

Generalizing Fisher's "reproductive value": Linear differential and difference equations of "dilute" biological systems†

(one-sex demography/eigenvectors/density dependence/asymptotic importance)

PAUL A. SAMUELSON

Department of Economics, Massachusetts Institute of Technology, Cambridge, Massachusetts 02139

Contributed by Paul A. Samuelson, August 22, 1977

ABSTRACT R. A. Fisher's 1930 "reproductive value" is defined as the contribution made by a population's initial age elements to its asymptotically dominating exponential growth mode. For the Leslie discrete-time model, it is the characteristic row vector of the Leslie matrix, and for the integral-equation model of Lotka the similar *eigenfunction*. It generalizes neatly to a 2-sex model of linear differential equations, and to general n -variable linear systems. However, when resource limitations end the "dilute" stage of linearity, reproductive value loses positive definability. The present linear analysis prepares the way for generalizing reproductive value to nonlinear systems involving first-degree-homogeneous relationships.

For a linear female-dominant demographic system like that of Sharpe and Lotka (1), or its discrete-time version of Leslie (2), R. A. Fisher (3) defined the "reproductive value" of an initial population element of a given age. Eschewing his analogies to the compound-interest concepts of economics, we may tersely define Fisher's concept as *the contribution made by the system's initial conditions to its asymptotically dominating exponential-growth mode*.

Review of discrete-time demography

Utilizing convenient matrix notation, we write our system as

$$x(t+1) = Lx(t) \quad [1]$$

in which $x = [x_i]$ is the column vector of a number of females of age j ; in which $[L_{ij}] = [m_j]$ is the row vector of nonnegative age-specific fertilities, with $m_n > 0$ if we ignore all post-fertile ages older than n , and with $m_k m_{k+1} > 0$ for some choice of k between 1 and $n-1$; and in which the only nonzeros in L s last $n-1$ rows are the positive age-specific survival fractions in the sub-diagonal, $0 < L_{i+1,i} = p_i \leq 1 = l_0, p_1 p_2 \dots p_k = l_k \leq l_{k-1}$ for $1 \leq k < n$.

Now with L assured to be a *primitive* (nonnegative, acyclic, irreducible) Perron-Frobenius matrix, it is well known that the system approaches an exponential rate of growth

$$\lim_{t \rightarrow \infty} \frac{x_i(t+1)}{x_i(t)} = 1 + r, \quad (i = 1, \dots, n), \quad x(0) > 0 \quad [2.1]$$

$$-1 < r < 0,$$

in which $1+r$ is the positive root of

$$\psi[\lambda] = \sum_{i=1}^n m_i l_{i-1} \lambda^{-i} = 1 \quad [2.2]$$

$$\lim_{t \rightarrow \infty} \frac{\sum_{i=1}^n x_i(t)}{(1+r)^t} = v[x_1^0, \dots, x_n^0]. \quad [2.3]$$

This is a uniquely defined function, fulfilling Fisher's purpose and obeying

$$v[x_1^0, \dots, x_n^0] = \sum_{i=1}^n v_i x_i(0) = vx(0) \quad [2.4]$$

$$\lim_{t \rightarrow \infty} \frac{x_i(t)}{\sum_{j=1}^n x_j(t)} = \bar{x}_i, \quad \sum_{i=1}^n \bar{x}_i = 1 \quad [2.5]$$

v and \bar{x} being row and column eigenvectors of L corresponding to its characteristic root of largest absolute value, $1+r$:

$$L\bar{x} = (1+r)\bar{x}, \quad \mathbf{1}\bar{x} = 1, \quad \mathbf{1} = (1, 1, \dots, 1) \quad [3.1]$$

$$vL = v(1+r), \quad v\bar{x} = 1. \quad [3.2]$$

[Remark: $\sum_{i=1}^n x_i(t) / \sum_{i=1}^n c_i x_i(t)$, where $c_i > 0$, approaches a constant as $t \rightarrow \infty$; so there is no intrinsic bias from adding units of different age on a one-for-one basis.]

Fisher's vector of *reproductive value* is, by definition, proportional to v . (He seems to suggest a normalization for v that makes the reproductive value at birth unity, *my* v/v_1 ; then his v_j/v_1 gives each age's reproductive value compared to that at birth.) It may be noted that, if we include in L some rows and columns for post-fertile ages, we shall have L reducible and shall have *zeros* for $[v_{n+1}, v_{n+2}, \dots]$.

Explicit formulas for \bar{x} and v are given, as by Samuelson (ref. 4, p. 396; ref. 5, pp. 400-401), by

$$\bar{x}^T = [\bar{x}_j] = b[1, l_1(1+r)^{-1}, \dots, l_{n-1}(1+r)^{-n+1}] \quad [4.1]$$

$$b^{-1} = 1 + l_1(1+r)^{-1} + \dots + l_{n-1}(1+r)^{-n+1} \quad [4.2]$$

$$v = [v_j] = a \left[\sum_{k=j}^n m_k l_{k-1} (1+r)^{-k} / l_{j-1} (1+r)^{j-1} \right] \\ = a[1, m_2(1+r)^{-1} + m_3(l_2/l_1)^{-2} + \dots \\ + m_n(l_{n-1}/l_1)(1+r)^{-n+1}, \dots, m_{n-1}(1+r)^{-1} \\ + m_n(l_{n-1}/l_{n-2})(1+r)^{-2}, m_n(1+r)^{-1}] \quad [4.3]$$

in which

$$a = 1/b\bar{g} \quad [4.4]$$

$$\bar{g} = -(1+r)\psi[1+r]$$

$$= [1, \dots, m_n(1+r)^{-1}] \begin{pmatrix} 1 \\ \vdots \\ l_{n-1}(1+r)^{-n+1} \end{pmatrix}. \quad [4.5]$$

Here b is the stable-age birth rate, $x_1(t) / \sum_{i=1}^n x_i(t)$, and \bar{g} is the stable-age "average length of a generation" (i.e., the weighted average age of mothers when giving birth, the weights being the stable-age $[\bar{x}_i] = \bar{x}$).

The costs of publication of this article were defrayed in part by the payment of page charges. This article must therefore be hereby marked "advertisement" in accordance with 18 U. S. C. §1734 solely to indicate this fact.

† This is the first of two related papers. Part 2, "Nonlinear, homogeneous, biparental systems," will appear in the December 1977 PROCEEDINGS.

Keyfitz (ref. 6, pp. 56-58) has provided a useful interpretation of this $v[x_1^0, \dots, x_n^0]$ function. It is the size that a stable-age population would have to be *today* to lead to the same *ultimate* population level as our system will generate out of its actual initial conditions $x(0)$. This defined "equivalent" stable-age system grows from the beginning at rate $1 + r$, and it continues to be "equivalent" to our actual system at t s after $t = 0$; therefore, $v[x_1(t), \dots, x_n(t)]$ must be a scalar with the remarkable property of growing immediately (and not just asymptotically) at rate $1 + r$. Mathematical proof of this Fisherine property follows.

From the orthogonality properties of the full set of column and row eigenvectors of L , we have

$$V(t + 1) = v x(t + 1) = v L x(t) = (1 + r) v x(t) \\ = (1 + r) V(t) = (1 + r)^t V(0) = (1 + r)^t [v x(0)]. \quad [5]$$

This verifies that Fisher's total reproductive value does grow from *the beginning* like $(1 + r)^t$, whereas any different linear combination of the $x_i(t)$ s will only *asymptotically* grow like $(1 + r)^t$. Reference may be made to Vincent (7), Goodman (8), and Keyfitz (6) for computations and interpretations of reproductive values.

Review of continuous-time case

The integral-equation counterpart of Eqs. [1-5] can be written in terms of total female births, $B(t)$, and of number of females of age y at time t , $N(y, t)$, once we are given invariant age-specific survival and fertility functions, $m(y)$ and $l(y)$, as follows:

$$B(t) = \int_{\alpha}^{\beta} m(y) N(y, t) dy, \quad 0 < \alpha < \beta < \infty. \quad [6.1]$$

$N(y, 0) = N^0(y) \geq 0$, a given nonnegative function

$$N(y, t) \equiv \frac{l(y)}{l(y - \theta)} N(y - \theta, t - \theta), \quad y \geq \theta, t \geq \theta \quad [6.2]$$

$$l(0) = 1; l'(y) \leq 0 < l(y), \quad 0 \leq y < \gamma; l(y) \equiv 0, \quad \gamma \leq y \\ m(y) > 0, \quad 0 < \alpha \leq y \leq \beta < \gamma; m(y) \equiv 0, \quad \beta < y$$

Provided $\int_{\alpha}^{\beta} N^0(y) dy > 0$, it is known that

$$\lim_{t \rightarrow \infty} \frac{\partial N(y, t) / \partial t}{N(y, t)} \equiv \rho \leq 0. \quad [7.1]$$

Fisher's *reproductive value* at age y is then definable as

$$\lim_{t \rightarrow \infty} \frac{\int_0^{\beta} N(y, t) dy}{\exp[\rho t]} = \int_0^{\beta} v(y) N^0(y) dy \quad [7.2]$$

$$\lim_{t \rightarrow \infty} \frac{N(y, t) dy}{\int_0^{\gamma} N(u, t) du} = \bar{N}(y), \quad \int_0^{\gamma} \bar{N}(y) dy = 1 \quad [7.3]$$

in which ρ is the real root of

$$\psi(\rho) = \int_{\alpha}^{\beta} m(y) l(y) e^{-\rho y} dy = 1 \quad [7.4]$$

and

$$\bar{N}(y) = b l(y) e^{-\rho y} \quad [7.5]$$

$$b^{-1} = \int_0^{\beta} l(u) e^{-\rho u} du \quad [7.6]$$

and

$$v(y) = a \int_y^{\beta} m(u) [l(u) / l(y)] e^{-\rho(u-y)} dy \quad [7.7]$$

$$\int_0^{\beta} v(y) \bar{N}(y) dy = 1 \quad [7.8]$$

$$a = 1 / b \bar{g}$$

$$\bar{g} = -\psi'(\rho) = + \int_0^{\beta} y m(y) l(y) e^{-\rho y} dy. \quad [7.9]$$

As in the discrete-time case of Eq. 4.4, \bar{g} and b are stable-age average generation length and birth rate (on a pre-menopausal population base).

Specifically, Eq. 7 shows that $N(y, t)$ can be written asymptotically as follows

$$N(y, t) \approx \bar{N}(y) e^{\rho t} \left[\int_0^{\beta} v(u) N^0(u) du \right]. \quad [8]$$

It is worth mentioning that, when fertility and mortality depend on total population, T , with

$$T(t) = \int_0^{\gamma} N(y, t) dy, \quad [9]$$

$$\partial m(y, T) / \partial T < 0, \quad \partial l(y, t) / \partial T < 0$$

the *nonlinear* integral equation for $B(t)$ becomes

$$B(t) = \int_{\alpha}^{\beta} m(y, T) l(y, T) B(t - y) dy, \quad t \geq \beta < 0 \quad [10.1]$$

and

$$\lim_{t \rightarrow \infty} B(t) = B^*, \quad \lim_{t \rightarrow \infty} T(t) = T^* \quad [10.2]$$

in which T^* is the positive root for T in

$$1 = \int_{\alpha}^{\beta} m(y, T) l(y, T) dt \quad [10.3]$$

and

$$B^* = T^* / \int_0^{\gamma} l(y, T^*) dy. \quad [10.4]$$

Leslie (ref. 9, section 5) and the vast Verhulst (10) and Pearl and Reed (11) literature recognize the realism of Eq. 10's nonlinearity.

For the nonlinear model of Eqs. 9-10, there is *no* existent useful $v(y)$ function that Fisher can find to employ to form

$$V(t) = \int_0^{\beta} v(y) N(y, t) dy$$

for which

$$V'(t) / V(t) \equiv \text{a constant.}$$

Similarly, for the *logistic* model of Verhulst and Pearl and Reed, which prevails in the post-dilute stage,

$$\dot{x} = x(a - ax^{-1}) \quad [10.5]$$

$$\lim_{t \rightarrow \infty} x(t) = \hat{x} \text{ for all } x(0) > 0 \quad [10.6]$$

and reproductive value of $x(0)$ is inevitably zero.

In other words, the concept of "reproductive value" loses existence for general nonlinear demographic systems. Unfortunately, the reality any theory of natural selection must face, as Fisher (ref. 3, pp. 41-46) clearly understands, is of the nature of Eq. 10 above rather than Eq. 6 above. Only in early *dilute* stages of Malthus-von Neumann growth (ref. 12) will Eqs. 1 and 6 have relevance; but it is precisely then that selection loses its sting!

In Price and Smith (13) some difficulties with Fisher's $v(y)$ concept are noted when $m(y)l(y)$ in Eq. 7.4 is a varying func-

tion of calendar time. The present critique cuts deeper: even if the *structure* of the nonlinear system shows *no* change with calendar t , Fisher's concept of "reproductive value" encounters grave definitional problems.

Linear differential and difference equations

Not all nonlinear systems render reproductive value nugatory. To pave the way for an important class of manageable nonlinear systems, those involving biparental nonlinearities of the type introduced by Kendall (14), we need first to generalize the concept of reproductive value for the linear differential equations of biparental reproduction like those of Goodman (15).

Thus, consider the *linear* version of Eq. 1 that ignores age differences but recognizes two sexes, x_1 for males and x_2 for females. So long as the $[x_i]$ are still so small that the resource limitations of the finite environment are not yet binding, we may model the system's "dilute" stage by the following linear version:

$$\begin{aligned} \dot{x}_1 &= \gamma_1(\beta_1 x_1 + \beta_2 x_2) - \delta_1 x_1 & [11] \\ \dot{x}_2 &= \gamma_2(\beta_1 x_1 + \beta_2 x_2) - \delta_2 x_2 \\ \gamma_1 + \gamma_2 &= 1; \gamma_i, \delta_i, \beta_i > 0, \dot{x}_i = dx_i/dt. \end{aligned}$$

This can be written in matrix notation as

$$\dot{x} = Ax. \tag{12}$$

As is well known,

$$\lim_{t \rightarrow \infty} \frac{\dot{x}_i(t)}{x_i(t)} = \rho \begin{cases} < 0, \\ > 0, \end{cases} \quad (i = 1, 2) \tag{13.1}$$

$$\lim_{t \rightarrow \infty} \frac{\sum_1^2 x_i(t)}{e^{\rho t}} = v[x_1^0, x_2^0] = [vx(0)] \tag{13.2}$$

$$\lim_{t \rightarrow \infty} \frac{x_i(t)}{\sum_1^2 x_j(t)} = \bar{x}_i, \quad \sum_1^2 \bar{x}_i = 1, \tag{13.3}$$

in which ρ is the largest real characteristic root of

$$\det[A - \lambda I] = (\rho - \lambda)(\lambda_2 - \lambda), \quad \rho > \lambda_2 \tag{13.4}$$

and \bar{x} and v are ρ 's normalized eigenvectors.

$$A\bar{x} = \rho\bar{x}, \quad \sum_1^2 \bar{x}_j = 1 \tag{13.5}$$

$$vA = v\rho, \quad v\bar{x} = \sum_1^2 v_j \bar{x}_j = 1 \tag{13.6}$$

$$V(t) = vx(t) \text{ obeys } V'(t) = \rho V(t). \tag{13.7}$$

Clearly $[v_1, v_2] = v$ is the exact rendition of Fisher's reproductive value for a *linear* 2-sex model. To verify this, consider the female-dominant version discussed by Goodman (ref. 15, p. 213) in which $\beta_1 = 0$.

In this case, males have no role in determining the ultimate growth rate of the system. Does v show this? Indeed it does, because now $[v_1, v_2] = [0, v_2]$. Thus, other things equal, it would be well to harvest only males for game, their reproductive value and role in system growth being zero.

Qualifications and generalizations

As observed by Kendall (14), Goodman (8, 15), and Yellin and Samuelson (16), and as Fisher does not fail to notice, the additive form for the biparental birth function of Eq. 11 has the unrealistic property that increasing the numbers of one sex alone

adds unflinchingly to the birth rate. How the concept of reproductive value is to be generalized for a more realistic nonadditive birth function must remain as a separate task for analysis.

The linear relations of Eq. 12 can easily be generalized to $n \geq 0$. If either A is a *primitive* Perron-Frobenius matrix, or if A has off-diagonal elements all positive, we are guaranteed that it has a real root ρ that is dominant, and whose characteristic row vector provides an appropriate measure of "reproductive value."

Similarly, if we replace L in Eq. 1 by any *primitive* matrix, B , so that our biological system takes the form

$$[x_i(t + 1)] = [b_{ij}][x_i(t)], \tag{14.1}$$

then for a dominating $1 + r$, we have the characteristic row vector

$$v[b_{ij}] = v(1 + r), \quad v > 0. \tag{14.2}$$

Thus, reproductive value is proportional to v . Even if some b_{ij} are negative, provided $\alpha I + B$ is for some real α a primitive matrix, all our results will apply. Of course, $(1 + r)^t$ for a difference equation system corresponds to $(e^\rho)^t$ for a differential equation system: indeed, $1 + r = e^\rho$ and the systems 12 and 14 are identical for equally spaced values of t if $B = e^A$.

What if the system is not irreducible, so that A or B are reducible matrices such that (i) either part of the system comes to grow at a slower exponential rate than the rest, or (ii) the whole system's ultimate level is independent of some of the variables' initial conditions? Then, as we've already seen in the female-dominant model below Eq. 13, some of the biological variables have a *zero* reproductive value in the Fisher sense.

What if the system is *cyclic*, so that B generates *asymptotically* a dominating $(1 + r)^t$ component, but one with coefficients for each exponential component that are each functions of the initial $[x_i(0)]$ that are periodic functions of integral period m ? Then, strictly speaking, we have m different $v[x_1^0, \dots, x_n^0]$ functions, $v[k; x_1^0, \dots, x_n^0]$, in which $v[k + m; x_1^0, \dots, x_n^0] \equiv [k; x_1^0, \dots, x_n^0]$. If we take a Cesaro mean of the biological solution,

$$[x(0) + x(1) + \dots + x(t)]/t = Y(t)$$

then a specifiable $\bar{v}[x_1^0, \dots, x_n^0]$ will give its reproductive value.

Finally, differential and difference equations like 12 and 14, but with no simple sign restrictions on the a_{ij} and b_{ij} coefficients, could chance to have dominant exponential-growth modes $v[x_1^0, \dots, x_n^0] \bar{x} \exp[\rho t]$ or $v[x_1^0, \dots, x_n^0] \bar{x} (1 + r)^t$. But now the $\sum_1^n v_j x_j(0)$ expression might involve some *negative* reproductive-value v_i coefficients. Before spending much time in giving such phenomena a biological interpretation, we have to remind ourselves that the linear modelling of a real-world system is at best useful for the restricted domain of the variables in which the system can be regarded as "dilute." *Logistic* and other saturation relationships, like that in Eq. 10, will soon enough apply in situations where natural selection has genuine relevance.

My greatest debt is to my collaborator Joel Yellin of the Massachusetts Institute of Technology. I owe thanks to the National Science Foundation Grant 7708959 and National Institutes of Health Grant 1 R01 HD 09081 for partial financial aid.

1. Sharpe, F. R. & Lotka, A. J. (1911) "A problem in age distribution," *Philos. Mag.* 21, 435-438.
2. Leslie, P. H. (1945) "On the use of matrices in certain population

- mathematics," *Biometrika* 33, 183-212.
3. Fisher, R. A. (1930) *The Genetical Theory of Natural Selection* (Clarendon Press, Oxford).
 4. Samuelson, P. A. (1943) "A simple method of interpolation," *Proc. Nat. Acad. Sci. USA* 29, 397-401. Reproduced as chapter 49 in *Collected Scientific Papers of Paul A. Samuelson*, Vol. I, ed. Stiglitz, J. E., (MIT Press, Cambridge, MA, 1966).
 5. Samuelson, P. A. (1943) "Efficient computation of the latent vectors of a matrix," *Proc. Nat. Acad. Sci. USA* 29, 393-397. Reproduced as chapter 50 in *Collected Scientific Papers of Paul A. Samuelson*, Vol. I, ed. Stiglitz, J. E. (MIT Press, Cambridge, MA, 1966).
 6. Keyfitz, N. (1968) *Introduction to the Mathematics of Population* (Addison-Wesley, Reading, MA).
 7. Vincent, P. (1945) "Potentiel de'accroissement d'une population stable," *J. Soc. Stat. Paris* 86, 16-29.
 8. Goodman, L. A. (1967) "On the reconciliation of mathematical theories of population growth," *J. R. Stat. Soc. Ser. A*, 130, 541-553.
 9. Leslie, P. H. (1948) "Some further notes on the use of matrices in population mathematics," *Biometrika* 35, 213-245.
 10. Verhulst, P. F. (1838) "Notice sur la loi que la population suit dans son accroissement," *Correspondance mathématique et Physique Publiée par A. Quetélet (Brussels)* 10, 113-121.
 11. Pearl, R. & Reed, L. J. (1920) "On the rate of growth of population of the United States since 1790 and its mathematical representation," *Proc. Nat. Acad. Sci. USA* 6, 275-288.
 12. von Neumann, J. (1945) "A model of general equilibrium," *Rev. Econ. Stud.* 13, 1-9.
 13. Price, G. R. & Smith, C. A. B. (1972) "Fisher's Malthusian parameter and reproductive value," *Ann. Hum. Genet.* 36, 1-7.
 14. Kendall, D. G. (1949) "Stochastic processes and population growth," *J. R. Stat. Soc. Ser. B*, 11, 230-264.
 15. Goodman, L. A. (1953) "Population growth of the sexes," *Biometrics* 9, 212-225.
 16. Yellin, J. & Samuelson, P. A. (1974) "A dynamical model for human population," *Proc. Nat. Acad. Sci. USA* 71, 2813-2817.