

25. On the Generation and Growth of a Population

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1. Some of the factors which complicate the theoretical and practical quantitative study of human populations may be negligible in the treatment of certain lower biological populations. The comparatively short lifetime and the regularity of breeding epochs is one simplification, which, incidentally suggests the interval between breeding epochs as a natural unit of age. It may also be that fertility and mortality rates at ages are more nearly constant in time—in any case, time fluctuations in these rates due to environment changes are more amenable to experimental control in colonies of lower animals or plants than in human populations.

2. Suppose a group y_1 of individuals to be 'born' at some epoch ($t=0$) and consider the population generated by this group. Assume that 'breeding' occurs at regular epochs $t=z, 2z, \dots, NZ, \dots$ and let us adopt z as the unit of age for individuals. Let f_r be the fertility factor per individual entering the r^{th} age group ($r-1z$ to rz) and let S_r be the survival factor per individual for survival from the r^{th} to the $(r+1)^{\text{th}}$ age group. Both f_r and S_r are taken to be constant in time and we assume, further, that for reproductive purposes there is no interaction between different age groups.

Under these somewhat stringent conditions, the relaxation of which can be considered later, the numerical history of the population generated by the original y_1 individuals, will, just after the third breeding epoch (say), be as follows:

	After epoch $t=0$	After epoch $t=Z$	After epoch $t=2Z$	After epoch $t=3Z$
No. aged $0+$	y_1	$f_1 y_1$	$(f_1^2 + f_2 s_1) y_1$	$(f_1^3 + 2f_1 f_2 s_1 + f_3 s_2 s_1) y_1$
No. aged $Z+$	0	$s_1 y_1$	$f_1 s_1 y_1$	$(s_1 f_1^2 + f_2 s_2^2) y_1$
No. aged $2Z+$	0	0	$s_2 s_1 y_1$	$f_1 s_2 s_1 y_1$
No. aged $3Z+$	0	0	0	$s_3 s_2 s_1 y_1$

If we now suppose that no individual survives the age nZ (i.e. $S_n=0$), the frequency distribution in the n age groups 0 to Z ; Z to $2Z, \dots, n-1Z$ to nZ will, after the N^{th} breeding epoch be given by the N^{th} power of the linear substitution.

$$A \equiv (f_1 y_1 + f_2 y_2 + \dots + f_n y_n, s_1 y_1 \dots s_{n-1} y_{n-1}), \quad (1)$$

the initial set of frequencies being $y_1 = y_1; y_2 = y_2 = \dots y_n = 0$.

3. Now consider the n age groups 0 to z, z to $2z$, etc. to be filled by an *arbitrary* set of y_1, y_2, \dots, y_n individuals and let the fertility and survival factors for age groups be $f_1 f_2 \dots f_n$ and $s_1, s_2 \dots s_{n-1}, 0$ as before. Then we may take the arbitrary column matrix

$$\{y\} = \{y_1, y_2 \dots y_n\}$$

as an initial age distribution corresponding to the epoch $t=0$. The age distribution after the first breeding epoch will now be given by

$$\{y'\} = \{y'_1, y'_2 \dots y'_n\}$$

where

$$y'_1 = f_1 y_1 + f_2 y_2 + \dots + f_n y_n$$

$$y'_2 = s_1 y_1$$

$$y'_3 = s_2 y_2$$

$$y'_n = s_{n-1} y_{n-1}$$

which is, of course, the linear substitution A of equation (1). The matrix of this substitution is the square matrix

$$M = \begin{vmatrix} f_1 & f_2 & \dots & f_{n-1} & f_n \\ s_1 & 0 & \dots & 0 & 0 \\ 0 & s_2 & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & s_{n-1} & 0 \end{vmatrix}$$

all elements not in the first row or sub-diagonal being zero. The age frequency distribution after the N^{th} breeding epoch will be given by the N^{th} power of A or, what is the same thing, by the column matrix $M^N \{y\}$.

Now the characteristic equation of M is easily shown to be

$$\lambda^n - f_1 \lambda^{n-1} - \dots - f_{n-1} s_1 s_2 \dots s_{n-2} \lambda - f_n s_1 s_2 \dots s_{n-1} = 0$$

where, of course $f_r \geq 0$ ($r=1, 2, \dots, n$) and $0 \leq s_r \leq 1$ ($r=1, 2, \dots, n-1$), $s_n = 0$. This equation determines the form to which the age distribution of the population envisaged ultimately settles down under the action of the given system of fertility and survival factors.

4. Under certain conditions however the initial age distribution will be repeated exactly after the cycle of n breeding epochs. This follows at once since the matrix M satisfies its own characteristic equation

$$M^n - f_1 M^{n-1} - \dots - f_{n-1} s_1 s_2 \dots s_{n-2} M - f_n s_1 s_2 \dots s_{n-1} I = 0$$

where I is the unit matrix of order n .

Now if $M^n - I = 0$ the initial distribution $\{y\}$ will be repeated exactly after n operations of M. We see that the condition for this is

$$f_1 = f_2 = \dots = f_{n-1} = 0 \quad \text{and} \quad f_n s_1 s_2 \dots s_{n-1} = 1.$$

If

$$f_1 = f_2 = \dots = f_{n-1} = 0 \quad \text{and} \quad f_n s_1 s_2 \dots s_{n-1} = k$$

then the distribution after n breeding epochs will be

$$\{k y_1, \dots, k y_n\}, \quad \text{i.e., } k \{y\}.$$

After $2n$ epochs it will be $k^2 \{y\}$ and so on.

5. In general, however, the age distribution will display no pure periodicity but will settle down to a definite (stable) distribution depending on the dominant root (root of maximum modulus) of the characteristic equation.

In this equation, namely

$$\lambda^n - f_1 \lambda^{n-1} - f_2 \lambda^{n-2} s_1 \dots - f_{n-1} s_1 s_2 \dots s_{n-2} \lambda - f_n s_1 \dots s_{n-1} = 0$$

the f and s are all positive so that the equation has at most one positive root, and moreover, it always has one. It can be shown that this positive root is also the dominant root¹ (a fact of itself not without interest). The only exception which can arise yields the periodicity mentioned in para 4.

6. Now when the characteristic equation has a single (non repeated) real dominant root l (say) the ratio of an element in the $(m+1)^{\text{th}}$ power of M to the corresponding element in the m^{th} power will, for large m , tend to l . The column matrix giving the age distribution, being acted upon successively by the matrix M , will also tend to a form in which an element of $M^{m+1}\{y\}$ will bear to the corresponding element in $M^m\{y\}$ the ratio l .

Now let Y_1, Y_2, \dots, Y_n be a set of frequencies such that

$$\left. \begin{aligned} \lambda Y_1 &= f_1 Y_1 + f_2 Y_2 \dots + f_n Y_n \\ \lambda Y_2 &= s_1 Y_1 \\ \lambda Y_3 &= s_2 Y_2 \\ &\vdots \\ \lambda Y_n &= s_{n-1} Y_{n-1} \end{aligned} \right\} \quad (2)$$

Eliminating Y_1, Y_2, \dots, Y_n we obtain the characteristic equation of M , the matrix of A .

The set Y_1, Y_2, \dots, Y_n constitutes a 'pole' of the substitution, A corresponding to the root λ of the characteristic equation. We have seen that the frequencies in all age groups will ultimately increase in the ratio l , it follows that the ultimate ratios of the n frequencies one to another will be Y_1, Y_2, \dots, Y_n where $Y_1 \dots Y_n$ is a pole corresponding to the dominant root l . Now from equation (2) with $\lambda=l$ we obtain

$$Y_1 : Y_2 : \dots : Y_n = 1 : \frac{s_1}{l} : \frac{s_1 s_2}{l^2} : \dots : \frac{s_1 s_2 \dots s_{n-1}}{l^{n-1}} \quad (3)$$

7. We see, therefore, that under the operation of the matrix M the age distribution column matrix $\{y\}$ will in general settle down to a form in which the relative frequencies in the different age groups are determined by the ratios (3) and that after each breeding epoch the numbers in each group (and so of course in the total population) will increase in geometric progression of ratio equal to the positive root of the characteristic equation of M . The population will

¹ This theorem and its consequences, which lead to a simple upper bound to the modulus of the roots of any equation, have been investigated by Mr. D. B. Lahiri and the present author in a paper awaiting publication.

increase, just maintain itself, or decrease ultimately according as $l \gtrless 1$. The number l is related to Kuczynski's net reproduction rate, the analogue of which would here be

$$(f_1 + f_2 s_1 + \dots + f_n s_1 \dots s_{n-1})$$

but l appears to be a better index of what can be called the true (ultimate) rate of increase. We have

$$1 = \frac{f_1}{l} + \frac{f_2 s_1}{l^2} + \dots + \frac{f_n s_1 \dots s_{n-1}}{l^n}$$

so that a net reproduction rate $\gtrless 1$ means $l \gtrless 1$ and *vice versa*, but the magnitudes of the two measures will be different.

8. The question of approximation to the case of pure periodicity discussed in para 4 may be of practical importance for some lower animals with few age groups. The rapidity with which an arbitrary initial age distribution settles down close to the 'ultimate' form depends on the difference between the dominant and sub-dominant root of the characteristic equation.

As for the relaxation of the conditions assumed in para 1, the question of interaction between age groups would in many cases be of no importance but to take account of time changes in f_r and s_r would mean assuming suitable laws of variation for the matrix elements. Such laws lead to much more complicated analysis but are being investigated.