

Generalizing Fisher's "reproductive value": Nonlinear, homogeneous, biparental systems*

(biparental models/dilute homogeneous systems/asymptotic growth states)

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ABSTRACT Biparental demographic models violate linearity. However, in their early "dilute" stages before limited environment resources bring need for competitive selection, first-degree-homogeneous relations obtain. For them, a reproductive-value function of the *initial coordinates* is defined to recapitulate their contribution to the asymptotically dominating mode of exponential growth: now the generalized Fisher reproductive value of one sex is altered by relative numbers of the other sex. The new reproductive-value function is also derived for general systems of homogeneous-first-degree differential and difference equations, and is shown to grow from the start at the asymptotic growth rate.

Review of general linear case

Samuelson (1) provided a comprehensive review of the concept of reproductive value defined by Fisher (2). For the discrete-time Leslie (3) matrix version and for the Sharpe-Lotka (4) integral-equation version of linear demographic systems, reproductive value summarizes the relative quantitative contribution to the system's long-run growth of each initial-condition element: thus, it is the normalizable dominant characteristic (row) eigenvector of the Leslie demographic matrix and the integral-equation equivalent in the continuous-time case.

Generalizing from the one-sex-dominant models of conventional Lotka demography, Samuelson showed how to define and calculate the reproductive-value vector, $[v_1, v_2] = v$, for a *linear* biparental system like that discussed by Kendall (5) or Goodman (6):

$$\begin{aligned} \dot{x} &= Ax & [1] \\ &= \begin{bmatrix} dx_1/dt \\ dx_2/dt \end{bmatrix} = \begin{bmatrix} \gamma_1\beta_1 - \delta_1 & \gamma_1\beta_2 \\ \gamma_2\beta_1 & \gamma_2\beta_2 - \delta_2 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} \\ \gamma_1 + \gamma_2 &= 1; \quad \gamma_i, \beta_i > 0 \\ x(t) &\approx \{vx(0)\} xe^{\rho t} \\ \det[A - \lambda I] &= (\rho - \lambda)(\lambda_2 - \lambda), \quad 0 \lesseqgtr \rho > \lambda_2 \\ Ax &= \rho x, \quad [1 \quad 1]x = 1 \\ vA &= v\rho, \quad vx = 1 \\ vx(t) &= e^{\rho t} vx(0). \end{aligned}$$

Bold-face type in the equations above denotes matrices and vectors. The above relations recapitulate Samuelson (ref. 1, equations 12-13).

First-degree-homogeneous biparental case

It is proposed here to show how Fisher's concept of reproductive value can be properly generalized for the manageable biparental

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rental nonlinear models of the type discussed by Kendall (5), Goodman (6), Pollard (7), Yellin and Samuelson (8), and others. Instead of the linear system in 1, we encounter

$$\begin{aligned} \dot{x}_1 &= \gamma_1 B[x_1, x_2] - \delta_1 x_1 & [2] \\ \dot{x}_2 &= \gamma_2 B[x_1, x_2] - \delta_2 x_2 \\ \gamma_1 + \gamma_2 &= 1; \quad \gamma_i, \delta_i > 0. \end{aligned}$$

Here, as before, δ_i is the force of mortality for the *i*th category. The sex ratio at birth is a constant, $\gamma_1/\gamma_2 \gtrless 1$. What is new is the jointly interacting *biparental* birth function, $B[x_1, x_2]$, which is biologically nonlinear: with zero males, births are zero; with zero females, births are zero; as one increases the number of one sex alone, the number of the other sex held constant, one encounters the law of diminishing returns in births; however, if one doubles *both* sexes together, births double so long as the environment's limitation of resources is not yet binding on the *dilute* system.

This means that $B[x_1, x_2]$ is a homogeneous-first-degree, concave, monotone-increasing function:

$$\begin{aligned} B[x_1, x_2] &\equiv \lambda^{-1} B[\lambda x_1, \lambda x_2] \equiv x_1 f[x_2/x_1] \geq 0 & [3] \\ 0 &\equiv B[x_1, 0] \equiv B[0, x_2]; \quad f'[v] > 0 > f''[v], \quad v > 0. \end{aligned}$$

What is not clear is whether, for x_i frozen, a large enough increase in x_j can raise the rate of birth above any preassigned level, as with the "geometric-mean" example

$$B[x_1, x_2] = a x_1^\alpha x_2^{1-\alpha}, \quad 0 < \alpha < 1 \quad [4.1]$$

$$\lim_{x_2 \rightarrow \infty} B[1, x_2] = \infty = \lim_{x_1 \rightarrow \infty} B[x_1, 1]$$

or whether, as would actually seem more realistic, limiting the number of one sex must limit the level of possible rate of births no matter how numerous is the other sex—as with the "harmonic-mean" example:

$$B[x_1, x_2] = a \frac{x_1 x_2}{\alpha x_1 + (1 - \alpha) x_2}, \quad 0 < \alpha < 1 \quad [4.2]$$

$$\lim_{x_2 \rightarrow \infty} B[1, x_2] = a(1 - \alpha)^{-1} < \infty > a\alpha^{-1} = \lim_{x_1 \rightarrow \infty} B[x_1, 1]$$

Still other examples are

$$B[x_1, x_2] = a \text{Min}[x_1/c_1, x_2/c_2] \quad [4.3]$$

$$B[x_1, x_2] = a[\alpha x_1^\theta + (1 - \alpha)x_2^\theta]^{1/\theta}, \quad 0 \neq \theta < 1. \quad [4.4]$$

The asymptotic solution of 2's nonlinear biparental model has the essential exponential-mode properties of the Lotka-Fisher model, or of 1's 2-parent linear model.

More precisely, for $|\delta_1 - \delta_2|$ and $|\gamma_1 - \gamma_2|$ not too large (or,

* This is the second paper of a pair; the first paper is ref. 1.

in 4.1's case where $B[1, x_2]$ and $B[x_1, 1]$ are unbounded, for any positive δ s and γ s), and for initial $[x_i^0]$ positive:

$$\lim_{t \rightarrow \infty} \frac{\dot{x}_i}{x_i} = \rho \geq 0, \quad (i = 1, 2), \quad x(0) > 0 \quad [5.1]$$

$$\lim_{t \rightarrow \infty} \frac{x_i(t)}{\sum_1^2 x_j(t)} = \bar{x}_i > 0, \quad \sum_1^2 \bar{x}_j = 1 \quad [5.2]$$

$$\lim_{t \rightarrow \infty} \frac{\sum_1^2 x_j(t)}{e^{\rho t}} = v[x_1^0, x_2^0] \equiv \lambda^{-1} v[\lambda x_1^0, \lambda x_2^0] \quad [5.3]$$

in which $(\rho; \bar{x}_1, \bar{x}_2)$ are the unique positive real roots of

$$\rho = \gamma_1 f[x_2/x_1] - \delta_1 \quad [6.1]$$

$$= \gamma_2 fx_2/x_1^{-1} - \delta_2 \quad [6.2]$$

$$x_1 + x_2 = 1, \quad x_i > 0 \quad [6.3]$$

and in which $v[x_1^0, x_2^0]$ is a determinate *generalized reproductive-value function* calculable from the existent solutions to 2, $[X_i; x(0)]$, and 5.3's limit.

[Remark: As shown by Yellin and Samuelson (ref. 8, table 1, sections 9–11) and by Samuelson (ref. 9, p. 110), there need not always be an exponential solution to a homogeneous demographic system: instead, the sex ratio may diverge to infinity—as for example when $f[\]$ is derived from 4.2 and the death rate of one of the sexes is *very* much larger than the other, so that the sex ratio goes to zero or infinity as both groups hasten to extinction.]

The reader will note the complete parallelism of the nonlinear relations of 5–6 to the already established linear reproductive-value relations given in 1.

The reproductive-value function

It remains to investigate the properties of 5.3's reproductive-value function, $v[x_1^0, x_2^0]$, which is the desired nonlinear *generalization* of Fisher's linear reproductive-value concept, $v_1 x_1^0 + v_2 x_2^0 + \dots$

Actually, it can be shown from the homogeneity property of $B[x_1, x_2]$ that $v[x_1^0, x_2^0]$ must have a similar first-degree-homogeneous property

$$v[\lambda x_1^0, \lambda x_2^0] \equiv \lambda v[x_1^0, x_2^0] \geq 0, \quad \lambda > 0 \quad [7.1]$$

$$v_i[\] = \partial v[x_1^0, x_2^0] / \partial x_i^0 > 0, \quad (i = 1, 2), \quad [x_j^0] > 0 \quad [7.2]$$

$$1 = \frac{x_1^0 v_1[x_1^0, x_2^0]}{v[x_1^0, x_2^0]} + \frac{x_2^0 v_2[x_1^0, x_2^0]}{v[x_1^0, x_2^0]} \quad [7.3]$$

Now that we have our generalized reproductive-value function, we shall find that it lacks some of the properties that Fisher was able to find in the linear case of $v[x_1^0, x_2^0] = v_1 x_1^0 + v_2 x_2^0$. No longer can Fisher speak of the reproductive value of one segment of the population *without regard to its plentitude relative to other segments*. How much an extra female is "worth" to Australia in 1911 cannot be put in a table like that of Fisher (ref. 2, figure 2, p. 28) without regard to how many males there are in Australia—as Fisher implicitly realizes elsewhere in his discussion. On the other hand, he seems to nod in inferring (ref. 2, p. 159):

If we consider the aggregate of an entire generation of such offspring [ready to reproduce, which would seem to be (x_1^0, x_2^0) in our modelling] it is clear that the total reproductive value of the males in this group is exactly equal to the total value of all females, because each sex must supply half the ancestry of all future generations of the species.

What can this mean? That half of $v[x_1^0, x_2^0]$ in some sense belongs to each sex? The least ambiguous measure of each sex's

separate total reproductive value would seem to be given by $x_i^0 \partial v(x_1^0, x_2^0) / \partial x_i^0$ from 7.3. For each of these to be *always* one-half because every diploid birth has both a mother and father, this last prosaic biological fact would have to imply that $v[x_1^0, x_2^0]$ is of the equally weighted geometric-mean type

$$v[x_1^0, x_2^0] \stackrel{?}{=} c[x_1^0 x_2^0]^{1/2} \quad [8]$$

This, however, is quite invalid—as any experimentation with actual admissible instances of $B[x_1, x_2]$ in 2 will confirm. Indeed I have not yet been able to find even one admissible $B[x_1, x_2]$ function for which 8 obtains!

What is a different and more trivial matter is that, under the singular assumption of *complete symmetry*,

$$B[x_1, x_2] \equiv B[x_2, x_1], \quad \gamma_1 = \gamma_2 = 1/2, \quad \delta_1 = \delta_2 = \delta \quad [9]$$

it is obvious that $v[x_1^0, x_2^0]$ is then a symmetric function, with each sex of "equal reproductive value" *when the sex ratio is balanced* (and *only* then):

$$v[x_1^0, x_2^0] \equiv v[x_2^0, x_1^0] \quad [10.1]$$

$$x_1^0 v_1[x_1^0, x_2^0] = x_2^0 v_2[x_1^0, x_2^0] = 1/2 v[x_1^0, x_2^0] \quad [10.2]$$

when

$$x_1^0 = x_2^0 \quad [10.3]$$

The *reproductive value* of each member of a sex, as measured by $\partial v[x_1^0, x_2^0] / \partial x_i^0$, will rise as it becomes scarce and x_i^0/x_j^0 falls; but one cannot predict in advance how the *total* reproductive value of *all* members of that sex moves when x_i^0/x_j^0 falls, because $x_i^0(\partial v[x_1^0, x_2^0] / \partial x_i^0)$ may rise or fall in the general case.

A counterexample

To grasp the meaning of these corrections to the conventional view, begin with the case that would seem most favorable to the Fisher quotation—the case of complete symmetry and 4.1's geometric mean:

$$\dot{x}_1 = \beta(x_1 x_2)^{1/2} - \delta x_1, \quad \dot{x}_2 = \beta(x_1 x_2)^{1/2} - \delta x_2; \quad \beta, \delta > 0. \quad [11]$$

For $x_1^0 = 0$, obviously the solution is given by $[x_j(t)] = [0, x_2^0 e^{-(\delta)t}]$. However, as soon as we move ever so little from either axis, making *both* $[x_j^0]$ positive, the system's asymptotic growth rate becomes the *faster* growth rate $\exp[(\beta - \delta)t]$. As will be seen below, the exact solution can be written as

$$x_i(t) = v[x_1^0, x_2^0] e^{(\beta - \delta)t} [1 + \epsilon(t)] \quad [12.1]$$

$$= [1/4 x_1^0 + 1/4 x_2^0 + 1/2 (x_1^0 x_2^0)^{1/2}] e^{(\beta - \delta)t} [1 + \epsilon(t)]$$

$$\lim_{t \rightarrow \infty} \epsilon(t) = 0 \text{ for all positive } (x_1^0, x_2^0). \quad [12.2]$$

From 12.1 we see that even in this case most favorable to Fisher's purported equal sharing of reproductive value among the two (needed!) sexes, it is actually the case that the *scarcest* sex has the *least* total reproductive value.

To verify 12 and handle more realistic cases of nonvanishing $|\gamma_1 - \gamma_2|$ and $|\delta_1 - \delta_2|$, we may analyze the one nonlinear case shown by Kendall (ref. 5, equation 72) to be exactly solvable. Put 4.1's symmetric geometric mean into 2 to get

$$\dot{x}_i = \gamma_i 2\beta(x_1 x_2)^{1/2} - \delta_i x_i, \quad (i = 1, 2) \quad [13]$$

$$\gamma_1 + \gamma_2 = 1; \quad \gamma_i, \delta_i, \beta > 0; \quad [x_j^0] > 0.$$

Transform the $[x_j]$ to new variables $[y_j]$:

$$x_1^{1/2} = y_1, x_2^{1/2} = y_2; x_1 = y_1^2, x_2 = y_2^2; x_i > 0 \quad [14.1]$$

$$\dot{x}_i = 2y_i \dot{y}_i, \quad (i = 1, 2). \quad [14.2]$$

Then 13 is transformed into the exactly linear system, with the following properties

$$\dot{y} = \begin{bmatrix} \dot{y}_1 \\ \dot{y}_2 \end{bmatrix} = Ay = \begin{bmatrix} -1/2\delta_1 & \gamma_1\beta \\ \gamma_2\beta & -1/2\delta_2 \end{bmatrix} \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} \quad [15.1]$$

$$\det[A - \lambda I] = \lambda^2 + 1/2(\delta_1 + \delta_2)\lambda + 1/4(\delta_1\delta_2 - 4\gamma_1\gamma_2\beta^2) \quad [15.2]$$

$$= (\rho - \lambda)(\lambda_2 - \lambda), \quad 0 \leq \rho < \lambda_2$$

$$A \begin{bmatrix} \bar{y}_1 \\ \bar{y}_2 \end{bmatrix} = \rho \begin{bmatrix} \bar{y}_1 \\ \bar{y}_2 \end{bmatrix}; \quad \bar{y}_i \geq 0, \quad \bar{y}_1 + \bar{y}_2 = 1 \quad [15.3]$$

$$[v_1 \ v_2]A = [v_1 \ v_2]\rho, \quad v_j \geq 0 \quad [15.4]$$

$$v_1\bar{y}_1 + v_2\bar{y}_2 = v\bar{y} = 1 \quad [15.5]$$

$$y_i(t) = [v_1 y_1^0 + v_2 y_2^0] \bar{y}_i e^{\rho t} \times \{1 + c_i \exp[(\lambda_2 - \rho)t]\} \quad [15.6]$$

$$x_i(t) = y_i(t)^2 = [v_1^2 x_1^0 + v_2^2 x_2^0 + 2v_1 v_2 (x_1^0 x_2^0)^{1/2}] \bar{y}_i^2 e^{2\rho t} \times \{1 + 2c_i \exp[(\lambda_2 - \rho)t] + c_i^2 \exp[2(\lambda_2 - \delta)t]\}, \quad (i = 1, 2). \quad [15.7]$$

Hence, for our nonlinear system 13, the correct reproductive value is calculated to be

$$v[x_1^0, x_2^0] = (v_1)^2 x_1^0 + (v_2)^2 x_2^0 + 2v_1 v_2 (x_1^0 x_2^0)^{1/2} \quad [16.1]$$

$$\partial v[x_1^0, x_2^0] / \partial x_i^0 = (v_i)^2 + v_1 v_2 (x_j^0 / x_i^0), \quad j \neq i \quad [16.2]$$

$$x_i \{ \partial v[x_1^0, x_2^0] / \partial x_i \} = (v_i)^2 x_i^0 + v_1 v_2 (x_1^0 x_2^0)^{1/2}, \quad \text{a rising function of } x_i^0. \quad [16.3]$$

Warning: For an $x_i^0 = 0$, the $e^{2\rho t}$ growth mode becomes irrelevant: so it is dangerous to go all the way to the limit $x_i^0 \rightarrow 0$, for the reason that the Kendall transformation of variables in 14 fails on either x_i axis. Always in 5 and 6 it is important to avoid cases where either x_i vanishes and where $\exp(-\delta_i t)$ solutions supercede the exponential growth modes of 6.

Invariant growth rate of reproductive value

Because we know from the established linear analysis that $v y(0)$ in 15.6 grows from the beginning like $e^{\rho t}$, we know that $\sum_j^2 v_j x_j(t)^{1/2}$ has the invariant growth rate of ρ . Its square has the invariant growth of 2ρ . So 16's reproductive-value function $v[x_1^0, x_2^0]$ does grow from the beginning at the nonlinear system's asymptotic growth rate of 2ρ . But, is this important Fisher property valid only for nonlinear systems that are merely a disguised transformation of a linear system in other variables—as in 13–14, which is admittedly a special, Santa Claus, case?

Fortunately, we can give the following proof that the nonlinear system's reproductive-value function, $v[x_1(t), x_2(t)]$, defined by 5, has Fisher's invariant growth rate property.

We have

$$\lim_{\tau \rightarrow \infty} \frac{\sum_1^2 x_j(t + \tau)}{e^{\rho \tau}} = v[x_1(t), x_2(t)], \quad \text{by 5.3's definition} \quad [17.1]$$

$$\equiv e^{\rho t} \lim_{t + \tau \rightarrow \infty} \frac{\sum_1^2 x_j(t + \tau)}{\exp[\rho(t + \tau)]}, \quad \text{by substitution}$$

$$\equiv e^{\rho t} v[x_1(0), x_2(0)] \quad \text{Q.E.D.} \quad [17.2]$$

Thus, for the most general nonlinear system that approaches asymptotically to a balanced state of exponential growth, we can define a reproductive-value function with the usual Fisher properties. Indeed, there is nothing of black magic involved in this invariant growth rate of the reproductive-value function from the beginning: that property is implicit in its original definition.

Generalizations

We have completed the task of properly defining a nonlinear function of so-called reproductive value. There remains the task of showing how this applies to any number of coordinates, (x_1, \dots, x_n) , $n \geq 2$; and the task of showing how the concept is defined for *difference* rather than *differential* equations.

Consider the alternative first-degree-homogeneous systems:

$$dx_i/dt = f^i[x_1, \dots, x_n], \quad (i = 1, \dots, n)$$

$$= \lambda^{-1} f^i[\lambda x_1, \dots, \lambda x_n], \quad \lambda > 0 \quad [18.1]$$

and

$$x_i(t + 1) = F^i[x_1(t), \dots, x_n(t)], \quad (i = 1, \dots, n) \quad [18.2]$$

$$= \lambda^{-1} F^i[\lambda x_1(t), \dots, \lambda x_n(t)], \quad \lambda > 0.$$

These can represent essentially the same system in the following sense. Write down the solution of 18.1 at $t + \tau$ in terms of its non-negative initial conditions at t , $[x_j(t)]$:

$$x_i(t + \tau) = X^i[\tau; x_1(t), \dots, x_n(t)], \quad (i = 1, \dots, n) \quad [18.3]$$

$$= \lambda^{-1} X^i[\tau; \lambda x_1(t), \dots, \lambda x_n(t)].$$

The indicated first-degree-homogeneity of 18.3's solution follows from that of 18.1. Now set $\tau = 1$ in 18.3 to derive

$$x_i(t + 1) = X^i[1; x_1(t), \dots, x_n(t)], \quad (i = 1, \dots, n). \quad [18.4]$$

It will now be obvious that 18.4 is identical in form and substance to 18.2: hence, it is seen that the differential-equation system 18.1 generates at equally spaced intervals of t exactly the same solution as 18.2 does.

The same exponential-growth mode will exist for 18.1 as for 18.2, $[\bar{x}_i](e^\rho)^t$ or $[\bar{x}_i](1 + r)^t$;

$$1 + r = e^\rho, \quad \rho = \log_e(1 + r) \quad [19.1]$$

and where the \bar{x}_i are the positive solutions of the equivalent alternative sets

$$\rho \bar{x}_i = F^i[\bar{x}_1, \dots, \bar{x}_n], \quad \sum_1^n \bar{x}_i = 1, \quad [19.2]$$

$$(1 + r)\bar{x}_i = F^i[\bar{x}_1, \dots, \bar{x}_n], \quad (i = 1, \dots, n). \quad [19.3]$$

It is of course not necessary that there exists a solution in 19, or that it be unique, or even that an existent unique solution be "locally stable." Thus, Yellin and Samuelson (ref. 8, table 1) give examples of null solutions and of locally unstable solutions that can obtain in feasible demographic models. In reducible examples—one such is the trivial case where $\dot{x}_1/x_1 = \dot{x}_2/x_2 = \rho$ —19 has an infinity of solutions; hence, there is a different reproductive-value function for each x_i or for any of an infinite number of homogeneous-first-degree functions of x_1 and x_2 ! Unfortunately, the standard Hardy-Weinberg case in genetics possesses just such degeneracy.

It is shown by Solow and Samuelson (10), that, provided the partial derivatives $(F_j^i[x_1, \dots, x_n])$ are all positive numbers in the non-negative orthant $[x_i] \geq 0$, such unique solutions will

exist. Indeed, if the off-diagonal elements of (F^t) or of (f^t) are positive for $x_i \geq 0$ and the diagonal elements are bounded, that will suffice to guarantee a unique and stable exponential growth mode, $\bar{x}_i(1+r)^t$.

The generalized *reproductive-value function* is now easily defined as $v[x_1^0, \dots, x_n^0]$ in 20.2

$$\lim_{t \rightarrow \infty} \frac{x_i(t+1)}{x_i(t)} = 1+r > 0, \quad (i=1, \dots, n) \quad [20.1]$$

$$\lim_{t \rightarrow \infty} \frac{\sum_1^n x_j(t)}{(1+r)^t} = v[x_1^0, \dots, x_n^0] \quad [20.2]$$

$$= \lambda^{-1} v[\lambda x_1^0, \dots, \lambda x_n^0].$$

This completes the generalization. One should conclude with a warning: Every environment has ultimately limited resources that serve in the end to terminate the dilute first-degree-homogeneous stage of Malthus and von Neumann (11). In that case, reproductive value is by definition zero because the initial conditions $[x_1^0, \dots, x_n^0]$ wash out in the limit:

$$\lim_{t \rightarrow \infty} X^t[t; x_1^0, \dots, x_n^0] \equiv x_i^*, \quad (i=1, \dots, n). \quad [21]$$

In concluding, one must warn that the concept of reproductive value has often been used in a loose way. There remains the analytic task of auditing its claims, as for example in connection with optimal harvesting and other problems. Unfortunately, the homogeneity assumptions underlying dilute systems then become peculiarly vulnerable and the whole concept of reproductive value must be handled with care.

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