



Some Further Notes on the Use of Matrices in Population Mathematics

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SOME FURTHER NOTES ON THE USE OF MATRICES IN POPULATION MATHEMATICS

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CONTENTS

	PAGE
1. Introduction	213
2. The stable female birth-rate	217
3. The biological significance of the row vectors	219
4. The total reproductive value of a population and the length of a vector	225
5. The limited type of population growth	227
6. The predator-prey relationship between two populations	238
References	245

1. INTRODUCTION

The use of matrices in population mathematics has been discussed in a previous paper (Leslie, 1945), and some of the properties of the basic matrix representing a system of age-specific fertility and mortality rates have been described both there, and also in an earlier paper by Lewis (1942).† The purpose of the following notes is to enlarge on a few points left over from the earlier work, and in the later sections to extend the use of matrices and vectors to the case of the logistic type of population growth and to the predator-prey type of relationship between two or more populations.

In order to save a troublesome amount of cross-referring, it may perhaps be a convenience if the definitions and properties of the basic vectors and matrices are summarized here, and also if a brief account is given of the various transformations which are at one time or another used in the theoretical development. For fuller details reference may be made to the appropriate section of the original paper.

As before, for the sake of simplicity, the female population only will be considered, and the same unit of age will be adopted as that of time. If m to $m+1$ is the last age group in the complete life-table distribution defined by $L_x = \int_x^{x+1} l_x dx$ (taking $l_0 = 1$), and we put

P_x ($x = 0, 1, 2, \dots, m-1$) = L_{x+1}/L_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 ($x = 0, 1, 2, \dots, m$) = 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 to 1 at time $t+1$,

† At the time my original paper was published I was not aware that the same problem had already been investigated by Lewis (1942). This author establishes the form of the basic matrix and discusses a number of its properties, including the role of the dominant latent root and the form of the stable age distribution. He suggests that the rapidity with which an arbitrary age distribution settles down to the latter form will depend on the difference between the dominant and subdominant root of the characteristic equation, and he also discusses the type of matrix in which there is only a single non-zero element in the first row. It is clear, therefore, that unwittingly I covered a good deal of ground which had already been covered by him. I am indebted to Prof. M. S. Bartlett and Dr S. Vajda for this reference.

we are led to consider the square matrix M of order $m+1$ which has the F_x figures in the first row and the P_x figures in the subdiagonal immediately below the principal diagonal. For many purposes, however, it may not be necessary to deal with the matrix M as a whole. Thus, if $x = k$ is the last age group within which reproduction occurs, all the F_x figures for $x > k$ will be zero and the determinant $|M| = 0$. Partitioning the matrix symmetrically at this point the principal, non-singular, submatrix is

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

As before an arbitrary age distribution will be written as the column vector ξ , different age distributions being distinguished by different subscripts. The number of elements composing a ξ vector may be either $m+1$ or $k+1$ depending on whether the particular age distribution considered is complete, or confined only to the pre-reproductive and reproductive age groups. Associated with each ξ_x there is a uniquely determined vector η_x , which in matrix notation is written as a row vector, the square of the length of the vector ξ_x being given by the scalar product $\eta_x \xi_x$. If the age distribution ξ_x is complete, consisting of $m+1$ elements, the last $m-k$ elements of the associated vector η_x will all be zero. Generally speaking, however, the post-reproductive age groups can be neglected, more particularly in the theoretical development, and unless otherwise stated it will be assumed that we are dealing with η and ξ vectors consisting of $k+1$ elements which are subject to the system of rates represented by the submatrix A .

It was shown in the previous paper (Leslie, 1945, §5) that it is convenient for many purposes to pass to a new frame of reference, the vectors η and ξ and the matrix A undergoing the non-singular linear transformations

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

where H is a diagonal matrix with elements $(P_0 P_1 P_2 \dots P_{k-1})$, $(P_1 P_2 P_3 \dots P_{k-1})$, ..., $(P_{k-2} P_{k-1})$, P_{k-1} , 1, which are derived entirely from the life table. (If the matrix M is the subject of the transformation instead of A , the matrix H may be suitably enlarged and will include all the P_x figures down to P_{m-1} .) It will be noted that in this collineatory transformation the square of the length of a vector is an invariant, and that the matrices A and B have the same characteristic equation and, therefore, the same latent roots.

The effect of this transformation on the elements of A is to replace the P_x figures in the principal subdiagonal by a series of units, and thus to reduce A to the rational canonical form. In biological terms it is equivalent to transforming the original population into one in which all the individuals live until the span of reproductive life is completed at the age of $x = k+1$. This imaginary type of population, with which in many ways it is more convenient to work, might be termed the canonical population.

When the relation between two column vectors is such that

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

where λ is a scalar, then ψ_a is termed a stable ψ appropriate to the matrix B . Similarly in the case of initial row vectors, if

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

then ϕ_a is a stable ϕ appropriate to B .

It may be shown that corresponding to each distinct latent root λ_a of the characteristic equation of B ,

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

there is a pair of stable vectors ϕ_a and ψ_a which in the usual way may be normalized so that $\phi_a \psi_a = 1$. In the case when all the $k+1$ latent roots of B are distinct, the normalized stable ψ form a set of $k+1$ independent and mutually orthogonal vectors of unit length, and any arbitrary ψ_x may be expanded in terms of them, viz.

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

where the coefficients c_a may be either real or complex. Similarly the associated row vector ϕ_x can be expanded in terms of the stable ϕ ,

$$\phi_x = \bar{c}_1 \phi_1 + \bar{c}_2 \phi_2 + \dots + \bar{c}_{k+1} \phi_{k+1},$$

where \bar{c}_a is the complex conjugate of c_a in the expansion of ψ_x . Similarly, by transforming back to the original co-ordinate system, any arbitrary ξ_x can be expanded in terms of the stable ξ and its associated vector η_x in terms of the stable η .

Since only one of the latent roots, and this the dominant one of the matrix B , is real and positive, only one of the stable ψ will consist of real and positive elements. It is this stable $\xi_1 = H^{-1}\psi_1$, associated with the dominant root λ_1 , which is ordinarily referred to as the stable age distribution appropriate to a given set of age-specific fertility and mortality rates. The relation between the inherent rate of increase (r) and the dominant root of the matrix is given by

$$\log_e \lambda_1 = r.$$

There is one further transformation of the matrix B which is of some theoretical importance. The expansion of an arbitrary ψ_x in terms of the normalized stable ψ may be written in matrix notation as

$$\psi_x = Q c_x,$$

where the columns of the matrix Q consist of the stable ψ arranged from left to right in descending order of the moduli of the roots with which they are associated. In the same way the expansion of an arbitrary ϕ_x may be written

$$\phi_x = \bar{c}'_x U,$$

where \bar{c}'_x is the transposed complex conjugate of the vector c_x , and the rows of the matrix U are formed by the stable ϕ arranged in a similar order from above down. Since the normalized stable vectors have the properties

$$\phi_a \psi_b \begin{cases} = 1 & (a = b), \\ = 0 & (a \neq b), \end{cases}$$

it follows that U and Q are reciprocal matrices ($UQ = I$). In this transformation to an orthogonal co-ordinate system the length of a vector remains an invariant and the matrix B becomes

$$UBQ = UHAH^{-1}Q = C,$$

where C is a diagonal matrix whose elements are the latent roots of B (reduction to classical canonical form).

Since an arbitrary age distribution $\psi_x = H\xi_x$ must necessarily consist of real and positive elements, and since $\psi_x = Qc_x$, $\phi_x = \bar{c}'_x U$, we have $\phi_x = \psi'_x \bar{U}' U = \psi'_x G$, where G is a

symmetrical matrix of real elements. Thus, in terms of the original co-ordinate system, since H is a diagonal matrix unaltered by transposition,

$$\eta_x = \xi'_x H G H.$$

The matrix $H G H$, or G if the work is being carried out in terms of the canonical population, has the important property of converting a column vector into the associated row vector. The reciprocal relationship is given by

$$\xi_x = H^{-1} G^{-1} H^{-1} \eta'_x,$$

where $G^{-1} = Q \bar{Q}'$. For further properties of the metric matrix G see the previous paper (Leslie, 1945, § 11).

It may perhaps be of interest if the actual values of some of these matrices are given for a simple numerical example, which will be used in some of the later sections in order to illustrate certain points. Although this example is purely a mathematical model bearing no relation to any known species, its properties are the same as those which might be observed for a population of living organisms considered in a small number of age groups, and for convenience biological terms will be used throughout in interpreting the results obtained with this matrix. Suppose, then, we have an entirely imaginary population which can be considered in four age groups, and let the life table or stationary age distribution be given by the L_x values forming the column vector $\{0.9, 0.7, 0.5, 0.3\}$. Further let the matrix

$$A = \begin{bmatrix} 0 & 45/7 & 18 & 18 \\ 7/9 & 0 & 0 & 0 \\ 0 & 5/7 & 0 & 0 \\ 0 & 0 & 3/5 & 0 \end{bmatrix}. \quad (1.1)$$

Then, since H is the diagonal matrix with elements $h_{11} = P_0 P_1 P_2$, $h_{22} = P_1 P_2$, $h_{33} = P_2$, $h_{44} = 1$, we have

$$H = \begin{bmatrix} 1/3 & 0 & 0 & 0 \\ 0 & 3/7 & 0 & 0 \\ 0 & 0 & 3/5 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

and

$$H A H^{-1} = B = \begin{bmatrix} 0 & 5 & 10 & 6 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \end{bmatrix}.$$

The characteristic equation $|B - \lambda I| = 0$ is, when expanded in powers of λ ,

$$\lambda^4 - 5\lambda^2 - 10\lambda - 6 = 0;$$

and the latent roots are therefore $\lambda_1 = 3$; $\lambda_2, \lambda_3 = -1 \pm i$; $\lambda_4 = -1$. In the transformation to the classical canonical form $UBQ = C$, the matrix

$$Q = \frac{1}{\sqrt{(68)}} \begin{bmatrix} 27 & 4.9985 + 6.4019i & 4.9985 - 6.4019i & \sqrt{(17)}i \\ 9 & 0.7017 - 5.7002i & 0.7017 + 5.7002i & -\sqrt{(17)}i \\ 3 & -3.2010 + 2.4992i & -3.2010 - 2.4992i & \sqrt{(17)}i \\ 1 & 2.8501 + 0.3509i & 2.8501 - 0.3509i & -\sqrt{(17)}i \end{bmatrix},$$

$$U = \frac{1}{\sqrt{(68)}} \begin{bmatrix} 1 & 3 & 4 & 2 \\ 2.8501 + 0.3509i & -3.2010 + 2.4992i & -13.5488 - 7.4545i & -7.4977 - 9.6029i \\ 2.8501 - 0.3509i & -3.2010 - 2.4992i & -13.5488 + 7.4545i & -7.4977 + 9.6029i \\ -\sqrt{(17)}i & \sqrt{(17)}i & 4.\sqrt{(17)}i & 6.\sqrt{(17)}i \end{bmatrix},$$

and

$$G = \bar{U}'U = \begin{bmatrix} 0.5072 & -0.4484 & -2.1539 & -2.1982 \\ -0.4484 & 0.8674 & 1.9041 & 1.5882 \\ -2.1539 & 1.9041 & 11.2688 & 11.2109 \\ -2.1982 & 1.5882 & 11.2109 & 13.4245 \end{bmatrix},$$

where in each case the elements have been rounded off to the fourth decimal place.

Since the a th row of the matrix U is the stable vector ϕ_a which is associated with the stable ψ_a vector given by the a th column of Q , it is possible to construct readily from their rows and columns the set of four matrices $S_a = \psi_a \phi_a$, which have the properties (Leslie, 1945, § 9)

$$S_a^2 = S_a, \quad S_a S_b = 0 \quad (a \neq b), \quad \sum_a S_a = I.$$

If $f(B)$ is a polynomial of the matrix B , we have when the latent roots of the matrix are distinct,

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

Thus

$$B^t = \lambda_1^t S_1 + \lambda_2^t S_2 + \dots + \lambda_{k+1}^t S_{k+1},$$

so that in the present example, when the matrix B is raised to a high power and λ_1^t is much greater than all the remaining λ_a^t ,

$$B^t \propto \begin{bmatrix} 27 & 81 & 108 & 54 \\ 9 & 27 & 36 & 18 \\ 3 & 9 & 12 & 6 \\ 1 & 3 & 4 & 2 \end{bmatrix},$$

and hence, by transforming back to the original co-ordinate system,

$$H^{-1}B^tH = A^t \propto \begin{bmatrix} 81 & 312.4283 & 583.2 & 486 \\ 21 & 81.0000 & 151.2 & 126 \\ 5 & 19.2857 & 36.0 & 30 \\ 1 & 3.8571 & 7.2 & 6 \end{bmatrix}$$

for large values of t .

2. THE STABLE FEMALE BIRTH-RATE

Once the dominant latent root of the matrix has been found, there is one comparatively simple way of calculating the stable age distribution. Thus, working in terms of the canonical population and $m+1$ age groups, the stable ψ_1 appropriate to the root λ_1 may be taken proportional to the column vector $\{\lambda_1^m, \lambda_1^{m-1}, \dots, \lambda_1, 1\}$, and by operating on this vector with the matrix H^{-1} , the stable age distribution ξ_1 can readily be obtained. The method which was used previously for calculating the stable female birth-rate was then to operate on this distribution with the maternal frequency figures† (m_x) and thus determine the total number

† The maternal frequency m_x is the mean number of live daughters born per unit of time to a female aged x to $x+1$. They are the figures tabulated in the usual type of fertility table and are not the same as the F_x figures forming the first row of the matrix.

of female births which might be expected per unit of time (Leslie, 1945, § 16). Although it seems likely that no very great error would be made in employing these methods, both the stable age distribution and the stable birth-rate can be defined rather more formally for the discontinuous case, and the appropriate equations can be derived for calculating them directly when the work is being carried out in terms of discrete age groups.

Consider at time t a stable age distribution $\xi(t)$ appropriate to the dominant latent root λ of the matrix M , and let n_x ($x = 0, 1, 2, \dots, m$) be the elements of this column vector. Then by the definition of a stable vector

$$\xi(t-x) = \lambda^{-x}\xi(t).$$

If $B(t)$ = the number of daughters born alive in the whole population in the interval of time t to $t+1$, it is easily seen that since n_x are the number of individuals alive aged x to $x+1$,

$$\lambda n_0 = L_0 B(t),$$

$$\begin{aligned}\lambda n_1 &= P_0 n_0 \\ &= L_1 B(t-1),\end{aligned}$$

and in general

$$\lambda n_x = L_x B(t-x).$$

If we put

π_x = the proportion of the stable population alive in the age group x to $x+1$,

and $N(t)$ = the total number of individuals alive in the stable population at time t ;

$$\pi_x = \frac{L_x B(t-x)}{N(t+1)}.$$

Defining the birth-rate

$$\beta = B(t)/N(t),$$

we have in the case of the stable population,

$$B(t-x) = \beta N(t-x) = \beta N(t) \lambda^{-x},$$

so that

$$\pi_x = \beta L_x \lambda^{-(x+1)}, \quad (2.1)$$

an expression which defines the matrix stable age distribution. From this it follows, since

$$\sum_0^m \pi_x = 1,$$

that

$$\frac{1}{\beta} = \sum_{x=0}^m L_x \lambda^{-(x+1)}. \quad (2.2)$$

This argument for the case of discrete age classes is, of course, developed along lines similar to those followed by Lotka (e.g. 1939, p. 16) for the continuous case, where, if c_x is the proportion of the stable population aged between x and $x+dx$ and b the instantaneous birth-rate,

$$c_x = b e^{-rx} l_x \quad \text{and} \quad \frac{1}{b} = \int_0^\infty e^{-rx} l_x dx. \quad (2.3)$$

The birth-rate β as defined by (2.2) is, however, a different type of birth-rate to that defined by (2.3). It is the total number of births taking place in the interval of time t to $t+1$ expressed per head of population at time t . If $D(t)$ is the number of deaths occurring in the same interval and $\delta = D(t)/N(t)$,

$$N(t+1) = N(t) + B(t) - D(t),$$

and thus, in the case of the stable population,

$$\lambda = 1 + \beta - \delta.$$

In order to express the relationship between β and b , we might consider that in the continuous case the number of births occurring during the interval of time t to $t+1$ will be given by

$$B(t) = bN(t) \int_0^1 e^{r\tau} d\tau,$$

whence

$$\beta = \frac{b}{r} (e^r - 1),$$

or, since $\log_e \lambda = r$,

$$b = \frac{\beta \log_e \lambda}{\lambda - 1}. \quad (2.4)$$

As an illustration of the comparative results obtained by applying these equations, we may take the same imaginary population of *Rattus norvegicus* as was used previously as a numerical example (Leslie, 1945). In the appendix to that paper it was shown that for the given system of fertility and mortality rates the value of r , estimated by the more usual methods of computation, was 0.44565, and that $b = 0.51265$, this value of the birth-rate being obtained by the numerical integration of (2.3). When the system of rates was expressed in the form of a matrix of order 21×21 , the dominant root was $\lambda_1 = 1.56246$, or $r = 0.44626$, and using equation (2.2) $\beta = 0.64839$, and from (2.4) $b = 0.5144$. The agreement between these estimates of the stable birth-rate is reasonably close and suggests that when we have already calculated the life table age distribution, which is so often the case, equations (2.2) and (2.4) of this section will provide an alternative method of calculating b , which would save a great deal of the tedious labour involved in the numerical integration of (2.3). Although theoretically it is necessary to consider the entire age span of the life table in applying these equations, this was not done in the present instance. In the numerical example given above the value of the rate of increase is so high that the post-reproductive age groups could be neglected without any very great error.

The stable birth-rate and death-rate of the transformed or canonical population (ψ_1 vector) are perhaps only of academic interest. In this connexion, however, there is a small point worth mentioning in order to correct a misstatement which was made in the previous paper. In a footnote (p. 208) it was there stated that 'in the transformed population the death-rate = 0'. Strictly speaking this would only be approximately true under certain conditions; for, if in the case of the stable canonical population

$$\lambda = 1 + \beta' - \delta',$$

where dashes are attached to the symbols in order to distinguish them from those used above, we have by putting $L_x = 1$ in (2.2) and carrying out the summation,

$$\beta' = \frac{\lambda^{m+1}(\lambda - 1)}{\lambda^{m+1} - 1},$$

and hence

$$\delta' = \frac{\lambda - 1}{\lambda^{m+1} - 1},$$

which will approach zero as λ^{m+1} becomes large. Actually in the numerical example given in the footnote referred to, the value of λ^{m+1} was sufficiently great for δ' to be taken as approximately zero without any very serious error being incurred.

3. THE BIOLOGICAL SIGNIFICANCE OF THE ROW VECTORS

The columns of the matrix M' are a measure of the contributions made by each age group to the total population at time t . Thus, for example, if there were n_j individuals alive in the age group j to $j+1$ at $t = 0$, the number and age distribution of their living descendants and

survivors at time t could be found by multiplying the elements in the $(j+1)$ th column of M^t by n_j , and hence their total contribution to the population at this time is given by n_j times the sum of these elements. It was shown previously (Leslie, 1945, § 4) that for values of $t \geq m-k$, where $x=k$ is the last age group within which reproduction occurs, the last $m-k$ columns of M^t will consist only of zero elements, an expression of the obvious fact that individuals alive in the post-reproductive age groups contribute nothing to the population after they themselves are dead. From the point of view of the contributions made to the future population by the individual age groups, it is the submatrix A^t which is principally of interest. When t becomes very large, A^t can be taken as being proportional to the matrix

$$H^{-1}S_1H = H^{-1}\psi_1\phi_1H = \xi_1\eta_1,$$

and therefore the sums of the elements in the columns of A^t must be proportional to the row vector η_1 . Since a population with an arbitrary age distribution tends ultimately to approach the stable form, provided that the system of age-specific fertility and mortality rates remains constant, it follows that the normalized row vector associated with the dominant latent root provides a measure of the relative contributions per head made to the stable population in the future by the individual age groups. Thus, supposing we have two arbitrary age distributions ξ_x and ξ_y , both subject to the same constant system of age-specific rates, the ratio between the total number of individuals in the two populations would, as time went on, tend to the figure

$$R = \frac{\eta_1\xi_x}{\eta_1\xi_y}.$$

If, instead of regarding ξ_x and ξ_y as two separate populations, we regard them as two components of an age distribution ξ_z , it is thus possible to estimate their relative contributions to the population in the future, subject to the condition that the system of rates represented by the matrix A remains constant.

If, in this expression for R , we put $\xi_y = \xi_1$, the normalized stable vector associated with the dominant root of the matrix, we may write

$$V = \eta_1\xi_x,$$

or, since the angle between two vectors ξ_x and ξ_y , of lengths x and y respectively, is

$$\cos \theta = \frac{\eta_y\xi_x}{yx}, \quad V = x \cos \theta_x,$$

where θ_x is the angle ξ_x makes with the stable vector ξ_1 of unit length. Thus, when ξ_x is the stable form of age distribution ($= c_1\xi_1$), the quantity V is the same as the length of the vector ξ_x , since $\cos \theta_x = 1$, and when the population is not distributed as to age in the stable form, $0 < V < x$. The rate of increase of V with regard to time is $dV/dt = rV$, since $V(t) = \lambda_1^t V(0)$.

This quantity V appears to be essentially the same as that termed the total reproductive value of a population by Fisher (1930, p. 27). In discussing the equation

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

by means of which the inherent rate of increase r is usually calculated, Fisher points out the close analogy between a population increasing geometrically and the growth of capital invested at compound interest. Thus the birth of a child can be regarded as the loaning to him of a life and the birth of his offspring as a subsequent repayment of the debt. Then, 'a unit investment has an expectation of a return $l_x m_x dx$ in the time interval dx , and the present value of this repayment, if r is the rate of interest, is $e^{-rx} l_x m_x dx$; consequently the

Malthusian parameter of population increase is the rate of interest at which the present value of births of offspring to be expected is equal to unity at the date of birth of their parent'. (In this quotation the original symbolism has been changed to that used here; Fisher writes m , the Malthusian parameter, instead of r , and the maternal frequency b_x instead of m_x .) Fisher then goes on to say that 'we may ask, not only about the newly born, but about persons of any chosen age, what is the present value of their future offspring; and if the present value is calculated at that rate determined as before, the question has a definite meaning—To what extent will persons of this age, on the average, contribute to this ancestry of future generations?' He then defines the reproductive value which can be assigned to a person aged x as

$$v_x = \frac{e^{rx}}{l_x} \int_x^\infty e^{-rt} l_t m_t dt.$$

Thus, by assigning to each of the n_x persons aged x the appropriate value v_x and summing over all age classes of a given age distribution, a figure which Fisher terms the total reproductive value of the population may be obtained. He also pointed out that this total reproductive value would increase or decrease according to the correct Malthusian rate r .

It was not difficult to show on an actual numerical example that the values of v_x were the same, apart from a scale factor, as the elements of the η_1 row vector after allowing for the fact that the latter refer to a population considered in discrete age groups, whereas the former refer to values of x which vary continuously; and it was evident that the calculation of the quantity V defined above was essentially the same as the calculation of Fisher's total reproductive value of the population.

There is, however, one important point in regard to the argument developed by Fisher which has been quoted. The present value of the repayment $l_x m_x dx$ is taken to be $e^{-rx} l_x m_x dx$, where r is the rate of interest. But, in the case of a population, this estimate of the present value would only be valid if the whole population were increasing at a rate r , and this would only be true when the stable form of age distribution was established. In other words, the reproductive value v_x assigned to a female aged x is the present value of her future daughters only when that female and her daughters are considered as members of a population with a stable age distribution. That this is so may be seen from a numerical example. Let us suppose we are given the age distribution

$$\xi_a = \{81, 21, 5, 1\},$$

which is a stable ξ appropriate to the dominant root $\lambda_1 = 3$ of the numerical matrix A (1.1) defined in the introduction. In one unit of time the population will be $A\xi_a = \lambda_1 \xi_a$ and these individuals will be either survivors or descendants of the original population. Each individual alive in the latter will contribute on the average so many living individuals to the population at $t = 1$, and we wish to assess the present value of that contribution. Consider first of all the solitary female alive in the last age group. In one unit's time this individual will be no longer alive, but she will have contributed $F_3 = 18$ living daughters to the population at that time. The present value of that contribution will therefore be $F_3/\lambda = 6$, and this is the present value which may be attached to each individual alive in this age group of a stable population at any given time. Passing to the five individuals in the next younger age group, $5F_2 = 3$ will be alive in the fourth age group at $t = 1$, and each of these three will be valued then at 6 or a total of 18. They will also have contributed $5F_2 = 90$ daughters. The present total value of the contribution made by these five individuals will be therefore

$$(90 + 18)/3 = 36.$$

or 7.2 per head. In the same way the 21 individuals in the second age group will each be valued at 3.85714 and the 81 in the first age group at 1 each. These values which have been determined in this way may be written as the row vector

$$\eta_1^* = [1, 3.85714, 7.2, 6],$$

where an asterisk is attached to the symbol in order to distinguish this vector from the true normalized form for this particular matrix, namely,

$$\eta_1 = \frac{1}{\sqrt{(68)}} [0.3, 1.28571, 2.4, 2],$$

and it will be noted that $\eta_1^* = 3 \cdot \sqrt{(68)} \eta_1$.

It is clear from this example that this method of assessing the present value of the contribution made by each female aged x to $x+1$ to the population at time $t+1$ is equivalent to determining the present value of her future daughters, and that the valuation can only be carried out in this way when that female and her daughters are considered as members of a stable age distribution. Symbolically the equation which defines the elements y_x ($x = 0, 1, 2, \dots, k$) of the vector η^* , and which is equivalent to that given by Fisher for v_x in the continuous case, is

$$y_x = \frac{\sum_x \lambda^{-(x+1)} L_x F_x}{L_x \lambda^{-x}},$$

and by an obvious extension to the case of stable 'age distributions' consisting of complex or negative individuals, the stable η_a^* representing the present value of the 'contributions' made by each individual could be calculated similarly for each distinct latent root λ_a of a given matrix A . Moreover, it is evident in each case $y_x = 0$ for all values of $x > k$, the last age group in which reproduction occurs.

The use of these row vectors in the form η_a^* has, however, certain disadvantages, more particularly when it is necessary to compare the total present values of two stable age distributions which are each subject to a different system of rates of death and reproduction. It will be seen from the above equation defining v_x that if the maternal frequency is measured in terms of daughters, we must have in all cases $v_0 = 1$, since

$$\int_0^\infty e^{-rx} l_x m_x dx = 1 \quad \text{and} \quad l_0 = 1.$$

Similarly in the discrete case, the value of y_0 may be written, making use of the relationship $(P_0 P_1 P_2 \dots P_x) = L_{x+1}/L_0$,

$$y_0 = \frac{F_0}{\lambda} + \frac{P_0 F_1}{\lambda^2} + \frac{P_0 P_1 F_2}{\lambda^3} + \dots + \frac{(P_0 P_1 P_2 \dots P_{k-1}) F_k}{\lambda^{k+1}},$$

which must be equal to unity, since from the characteristic equation of the matrix

$$\lambda^{k+1} - F_0 \lambda^k - P_0 F_1 \lambda^{k-1} - \dots - (P_0 P_1 \dots P_{k-2}) F_{k-1} \lambda - (P_0 P_1 \dots P_{k-1}) F_k = 0.$$

Thus, as exemplified in the numerical illustration given above, the vector η_1^* will always have its first element equal to unity and will in general differ from the normalized η_1 by some scalar factor. The vector η_1^* measures the total value of a stable population on a different scale, or in a different system of units, to those in which the present value is measured by the vector η_1 . But the question of the respective units in which a number of such values are expressed might become of importance if two or more stable populations subject to different systems of rates were being compared. Suppose these rates are represented by a number of different

matrices A_1, A_2, \dots, A_n , which will be assumed to be all of the same order. If the series of reproductive values for the individual age groups is taken as the row vector η_1^* appropriate to each of the given matrices, the first element of each vector will necessarily be unity as has been shown above. That the use of these vectors in this form for calculating the total present value may lead to unsatisfactory results for the comparison between two stable populations, can be seen from a simple example. Suppose each element of the numerical matrix A defined in the introduction (1.1), and which we will now call A_1 , is divided by a factor of 3. The resulting matrix—say A_2 —can then be taken as representing a new system of rates which has a dominant latent root $\lambda_1 = 1$. The stable age distribution $\xi_a = \{81, 21, 5, 1\}$ of A_1 is, however, also a stable ξ_a of A_2 appropriate to this root. If the stable η_1^* for the second matrix is calculated as before the elements will be the same as those given above for the original matrix. The total present value of the population represented by ξ_a would therefore be estimated at the same figure whichever of the two systems of rates it was subject to. If then these were two separate populations with rates A_1 and A_2 , which happened to have identical age distributions, a comparison between them by means of the total values calculated in this way is not very informative. The easiest way out of this difficulty would be to use only the normalized η_1 associated with the dominant latent root of each matrix in calculating the total present value of a stable population for the purpose of comparing it with that of another. This procedure allows for any difference in what may be termed the respective scales of the two matrices. For this particular example, the normalized η_1 associated with the root $\lambda_1 = 1$ of the matrix A_2 is

$$\begin{aligned}\eta_{21} &= \frac{0.19245}{\sqrt{(68)}} [0.3, 1.28571, 2.4, 2] \\ &= 0.19245\eta_{11},\end{aligned}$$

where the initial of the two suffixes refers to the matrix with which the vector is associated. The total value of a population with an age distribution ξ_a would therefore be 8.2462 if it was subject to the system of rates represented by the matrix A_1 , and 1.5870 when subject to A_2 . Thus the use of the normalized row vectors instead of the form η_1^* leads to a different value being placed on each of the two populations corresponding to a difference in the systems of rates to which they are respectively exposed.

We may conclude, therefore, that in calculating the total value of a stable population it will in general be preferable to use the normalized stable row vector η_1 and not the form η_1^* . The one form, however, can be readily transformed into the other. For, working in terms of age distributions confined to the prereproductive and reproductive age groups, if the elements of η_1^* are calculated by means of the above equation for y_x , the relationship between η_1^* and η_1 is given by

$$\eta_1 = (P_0 P_1 P_2 \dots P_{k-1}) \left\{ \frac{df(\lambda)}{d\lambda} \right\}^{-\frac{1}{2}} \eta_1^*,$$

where $df(\lambda)/d\lambda$ is the characteristic equation of the matrix differentiated with respect to λ , in which the numerical value of the dominant root is inserted and the square root taken with a positive sign. Thus, for the numerical example which has been used previously in this section, the characteristic equation of the matrix A defined by (1.1) is

$$f(\lambda) = \lambda^4 - 5\lambda^2 - 10\lambda - 6,$$

and

$$\frac{df(\lambda)}{d\lambda} = 4\lambda^3 - 10\lambda - 10.$$

For $\lambda_1 = 3$, we have

$$\left\{ \frac{df(\lambda)}{d\lambda} \right\}^{\frac{1}{2}} = \sqrt{(68)},$$

and, since $P_0 P_1 P_2 = \frac{1}{3}$ for this matrix,

$$\eta_1 = \frac{1}{3\sqrt{(68)}} \eta_1^*,$$

corresponding to the difference between these two vectors which was noted above. Although this procedure has been illustrated in terms of the dominant root of the matrix, it can be similarly carried out for any stable η_a^* appropriate to a latent root λ_a . Alternatively, the normalized row vectors may be readily calculated in terms of the canonical population and the matrix $B = HAH^{-1}$ by the methods described in the previous paper (Leslie, 1945, §§ 7 and 8), and transformed back again by means of the relationship $\eta = \phi H$.

If Fisher's total reproductive value of a population is written in terms of vectors as the scalar

$$V = \eta_1 \xi_x = x \cos \theta_x,$$

it follows, as was pointed out earlier in this section, that when the population represented by the vector ξ_x is of the stable form of age distribution, we have $V = x$, the length of ξ_x . The total reproductive value, or the total present value, of a stable population is therefore given by the length of the vector representing the age distribution of the population. Now any population of individuals with a stable form of age distribution ξ_a can be represented as a multiple $c_1 \xi_1$ of the normalized stable ξ associated with the dominant root of the matrix, and its associated vector η_a as a multiple $\bar{c}_1 \eta_1$ of the normalized η_1 , the square of the length of ξ_a being given by $\eta_a \xi_a$. We may thus regard the vector $\eta_a = \bar{c}_1 \eta_1$, which is associated with the vector $\xi_a = c_1 \xi_1$, as the representative of the population in terms of the individual present values according to age, just as the vector ξ_a is the representative of the population in terms of numbers according to age. Although we have been here considering only the total present value of a population of real positive individuals distributed as to age in the stable form, which must necessarily involve only one of the stable η or ξ for a given matrix, there is little difficulty from the mathematical point of view in considering 'populations' consisting of negative or complex individuals, and we may extend the arguments used for the real case so as to include all the stable vectors for the matrix. Thus, the length of any stable vector, ξ_a say, which fulfils the condition $A\xi_a = \lambda_a \xi_a$, can be regarded as the total present value of the 'population' represented in terms of numbers by ξ_a and in terms of individual present values by its associated vector η_a .

Since any arbitrary age distribution of real individuals ξ_x can be regarded as the sum of one or more mutually orthogonal stable ξ , viz. .

$$\xi_x = c_1 \xi_1 + c_2 \xi_2 + \dots + c_{k+1} \xi_{k+1},$$

and its associated vector η_x similarly as the sum of a number of associated stable η

$$\eta_x = \bar{c}_1 \eta_1 + \bar{c}_2 \eta_2 + \bar{c}_3 \eta_3 + \dots + \bar{c}_{k+1} \eta_{k+1},$$

and since the total present value of each of the component stable vectors is given by the length of that vector, namely $\sqrt{(\bar{c}_a c_a)}$, the total present value of the resultant ξ_x will be given by $\sqrt{(\sum \bar{c}_a c_a)}$, which is the length of the vector ξ_x .

The row vectors which were originally introduced into this theoretical discussion solely for mathematical reasons are thus not entirely without interest from the biological point of view. The uniquely determined vector η_x which was assumed to be associated with each ξ_x is a measure of the present value of the contribution made to future generations by an

individual aged x to $x+1$ when that individual is considered as a member of a population with an age distribution ξ_x . The row vectors appear to form a more generalized system of weights or values which we attach to an individual aged x to $x+1$ than the reproductive values v_x defined by Fisher. The latter are represented by a single member of this class of vectors, though one of particular importance owing to its association with the dominant root of the matrix.

Finally there is one further row vector which is very easily calculated for a given system of age-specific fertility and mortality rates, and which on occasion may be useful in studying the comparative fertility of different populations. The net reproduction rate,

$$R_0 = \int_0^\infty l_x m_x dx,$$

in addition to its usual meaning, may also be defined as the expected number of daughters which will be born on the average by a female now aged 0 during the remainder of her lifetime. It is in fact a figure which is analogous to the expectation of life at birth, only in terms of future daughters. Now, in addition to the newly born, we may also enquire what this expected number of daughters will be in the case of a female alive at any age x . Clearly this figure is given by,

$$u_x = \frac{1}{l_x} \int_x^\infty l_x m_x dx,$$

with $u_0 = R_0$. Similarly, in the discrete case, we may consider an η row vector of which the elements z_x ($x = 0, 1, 2, \dots, k$) are

$$z_x = \frac{1}{L_x} \sum_x^k L_x F_x,$$

and it will be found that this is merely a multiple of the η_1^* vector appropriate to the dominant root $\lambda_1 = 1$ of the matrix for a stationary population which is obtained by dividing each of the F_x figures in the first row of the matrix A by the net reproduction rate.

4. THE TOTAL REPRODUCTIVE VALUE OF A POPULATION AND THE LENGTH OF A VECTOR

It appears from the foregoing discussion that the elements of the normalized row vector η_1 can be regarded from two slightly different points of view. On the one hand they provide a measure of the relative contributions per head made by each age group to the stable population in the future, and this property arises from the fact that the sums of the columns of the matrix A^t can be taken as proportional to the elements of this vector when t becomes very large. On the other hand this vector is also associated with the column vector ξ_1 representing the stable age distribution appropriate to a given matrix, and in this sense its elements are a measure of the present value of the contribution made to future generations by an individual aged x to $x+1$ when that individual is considered as a member of a population with a stable age distribution. This difference is of importance in making any practical use of Fisher's total reproductive value of a population, which is defined here as $V = \eta_1 \xi_x$, where ξ_x is an arbitrary age distribution.

Thus, if we have two populations ξ_x and ξ_y both of which are subject to the same system of rates A , or alternatively if ξ_x and ξ_y are two subdivisions of one population subject to A , we can calculate for each the total reproductive values V_x and V_y , and determine the ratio $R = V_x/V_y$. This quantity, as was shown at the beginning of the previous section, is the ratio at time t , when t becomes very great, of the total number of individuals in the two populations which at $t = 0$ had the age distributions ξ_x and ξ_y . But the quantity R cannot be interpreted in this way when the two populations are not subject to the same system of rates.

Again, if a population happens to have a stable form of age distribution ξ_a , then $V = \eta_1 \xi_a = a$, the length of the vector ξ_a and this figure represents the total present value of the stable population ξ_a . But, apart from the case when an arbitrary ξ_x is of the stable form, it is difficult to define the meaning of V simply by itself in any precise biological terms. From the mathematical point of view, when an arbitrary ξ_x is expanded in terms of the stable ξ , and

$$\xi_x = c_1 \xi_1 + c_2 \xi_2 + \dots + c_{k+1} \xi_{k+1},$$

we have

$$\eta_x \xi_x = \sum_{a=1}^{k+1} \bar{c}_a c_a,$$

which is the same thing as x^2 , the square of the length of the vector ξ_x . Then it can be seen that since $V = \eta_1 \xi_x = c_1 = x \cos \theta_x$, the calculation of Fisher's total reproductive value is essentially the determination of one component of a set of mutually orthogonal sums of squares which together make up the total sum of squares represented by x^2 . Thus $V^2 = c_1^2$ which is the first term in $\eta_x \xi_x = \sum_a \bar{c}_a c_a$, since c_1 is necessarily a real positive number.

The two methods of valuation which have been mentioned here are the calculation of the length of the vector ξ_x representing the age distribution of the population, and the calculation of the total reproductive value V . Which of these two figures is the more important from the point of view of assessing the state of a population subject to a given system of fertility and mortality rates is a matter for discussion and further investigation. Certainly the total reproductive value V is a figure which is the more easily determined. It requires only a knowledge of the row vector η_1 associated with the dominant root of the matrix representing the given system of rates to which the population is subject. On the other hand the calculation of the length of the vector ξ_x , is much more complicated. For, in order to arrive at the associated vector $\eta_x = \xi'_x HGH$, it is necessary to know the numerical values of the elements of the matrix G , and hence HGH , which in turn cannot be computed unless all the latent roots of the matrix A are known. Thus, purely from the practical point of view, the calculation of the total reproductive value $V = \eta_1 \xi_x$ offers a number of advantages and, within the limitations set out above, this figure may prove useful in comparing one population with another.

It is perhaps worth mentioning in passing one further type of problem. If the length of the vector ξ_x is regarded as the present value of the population when it is subject to a particular system of fertility and mortality rates, it may be of interest on occasion to consider the maximum or minimum of the quadratic form $\xi' HGH \xi$ given one or more restrictive conditions. Thus, for example, we might consider the problem of determining the column vector ξ_s which would give rise to the minimum total value when the sum of its elements was equal to a number N . If n_x ($x = 0, 1, 2, \dots, k$) are the elements of ξ_s and the symbol $\{1\}$ represents a column vector of $(k+1)$ units, we have, after differentiating with respect to the n_x and introducing a Lagrange multiplier λ ,

$$HGH \xi_s - \lambda \{1\} = 0,$$

$$\sum n_x = N,$$

a set of $(k+2)$ equations for determining the values of n_x which will make the length of the vector ξ_s a minimum subject to the restrictive condition imposed. It will be seen from these equations that the solution of this problem is equivalent to that of determining the column vector ξ_s which will have all the elements of its associated row vector η_s the same value. Thus, by reversing the process, and starting with an arbitrary row vector of $(k+1)$ units, it

follows that the required column vector is proportional to the sums of the columns of the matrix $H^{-1}G^{-1}H^{-1}$. As an example of the type of vector which has the minimum value, the solution of these equations in the case of the simple 4×4 matrix given in the introduction was for $N = 108$,

$$\xi_s = \{84.5686, 17.4054, 4.5059, 1.5201\},$$

whereas the stable population of 108 individuals was

$$\xi_1 = \{81, 21, 5, 1\}.$$

This problem has been considered here in terms of the vector of shortest length, without imposing the full restrictive conditions which strictly speaking would be necessary when considering a population of living individuals, namely that the elements n_x of the column vector are positive integers with $\Sigma n_x = N$. But the vector ξ_s in this example consists of positive elements and may be taken as representing, in the case of this numerical system, the type of proportionate age distribution which would give rise to the minimum value. Actually the difference between the two distributions ξ_s and ξ_1 is not very marked in this example. The square of the length of the stable vector is 68, while that of the vector of shortest length is 64.4. But that this difference between the total values does correspond to a difference between the properties of the two age distributions may be seen by operating on each of them with the matrix A and determining the total number of individuals in the two populations at successive intervals of time. The numbers in the population which starts with an age distribution ξ_s will always be lower than those in the population starting with the stable form ξ_1 , until ultimately there would be about 5.3 % fewer individuals in the former than in the latter.

5. THE LIMITED TYPE OF POPULATION GROWTH

Hitherto it has been assumed that the system of age-specific fertility and mortality rates represented by the matrix A remains constant, and that therefore the population increases geometrically to an unlimited extent at a rate $dN/dt = rN$, when the stable age distribution is established. The next case which is usually considered in population mathematics is that of the logistic population, where the rate of increase in numbers is defined by the differential equation

$$\frac{dN}{dt} = (r - aN)N,$$

r and a being constants > 0 , from which the well-known result follows that such a population will approach asymptotically an upper limit to the numbers given by $K = r/a$, according to the equation

$$N = \frac{K}{1 + Ce^{-rt}}.$$

It is therefore of interest to consider in terms of matrices and vectors the type of population growth in which the system of rates is dependent on the number of individuals present in the population at a given time.

Suppose that the system of rates to which a population is exposed when no limitations are placed upon the growth in numbers is represented by the matrix A with a dominant latent root λ_1 . This might be called the optimum system of rates for the particular species or genetic stock. When the population is increasing in a limited environment let us suppose that at time t there is an age distribution $\xi(t)$ consisting of a total number $N(t)$ of individuals, and that at this time the elements of A are altered so that we have a new matrix A_t with a dominant latent root $\lambda_1/q(t)$, where $q(t)$ is dependent on $N(t)$. Then the age distribution of

the population at time $t+1$ will be given by $A_t \xi(t) = \xi(t+1)$, and the process can be obviously extended so that at time $t+1$ we have a matrix A_{t+1} with a dominant root $\lambda_1/q(t+1)$, $q(t+1)$ depending on $N(t+1)$, and so on. At each integral value of t , therefore, the original inherent rate of increase $r = \log_e \lambda_1$ will in general change to a new rate $r' = \log_e (\lambda_1/q)$, where q is some function of N , the number of individuals present in the population.

The changes which are thus assumed to occur in the optimum age-specific rates of fertility and mortality represented by the matrix A might take place in an innumerable variety of different ways. But, from the theoretical point of view, there are two extreme cases which are particularly of interest; on the one hand, when the decrease in the optimum rate of increase is due to a lowered degree of fertility, while the age-specific death-rates remain the same: and on the other when it is due to an increased rate of mortality and fertility remains constant. Even under these simplified conditions it is necessary to make some assumption as to the way in which the rates are actually affected, and in order to define the problem in concrete terms, it will be assumed here that the changes which occur either in the degree of fertility or in that of mortality are due to the operation of a factor which is independent of age. In addition one further type of change in the rates of fertility, involving a factor which increases geometrically with age, will be mentioned in passing. For simplicity the two main cases will be considered separately.

(a) *Mortality affected by a factor independent of age, fertility remaining constant*

If l_x and m_x are respectively the life table and fertility table for a population living under optimum conditions where no limitations are placed upon the growth in numbers, the inherent rate of increase (r) of the population is defined by

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

and the stable age distribution (c_x) and the stable birth-rate (b) by

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

If now a force of mortality (γ) which is independent of age is superimposed on the original force of mortality (μ_x), represented by the optimum life table l_x , the new life table l'_x will be given by

$$\frac{1}{l'_x} \frac{dl'_x}{dx} = -(\gamma + \mu_x) \quad \text{or} \quad l'_x = e^{-\gamma x} l_x;$$

and, if the original fertility table remains unaltered, the new inherent rate of increase will be $r' = r - \gamma$. The stable age distribution (c'_x) and stable birth-rate (b') of the population when it is subject to this new life table will then be

$$c'_x = b' e^{-r'x} l'_x, \quad \frac{l}{b'} = \int_0^{\infty} e^{-r'x} l'_x dx;$$

and it follows, since $l'_x = e^{-\gamma x} l_x$ and $r' = r - \gamma$, that $1/b' = 1/b$ and $c'_x = c_x$. The imposition of a force of mortality independent of age on a given life table thus leaves the original stable age distribution and stable birth-rate unchanged.

Similarly in terms of matrices, if A is the matrix representing the age-specific rates of fertility and mortality for a population living under optimum conditions, we are led to consider the matrix $q^{-1}A$ in which each element of the original matrix A is divided by a scalar q . Approximately, in the discrete case, this is equivalent to imposing on the original

life table a force of mortality which is independent of age. Then in the reduction of $q^{-1}A$ to rational canonical form, if

$$H_q = \begin{bmatrix} (P_0 P_1 P_2 \dots P_{k-1}) q^{-k} & & \dots & & & & \\ & (P_1 P_2 \dots P_{k-1}) q^{-(k-1)} & & \dots & & & \\ \dots & \dots & \dots & \dots & \dots & \dots & \\ & & & & (P_{k-2} P_{k-1}) q^{-2} & & \\ & & & & & & (P_{k-1}) q^{-1} \\ & & & & & & & 1 \end{bmatrix},$$

the first row of $B_q = H_q(q^{-1}A)H_q^{-1}$ is

$$F_0 q^{-1}, \quad P_0 F_1 q^{-2}, \quad P_0 P_1 F_2 q^{-3}, \quad \dots, \quad (P_0 P_1 P_2 \dots P_{k-1}) F_k q^{-(k+1)},$$

the remaining elements consisting in the usual way of a series of units in the principal subdiagonal.

The characteristic equation of the matrix B_q is

$$\lambda^{k+1} - F_0 q^{-1} \lambda^k - P_0 F_1 q^{-2} \lambda^{k-1} - \dots - (P_0 P_1 \dots P_{k-2}) F_{k-1} q^{-k} \lambda - (P_0 P_1 \dots P_{k-1}) F_k q^{-(k+1)} = 0$$

while that of the original matrix $B = HAH^{-1}$ is obtained by putting $q = 1$. Comparing these two equations term by term it will be seen that the latent roots of B_q are merely those of B each divided by the factor q . Thus, in terms of the canonical population, the stable age distribution appropriate to the dominant latent root λ_1/q of the matrix B_q may be taken as a multiple of the vector

$$\psi_1 = \left\{ \left(\frac{\lambda_1}{q} \right)^k, \quad \left(\frac{\lambda_1}{q} \right)^{k-1}, \quad \dots, \quad \left(\frac{\lambda_1}{q} \right), \quad 1 \right\};$$

and since $\xi_1 = H_q^{-1} \psi_1$,

$$\xi_1 = \{(P_0 P_1 P_2 \dots P_{k-1})^{-1} \lambda_1^k, (P_1 P_2 \dots P_{k-1})^{-1} \lambda_1^{k-1}, \dots, (P_{k-1})^{-1} \lambda_1, 1\},$$

which is the same as the $\xi_1 = H^{-1} \psi_1$ appropriate to the root λ_1 of the original matrix A . Moreover, since the time which it takes for an arbitrary ξ_x to approach the stable form of age distribution associated with the dominant root of the matrix will depend on the ratios of this root to the other roots of the matrix, as may be seen from the expansion of $\xi_x(t)$ at time t in terms of the stable ξ ,

$$\xi_x(t) = c_1 \lambda_1^t \xi_1 + c_2 \lambda_2^t \xi_2 + \dots + c_{k+1} \lambda_{k+1}^t \xi_{k+1},$$

it follows that a population with any arbitrary form of age distribution which is subject to the matrix $q^{-1}A$ will approach the stable form at the same rate for all values of q . This result is of interest in the theoretical study of wild mammalian populations, since it might be assumed, at least as a first approximation, that any increase of mortality due to predation, hunger, etc., falling on some optimum system of age-specific death-rates could be represented by a factor which tended to be independent of age.

If then we consider at time t a population with an age distribution $\xi(t)$ which is subject to the system of rates represented by the matrix $q^{-1}A$, and we regard q as some function of N , the number of individuals present in the population at time t , we might put as a first approximation

$$q = \alpha + \beta N.$$

For the stationary state we must have $q = \lambda_1$, the dominant latent root of the matrix A ,

and in addition, as N tends to zero, q must approach 1. When the dominant latent root of $q^{-1}A$ is equal to unity, the condition for a stationary population,

$$N = \frac{\lambda_1 - 1}{\beta} = K,$$

and therefore we may write $q = 1 + \frac{(\lambda_1 - 1)N}{K}$.

Then, assuming at time t there are $N(t)$ individuals distributed as to age in the stable form of distribution (ξ_a) for the matrix $q^{-1}A$, which distribution is the same for all values of q as has been shown above,

$$q^{-1}A\xi_a(t) = \xi_a(t+1) = \frac{\lambda_1 \xi_a(t)}{q},$$

or

$$N(t+1) = \frac{\lambda_1 N(t)}{1 + \frac{\lambda_1 - 1}{K} N(t)},$$

and

$$\frac{K - N(t+1)}{N(t+1)} = \lambda_1^{-1} \left\{ \frac{K - N(t)}{N(t)} \right\},$$

which, as $\log_e \lambda_1 = r$, is the same thing as the logistic type of population growth,

$$N = \frac{K}{1 + Ce^{-rt}}.$$

Thus, when fertility remains constant and mortality is affected by a factor which is independent of age, this factor being regarded as a simple linear function of the numbers present in the population at time t , the total number of individuals in the population will increase according to the logistic form of population growth, provided that the age distribution of the population at $t = 0$ is the stable form appropriate to the dominant latent root of the matrix A . But, when this condition is not fulfilled, and the initial age distribution is not of the stable form, there may be quite considerable departures from the curve given by this actual logistic equation. The form of the curves representing the total number of individuals at successive intervals of time will, however, still tend to be S-shaped, and in some cases there is little doubt that a logistic type of equation could be fitted empirically to the data over a considerable portion of the total curve. The type of variation which might be expected in these growth curves owing to a departure from the stable form of age distribution is illustrated in the following simple examples.

Suppose that an entirely imaginary population, which can be considered in four age groups, is subject to the optimum system of rates of death and reproduction represented by the matrix defined originally in the introduction,

$$A = \begin{bmatrix} 0 & 6.4286 & 18 & 18 \\ 0.7778 & 0 & 0 & 0 \\ 0 & 0.7143 & 0 & 0 \\ 0 & 0 & 0.6000 & 0 \end{bmatrix},$$

which has a dominant root $\lambda_1 = 3$, or $r = 1.09861$, and suppose that for the matrix $q^{-1}A$,

$$q = 1 + 0.000185185N.$$

where N is the number of individuals in the population at integral values of time t . When

$q = 3$, the stationary state, $N = 10800$; and at $t = 0$ let there be 108 individuals present in the population. These conditions are fulfilled by the logistic equation

$$N = \frac{10800}{1 + 99e^{-1.09861t}}.$$

If at $t = 0$ we consider three different age distributions each consisting of 108 individuals and represented by the vectors

$$\xi_a = \{81, 21, 5, 1\}, \quad \xi_s = \{85, 17, 4, 2\}, \quad \xi_x = \{0, 0, 108, 0\},$$

where ξ_a is a stable age distribution of the matrix A , ξ_s the vector of shortest length given in the previous section and expressed to the nearest integer, and ξ_x a very skew form of age distribution in which all the individuals are concentrated in an age class for which fertility is high, the age distributions and therefore the total number in each population can be readily calculated by successive applications of the matrix $q^{-1}A$. The following are the results obtained in each case, together with the values of N calculated from the logistic equation

Values of N

t	From logistic	Initial age distribution		
		ξ_a	ξ_s	ξ_x
0	108.0	108	108	108
1	317.6	318	292	1970
2	900.0	901	844	1930
3	2314.3	2316	2215	6199
4	4860.1	4862	4660	8423
5	7673.7	7675	7540	9389
6	9508.7	9509	9433	10694
7	10332.3	10332	10298	10609
8	10639.5	10641	10628	10741
9	10745.9	10745	10742	10804
10	10781.9	10781	10780	10781

which are given in the first column. It will be seen that in the case of the stable age distribution ξ_a the values of N follow those calculated from the logistic equation, apart from small discrepancies at times in the last figure due to errors of rounding off. (The elements of the vector $\xi(t+1) = q^{-1}A\xi(t)$ were in each case expressed to the nearest whole number.) In the case of ξ_s , an age distribution which does not differ very greatly from the stable form, the numbers lie below those for the initial distribution ξ_a until $t = 10$, the stable age distribution being approximately established in this population round about $t = 7$; while for ξ_x the numbers are very erratic owing to the very skew form of the initial distribution leading to a very rapid increase in numbers during the early stages. The stable form of age distribution was approximately established in this last population at $t = 10$. It is evident from these examples that the initial form of age distribution may have a marked effect on the course of development followed by a population which inherently is increasing towards some upper limit according to the type of growth in numbers assumed here.

The initial number of individuals in these three examples is small relative to the upper limit of $K = 10800$, so that even a thoroughly skew form of distribution such as ξ_x has time

in which to approach the stable form of age distribution before the upper limit in numbers is achieved. Actually in the case of ξ_x the stable form is not established before $t = 10$, and a tendency to overshoot the upper limit will be noticed before that time. If the initial number of individuals had been chosen much greater relative to K this tendency would only have been emphasized. An extreme case would have been to assume that the initial number of individuals in each of the three examples was equal to 10800. Then it is evident that whereas the population represented by ξ_a , the stable form, would have remained constant at the same figure, those represented by ξ_s and ξ_x would vary on either side of the upper limit to begin with and would tend to approach the steady state by a series of damped oscillations as the stable age distribution was in the process of being established.

(b) *Fertility affected by a factor independent of age, mortality remaining constant*

This problem raises a number of difficulties not all of which have been satisfactorily resolved. But, before considering the main problem as defined here, namely when fertility is affected by a factor independent of age, there is another case which arises from the foregoing discussion, and which is perhaps worth mentioning. The canonical matrix

$$B_q = H_q(q^{-1}A)H_q^{-1}$$

defined above, is when written in full, to take a simple example of a 4×4 matrix,

$$B_q = \begin{bmatrix} F_0 q^{-1} & P_0 F_1 q^{-2} & P_0 P_1 F_2 q^{-3} & P_0 P_1 P_2 F_3 q^{-4} \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \end{bmatrix};$$

and it can be seen that in addition to being the canonical form of $q^{-1}A$, B_q is also the canonical form of

$$A_q = \begin{bmatrix} F_0 q^{-1} & F_1 q^{-2} & F_2 q^{-3} & F_3 q^{-4} \\ P_0 & 0 & 0 & 0 \\ 0 & P_1 & 0 & 0 \\ 0 & 0 & P_2 & 0 \end{bmatrix},$$

the diagonal matrix H of the transformation HA_qH^{-1} having elements $h_{11} = P_0 P_1 P_2$, $h_{22} = P_1 P_2$, $h_{33} = P_2$, $h_{44} = 1$. This matrix A_q can be regarded as representing some system of age-specific rates in which an original level of fertility included in the F_x figures has been affected by a factor which increases geometrically with age, and as before this factor q might be taken as being linearly related to N , the number of individuals present in the population at time t . But in contradistinction to the matrix $q^{-1}A$, the age distribution of a population subject to the matrix A_q will no longer remain stable. For suppose that in terms of the canonical population the stable age distribution associated with the dominant root λ_1/q of A_q is

$$\psi_1 = \left(\left(\frac{\lambda_1}{q} \right)^k, \left(\frac{\lambda_1}{q} \right)^{k-1}, \dots, \left(\frac{\lambda_1}{q} \right), 1 \right),$$

the transformation $\xi_1 = H^{-1}\psi_1$ gives

$$\xi_1 = \left\{ (P_0 P_1 P_2 \dots P_{k-1})^{-1} \left(\frac{\lambda_1}{q} \right)^k, (P_1 P_2 \dots P_{k-1})^{-1} \left(\frac{\lambda_1}{q} \right)^{k-1}, \dots, P_{k-1}^{-1} \left(\frac{\lambda_1}{q} \right), 1 \right\},$$

which is not the same as the ξ_1 associated with the dominant root λ_1 of the original matrix A .

If then at time t a population happened to have the stable form of age distribution appropriate to the matrix $A_q(t)$, it will not in general have the stable form of distribution at $t+1$ appropriate to $A_q(t+1)$, except in the case of the stationary population with $N = K$ and $\lambda_1/q = 1$, when the life table age distribution is established.

By extending this argument for the matrix A_q to the perfectly general case, it can be seen that the age structure of a population will be constantly changing when the degree of fertility is affected and the life table remains constant, until in the terminal stages of its growth the population approaches the stationary state. This is, of course, essentially the same type of changing age distribution as that shown to occur by Lotka (1931) in the case of a population growing in numbers according to the logistic law with a constant form of life table. A numerical example is given later of a population subject to the matrix A_q when q is taken as a simple linear function of N .

Although, biologically speaking, it is not impossible for fertility to be affected by a factor which increases geometrically with age and which depends on the number of individuals present in the population at a given time, it is perhaps of greater interest to consider the case in which the fractional decrease in fertility is the same at all ages. In other words, it is necessary to consider the matrix A_s , say, in which the elements in the first row of a matrix A representing the optimum rates of death and reproduction are each divided by a factor s , so that

$$A_s = \begin{bmatrix} F_0 s^{-1} & F_1 s^{-1} & F_2 s^{-1} & \dots & F_k s^{-1} \\ P_0 & . & . & \dots & . \\ . & P_1 & . & \dots & . \\ \dots & \dots & \dots & \dots & \dots \\ . & . & . & P_{k-1} & . \end{bmatrix}.$$

Now, if the $(x+1)$ th element in the first row of the canonical form $B = HAH^{-1}$ is written as

$$(P_0 P_1 P_2 \dots P_{x-1} F_x) = f_x,$$

the characteristic equation of the original matrix A is

$$\lambda^{k+1} - \left(\sum_{x=0}^k f_x \lambda^{k-x} \right) = 0,$$

and that of the matrix A_s is $\lambda^{k+1} - \left(s^{-1} \sum_{x=0}^k f_x \lambda^{k-x} \right) = 0$.

If the real positive root of the first equation is λ_1 , the real positive root of the second can be written as λ_1/q , and the inherent rate of increase of a population subject to the system of rates A_s will be $r' = \log_e (\lambda_1/q)$. Since we are considering as before the case when q is a function of N , say

$$q = 1 + \frac{\lambda_1 - 1}{K} N,$$

it is necessary, in order to solve the problem of a population in which fertility is affected by a factor independent of age, that s should be expressed as a function of q .

This point proved to be rather troublesome, and the following solution needs a much fuller investigation than it has received here. It depends on the relation between the first row of the canonical form $B = HAH^{-1}$ and the $L_x m_x$ column which was touched on in the previous paper (Leslie, 1945, § 6). It is evident that the division of the elements in the first row of the

matrix A or B by a scalar s is the same thing as dividing the maternal frequency figures (m_x) by the same quantity. The original net reproduction rate, $R_0 = \int_0^\infty l_x m_x dx$, will therefore become R_0/s . Now, in the solution of the equation

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

we have
$$\log_e R_0 = m_1 r - \frac{m_2}{2!} r^2 + \frac{m_3}{3!} r^3 - \frac{m_4 - 3m_2^2}{4!} r^4 + \dots, \quad (5.1)$$

where
$$m_1 = \int_0^\infty x l_x m_x dx / \int_0^\infty l_x m_x dx,$$

and m_n ($n = 2, 3, 4, \dots, n$) is the n th moment about this mean. When the maternal frequency is divided by s the moments of the distribution will not be affected, but the value of r will change to a new value r' , and

$$\log_e (R_0/s) = m_1 r' - \frac{m_2}{2!} r'^2 + \frac{m_3}{3!} r'^3 - \frac{m_4 - 3m_2^2}{4!} r'^4 + \dots \quad (5.2)$$

The moments are usually calculated by treating the $L_x m_x$ figures ($L_x = \int_x^{x+1} l_x dx$) as a frequency distribution, the individual frequencies being regarded as centered at the mid-point of each age group. Alternatively they are sometimes calculated from $l_x m_x$, where l_x is the value of the usual life table function taken at each midpoint. When a system of rates is expressed in the form of a matrix the elements of the first row of the canonical form $B = HAH^{-1}$ are not the same as the $L_x m_x$ figures. But it was found (Leslie, 1945, § 6) that the sum of these elements was equal to the net reproduction rate and that if each element ($P_0 P_1 P_2 \dots P_{x-1} F_x$) was regarded as centered at the age of $x + 1$, the mean and semiinvariants of the distribution were the same as those obtained from the $L_x m_x$ column.

These relationships suggested a possible way of relating s to q . If for the matrix A , with a dominant latent root $\lambda_1 = e^r$, the sum of the elements in the first row of $B = HAH^{-1}$ is equal to R_0 , and if the dominant latent root of the matrix A_s is $\lambda_1/q = e^{r'}$, we might, as a first approximation, take only the first terms in each of the equations (5.1) and (5.2), and put

$$\log_e R_0 = m_1 r, \quad \log_e (R_0/s) = m_1 r',$$

and
$$\frac{r'}{r} \log_e R_0 = \log_e (R_0/s),$$

or, since
$$\frac{r'}{r} = 1 - \frac{\log_e q}{r},$$

$$\log_e s = \frac{\log_e R_0}{r} \log_e q. \quad (5.3)$$

For a greater degree of accuracy the first two terms could be taken as (5.1) and (5.2), viz.

$$\log_e R_0 = m_1 r - \frac{m_2}{2} r^2, \quad \log_e (R_0/s) = m_1 r' - \frac{m_2}{2} r'^2;$$

and
$$\frac{r'}{r} \left(1 + \frac{r - r'}{\frac{2m_1}{m_2} - r} \right) \log_e R_0 = \log_e (R_0/s).$$

From which, putting $\log_e q = w$ and $\frac{2m_1}{m_2} - r = c$,

$$\log_e s = -\frac{\log_e R_0}{rc} \{(r-c)w - w^2\}. \quad (5.4)$$

For a greater degree of accuracy still, further terms on the right-hand side of (5.1) and (5.2) could be included, though the algebra tends to become somewhat tedious. Presumably the number of terms which it would be necessary to include in any particular case would depend on the magnitude of r and upon the form of the distribution relating net fertility to age. Actually in the elementary numerical example which has been used here so far, equation (5.4) appears to be fairly accurate. Thus the characteristic equation of A with $\lambda_1 = 3$ and $R_0 = 21$ is

$$\lambda^4 - 5\lambda^2 - 10\lambda - 6 = 0.$$

Dividing these numerical coefficients by $s = 5$, for example,

$$\lambda^4 - \lambda^2 - 2\lambda - 1.2 = 0,$$

of which the real positive root is $\lambda_1/q = 1.63476$, or $q = 1.83513$. The values of m_1 and m_2 were 3.04762 and 0.52154 respectively, and equation (5.4) was in common logarithms

$$\log s = 2.48366 \log q + 0.60263 (\log q)^2. \quad (5.5)$$

For $q = 1.835$, the estimated value of s is 4.975, whereas the true value is $s = 5$. If s is estimated from equation (5.3) for $q = 1.835$ the value is 5.379, so that the second degree equation in $\log q$ is an improvement on the first and gives a reasonably close approximation to s for values lying in this region. It will be noted that if $q = 3$, $s = 21$ from this second degree equation (5.5), as it should do.

In order to compare the operational effect of the matrix A_s with that already determined for $q^{-1}A$, two examples are given below for the initial age distributions

$$\xi_a = \{81, 21, 5, 1\}, \quad \xi_x = \{0, 0, 108, 0\},$$

ξ_a being the stable age distribution of 108 individuals for the matrix A , and ξ_x the same form of skew distribution used previously. As before, q was taken as

$$q = 1 + 0.000185185N,$$

and the appropriate value of s at each stage was calculated by means of equation (5.5). In addition one example is given of the operation of the matrix A_q in which fertility is affected by a factor which increases geometrically with age, taking ξ_a as the initial distribution. The results were as follows:

Values of N

t	From logistic	Matrix A_q ξ_a	Matrix A_s	
			ξ_a	ξ_x
0	108.0	108	108	108
1	317.6	312	312	1915
2	900.0	867	867	1976
3	2314.3	2118	2115	5603
4	4860.1	4194	4120	7315
5	7673.7	6659	6393	8616
6	9508.7	8857	8362	10464
7	10332.3	10268	9696	10369
8	10639.5	10876	10384	10695
9	10745.9	10984	10673	10901
10	10781.9	10900	10766	10715

Comparing the two cases in which the initial distribution was of the stable form ξ_a with the figures derived from the logistic curve, it will be seen that in both cases the numbers of individuals are less than those for the logistic particularly in the early stages of development. Broadly speaking, however, all these three curves are similar in their general outlines, though there is an obvious tendency in the case of the matrix A_q for the population to overshoot the upper limit of $N = 10800$ in the later stages. Similarly, in the case of the initial distribution ξ_x and the matrix A_s , the course of events is not very different from that for the previous example with this distribution, when it was assumed that mortality was changing and fertility remained constant, though, again here, the numbers of individuals are less when fertility is changing and mortality remains the same. The chief difference between these examples and those given previously lies, of course, in the forms of the age distribution. When the matrix $q^{-1}A$ was assumed to be in operation, the ultimate age distribution to which all populations would tend, whatever their initial conditions and numbers might be, was

$$\xi = \{8100, 2100, 500, 100\};$$

whereas, both for the matrix A_q and A_s , the stationary age distribution of 10800 individuals is

$$\xi = \{4050, 3150, 2250, 1350\};$$

and throughout the whole course of development of each population an approach is being made to one or other of these very different distributions.

Although the two extreme cases of either fertility or mortality changing through the operation of a factor which is independent of age have been considered here separately, there should be little difficulty in extending the methods so as to include the case where both fertility and mortality are affected in varying degrees at the same time. Thus, we might consider the scalar q of the dominant latent root λ_1/q at time t as being the product, $q = uv$, of two factors, one of which, u say, represents an increase in mortality independent of age, and the other v represents the effect of a decrease in fertility at all ages by means of the factor s . Various possibilities then arise, depending on whether the ratio u/v was regarded as a constant, or as varying in some predetermined manner. However, these questions have not been gone into any further at present.

It will be noticed that the problem considered in this section of a growing population subject to a changing degree of fertility and a constant life table is not precisely the same as that discussed by Lotka (1931). In the first part of that paper Lotka showed how the birth-rate, death-rate, age distribution and inherent rate of increase of such a population would change when the total number of individuals in the population increased according to the logistic law. Here no assumption is made as to the way in which the number of individuals is increasing, but it is assumed that at equal intervals of time, which intervals in practice can be made as small as we please according to the degree of accuracy required, the inherent rate of increase of the population $r' = \log_e (\lambda_1/q)$ is dependent on the number of individuals (N) present at time t , and, as a first approximation, q has been taken as a linear function of N . The most important feature of this form of population growth is the marked effect which the initial age distribution and numbers have on the subsequent course of development of the population. Only in one case, namely when mortality is increased owing to the operation of a factor independent of age, fertility remaining constant, and when the initial age distribution is of the stable form appropriate to the matrix A , is the true logistic form of growth in numbers realized. However, the result of operating on a not too abnormal initial distribution with either of the matrices $q^{-1}A$, A_q or A_s is, broadly speaking, a very similar type

of S-shaped curve, if the initial numbers are small relative to the upper limit K , and in some cases there is little doubt that a logistic equation could be fitted empirically to such a series of points, more particularly when the figures for the total number of individuals are not available over the complete range of development of the population. But, in general, we shall have for a given matrix A and a given value of K in the equation $q = 1 + (\lambda_1 - 1)N/K$, a family of S-shaped or partially S-shaped curves (or even the type of curve which descends towards the upper limit K), the differences between the individual members depending on the initial state of the population and on the way in which the decrease in the inherent rate of increase takes place, whether through a decrease in fertility, or an increase in mortality, or a combination in varying degrees of both factors. Among the more interesting features of this type of population growth is the possibility, under suitable initial conditions, of the total numbers in the population becoming greater than K and then of finally approaching the stationary state by means of a series of damped oscillations around this limit.

It is interesting to consider in the light of these results some of the population growth curves which have been published for one or other species of insect living alone in a limited environment (e.g. Chapman, 1928; Crombie, 1945). Certainly the initial age distribution of some of these populations must have been extremely skew, consisting as they did in many cases of only a small number, perhaps only a pair, of adults. It is a little difficult, on looking through the figures given in these various papers, to rid oneself of the impression that some of the curves may have been influenced, in part at least, by these rather extreme initial conditions. But at present this remains an impression and nothing more; it does suggest, however, that the part played by the initial age distribution is worth investigating further in these experimental populations.

Although the dominant latent root of the matrix operating between t and $t+1$ has been considered here only as a function of the number of individuals present at time t , there should be little difficulty in extending the argument so as to include the case when q is assumed to be a function not of $N(t)$ but of $N(t-a)$ where a is an integer, or even of an integral, $\int_0^t N dt$ say. This last would be equivalent to assuming that the growth of the population was defined by a type of integro-differential equation such as is introduced by Volterra in his development of population mathematics (e.g. Volterra, 1931, p. 141; Volterra & D'Ancona, 1935, p. 22). Moreover, there is another and more speculative approach which is not without interest. In all these various forms of population growth the inherent rate of increase is regarded as dependent on the total numbers and thus each individual is counted as being of the same value for all age distributions of which it is a member. In other words, the factor q is taken to be some function of the scalar $[1]\xi$, where $[1]$ is a row vector of units. Now, from the biological point of view, it is not unreasonable to suppose that the form of the age distribution may also be of importance. For a given value of N we might have two entirely different age distributions, one of which was composed largely of adult individuals and only a small number of young, and the other with these proportions reversed. The question naturally arises whether one is justified in assuming that both the populations are of equal value and that they both influence the system of rates to the same extent. The one with the larger proportion of adults might exert a greater degree of influence on the rate of increase owing, for instance, to a proportionately greater consumption of food, or an enhanced mutual interference between the individual members of the population. But this is at present purely

speculative, and so far as the writer is aware, there is no experimental evidence for the occurrence of such differential effects associated with the form of the age distribution when the populations are of the same size. As a possibility, however, it is of interest theoretically and it suggests that instead of counting all individuals as equal, some system of weighting the individual age classes would be required. A mathematical model which immediately comes to mind is that of a matrix whose dominant latent root is affected by the length of the vector on which it is operating; that is to say, it would be assumed that the inherent rate of increase was dependent on the present value of the population at a given time.

6. THE PREDATOR-PREY RELATIONSHIP BETWEEN TWO POPULATIONS

It is of interest to consider very briefly a simple type of predator-prey relationship between two species of which the one, S_1 , is preyed upon by the other, S_2 . If the matrix A_1 with a dominant latent root λ_1 represents the optimum system of rates for the prey and the matrix A_{1t} for this population at time t has a dominant root λ_1/q_1 , we might regard the factor q_1 as a function of N_2 , the number of the predatory species S_2 , and write as a first approximation,

$$q_1 = 1 + \alpha_1 N_2, \quad (6.1)$$

where $\alpha_1 > 0$ is a constant. In the same way there will be some optimum system of rates A_2 for the species S_2 , though in fact this system may never be realized in full save under exceptional circumstances, for instance when the prey are extremely numerous in comparison with the predator, and everything in the environment is favourable to the latter species. (From the biological point of view there must be some upper limit to the possible inherent rate of increase of which a particular species is capable. For instance, in the case of mammals, this limit will be determined in part by physiological factors, such as the length of the gestation period, the shortest interval between litters, the maximum average number of daughters per litter, the age at which breeding first starts, and so forth, as well as the form of life table under the most favourable circumstances.) Then at time t the matrix A_{2t} will have a dominant root λ_2/q_2 and we will write

$$q_2 = 1 + \alpha_2 \frac{N_2}{N_1}, \quad (6.2)$$

where $\alpha_2 > 0$ is another constant and N_1 the number of the species S_1 at time t . This equation expresses in a simple fashion the main biological consequences to the species S_2 of its dependence upon S_1 as a source of food. For when $N_1 \rightarrow 0$, $q_2 \rightarrow \infty$, and the inherent rate of increase of the predator $r'_2 = \log_e(\lambda_2/q_2) \rightarrow -\infty$ (disappearance of predator in the absence of any prey). Conversely, when N_1 becomes very large, $q_2 \rightarrow 1$ and the inherent rate of increase of the predator approaches its optimum value $r_2 = \log_e \lambda_2$.

Adopting, then, the simple system represented by (6.1) and (6.2) we shall have for the stationary state, putting $q_1 = \lambda_1$ and $q_2 = \lambda_2$,

$$N_1 = \frac{\alpha_2(\lambda_1 - 1)}{\alpha_1(\lambda_2 - 1)} = K_1, \quad N_2 = \frac{\lambda_1 - 1}{\alpha_1} = K_2,$$

which will be real positive quantities when both λ_1 and $\lambda_2 > 1$. Moreover, assuming for the moment that a stable stationary state is possible, we must have $\alpha_2(\lambda_1 - 1) > \alpha_1(\lambda_2 - 1)$ and

$(\lambda_1 - 1) > \alpha_1$ for both species to coexist in appreciable numbers. Then, expressing α_1 and α_2 in terms of the λ 's and K 's,

$$q_1 = 1 + (\lambda_1 - 1) \frac{N_2}{K_2}, \quad (6.1a)$$

$$q_2 = 1 + (\lambda_2 - 1) \frac{K_1 N_2}{K_2 N_1}. \quad (6.2a)$$

This simple system, however, can be improved upon to some extent. It will be noticed that if in equation (6.1) $N_2 = 0$, $q_1 = 1$ and thus in the absence of the predator it is assumed that the prey will increase to an unlimited extent. In order to introduce the conception of a limited environment, we might put

$$q_1 = 1 + \alpha_1 N_2 + \beta_1 N_1, \quad (6.3)$$

so that when $N_2 = 0$, the species S_1 will approach some upper limit in numbers. A slightly more general system is represented then by equations (6.3) and (6.2), for which the stationary state is

$$N_1 = \frac{\alpha_2(\lambda_1 - 1)}{\alpha_1(\lambda_2 - 1) + \alpha_2\beta_1}, \quad N_2 = \frac{(\lambda_1 - 1)(\lambda_2 - 1)}{\alpha_1(\lambda_2 - 1) + \alpha_2\beta_1}.$$

It would thus be possible to examine the consequences of various hypotheses as to the way in which the reduction in the optimum inherent rates of increase for the two species are effected. The possible combinations are, however, so numerous that it is difficult to cover at all adequately any more than one of the most obvious cases. In order to illustrate the properties of such a system, the simplest, and also the possibly not unrealistic example of the reduction in the rates for both species taking place through the operation of an additional force of mortality independent of age will be considered here. That is to say, it will be assumed that the effect of the species S_2 on system of rates for the species S_1 will be to divide the elements of the matrix A_1 by the factor q_1 , and similarly that the effect of the species S_1 on the species S_2 and the matrix A_2 will be to divide the elements of the latter by q_2 . This simplifies a number of the actual computations and also the analysis of the properties of the equations.

If at time t the age distributions of the $N_1(t)$ and $N_2(t)$ individuals of the species S_1 and S_2 are of the stable forms appropriate to the dominant latent roots λ_1 and λ_2 of the matrices A_1 and A_2 respectively, then from the properties of a matrix $q^{-1}A$ which were discussed in the previous section, the two populations will retain their initial forms of age distribution unchanged. The total numbers of individuals in the two populations, supposing these are subject to the system defined by equations (6.1a) and (6.2a) respectively, will therefore be at time $t + 1$

$$N_1(t+1) = \frac{\lambda_1 N_1(t)}{1 + (\lambda_1 - 1) \frac{N_2(t)}{K_2}},$$

$$N_2(t+1) = \frac{\lambda_2 N_2(t)}{1 + (\lambda_2 - 1) \frac{K_1 N_2(t)}{K_2 N_1(t)}},$$

whence

$$N_1(t+1) - N_1(t) = \frac{(\lambda_1 - 1) N_1(t) \left\{ 1 - \frac{N_2(t)}{K_2} \right\}}{1 + (\lambda_1 - 1) \frac{N_2(t)}{K_2}},$$

and

$$N_2(t+1) - N_2(t) = \frac{(\lambda_2 - 1) N_2(t) \left\{ 1 - \frac{K_1 N_2(t)}{K_2 N_1(t)} \right\}}{1 + (\lambda_2 - 1) \frac{K_1 N_2(t)}{K_2 N_1(t)}}.$$

Before discussing the limits to which these difference equations will tend when the time interval is made smaller and smaller, it is necessary to consider the question of the value to which the dominant latent root of the matrix will tend when the latter becomes of a very large order. Suppose that working in some convenient unit of age and time we have the matrix A_1 , with a real positive root λ_1 , representing some given system of age-specific fertility and mortality rates. We can also construct a new matrix— $A_{\frac{1}{2}}$ say—for the same system of rates when the time interval is taken to be a half-unit. This new matrix will be twice the order of the original one and it will have a dominant root— $\lambda_{\frac{1}{2}}$ say—which will be less than λ_1 . Continuing the process further, we shall have for an interval of age and time h a matrix A_h with a dominant root λ_h , this root representing in the case of a population with a stable age distribution, the ratio $N(t+h)/N(t)$. In order to compare the successive values of λ_h which would be obtained by making the interval h smaller and smaller, it is necessary to express them in some common unit of time and we can write

$$\Lambda = (\lambda_h)^{1/h} \quad \text{or} \quad \lambda_h = \Lambda^h.$$

Then, when the matrix remains constant in time, we shall have for a population with a stable age distribution,

$$\frac{N(t+h) - N(t)}{h} = \frac{\lambda_h - 1}{h} N(t) = \frac{\Lambda^h - 1}{h} N(t),$$

or, when $h \rightarrow 0$,

$$\frac{dN}{dt} = (\log_e \Lambda) N,$$

since

$$\lim_{h \rightarrow 0} \frac{\Lambda^h - 1}{h} = \log_e \Lambda.$$

Thus, as the matrix is made larger and larger, the value of $\log_e \Lambda$ tends to ρ , the true instantaneous relative rate of increase of the stable population per unit of time.

In a similar fashion we may write for an interval h the above difference equations in the form

$$\begin{aligned} \frac{N_1(t+h) - N_1(t)}{h} &= \frac{\left(\frac{\Lambda_1^h - 1}{h}\right) N_1(t) \left\{1 - \frac{N_2(t)}{K_2}\right\}}{1 + (\Lambda_1^h - 1) \frac{N_2(t)}{K_2}}, \\ \frac{N_2(t+h) - N_2(t)}{h} &= \frac{\left(\frac{\Lambda_2^h - 1}{h}\right) N_2(t) \left\{1 - \frac{K_1 N_2(t)}{K_2 N_1(t)}\right\}}{1 + (\Lambda_2^h - 1) \frac{K_1 N_2(t)}{K_2 N_1(t)}}, \end{aligned}$$

which, as $h \rightarrow 0$, may be replaced by

$$\frac{dN_1}{dt} = (\log_e \Lambda_1) N_1 \left(1 - \frac{N_2}{K_2}\right), \quad \frac{dN_2}{dt} = (\log_e \Lambda_2) N_2 \left(1 - \frac{K_1 N_2}{K_2 N_1}\right).$$

Thus, when the age distributions of the populations S_1 and S_2 are each initially of the appropriate stable form, and when it is assumed that their respective systems of rates are represented by the matrices $q_1^{-1}A_1$ and $q_2^{-1}A_2$, the system of interrelations between the two populations which is defined by

$$q_1 = 1 + \alpha_1 N_2, \quad q_2 = 1 + \alpha_2 \frac{N_2}{N_1},$$

is equivalent to that defined by the differential equations

$$\frac{dN_1}{dt} = (r_1 - a_1 N_2) N_1, \quad \frac{dN_2}{dt} = \left(r_2 - a_2 \frac{N_2}{N_1} \right) N_2, \quad (6.4)$$

or, when q_1 is defined by (6.3), to

$$\frac{dN_1}{dt} = (r_1 - a_1 N_2 - b_1 N_1) N_1, \quad \frac{dN_2}{dt} = \left(r_2 - a_2 \frac{N_2}{N_1} \right) N_2, \quad (6.5)$$

where in both sets $r_1 = \log_e \lambda_1$, $r_2 = \log_e \lambda_2$ and a_1 , a_2 , b_1 are constants > 0 . This result is analogous to that discussed in the previous section for a single population increasing in a limited environment, where it was shown that when mortality was affected by a factor independent of age and the initial distribution was of the appropriate stable form, the numbers of individuals increased according to the logistic law, and that consequently under these conditions the type of population growth resulting from the operation of the matrix $q^{-1}A$, where

$$q = 1 + \frac{\lambda_1 - 1}{K} N,$$

was equivalent to that defined by the differential equation,

$$\frac{dN}{dt} = (r - aN) N.$$

The system of equations (6.4) differs somewhat from the classical Lotka-Volterra equations (Lotka, 1925, Chap. 8; Volterra, 1931, p. 14) for a simple predator-prey relationship between two species, in which the second member would be written

$$\frac{dN_2}{dt} = (-r_2 + a_2 N_1) N_2.$$

The form of the second member in (6.4) was originally suggested by the results of an analysis made by the author (unpublished observations) of some data given by Gause (1934) for the growth in numbers of *Paramecium caudatum* and *Paramecium aurelia* cultures, in which the food supply consisted of a suspension of *Bacillus pyocyaneus* in a buffered medium. Two different concentrations of bacteria—called by Gause ‘one loop’ and ‘half-loop’—were used for both species of *Paramecium*, and under the conditions of the experiments these populations could be regarded as living in a limited environment with a constant supply of food. It was apparent from the results that for each species living alone the upper limit to the number of individuals depended on the concentration of food, being in each case approximately twice as great in the cultures with the ‘one loop’ concentration as in those with the ‘half-loop’. If logistic equations are fitted to the four series of data given by Gause (1934, table 4, p. 145), it will be found that whereas the constant r in the equation $dN/dt = (r - aN) N$ remains approximately the same in the pair of experiments on each species of *Paramecium*, the constant a is inversely proportional to the concentration of food (see also on this point Kostitzin, 1937, p. 77). Thus, when the food supply (F) was kept constant, the form of population growth in numbers could be written

$$\frac{dF}{dt} = 0, \quad \frac{dN_2}{dt} = \left(r_2 - \frac{a_2}{C} N_2 \right) N_2,$$

where C represents the relative concentration of food in the different experiments. This relationship suggested a system of equations such as (6.4) for the theoretical case of a food supply consisting of a population of individuals which when living alone would increase at

a rate $dN_1/dt = r_1 N_1$. However, apart from these considerations, the form of the second member of (6.4) is linked with the type of expression used here to define q_2 in terms of N_1 and N_2 , and the latter arose as one of the simplest and most obvious ways of expressing the dependence of the species S_2 on S_1 , bearing in mind that the elements of the matrix representing the system of rates at a given time must be positive quantities ($F_x \geq 0$, $0 < P_x \leq 1$). The difficulties which arise when this is not the case will be appreciated on endeavouring to find a working model in terms of matrices and vectors which will reduce to the classic Lotka-Volterra equations under suitable initial conditions. For, in the case of the predatory species S_2 we should have to consider a reciprocal matrix A_2^{-1} with a real positive root λ_2^{-1} , and at time t the matrix $q_2 A_2^{-1}$ would be regarded as operating on the vector $\xi(t)$ representing the age distribution of S_2 . Then, if as before the matrix $q_1^{-1} A_1$ represents the system of rates for the species S_1 and

$$q_1 = 1 + \frac{\lambda_1 - 1}{K_2} N_2, \quad q_2 = 1 + \frac{\lambda_2 - 1}{K_1} N_1,$$

we have a system which will reduce to the Lotka-Volterra differential equations when the initial age distributions of both populations are of the stable form appropriate to their respective matrices A_1 and A_2 . Now, apart from the fact that here no upper limit is placed on the inherent rate of increase, $r'_2 = \log_e(q_2/\lambda_2)$, of the species S_2 , there is an added complication that a number of the elements of A_2^{-1} will be negative (for the form of the matrix A^{-1} see the previous paper, § 4). Although no difficulties arise in the special case, when the age distribution of S_2 is of the stable form, in the perfectly general case of an arbitrary $\xi(t)$ some of the elements of $\xi(t+1) = q_2 A_2^{-1} \xi(t)$ can become negative and thus meaningless from the biological point of view. For these various reasons, therefore, the form of interrelationship between the two species defined by equations (6.1a) and (6.2a) was adopted here as a working model, and these reduce in the special case to the system of differential equations (6.4).

The writer has to confess that he has been unable to integrate either of the sets (6.4) and (6.5). Their main properties, however, seem to be quite clear. Taking the simplest system (6.4) first, we have for $dN_1/dt = dN_2/dt = 0$,

$$N_1 = \frac{r_1 a_2}{r_2 a_1} = K_1, \quad N_2 = \frac{r_1}{a_1} = K_2,$$

and, introducing for simplicity the variables $n_1 = N_1/K_1$, $n_2 = N_2/K_2$,

$$\frac{dn_1}{dt} = r_1 n_1 (1 - n_2), \quad \frac{dn_2}{dt} = r_2 n_2 \left(1 - \frac{n_2}{n_1}\right).$$

We will suppose that we are dealing with the case when $r_1 a_2 > r_2 a_1$, $r_1 > a_1$, in order that the stationary state may have a real meaning from the biological point of view. Then, in considering small departures from the stationary state, let $v_1 = n_1 - 1$, $v_2 = n_2 - 1$; and, disregarding in the usual way terms such as $v_1 v_2$, v_1^2 , etc.;

$$\frac{dv_1}{dt} = -r_1 v_2, \quad \frac{dv_2}{dt} = r_2 v_1 - r_2 v_2.$$

This linear system will have a solution of the type $v_1 = A_1 e^{\mu_1 t} + B_1 e^{\mu_2 t}$, $v_2 = A_2 e^{\mu_1 t} + B_2 e^{\mu_2 t}$, where the values of μ will be given by the roots of the characteristic determinant

$$\begin{vmatrix} -\mu & -r_1 \\ r_2 & -(r_2 + \mu) \end{vmatrix} = 0$$

or

$$2\mu = -r_2 \pm \sqrt{(r_2^2 - 4r_1 r_2)}.$$

Thus, both roots μ_1 and μ_2 will be complex so long as $r_2 < 4r_1$, and the real part of this pair will be negative since $r_2 > 0$. The system under these conditions will therefore approach the stationary state by a series of damped oscillations. When $r_2 > 4r_1$, both μ_1 and μ_2 will be negative; and consequently the stationary state will be stable, since in both cases v_1 and v_2 tend to zero as time increases.

The analysis of the system represented by equations (6.5) leads to very similar results. For

$$\frac{dN_1}{dt} = \frac{dN_2}{dt} = 0,$$

$$N_1 = \frac{r_1 a_2}{r_2 a_1 + a_2 b_1} = K_1, \quad N_2 = \frac{r_1 r_2}{r_2 a_1 + a_2 b_1} = K_2.$$

And, in the same way as before, putting $n_1 = N_1/K_1$, $n_2 = N_2/K_2$, $v_1 = n_1 - 1$, $v_2 = n_2 - 1$, and neglecting terms in $v_1 v_2$, etc., we have

$$\frac{dv_1}{dt} = -r_1(1-k)v_1 - r_1 k v_2, \quad \frac{dv_2}{dt} = r_2 v_1 - r_2 v_2,$$

where

$$k = \left(1 + \frac{a_2 b_1}{r_2 a_1}\right)^{-1} \quad (0 < k < 1).$$

Then, putting the characteristic determinant

$$\begin{vmatrix} -\{r_1(1-k) + \mu\} & -r_1 k \\ r_2 & -(r_2 + \mu) \end{vmatrix} = 0,$$

we have

$$\mu^2 + \{r_2 + r_1(1-k)\}\mu + r_1 r_2 k = 0.$$

The roots of this equation will be either both negative or both complex with the real part negative, depending on the relation between the various constants, and consequently both v_1 and v_2 will tend to zero as time goes on, the stationary state thus being stable as before. It will be noticed, however, that if $\mu = u \pm iv$, the damping term represented by the real part, $u = -\{r_2 + r_1(1-k)\}$, will be greater than in the case of the first system of equations (6.4) where $u = -r_2$. Again, for a given set of values of r_1, r_2, a_1, a_2 , the number of individuals $N_1 = K_1$, $N_2 = K_2$ must be less for the second set of equations than for the first, since by definition $b_1 > 0$. Thus we might expect that for a population subject to equations (6.5) the stationary numbers will be lower and the approach to the stationary state more rapid than for a population subject to equations (6.4), provided that the values of r_1, r_2, a_1 and a_2 are the same in both cases.

As a numerical example of these predator-prey equations, suppose that the optimum system of rates for two imaginary species were the same and that they were represented by the matrix A which has been used previously to illustrate various points. Then $A_1 = A_2$, $\lambda_1 = \lambda_2 = 3$ and $r_1 = r_2 = 1.09861$. If, for the first set of equations (6.1) and (6.2) we put

$$q_1 = 1 + 0.002N_2, \quad (6.6)$$

$$q_2 = 1 + 10N_2/N_1 \quad (6.7)$$

and for the second, (6.3) and (6.2)

$$q_1 = 1 + 0.002N_2 + 0.000185185N_1, \quad (6.8)$$

q_2 remaining as before, the number of individuals for the stationary state are in the first case $K_1 = 5000$, $K_2 = 1000$, and in the second $K_1 = 3418$, $K_2 = 684$. Then, assuming that at $t = 0$, $N_1 = N_2 = 108$, and that each of these populations had the same stable form of age distribution

$$\xi_1 = \{81, 21, 5, 1\},$$

the results of operating on these two age distributions with the matrices $q_1^{-1}A_1$ and $q_2^{-1}A_2$ were as follows for the two sets of equations. The first two columns give the numbers of prey (N_1) and predators (N_2) when no upper limit is placed on the number of prey (equations (6.6) and (6.7)), and the second two columns give the respective numbers when the upper limit to N_1 would be 10800 individuals, if the predatory species was absent (equations (6.8) and (6.7)). (This is the same logistic population as was used in the previous section as an illustration.)

t	I		II	
	N_1	N_2	N_1	N_2
0	108	108	108	108
1	266	30	262	30
2	755	42	710	42
3	2089	81	1754	79
4	5393	175	3550	163
5	11983	396	5371	335
6	20050	894	6046	619
7	21583	1854	5403	917
8	13756	2991	4227	1020
9	5910	2826	3317	897
10	2665	1466	2921	726
11	2033	677	2928	625
12	2592	469	3146	598
13	4012	501	3396	618
14	6011	668	3555	658
15	7717	949	3587	692
16	7986	1277	3529	709
17	6741	1474		
18	5122	1388		
19	4071	1122		
20	3763	896		
21	4043	795		
22	4684	804		

In both cases the approach to the stationary state by means of a series of damped oscillations is very evident, this approach being made more rapidly in the second series than in the first as was to be expected from the results of the foregoing analysis. Probably the clearest graphical illustration of these functions is obtained by plotting $\log N_2$ against $\log N_1$, the result being a spiral curve which gradually approaches the stationary point.

Although these predator-prey equations have been studied here only in the special case of the reduction in the rates of increase of the two populations being effected by an increase in the degree of mortality which is independent of age, there would be little difficulty in investigating, for instance, the type of case in which a relative absence of prey affected the fertility of the predator, and so forth. Moreover, there will be in all cases the effect on such a system of any abnormalities in the initial age distributions, or of any chance disturbances of the existing age distributions at some point in the development of the populations. Without working out any actual examples, however, it might be expected from the results obtained in the case of a logistic-type population that the general effect of all these factors would be to add further oscillatory features to those which already are inherent in the system itself, even when the stability of the age-distributions is established as in the above numerical examples. It seems likely, too, that these additional factors will increase the chance of one or other of the two species being reduced to such low numbers as would be equivalent in practice to the extinction of the population. This possibility will, however, greatly depend on the numerical relations between the various constants which enter into the equations

and upon the initial conditions of the particular system. Finally, just as in the case of a solitary population increasing in a limited environment, there is the possibility of studying the more complicated cases in which q_1 and q_2 are taken to be functions not only of N_1 and N_2 at time t , but of the numbers at some previous time, or of an integral of N_1 or N_2 between some time limits. Similar methods could also be used in order to study a chain of such predator-prey relations.

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