{k-1})F_k \\ 1 & . & . & . & \dots & . \\ . & 1 & . & . & \dots & . \\ . & . & 1 & . & \dots & . \\ . & . & . & 1 & \dots & . \\ \dots & \dots & \dots & \dots & \dots & \dots \\ . & . & . & . & \dots 1 & . \end{bmatrix}.$$

Comparing this matrix B with the original form A, it can be seen that the latter has been simplified to the extent that the original P_x figures in the principal subdiagonal are now replaced by a series of units, and the matrix A has been reduced to the rational canonical form $B = HAH^{-1}$ (see Turnbull & Aitken, 1932, chap. v). In this way any computations with the matrix A are made easier, and we may work henceforward in terms of ϕ and ψ vectors together with the matrix B, instead of with the original η and ξ vectors, and the matrix A. Any results obtained in this new system of co-ordinates may be transformed back again to the original system whenever necessary. It is evident that by suitably enlarging H the original matrix M may be transformed in a similar way.

This linear transformation of the original co-ordinate system is equivalent biologically to the transformation of the original population we were considering into a new and completely imaginary type which, although intimately connected with the old, has certain quite different properties. Thus, it can be seen from the transformed matrix B that the individuals in this new population, instead of dying off according to age as the original ones did, live until the whole span of life is completed, when they all die simultaneously. This is indicated by the P_x figures being now all equal to unity; an individual alive in the age group x to $x+1$ at $t = 0$ is certain of being alive at $t = 1$, excepting in the last age group of all where none of the individuals will be alive in one unit's time. Accompanying this somewhat radical change in the life table, there is a compensatory adjustment made in the rates of fertility so that the new population has the same inherent power of natural increase (r) as that of the old. This follows from the fact that the latent roots of the matrices A and B are the same, and, as will be shown later, the dominant latent root is closely related to the value of r obtained by the usual methods of computation. Insomuch as the transformation is reversible and $A = H^{-1}BH$, it can be seen that by changing H we could transform the canonical form B, if we wished, into another matrix in which the P_x subdiagonal might be a specified set of

figures derived from some other form of life table. But, for our present purposes, the canonical form B, in which all the P_x figures are units, offers advantages over any other matrix of a similar type owing to the greater ease with which it can be handled.

6. Relation between the canonical form B and the $L_x m_x$ column

The actual computation of the matrix B by way of the steps indicated in the theoretical development is by no means difficult, although it is a somewhat tedious process, particularly if the matrix is of a large order. The numerical elements in the first row of B for the brown rat are given in Table 5 of the Appendix. These values were obtained from the F_x and P_x figures which have already been used in the numerical example in § 3 and which will be found in the same table. Further reflection suggested, however, that instead of first of all obtaining A and then transforming to B, a short cut could be taken which would save labour and which also would tend to eliminate some of the small cumulative errors arising in the longer method.

The series of values P_0, P_0P_1, $P_0P_1P_2$, ..., $(P_0P_1P_2 \dots P_{k-1})$ by which the individual F_x figures are multiplied in order to obtain the first row of B, is essentially a stationary age distribution. For, since by definition,

$$P_x = \frac{L_{x+1}}{L_x},$$

$$(P_0P_1P_2 \dots P_x) = \frac{L_{x+1}}{L_0},$$

where $L_0 = \int_0^1 l_x dx$. Hence the required series of multipliers is given by a stationary age distribution in which only one individual is alive in the age group 0–1. Now, the F_x figures, as defined in § 2, already contain within them some allowance not only for the probability of survival during the first unit of life, but also for the fact that some adult individuals in each age group are dying off during the interval of time 0–1. The process of multiplying F_x by $(P_0P_1P_2 \dots P_{x-1})$ is thus analogous to the formation of the $L_x m_x$ column, by means of which the net reproduction rate is estimated. The chief difference between the first row of B and the $L_x m_x$ distribution is that in the former the maternal frequency is expressed as between the ages of $x+\frac{1}{2}$ to $x+1\frac{1}{2}$, instead of between x to $x+1$ as in the latter. If each element $(P_0P_1P_2 \dots P_{x-1}F_x)$ of the first row of B is regarded as centred at the age of $x+1$, the sum, mean and seminvariants of this 'distribution' may be estimated and compared with the values which are obtained from the $L_x m_x$ column in the process of calculating r by the usual methods. In the present numerical example the results of this comparison were as follows:

Parameter	$L_x m_x$ column	First row of B
Sum (R_0)	25·65786	25·6603
Mean	9·60604	9·5948
m_2	14·14397	14·1839
m_3	22·15696	21·9358
$m_4 - 3m_2^2$	−117·6480	−117·920

After allowing for the small cumulative errors which might be expected to occur in the calculation of the matrix elements, there is a substantial agreement between the respective

estimates. This agreement strongly suggests that if we had wished to pass immediately to the matrix B without going through the laborious process of calculating the F_x and P_x figures, the elements of the first row could have been obtained by forming a new $L_x m_x$ column in which the age group limits were shifted a half unit later in life. This could readily be done by interpolating in the integral curve of the $L_x m_x$ values for the ages $x+\frac{1}{2}$. This method of forming the first row of B has been adopted in other instances, when the matrix A was not of any immediate interest. It proved to be relatively quick and certainly less laborious than the method of first establishing A and then transforming to B which was the one used in the present numerical example.

7. THE STABLE AGE DISTRIBUTION

The result of operating on an age distributon ψ_x with the matrix B is, in general, a different distribution ψ_y. But, in the special case when the relation between the two distributions is such that

$$B\psi_a = \lambda\psi_a,$$

where λ is an algebraic number, then ψ_a may be said to be a stable age distribution appropriate to the matrix B. For the sake of brevity it will be referred to as a stable ψ. Similarly for initial row vectors, if

$$\phi_a B = \lambda\phi_a,$$

then ϕ_a is said to be a stable ϕ.

The matrix equation defining a stable ψ may be written as $k+1$ linear equations, of which the ith is

$$\sum_{j=1}^{k+1} b_{ij}n_j - \lambda n_i = 0,$$

where n_i $(i = 1, 2, \ldots, k+1)$ are the co-ordinates of the stable ψ, and b_{ij} the element in the ith row and jth column of B. Eliminating the n_i from this system of equations, we obtain the characteristic equation of B, namely,

$$|B - \lambda I| = 0;$$

and, expanding this determinant in powers of λ, we have in the present case,

$$\lambda^{k+1} - F_0\lambda^k - P_0F_1\lambda^{k-1} - P_0P_1F_2\lambda^{k-2} - \ldots - (P_0P_1\ldots P_{k-2})F_{k-1}\lambda - (P_0P_1\ldots P_{k-1})F_k = 0.$$

The $k+1$ roots λ_a of this equation are the latent roots of B, and corresponding to each distinct λ_a there is a pair of stable vectors, ϕ_a and ψ_a, determined except for an arbitrary scalar factor.

Once a latent root λ_a has been determined, it is a comparatively simple matter to find the appropriate stable ψ_a and ϕ_a vectors. Thus, it is easily shown that the stable ψ_a is the column vector $\{\lambda_a^k \lambda_a^{k-1} \lambda_a^{k-2} \ldots \lambda_a 1\}$. A short method of estimating ϕ_a is the following. Suppose, to take a simple case, that

$$B = \begin{bmatrix} a & b & c & d \\ 1 & . & . & . \\ . & 1 & . & . \\ . & . & 1 & . \end{bmatrix}$$

and let y_x $(x = 1, 2, 3, 4)$ be the elements of the stable ϕ_a appropriate to the root λ_a. Then

$$\begin{aligned} \phi_a B &= [ay_1 + y_2 \quad by_1 + y_3 \quad cy_1 + y_4 \quad dy_1] \\ &= [\lambda_a y_1 \quad \lambda_a y_2 \quad \lambda_a y_3 \quad \lambda_a y_4]. \end{aligned}$$

By equating similar elements and putting $y_1 = 1$, $y_4 = d/\lambda_a$, $y_3 = \dfrac{c+y_4}{\lambda_a}$, etc., it is easy to see how the required row vector can be built up. Having in this way obtained the stable ψ and ϕ vectors for the matrix B, they may be transformed to the appropriate stable ξ and η for the matrix A by means of the relations

$$\eta = \phi H, \quad \xi = H^{-1}\psi.$$

The characteristic equation of the matrix B, when expanded, is of degree $k+1$ in λ, and once B has been obtained this equation can immediately be written down, since the numerical coefficients of $\lambda^k, \lambda^{k-1}, \lambda^{k-2}$, etc., are merely the elements of the first row taken with a negative sign. Since there is only one change of sign in this equation, only one of the latent roots will be real and positive. Excluding the rather special case when the first row of B has only a single non-zero element, and taking the more usual type of matrix which will be met with, namely, that for a species breeding continuously over a large proportion of its total life span, it will be found that the modulus of this root (λ_1) is greater than any of the others,

$$|\lambda_1| > |\lambda_2| > |\lambda_3| > \ldots > |\lambda_{k+1}|,$$

the remaining roots being either negative or complex.

This dominant latent root λ_1, which will be $\gtreqless 1$ according as to whether the sum of the elements in the first row of B is $\gtreqless 1$, is the one which is principally of interest. Since it is real and positive, it is the only root which will give rise to a stable ψ or ξ vector consisting of real and positive elements. It is this stable ξ_1 associated with the dominant root λ_1 which is ordinarily referred to as the stable age distribution appropriate to the given age specific rates of fertility and mortality. Since

$$A^t\xi_1 = \lambda_1^t \xi_1,$$

it can be seen that the latent root λ_1 of the matrix A and the value of r obtained in the usual way from

$$\int_0^\infty e^{-rx} l_x m_x dx = 1,$$

are related by

$$\log_e \lambda_1 = r.$$

From the mathematical point of view, however, the negative and complex roots of the characteristic equation are of importance in the further theoretical development. Moreover, as will be shown later, the stable vectors associated with them are not entirely without interest. Two main cases then arise: when the remaining roots are all distinct, and when there are repeated roots. For the present it will be assumed that the latent roots of the matrix are all distinct.

8. Properties of the stable vectors

Before proceeding further it is necessary to mention briefly the reasons why the methods given above for the computation of the stable ψ and ϕ vectors were adopted, apart from their simplicity in practice. If the $k+1$ distinct roots of the characteristic equation are known, we may form a set of $k+1$ matrices $f(\lambda_a)$ by inserting in turn the numerical value of each root in the matrix $[B-\lambda_a I]$. The adjoint of $f(\lambda_a)$ is

$$F(\lambda_a) = \prod_{b \neq a} [B-\lambda_b I] \quad \text{and} \quad f(\lambda_a)\, F(\lambda_a) = 0.$$

It may be shown that the stable ψ_a appropriate to the root λ_a can be taken proportional to any column, and the stable ϕ_a proportional to any row of the matrix $F(\lambda_a)$ (see e.g. Frazer, Duncan & Collar, 1938, chap. III). Moreover, $F(\lambda_a)$ is a matrix product of the type $\psi\phi$,

where the ψ vector is given by the first column and the ϕ vector by the last row of $F(\lambda_a)$, each divided by the square root of the element in the bottom left-hand corner; and the trace of the matrix is equal to the scalar product $\phi\psi$. Now $[B-\lambda_a I]$ is a square matrix of order $k+1$ with only zero elements below and to the left of the principal subdiagonal, which itself consists of units. The product of k such matrices, which gives $F(\lambda_a)$, will have therefore a unit in the bottom left-hand corner. Since the stable ϕ_a and ψ_a vectors obtained by the methods suggested in § 7 have respectively their first and last elements $= 1$, it follows that

$$\psi_a\phi_a = F(\lambda_a), \quad \phi_a\psi_a = \text{trace } F(\lambda_a).$$

The stable vectors may now be normalized. If the scalar product, $\phi_a\psi_a = z^2$, say, then

$$\frac{\phi_a}{|z|}\frac{\psi_a}{|z|} = 1.$$

From now on it will be assumed that the stable vectors appropriate to each of the latent roots have been normalized in this way.

These vectors have the following important properties:

(1) The $k+1$ stable ψ are linearly independent. There is thus no such relationship, with non-zero coefficients c, as

$$c_1\psi_1 + c_2\psi_2 + c_3\psi_3 + \ldots + c_{k+1}\psi_{k+1} = 0.$$

(2) The scalar product of a stable ψ, ψ_a with the associated vector of another stable ψ, ψ_b is zero, i.e.

$$\phi_b\psi_a = 0 \quad (a \neq b).$$

The normalized stable ψ thus form a set of $k+1$ independent and mutually orthogonal vectors of unit length.

(3) Any arbitrary ψ—ψ_x say—can be expanded in terms of the stable ψ, thus

$$\psi_x = c_1\psi_1 + c_2\psi_2 + c_3\psi_3 + \ldots + c_{k+1}\psi_{k+1},$$

where the coefficients c may be either real or complex. Similarly an arbitrary vector ϕ_x can be expanded in terms of the stable ϕ.

9. THE SPECTRAL SET OF OPERATORS

The matrix product $\psi_a\phi_a$ of the normalized stable vectors associated with the latent root λ_a will be termed the matrix S_a. From the relationships which have already been given, it can be seen that S_a is merely the adjoint matrix $F(\lambda_a)$ of the previous section after each element in the latter has been divided by the sum of the elements in the principal diagonal; in other words it is the normalized $F(\lambda_a)$. In the case of all the latent roots being distinct, there are thus $k+1$ matrices S_a, and these S_a form a spectral set of operators with the following properties:

$$S_a^2 = S_a, \quad S_aS_b = 0 \quad (a \neq b), \quad \sum_{a=1}^{k+1} S_a = I.$$

Moreover, if $f(B)$ is a polynomial of the matrix B, we have by Sylvester's theorem (Turnbull & Aitken, 1932, chap. VI, § 8)

$$f(B) = \sum_{a=1}^{k+1} f(\lambda_a)\, S_a,$$

so that the matrix

$$B = \lambda_1 S_1 + \lambda_2 S_2 + \ldots + \lambda_{k+1} S_{k+1}, \quad \text{and} \quad B^t = \lambda_1^t S_1 + \lambda_2^t S_2 + \ldots + \lambda_{k+1} S_{k+1}.$$

If the latent roots in the expansion of B are raised to a high power, the term associated with the positive real root predominates over all the others, so that when t is large, we have approximately

$$B^t = \lambda_1^t S_1.$$

In any particular case the power to which B will have to be raised in order that this equation should be approximately true, will depend both on the order of the matrix and on the relative magnitude of the dominant root as compared with that of the remaining roots.

At this point it is possible to attach some biological meaning to one of the ϕ or η row vectors, which in the first place were introduced into the theory for reasons of symmetry, and which were defined solely in terms of their mathematical properties. If at a given moment a transformed population has an arbitrary age distribution ψ_x, and the sequence $B\psi_x, B^2\psi_x, \ldots, B^t\psi_x$ is formed, it can be seen that when t is large and ψ_x is expanded in terms of the stable ψ, we have approximately

$$B^t\psi_x = c_1\lambda_1^t\psi_1.$$

Thus, a population with any arbitrary age distribution tends ultimately to approach the stable form appropriate to the given rates of fertility and mortality, provided that these age-specific rates remain constant. This theorem is, of course, well known; and it is clear that the achievement of the stable form of age distribution associated with the dominant latent root is very unlikely to occur in practice, except in the case when the initial distribution is already of that form or exhibits only small departures from it. Now, it has already been shown that the sums of the columns of a matrix B^t provide a measure of the contributions made to the population at time t per individual alive in the respective age groups at $t = 0$. When t is large, the matrix B^t is equivalent to the matrix S_1 multiplied by a scalar factor. From the way in which this latter matrix was constructed by the outer multiplication of ψ_1 and ϕ_1, it is evident that the sums of the columns of S_1 are proportional to the vector ϕ_1. Thus, transforming back again to the original co-ordinate system, the stable η_1 associated with the dominant latent root provides a measure of the relative contributions per head made to the stable population by the individual age groups.

10. Reduction of B to classical canonical form

From the $k+1$ stable ψ a matrix Q can be constructed, whose columns are the stable ψ arranged, reading from left to right, in descending order of the moduli of the roots with which they are associated. Corresponding to every pair of complex roots, $u \pm iv$, there will be in this matrix a pair of columns consisting of complex elements, the one column being the conjugate complex of the other. Some of the columns associated with the negative roots may be purely imaginary owing to the normalization of the corresponding ψ and ϕ vectors. In a similar way a matrix U may be formed, whose rows, reading from above down, are the stable ϕ arranged in the same order. Since the stable ϕ and ψ are normalized, and $\phi_a\psi_b = 0$ for $a \neq b$,

$$UQ = I,$$

and, therefore, U and Q are reciprocal matrices. By premultiplying and postmultiplying respectively with U and Q, the matrix B may be reduced to the classical canonical form C, in which the only elements lie in the principal diagonal and consist of the latent roots arranged in the order prescribed above. This reduction of B to a purely diagonal form by means of the collineatory transformation $UBQ = C$ is, however, only possible in the type of matrix we are considering, when the latent roots are all distinct.

The expansion of an arbitrary ψ_x in terms of the stable ψ,

$$\psi_x = c_1\psi_1 + c_2\psi_2 + \ldots + c_{k+1}\psi_{k+1},$$

may be written in matrix notation as $\psi = Qc$,

where c is the column vector $\{c_1 c_2 c_3 \ldots c_{k+1}\}$. Similarly, the expansion of the vector ϕ_x associated with ψ_x may be written $\phi = dU$,

where d is the row vector $[d_1 d_2 d_3 \ldots d_{k+1}]$. This is again a transformation to another co-ordinate system, but this time the reference axes are at right angles to one another. Since the variables transform contragrediently, $dc = \phi\psi = \eta\xi$. At this point it is necessary to make some assumption as to the relationship between the elements of the vectors d and c. Since these elements may be either real or complex, it will be assumed that

$$d = \bar{c}',$$

where the row vector $\bar{c}'$ is the transposed conjugate complex of the column vector c. Hence, the square of the length of a vector referred to this orthogonal co-ordinate system is given by $\bar{c}'c$, a number which is essentially real and non-negative. (The assumption that $d = c'$ will be found, in the particular case studied here, to lead to values of $c'c$ which, although real, may be negative.)

11. THE RELATION BETWEEN ϕ AND ψ VECTORS

Since $\psi_x = Qc_x$, and the associated $\phi_x = \bar{c}_x' U$, it may be seen from the relations given in the two previous sections that $\bar{\phi}_x' = \bar{U}'U\psi_x = G\psi_x$.

The matrix $G = \bar{U}'U$ is symmetrical and all its elements are real numbers, those in the principal diagonal being necessarily positive in sign. It therefore remains unaltered after transposition. Since the elements of the vector ψ_x, which is by definition an age distribution transformed by the matrix H, are also necessarily real, we may write

$$\phi_x = \psi_x' G.$$

The role of the matrix G is therefore the same as that of the double covariant metric tensor g_{mn} in the tensor calculus. It transforms any ψ vector into its associated ϕ vector. This process is reversible, the reciprocal matrix being given by $G^{-1} = Q\bar{Q}'$.

The magnitude of a vector ψ_x is defined by the equation

$$x = (\psi_x' G\psi_x)^{\frac{1}{2}},$$

where the square root is taken with a positive sign. If we have two vectors ψ_x and ψ_y, both radiating from the common origin, the angle between them is given by

$$\cos\theta = \frac{\psi_x' G\psi_y}{xy},$$

from which it follows that when $\psi_x' G\psi_y = \phi_x\psi_y = 0$, the two vectors are at right angles to one another, and when $\cos\theta = 1$ their directions are the same. If, in the last equation, we take ψ_y to be the stable vector ψ_1 associated with the dominant latent root λ_1, then knowing the magnitude of a vector $B^t\psi_x$ and the angle which it makes with the ψ_1 axis, we can obtain a graphical representation of the way in which a particular age distribution approaches the stable form.

The matrix G also defines the angles between the reference axes of the co-ordinate system. If we introduce into the vector space of the ψ's a system of reference axes defined by the unit column vectors

$$\begin{aligned} e_1 &= \{1 \quad 0 \quad 0 \quad \dots \quad 0\} \\ e_2 &= \{0 \quad 1 \quad 0 \quad \dots \quad 0\} \\ e_3 &= \{0 \quad 0 \quad 1 \quad \dots \quad 0\} \\ &\vdots \\ e_{k+1} &= \{0 \quad 0 \quad 0 \quad \dots \quad 1\} \end{aligned}$$

then the distance from the origin of the unit point e_j is

$$Oe_j = \sqrt{g_{jj}},$$

and the angle between any two of the co-ordinate axes is given by

$$\cos\theta_{ij} = \frac{g_{ij}}{\sqrt{(g_{ii}g_{jj})}},$$

where, in both cases, g_{ij} is the element in the ith row and jth column of G.

By transforming back to the original co-ordinate system, the metric matrix associated with the vector space of the ξ's will be found to be

$$G_\xi = HG_\psi H.$$

Hitherto we have been chiefly concerned with an operator B which, acting in the vector space of the ψ's, has the power of transforming a vector ψ_x into what is in general a new vector ψ_y. We may now have reason to inquire how the associated vectors ϕ_x and ϕ_y are related in the vector space of the ϕ's, whenever

$$B\psi_x = \psi_y.$$

Since $$\psi_x = G^{-1}\phi_x' \quad \text{and} \quad \psi_y = G^{-1}\phi_y',$$

we have $$GBG^{-1}\phi_x' = \phi_y',$$

and hence, by transposing,

$$\phi_x G^{-1}B'G = \phi_y.$$

Thus, the matrix which transforms ϕ_x into ϕ_y is not the same as that which transforms ψ_x into ψ_y. In order to distinguish these two operators, they will be referred to as B_ϕ and B_ψ respectively. In the few numerical examples which have been worked out, the matrix B_ϕ differed greatly from the rational canonical form B_ψ, and consisted of $(k+1)^2$ real elements, some of which were negative. In addition to the relationship

$$B_\phi = G^{-1}B_\psi' G,$$

it was also found that in the case of distinct latent roots

$$B_\phi = \bar{\lambda}_1 S_1 + \bar{\lambda}_2 S_2 + \bar{\lambda}_3 S_3 + \dots + \bar{\lambda}_{k+1} S_{k+1},$$

where the S_a matrices are the spectral set of operators defined in § 9 and $\bar{\lambda}_a$ is the conjugate complex of the latent root λ_a. It may be seen from this expansion of B_ϕ that the necessary condition for $B_\phi = B_\psi$ is that all the latent roots of B should be real, the one positive and the remainder negative. (It is to be noted that we are dealing here with the case of distinct latent roots; it would appear that even if all the λ were real, $B_\phi \neq B_\psi$ in the case of repeated roots.) Unless, however, the matrix B is of a small order, it is unlikely that this condition would be fulfilled, since in the more usual-sized matrix we shall be dealing with in the case

of human or other mammalian populations, some of the roots will almost certainly be complex.*

It seems unlikely that the equations given in this section will have very much practical application at the moment; they have been included merely to fill in the picture of the relationship between the two types of vector. For all ordinary purposes no one would choose to work in terms of ϕ vectors and the operator B_ϕ, instead of the more obvious ψ vectors and the more simple matrix form B_ψ. Nevertheless, since it has been necessary to assume that there are such vectors as η or ϕ associated with every ξ or ψ, and since these vectors play such an important part in the mathematical theory, the question naturally arises as to what significance must be attached to them from the biological point of view. Have they in fact any real meaning at all? Or must they be regarded purely as mathematical abstractions? At the end of § 9 it has been suggested that the row vector associated with the stable ξ_1 appropriate to the dominant latent root is a measure of the contributions made to the stable population per individual female alive in the respective age groups of the initial distribution; but this is a special case and the interpretation offered here is not applicable, even in a wider form, to η vectors in general. It may well be, of course, that the latter as a class have no concrete meaning: and that in seeking to define them in terms of some property or characteristic of an age distribution one is merely attempting the impossible. But the fact of one η vector having been defined in non-mathematical terms, even though on further consideration some revision may be needed of the actual definition given here, suggests that impossible may perhaps be too final a word to use in this connexion.

12. CASE OF REPEATED LATENT ROOTS

When any of the latent roots other than the real positive dominant root are repeated, a number of the relations given in the previous sections no longer hold good and certain equations must therefore be modified. Suppose a root λ_a has a multiplicity s, and consider the matrix $f(\lambda_a)$ such as, to take a simple example,

$$f(\lambda_a) = \begin{bmatrix} a-\lambda_a & b & c & d \\ 1 & -\lambda_a & 0 & 0 \\ 0 & 1 & -\lambda_a & 0 \\ 0 & 0 & 1 & -\lambda_a \end{bmatrix}.$$

Then, since the determinant $|f(\lambda_a)| = 0$ and at least one of the first minors of order 3 is not equal to zero, the above matrix has rank 3 and, therefore, nullity 1. Hence it can be seen that $f(\lambda_a)$ of whatever order it may be has nullity 1. Since $f(\lambda_a)$ is thus simply degenerate, there is only one stable ψ appropriate to the s equal roots λ_a (see e.g. Frazer, Duncan & Collar, 1938, chap. III).

Certain consequences immediately follow. Since the matrices Q and U cannot be constructed in the way given in § 10, the reduction of B to a purely diagonal matrix by means of the collineatory transformation UBQ can no longer be carried out. Neither is the expansion of B in terms of the spectral set of S_a matrices, nor the expansion of an arbitrary ψ_x

* The interesting theoretical case of the matrix A or B having a number of its latent roots real and positive, with the remainder real and negative, is outside the scope of the present study. The necessary conditions for this to be true would involve a number of the F_x figures becoming negative, a case not considered here, but which biologically might be held to correspond with the destruction of eggs, or the very young, by certain age groups, e.g. as observed by Chapman (1933) in experimental populations of the flour beetle, *Tribolium confusum*.

in terms of the stable ψ, possible in the actual forms given in §§ 9 and 8. We may, however, proceed as follows.

The matrix Q is essentially an alternant which has been postmultiplied by a diagonal matrix N, the elements in the latter being given by the reciprocals of the scalar factors $|z|$ by which the stable vectors were divided in the process of normalization $\left(\frac{\phi_a}{|z|}\frac{\psi_a}{|z|} = 1\right)$, so that $Q = XN$, where

$$X = \begin{bmatrix} \lambda_1^k & \lambda_2^k & \dots & \lambda_{k+1}^k \\ \lambda_1^{k-1} & \lambda_2^{k-1} & \dots & \lambda_{k+1}^{k-1} \\ \vdots & \vdots & & \vdots \\ \lambda_1 & \lambda_2 & \dots & \lambda_{k+1} \\ 1 & 1 & \dots & 1 \end{bmatrix}.$$

When a root λ_a is repeated s times, s of the columns in X become the same, and therefore the matrix becomes singular. In place of this alternant matrix we have the confluent alternant form (see Turnbull & Aitken, 1932, chap. VI) in which the s columns ($s = 0, 1, 2, 3, \dots, s-1$) corresponding to the repeated root λ_a are written

$$\begin{array}{llll} \lambda_a^k & k\lambda_a^{k-1} & \frac{k(k-1)\lambda_a^{k-2}}{2!} & \dots \\ \lambda_a^{k-1} & (k-1)\lambda_a^{k-2} & \frac{(k-1)(k-2)}{2!}\lambda_a^{k-3} & \dots \\ \vdots & \vdots & \vdots & \dots \\ \vdots & \vdots & 3\lambda_a & \dots \\ \vdots & 2\lambda_a & 1 & \dots \\ \lambda_a & 1 & 0 & \dots \\ 1 & 0 & 0 & \dots \end{array}$$

the column s being obtained from column 0 (the non-normalized stable ψ_a) by the operation $\left(\frac{d}{d\lambda_a}\right)^s \Big/ s!$. This confluent alternant form of X is non-singular and therefore a reciprocal matrix can be determined (see Aitken, 1939, § 50). The general classical canonical form of B obtained by the collineatory transformation, $X^{-1}BX = C$, has corresponding to the repeated root λ_a a diagonal submatrix:

$$\begin{bmatrix} \lambda_a & 1 & . & . & . & . \\ . & \lambda_a & 1 & . & . & . \\ . & . & \lambda_a & 1 & . & . \\ \dots & \dots & \dots & \dots & \dots & \dots \\ . & . & . & . & \lambda_a & 1 \\ . & . & . & . & . & \lambda_a \end{bmatrix}.$$

The matrix product of a column of X with the appropriate row of the reciprocal X^{-1} gives as before S_a and the $k+1$ S_a form a spectral set with the same properties as those defined in § 9, except that

$$B \neq \sum_{a=1}^{k+1} \lambda_a S_a.$$

In place of this expansion of B in terms of the S_a matrices, we have in the case of repeated roots the confluent form of Sylvester's theorem, for details of which reference may be made to Frazer, Duncan & Collar, 1938, chap. III. Apart from this modification, however, we may obtain by inspection of the S_a the factors by which the respective columns of X must be divided in order to express this matrix in a form comparable to that of Q in § 10. Similarly, when the respective rows of X^{-1} are multiplied by the appropriate factors, the matrix U is found and hence $G = \overline{U}'U$ can be constructed. (It is to be noted that $(\overline{X^{-1}})' X^{-1}$ is neither equal to, nor directly proportional to $\overline{U}'U$.) An arbitrary ψ_x can be expanded in terms of the column vectors of Q, though in the case of only one column associated with the repeated root λ_a does the relationship $B\psi_a = \lambda_a \psi_a$ hold.

13. THE APPROACH TO THE STABLE AGE DISTRIBUTION

A stable age distribution appropriate to the matrix B has been defined mathematically by the equation

$$B\psi = \lambda\psi,$$

and it has already been shown that since only one latent root of B is real and positive, only one of the stable ψ will consist of real and positive elements. But, in addition to this Malthusian age distribution, it is also of some interest to inquire whether any significance can be attached to the remaining stable ψ associated with the negative and complex roots of the characteristic equation.

Any age distribution ψ_x, the elements of which are necessarily $\geqq 0$, may be expressed as a vector of deviates from the stable ψ_1 associated with the dominant latent root, and we may therefore write the expansion of ψ_x in terms of the stable ψ as

$$(\psi_x - c_1\psi_1) = c_2\psi_2 + c_3\psi_3 + \ldots + c_{k+1}\psi_{k+1} = \psi_d,$$

where the coefficients c are given by the vector $c = U\psi_x$. Thus, the way in which a particular type of age distribution will approach the stable form may be studied by means of the vector ψ_d.

Among the terms occurring in the right-hand side of this expression there will be, corresponding to each negative root, a single term $c_a\psi_a$ which will consist of real elements alternately positive and negative in sign. (Even if the normalized ψ_a is imaginary this term will consist of real numbers, since in this case c_a will also become imaginary.) Moreover, corresponding to every pair of complex roots there will be a pair of terms $(c_m\psi_m + c_n\psi_n)$ which taken together will also give a single vector with real elements. This follows from the fact that c_m is the conjugate complex of c_n owing to the way in which the matrix U is constructed. Then, apart from the scalar c_1 which must necessarily be > 0, some of the remaining coefficients $c_2, c_3, \ldots, c_{k+1}$ in the expansion of ψ_d may be zero. The first and most obvious case is when they are all zero, and the age distribution ψ_x is therefore already of the stable form. But, if either

$$\psi_d = c_a\psi_a,$$

where ψ_a corresponds to a negative latent root, or

$$\psi_d = c_m\psi_m + c_n\psi_n,$$

where ψ_m and ψ_n are associated with a conjugate pair of complex roots, then it follows that the age distribution ψ_x will, as time goes on, approach the stable form in a particular way defined by either

$$B^t\psi_d = c_a\lambda^t\psi_a \quad \text{or} \quad B^t\psi_d = c_m\lambda^t\psi_m + c_n\overline{\lambda}^t\psi_n,$$

in which λ^t for a pair of complex roots $u+iv$ with modulus r may be written in the form of $r^t(\cos\theta t \pm i\sin\theta t)$. Thus, the negative and complex latent roots of B serve to determine a number of age distributions which are of some interest owing to the fact that they will approach the Malthusian form in what may be termed a stable fashion.

Since $|\lambda_1| > |\lambda_2| > |\lambda_3| > \ldots > |\lambda_{k+1}|$, the vector of deviates ψ_d will tend towards zero as $t \to \infty$ whenever $\lambda_1 \gtrless 1$. Thus, in the case of a stationary population, any ψ_x will converge to the stable form of age distribution. But if $\lambda_1 > 1$, there is a possibility of one or more of the remaining roots having a modulus $\geqq 1$, e.g. $|\lambda_2| \geqq 1$. In the latter case there may be certain age distributions with $c_2 \neq 0$ for which the amplitude of the deviations from the stable form tend either to increase ($|\lambda_2| > 1$), or to remain constant ($|\lambda_2| = 1$). From the practical point of view, however, we may still say that a population with such an age distribution approaches or becomes approximately equal to the stable population, since λ_1^t is much greater than λ_2^t when t is large.

14. Special case of the matrix with only a single non-zero F_x element

The interesting case of the matrix A having only a single non-zero element in the first row has been illustrated in a numerical example by Bernardelli (1941).* This author has also used a matrix notation in the mathematical appendix to his paper, and the form of his basic matrix is the same as that referred to here as M or A. It is not clear, however, from the definitions which he gives whether he regards the elements in the first row of his matrix as being constituted by the maternal frequency figures (m_x) themselves, or by a series of values similar to those defined here as the F_x figures. He refers to them merely as the specific fertility rates for female births.

In discussing the causes of population waves, Bernardelli describes a hypothetical species, such as a beetle, which lives for only three years and which propagates in the third year of life. He assumes, for the sake of argument, that—to employ the terminology used here—$P_0 = \frac{1}{2}$ and $P_1 = \frac{1}{3}$, and that 'each female in the age 2–3 produces, on the average, 6 new living females'. Assuming for the moment that he is here defining a F_x figure, we may write this system of mortality and fertility rates as

$$A = \begin{bmatrix} 0 & 0 & 6 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{bmatrix}, \quad B = HAH^{-1} = \begin{bmatrix} 0 & 0 & 1 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{bmatrix}.$$

The characteristic equation expanded in terms of λ is $\lambda^3 - 1 = 0$; and the latent roots are therefore 1, $-\frac{1}{2} \pm \frac{\sqrt{3}}{2}i$, all three being of equal modulus. The matrix A has the interesting properties

$$A^2 = A^{-1}, \quad A^3 = I,$$

so that any initial age distribution repeats itself regularly every three years. Thus, as Bernardelli shows, a population of 3000 females distributed equally among the three age

* At this point I should like to acknowledge the gift of a reprint of this paper, which was received by the Bureau of Animal Population at a time when I was in the middle of this work, and when I was just beginning to appreciate the interesting results which could be obtained from the use of matrices and vectors: also a personal communication from Dr Bernardelli, received early in 1942, at a time when it was difficult to reply owing to the developments of the war situation in Burma. Although the problems we were immediately interested in differed somewhat, this paper did much to stimulate the theoretical development given here, and it is with great pleasure that I acknowledge the debt which I owe to him.

groups becomes a total population of 6833 at $t = 1$; of 5166 at $t = 2$; and again 3000 distributed equally among the age groups at $t = 3$. Unless a population has already an initial age distribution in the ratio of $\{6:3:1\}$, no approach will be made to the stable form associated with the real latent root, and the vector of deviates ξ_d will continue to oscillate with a stable amplitude, which will in part depend on the form of the initial distribution. Although this numerical example refers specifically to a stationary population, it is evident that a similar type of argument may be developed in the case when $|\lambda| > 1$ and $A^3 = \lambda^3 I$.

We have assumed here that his definition of the fertility rate refers to a F_x figure. But, if we were to interpret the words quoted above as referring to a maternal frequency figure, namely that every female alive between the ages 2–3 produces on the average 6 daughters per annum, then the results become entirely different. For, deriving the appropriate F_x figures by the method described in § 2, the matrix is now

$$A = \begin{bmatrix} 0 & 1 & 3 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{bmatrix}, \quad B = HAH^{-1} = \begin{bmatrix} 0 & \frac{1}{2} & \frac{1}{2} \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{bmatrix},$$

and the latent roots are $1, -\frac{1}{2} \pm \frac{1}{2}i$. The modulus of the pair of complex roots is $1/\sqrt{2}$, which is < 1, so that every age distribution will now converge to the stable form associated with the real root. Thus, to take the same example as before, 3000 females distributed equally among the age groups will tend towards a total population of 4000 distributed in the ratio of $\{6:3:1\}$, and it was found that this age distribution would be achieved at approximately $t = 23$. During the approach to this stable form periodic waves are apparent both in the age distribution and in the total number of individuals, but these oscillations are now damped, in contrast with the results obtained with the first type of matrix.

This simple illustration serves to emphasize the importance which must be attached to the way in which the basic data are defined and to the marked difference which exists between what are termed here the m_x and F_x figures. Nevertheless, apart from the question of the precise way in which the definition of the fertility rates is to be interpreted in this example, the first type of matrix with only a single element in the first row does correspond to the reproductive biology of certain species. Thus, in the case of many insect types the individuals pass the major portion of their life span in various immature phases and end their lives in a short and highly concentrated spell of breeding. The properties of this matrix suggest that any stability of age structure will be exceptional in a population of this type, and that even if the matrix remains constant we should expect quite violent oscillations to occur in the total number of individuals.

15. Numerical comparison with the usual methods of computation

From the practical point of view it will not always be necessary to estimate the actual values of all the stable vectors and of the associated matrices which are based on them. Naturally, much will depend on the type of information which is required in any particular case. In order to compute, for instance, the matrices U, Q and G, it is necessary first of all to determine all the latent roots of the basic matrix. The ease with which these may be found depends very greatly upon the order of the matrix. Thus, in the numerical example for the brown rat used previously in § 3, the unit of age and time is one month and the resulting square matrix A is of order 21. To determine all the 21 roots of the characteristic equation would be

a formidable undertaking. It might be sufficient in this case to estimate the positive real root and the stable vector associated with it. On the other hand, it is possible to reduce the size of the matrix by taking a larger unit of age, and in some types of problem, where extreme accuracy is not essential, a unit say three times as great might be equally satisfactory, which would reduce the matrix for the rat population to the order of 7×7. It is not too difficult to find all the roots of a seventh degree equation by means of the root-squaring method (Whittaker & Robinson, 1932, p. 106). But the reduction of the matrix in this way will generally lead to a value of the positive real root which is not the same as that obtained from the larger matrix, and it is therefore necessary to see by how much these values may differ owing to the adoption of a larger unit of time.

Another important point which must be considered is the following. By expressing the age specific fertility and mortality rates in the form of a matrix and regarding an age distribution as a vector, an element of discontinuity is introduced into what is ordinarily taken to be a continuous system. Instead of the differential and integral calculus, matrix algebra

Table 2

Age group (units of 30 days)	'True' stable age distribution	Matrix stable age distribution	Age group (units of 30 days)	'True' stable age distribution	Matrix stable age distribution
0–	37,440	37,362	12–	161	160
1–	22,595	22,644	13–	101	101
2–	14,417	14,444	14–	64	63
3–	9,227	9,238	15–	40	40
4–	5,903	5,906	16–	25	24
5–	3,775	3,775	17–	15	15
6–	2,413	2,412	18–	9	9
7–	1,542	1,540	19–	6	5
8–	984	982	20–	3	3
9–	627	626			
10–	399	398			
11–	254	253	Total	100,000	100,000

is used, a step which leads to a great economy in the use of symbols and consequently to equations which are more easily handled. Moreover, many quite complicated arithmetical problems can be solved with great ease by manipulating the matrix which represents the given system of age specific rates. But the question then arises whether these advantages may not be offset by a greater degree of inaccuracy in the results as compared with those obtained from the previous methods of computation. It is not easy, however, to settle this point satisfactorily. In the way the usual equations of population mathematics are solved, a similar element of discontinuity is introduced by the use of age grouping. Thus, in the case of a human population, if we were estimating the inherent rate of increase in the ordinary way, we should not expect to obtain the same value of r from the data grouped in five year intervals of age as that from the data grouped in one year intervals. The estimates of the seminvariants would not be precisely the same in both cases. Nevertheless, the estimate from the data grouped in five year intervals is usually considered to be sufficiently accurate for all ordinary purposes, and there is little doubt that if we merely require the inherent rate of increase and the stable age distribution, these methods of computation are perfectly satisfactory when applied to human data. But, in the case of rodents, and probably also

other species with high gross and net reproduction rates, it will be found that even a 4th degree equation in r with the coefficients based on the seminvariants of the $L_x m_x$ distribution is, in many examples, not sufficient to give an accurate estimate of the rate of increase, and it is necessary to arrive at a better value of r in a somewhat roundabout way. Here, the determination of the positive real root of the characteristic equation for the matrix, once the latter has been established, may be even quicker than finding a solution from the $L_x m_x$ column by a method such as that described in the appendix.

In order to compare the values of r obtained from the characteristic equation of the matrix with those obtained from the $L_x m_x$ column, both methods were used in the numerical example for the brown rat, and a comparison was also made between the values when the data were grouped in 1 month and in 3 month age intervals. In addition, the stable age distribution appropriate to the positive real root of the matrix was also calculated in both cases. The results were as follows.

(*a*) *One month unit of grouping; matrix of order* 21×21. Using the method of computation indicated in the appendix, the value of r was estimated to be 0·44565 per month of 30 days. The positive real root of the characteristic equation was $\lambda_1 = 1{\cdot}56246$, whence $r = 0{\cdot}44626$, a value which differs from the former only in the fourth decimal place. The appropriate age distributions, expressed per 100,000, are given in Table 2, the 'true' stable being obtained from

$$n_x = 100{,}000b\int_x^{x+1} e^{-rx} l_x \, dx.$$

The agreement between these distributions is very good, although the one derived from the matrix shows certain small rhythmical departures from the 'true' distribution particularly in the earlier age groups. The maximum difference between them in this region, however, is not greater than 2·2 per thousand. Since the matrix stable distribution is proportional to the columns of the matrix $H^{-1}S_1H$, which in turn is proportional to A^t when t is large, this agreement between the two distributions also indicates that the cumulative errors which might be expected in forming the series A^2, A^3, A^4, etc., owing to the P_x figures being based on the life table age distribution, are not very serious. Judging by this example it seems that satisfactory estimates of the inherent rate of increase and of the stable age distribution may be made from a large order matrix.

(*b*) *Three months unit of grouping; matrix of order* 7×7. Clearly there are several ways in which a large order matrix may be condensed into one of a smaller order. The method which was used in the present instance was to construct the first row of the condensed canonical form B by interpolating in the integral curve of the original $L_x m_x$ column (1 month units of grouping) for the ages 4·5, 7·5, 10·5, etc., and taking the first differences of the seven values thus obtained. Since interpolation was not very satisfactory in the earlier part of the integral curve—the differences converged rather slowly in this region—the elements were expressed to only three places of decimals. (Some preliminary transformation of the integral $L_x m_x$ figures might have been better in this case.) The characteristic equation, expanded in terms of λ, was found to be

$$\lambda^7 - 1{\cdot}756\lambda^6 - 6{\cdot}899\lambda^5 - 7{\cdot}203\lambda^4 - 5{\cdot}344\lambda^3 - 3{\cdot}244\lambda^2 - 1{\cdot}110\lambda - 0{\cdot}102 = 0.$$

It will be seen that the sum of the coefficients, $R_0 = 25{\cdot}658$, which is necessarily the same as the original net reproduction rate owing to the way in which the coefficients were derived. For interest, the seven roots of this equation were then determined by the root-squaring

method, using 4-place tables of logarithms and Barlow's tables of squares (Whittaker & Robinson, 1932, p. 110). The approximate values of the roots, arranged in descending order of their moduli, are

$$\begin{aligned}
\lambda_1 &= \ \ 4{\cdot}016, \\
\lambda_2 &= -1{\cdot}032, \\
\lambda_3\lambda_4 &= -0{\cdot}0215 \pm 0{\cdot}6762i \quad (\text{mod.} = 0{\cdot}6765), \\
\lambda_5\lambda_6 &= -0{\cdot}5245 \pm 0{\cdot}3486i \quad (\text{mod.} = 0{\cdot}6298), \\
\lambda_7 &= -0{\cdot}135.
\end{aligned}$$

Thus, apart from the positive real root, there are two negative and two pairs of complex roots. It is interesting to note in passing that in this example the modulus of the second latent root is > 1 (vide § 13). From the value of the dominant root we find $r = 0{\cdot}4634$ per head per month of 30 days, an estimate of the rate of increase which is 1·71 % per month higher than that from the large order matrix.

Table 3. *Stable age distributions*

Age group (in months)	$100{,}000b\int_x^{x+3} e^{-rx} l_x dx$	From condensed matrix	Summation of 'true' distribution
0–	75,960	75,762	74,452
3–	18,055	18,267	18,905
6–	4,514	4,519	4,939
9–	1,120	1,111	1,280
12–	273	267	326
15–	64	61	80
18–	14	13	18
Total	100,000	100,000	100,000

The net reproduction rate given by the new $L_x m_x$ column which was obtained by working in units of three months, was 25·6162, a figure somewhat lower than the original one of 25·6579. The rate of increase, estimated in a similar way to the former example for one month age units, was $r = 0{\cdot}46034$, again a higher figure, though one of much the same order as that obtained from the condensed matrix.

The appropriate age distributions are given in Table 3, together with the 'true' distribution of Table 2 summed in three month age groups.

Compared with the last column, both of the stable distributions for the data grouped in three month age intervals are tilted towards the younger age classes, so that the number of immature females (< 3 months of age) is overestimated, while the remaining age groups are underestimated. The distributions derived from the integral and from the matrix are again of much the same order, and the differences between them and the last column, although not very great, are quite marked.

The four estimates of the inherent rate of increase which have obtained from these numerical data may be compared in the following table.

In both cases the estimates from the $L_x m_x$ column and from the matrix agree very well: for a given unit of grouping both methods would seem to give comparable results. The differences between the estimates made by the same method are much greater, and the effect

of increasing the unit of grouping, and in this way shortening the labour, is to increase the value of r quite appreciably. Whether, or not, we should regard these estimates for the three months age grouping as satisfactory would depend on the degree of accuracy required in any particular calculation. It must be remembered, however, that the basic numerical data are of rather an extreme type in this example. It is doubtful whether any naturally living rat population would have so good a life table and so high a degree of fertility as that assumed for this imaginary population. In fact it was for these very reasons that these data were

	$L_x m_x$ column	Matrix	Difference
1 month age groups	0·44565	0·44626	0·00061
3 „	0·46034	0·4634	0·0031
Difference	0·01469	0·0171	

chosen as the basis of the numerical calculations in this work. For, if it could be shown that the two methods of computation gave comparable results in this case, it was felt that an even better agreement should be obtained in less extreme examples and more particularly with data relating to populations whose rate of increase is nearer to the stationary state. Although in this example the larger unit of grouping leads to rather unsatisfactory estimates of the rate of increase and the stable age distribution, it seems probable that, for the reasons just given, the differences would be less for instance in the case of human data. Hence, the question of the unit to be adopted is likely to become of less importance in the type of data more commonly met with, though it would be necessary to work out an example for such a population in order to check this point.

There is, however, one way to avoid this difficulty of the working unit for populations with a high relative rate of increase. For example, returning to the numerical data used here, supposing that it was necessary in some particular problem to have a fairly high degree of accuracy in the results, but that the work involved in manipulating the large order matrix of 21×21 was too excessive. It might be sufficient in the case we are imagining to know the age distribution of the population in three month age groups at some particular time in the future, which we will take to be a multiple of three. Then, once the real latent root (λ_1) of the large matrix and its associated stable vector have been determined, it is possible to construct a small order matrix of 7×7 which has λ_1^3 as its dominant root and therefore the same real stable age distribution as the larger matrix, only expressed in three month instead of in one month age units. It is convenient to carry out the calculation in terms of the canonical form B and of ψ vectors. Having determined the dominant latent root and the stable vector for the larger matrix, the elements of the first three rows of B^3 are then written down and summed in columns. This can be done very quickly in the present example, where reproduction does not start until the age of 3 months, for the third row of B^3 is the same as the first row of B; the second row is merely the first row of B shifted one age group to the left; and similarly again for the first row. The sums of the columns are then weighted with the number alive in the appropriate age group in the stable population (ψ_1 vector), and by summing the weighted column totals in groups of three and taking the weighted mean, we obtain the elements of the first row of a 7×7 matrix which has λ_1^3 as its domi-

nant latent root. Thus, the characteristic equation of the original matrix condensed in this way was

$$\lambda^7 - 1{\cdot}5056\lambda^6 - 6{\cdot}4694\lambda^5 - 7{\cdot}2047\lambda^4 - 5{\cdot}5371\lambda^3 - 3{\cdot}4537\lambda^2 - 1{\cdot}3451\lambda - 0{\cdot}1447 = 0,$$

and, out of idle curiosity, all the seven roots were extracted in order to compare them with those of the previous example of a condensed matrix. The estimation in this case was carried out to a higher degree of accuracy. The results were:

$$\begin{aligned}
\lambda_1 &= 3{\cdot}81452, \\
\lambda_2 &= -1{\cdot}02526, \\
\lambda_3\lambda_4 &= -0{\cdot}5905 \pm 0{\cdot}3782i \quad (\text{mod.} = 0{\cdot}70125), \\
\lambda_5\lambda_6 &= 0{\cdot}0280 \pm 0{\cdot}6879i \quad (\text{mod.} = 0{\cdot}68847), \\
\lambda_7 &= -0{\cdot}15876.
\end{aligned}$$

The dominant root of the original matrix was 1·56246 and the cube root of λ_1 is 1·56248. The remaining roots may be compared with those given for the previous example. The two negative roots are very similar and, in the second case, the two pairs of complex roots appear to have changed places, the real part of one pair becoming positive instead of negative. Although the cube root of λ_1 is equal to the dominant root of the original matrix, it is unfortunately not true that a similar relationship holds for the remaining six values of λ. There is, for instance, no negative latent root > 1 for the larger form in this actual example.

This point, however, raises an extremely interesting question. For a given series of data a finite matrix of a relatively small order may be constructed, as in the first example given here of a condensed matrix. Supposing that the order of this matrix is increased step by step and that in each case the latent roots are found. Then, in this approach to an infinite matrix, how do the latent roots behave and what relation does the array of roots in each case bear to those of the preceding steps? For the purposes of comparison it will be necessary to express the roots in terms of some suitable unit of time, e.g. per month or per year. So far as the real positive root is concerned, it seems likely that the series of individual roots will approach nearer and nearer to a limiting value. For the root λ_1 is the ratio N_{t+h}/N_t, or the number of times the stable population has increased at the end of the interval of time h. Then, expressing λ_1 in the chosen unit of time, we have $\Lambda_1 = (\lambda_1)^{1/h}$, and taking logarithms;

$$\log_e \Lambda_1 = \frac{\log_e N_{t+h} - \log_e N_t}{h},$$

so that, when the interval of time becomes very small, corresponding to a matrix of a very large order, and $h \to 0$, the right-hand side of this equation approaches the limit $\frac{1}{N}\frac{dN}{dt} = \rho$, the true instantaneous relative rate of increase of the stable population. This argument is put forward with a certain amount of diffidence; it is only too easy for the biologist to overlook some flaw which will be immediately obvious to the trained mathematician. But, even if it were a valid argument for the behaviour of the dominant root, it can hardly be extended in this form to the case of the remaining roots; and thus the main question is left unanswered. From the point of view of the biologist, it would be interesting to know whether with an increase in the size of the matrix the array of secondary roots tends to coalesce round certain values of $\lambda^{1/h}$.

16. FURTHER PRACTICAL APPLICATIONS

If we wish merely to estimate the inherent rate of increase and the stable age distribution appropriate to some system of age specific fertility and mortality rates, there is evidently little to choose between the matrix and the ordinary methods of computation. The advantages of expressing the basic rates in the form of a matrix are more clearly seen in considering the type of problem such as the following. Let us suppose that a species of mammal at a certain season of the year invades a fresh environment where there is an ample food supply, a freedom from predators, and plenty of space to accommodate any rapid increase in numbers which might take place. Under these conditions it might be assumed for theoretical purposes that some age specific rates of fertility and mortality would remain approximately constant over a period of time. The age distribution of these immigrants then becomes of some importance owing to the effect which it must necessarily have on the future course of events. For this initial distribution must clearly be very different from that which would ultimately be established in the case of a species, such as a rodent, with possibly a very rapid rate of increase, since nestlings will not be represented in it and young individuals may be present in only relatively small numbers. Supposing then that we have a number of such populations subject to the same age schedules of fertility and mortality, but differing in the age distribution of the original immigrants, we may have reason to enquire how far the development of these populations is affected over a limited period of time by the varying form of this initial distribution, assuming for simplicity that no further waves of immigration occur.

If an estimate of the number and age distribution of the female population at successive intervals of time is alone required, the answer for any form of initial distribution is readily obtained once the series of matrices M, M^2, M^3, ..., M^t have been constructed. But, in addition, we may require to know the changes which might be expected to occur in the birth rate and death rate, and also, for example, in some such rate as the percentage of adult females pregnant, a figure which is one of the simplest measures we have of the degree of fertility among wild populations. Again, in a species like the wild rat we never know the exact age of individuals caught in the field, and thus the only measure of the form of the female age distribution is the percentage of immature females, provided, of course, we are sampling the complete population. Some method is therefore required for calculating such rates at successive intervals of time.

Once the age distribution of the female population at time t is known, an estimate of the expected number of female births per unit of time may be obtained by operating on the age distribution with the maternal frequency figures. Thus, in matrix notation we may write, the number of female births equals $m_x M^t \xi_0$, where ξ_0 is the initial age distribution and the m_x figures are treated as a row vector. Similarly the estimated number of deaths per unit of time may be obtained with the help of the age specific death rates (D_x). The relative rate of increase calculated in this way is not necessarily exact, but it may be sufficiently accurate for our present purposes. As an example of the degree of error involved in this method, we may compare the values of the stable birth rate and death rate, as given in the appendix, with those derived from the matrix stable distribution in Table 2 by operating with the m_x and D_x figures. The latter were in this case computed from the stationary age distribution and the d_x column of the life table ($D_x = d_x/L_x$). The results were as follows:

	'True' values from appendix	By operating with m_x and D_x on matrix stable distribution
Birth-rate (b)	0·51265	0·51257
Death-rate (d)	0·06700	0·06154
$b-d=r$	0·44565	0·45103

The rate of increase is overestimated by about 5·4 per thousand per month, the principal error being in the death rate. This discrepancy is due to the fact that the number of deaths under 2 months of age is underestimated by applying age specific death rates, which are based on the stationary age distribution, to the stable population grouped in one month intervals at these ages. The difference between these distributions happens to be quite marked in this example. The degree of error, however, is not very great; and in the type of problem we are considering, when the age distribution of a population may take any form, this seems to be the only practical method of estimating the rate of increase.*

Supposing, then that in the case of the rat population used here as a numerical illustration, we wished to estimate the number of females, the birth rate and death rate, and the percentage of immature females at monthly intervals up to—say—7 months from the origin of the time scale, when the initial immigration is assumed to take place. Since the jth column of the matrix gives the age distribution of the survivors and the surviving descendants per individual female alive in the age group $j-1$ to j at $t=0$, the sum of the elements in this column gives the number of times the original population in this age group has increased, or decreased, at time t. The percentage of immature females may be obtained once the sum of the first three elements in the column is known (reproduction begins at the age of 3 months in this example); and the number of births and deaths per unit of time may be found by operating on the column with the m_x and D_x figures. Each of these totals, of course, will have to be multiplied in the end by the number of females alive in this age group at $t=0$. Since the initial age distribution may be of any form under the conditions of the problem, it will be necessary first of all to calculate these four totals for every column of each of the seven matrices M^t. Now, to add up the elements forming each column of a matrix is equivalent to premultiplying the matrix by a row vector of units; the sum of the first three elements may be obtained by premultiplying with a row vector of which the first three elements are units and the remainder zeros; and similarly the numbers of births and deaths are found with the help of the row vectors m_x and D_x. Thus, the operations which it is necessary to perform on

* Another similar method, which avoids the actual calculation of the number of deaths by means of the age specific death rates, is suggested by the following relationship. If the transformed age distribution $\psi = H\xi$, where H is the matrix defined in § 5, is operated on with a row vector which consists of the $L_x m_x$ figures (Appendix, Table 4), and the resulting scalar is divided by the sum of the elements of ψ, an estimate is obtained of the relative rate of increase of a population with an age distribution ξ in the original co-ordinate system. This follows from the properties of the transformed population discussed at the end of § 5 and from the relationship between the first row of the canonical form $B = HAH^{-1}$ and the $L_x m_x$ column (§ 6). In the transformed population the death rate $=0$, and the maternal frequency is given by $L_x m_x$. Thus, by transforming back again to the original co-ordinate system

$$r = \frac{[L_x m_x]\, H\xi}{[1]\, H\xi},$$

where [1] defines a row vector of units. Taking ξ as the matrix stable distribution of Table 2, and calculating the row vectors $[L_x m_x]\, H$ and $[1]\, H$, the value of r was estimated by this method to be 0·44468.

each of the columns of M^t may be written as the matrix R, which will consist of $m+1$ columns and n rows, the number of the latter depending on the number of operations. Then the required totals for the matrix M^t will be given by

$$Z^t = RM^t = RMMM \ldots M,$$

and it is easy to see how the Z matrices may be built up in succession without calculating the actual matrices M^2, M^3, M^4, etc. Once the series of Z matrices have been constructed, we can obtain from $Z^t\xi_0$ the necessary figures from which the required rates at time t for a population with an initial age distribution ξ_0 may be calculated. Moreover, if we wish, the contributions made, for instance, to the total number of births or deaths by any particular age group in the initial distribution can also be determined.

The computations in this illustration have been greatly simplified by the assumption that the system of age specific fertility and mortality rates remains constant. In the case when the basic matrix M is changing with time and the age distribution at time t is given by $M_t \ldots M_3 M_2 M_1 \xi_0$, some of the rows of R will also be varying. Hence the series of Z matrices could not be built up without first computing M_2M_1, $M_3M_2M_1$, etc. The latter, however, may often be of interest in themselves. For, if each column of M^t—or $M_t \ldots M_3M_2M_1$ in the case of a variable matrix—is multiplied by the number of females alive in the appropriate age group at $t = 0$, the complete age structure of the population at time t is represented in the form of a two-dimensional array. Since the sum of the elements in each row is the total number alive in the age group x to $x+1$ at time t, the number contributed to this total by each age group at $t = 0$ is given by the individual entries.

APPENDIX

(1) *The tables of mortality and fertility*

The basic life table and fertility table which have been used in the numerical part of this study are given in Table 4. The adult l_x figures from the age of 2 months onwards are based on the mortality observed among the females of a domesticated brown rat stock housed at the Wistar Institute, Philadelphia. According to the data for 26 generations of this laboratory stock published by King (1939) it appears that out of 1384 females alive at the age of 2 months (60 days), 1337 were alive at 12 months, and 984 at 20 months. This information gave three points on the l_x curve, supposing that these survivors could be regarded as ordinates at these exact ages. In order to interpolate for other ages, a logistic type of curve was fitted to the data, the values of the constants being chosen so that the curve passed through these three points. The l_x values in Table 4 are given by

$$l_x = \frac{0{\cdot}85156355}{1 + 0{\cdot}00101065e^{0{\cdot}30016x}}, \quad \text{for} \quad x \geqq 2.$$

Although the original data did not extend beyond the age of 20 months, by which time the vast majority of the females had ceased breeding (King, 1939), this l_x curve was extrapolated to later ages, whenever necessary, simply for the purposes of this theoretical study.

The degree of infant mortality assumed here, namely 15 % between birth and the age of 2 months, is entirely arbitrary; it represents a moderate degree of loss at these early ages. Some care, however, was taken to weld the infant mortality smoothly on to the remainder of the l_x curve, and it was assumed that the number of deaths according to age (d_x) decreased

geometrically between birth and the age of 2 months. The actual calculations for these age groups were carried out in units of 1/8 of a month and the resulting l_x curve was integrated by means of Simpson's rule. The same method of numerical integration was used also for the adult part of the life table in order to obtain the L_x figures.

The fertility table is partly artificial and was constructed in the following way. The gross reproduction rate of these domesticated brown rats was estimated from the data published by King (1939) to have been just under 10 litters for the later generations, when the stock was thoroughly adapted to life in the laboratory. The frequency of litter production according to the age of the mother has been found by the author (unpublished observations) to be represented closely by a Pearsonian type I curve in the case of certain litter fertility tables, for example in the cross-albino rat, the vole and some human populations with a high degree of fertility; and, moreover, the values of β_1 and β_2 were very similar for all three species. The actual equation for the curve used here may be written

$$y = y'x^{1\cdot5-1}(a-x)^{2\cdot5-1},$$

and the range was assumed to be from 3 to 21 months, which for grouping purposes represents the span of the reproductive ages observed by King in this Wistar strain of brown rats. The ordinates of the integral curve of the above equation were taken from the tables of the incomplete Beta function and, in this way, a column was formed which gave a gross reproduction rate of 10 litters. The individual entries were then multiplied by the mean number of daughters per litter according to the age of the mother, which was recorded by King, and thus the m_x figures in Table 4 were obtained. The gross reproduction rate is 31·21 daughters and the net rate 25·66. These tables of fertility and mortality were originally constructed in order to determine the relative rate of increase and the type of stable age distribution which might be expected in a brown rat population living under more or less optimum conditions.

(2) *Calculation of the rate of increase*

Some difficulty was experienced in obtaining a satisfactory estimate of the rate of increase (r) from the usual solution (Dublin & Lotka, 1925) of the equation:

$$\int_0^\infty e^{-rx} l_x m_x dx = 1.$$

The 4th degree equation in r with the numerical coefficients based on the seminvariants of the $L_x m_x$ distribution, the estimates of which are given in § 6, was

$$4\cdot90199r^4 + 3\cdot69283r^3 - 7\cdot07198r^2 + 9\cdot60604r - 3\cdot2448498 = 0,$$

and the real root was found to be 0·42447. This value of r was, however, clearly too low and a better estimate had to be obtained in a rather roundabout way, since it was thought that the use of higher moments than the fourth would be unsatisfactory in the present example.

If the force of mortality represented by the original life table is increased by a constant factor (r) which is independent of age, the new life table is

$$l'_x = e^{-rx} l_x,$$

and the net reproduction rate will be given by $R_r = \Sigma L'_x m_x$, where L'_x are the integrals of the new l'_x curve. Clearly, the greater r is taken to be, the smaller R_r becomes. Then, suppose that the relation between R_r and r is given by

$$\log_e R_r = a + br + cr^2 + dr^3 + \ldots,$$

Table 4

Age (x) Units of 30 days	Life table		Fertility table	
	l_x	L_x	m_x	$L_x m_x$
0	1·00000	0·46544	—	—
0·5	0·88706	0·43489	—	—
1	0·85882	0·42725	—	—
1·5	0·85176	0·42534	—	—
2	0·85000	0·84973	—	—
3	0·84945	0·84910	1·1342	0·96305
4	0·84871	0·84824	2·0797	1·76408
5	0·84772	0·84708	2·6596	2·25289
6	0·84638	0·84553	2·8690	2·42582
7	0·84458	0·84344	2·9692	2·50434
8	0·84217	0·84063	2·9535	2·48280
9	0·83893	0·83687	2·8143	2·35520
10	0·83459	0·83184	2·6114	2·17227
11	0·82881	0·82515	2·2455	1·85287
12	0·82113	0·81629	2·0533	1·67609
13	0·81098	0·80463	1·7971	1·44600
14	0·79768	0·78940	1·5561	1·22839
15	0·78039	0·76975	1·2175	0·93717
16	0·75821	0·74472	0·9548	0·71106
17	0·73018	0·71342	0·6610	0·47157
18	0·69548	0·67512	0·4043	0·27295
19	0·65354	0·62953	0·1846	0·11621
20	0·60434	0·57696	0·0435	0·02510
21	0·54859	—	—	—
Total	—	—	31·2086	25·65786

where $a = \log_e R_0$, and the constants b, c, d, etc. are to be determined. It was assumed in the present instance that a 4th degree polynomial in r would be sufficient, and four new life tables were constructed taking r to be in turn 0·1, 0·2, 0·4 and 0·5. The L'_x integrals were obtained by Simpson's rule for the reproductive ages and the four values of R_r calculated. The equations for finding the values of the constants were:

$$0{\cdot}0001e + 0{\cdot}001d + 0{\cdot}01c + 0{\cdot}1b = -0{\cdot}8934974,$$
$$0{\cdot}0016e + 0{\cdot}008d + 0{\cdot}04c + 0{\cdot}2b = -1{\cdot}6708610,$$
$$0{\cdot}0256e + 0{\cdot}064d + 0{\cdot}16c + 0{\cdot}4b = -2{\cdot}9792984,$$
$$0{\cdot}0625e + 0{\cdot}125d + 0{\cdot}25c + 0{\cdot}5b = -3{\cdot}5490542,$$

whence

$$b = -9{\cdot}617235,$$
$$c = \ \ 7{\cdot}371816,$$
$$d = -5{\cdot}698291,$$
$$e = \ \ 2{\cdot}062332.$$

Inserting these values of the constants in the equation for $\log_e R_r$, the value of r for which $\log_e R_r = 0$ was found to be 0·44565.

The stable birth rate was estimated in the usual way from

$$\frac{1}{b} = \int_0^\infty e^{-rx} l_x \, dx.$$

The integrals were computed by means of Simpson's rule, treating the age groups 0–2 separately from the remainder of the life table, the units adopted being 1/4 month for the early ages compared with 1 month for the later. It was found that

$$\int_0^{21} e^{-0\cdot44565x} l_x dx = 1\cdot95064,$$

$$b = 0\cdot51265,$$

and hence the death rate,

$$d = 0\cdot06700.$$

The value of r is so high in this case that the error in the estimate of b due to neglecting the ages from 21 onwards would only be in the last figure. The stable age distribution is given in Tables 1 and 2 of the text. Owing to the way in which the value of r was determined, it will be found that the birth rate of the stable population obtained by operating on this age distribution with the maternal frequency figures is precisely the same as that given by the above integral.

(3) *Numerical values of the matrix elements*

The numerical elements of the matrices A and B to which reference has been made in §§ 3 and 6 of the text are given in Table 5.

Table 5

Age group x	Matrix A		Matrix B
	P_x	F_x	Elements of first row
0–	0·94697	0	0
1–	0·99665	0	0
2–	0·99926	0·3964	0·3741
3–	0·99899	1·4939	1·4089
4–	0·99863	2·1777	2·0517
5–	0·99817	2·5250	2·3756
6–	0·99753	2·6282	2·4682
7–	0·99667	2·6749	2·5059
8–	0·99553	2·6018	2·4293
9–	0·99399	2·4419	2·2698
10–	0·99196	2·1865	2·0202
11–	0·98926	1·9044	1·7454
12–	0·98572	1·7259	1·5648
13–	0·98107	1·4918	1·3332
14–	0·97511	1·2415	1·0885
15–	0·96748	0·9522	0·8141
16–	0·95797	0·7141	0·5907
17–	0·94631	0·4618	0·3659
18–	0·93247	0·2518	0·1888
19–	0·91649	0·0901	0·0630
20–		0·0035	0·0022

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