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Population Biology

Equivalence of maximizing reproductive value and fitness in the case of reproductive strategies

(evolution/life histories/demography)

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ABSTRACT The proposed equivalence of maximizing reproductive value and fitness is examined for two model life histories. In the first instance, it is assumed that offspring are fledged before the start of the next breeding season. In this case the proposed equivalence is verified. In the second model, parents care for their progeny for more than 1 year. In this case the optimal reproductive expenditure at a particular age is shown to depend on both current reproductive value and the diminution in survival rates of previously conceived young still dependent on parental protection.

Recently, there has been considerable theoretical interest in the evolution of life history phenomena (1–8). The problem, first stated explicitly by Gadgil and Bossert (4), is as follows. Consider an organism with limited (i.e., finite) resources at its disposal. Further suppose that there exists heritable variation with regard to the manner in which these resources are allocated. Then, one wishes to determine the schedule of allocation—to growth, to reproduction, and to maintenance—that maximizes the individual's contribution to subsequent generations.

In attempting to answer this question, several authors (5, 6, 8, 9) have proposed that the allocation schedule in question is that which maximizes reproductive value (10) at all ages. More recently, however, this view has been questioned (1, 2). In particular, it has been suggested that maximizing fitness and reproductive value and fitness are equivalent only under the restrictive circumstance that trade-offs between current fecundity and subsequent survival and growth are confined to operate within (and not between) age classes. The purpose of the present paper is to examine this question in detail. Specifically, it is argued that maximizing fitness and reproductive value is indeed equivalent, ***provided*** that increased expenditures for reproduction at age x do not adversely affect fecundity and survivorship at previous ages y ($y < x$). This assumption would appear to be met in nearly all cases, save those in which there is extended parental care. In such instances, offspring as yet unfledged can suffer increased mortality if the parents breed a second time and turn their attention to the more recent litter. Mathematically, this is equivalent to reducing the parents' fecundity at earlier ages and, in such cases, natural selection can be expected to maximize reproductive value plus a weighted sum of prior years' reproduction. An analysis of this case is given.

ANALYSIS

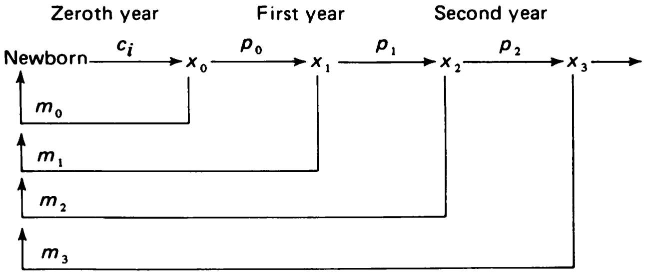

FIG. 1. Schematic representation of a population in which individuals reproduce at discrete (yearly) intervals. The number of individuals in each age class present during the breeding season is x_i. Each of these produces m_i offspring of which c_i survive to the breeding season in their first year of life (zeroth age class). The product $c_i m_i = B_i$ is termed the effective fecundity of an i-year-old individual. The p_i are postbreeding survival probabilities. Thus, p_0 is the probability that a 0-year-old individual alive during the breeding season at time t survives to become a 1-year-old individual during the breeding season the following year.

Preliminaries. Consider an organism with the life cycle depicted in Fig. 1. The population is censused once a year during the breeding season, $n_x(t)$ being the number of x-year-old individuals alive in year t. Let m_x be the number of offspring produced by an x-year-old individual. Of these, c_x survive to be counted as young of the year (yearlings) the following year. Furthermore, let p_x be the probability that an x-year-old individual survives to breed again at age $x + 1$ in year $t + 1$. On achieving stable age distribution (11, 12), this population will multiply annually at rate λ_1. λ_1 is the positive root of the "stable age" equation (13):

$$1 = \sum_{0}^{w} \lambda^{-(x+1)} l_x B_x. \qquad [1]$$

Here, $B_x = c_x m_x$, $l_0 = 1$, and $l_x = \Pi_0^{x-1} p_k$, $x \geq 1$. More generally, if $N(t)$ is a vector whose elements are the numbers of individuals in the various age class at time t,

$$n(t) = \sum_{1}^{w+1} \alpha_i \lambda_i{}^t N_i. \qquad [2]$$

Here, λ_i and N_i are the ith eigenvalues and eigenvectors (13) of the so-called Leslie (11, 12) matrix which maps $N(t)$ into $N(t + 1)$. The αs are constants chosen to reflect initial conditions—i.e., so that $N(0) = \Sigma\, \alpha_i N_i$. Eq. 1 is thus the characteristic equation of the Leslie matrix. Note that, because it is generally true (14) that

$$\lambda_1 > |\lambda_{j \neq 1}|,$$

we have in the limit as $t \rightarrow \infty$, $N(t) \rightarrow N_1$, which is therefore called the stable age distribution. Additionally, note that the population comes to multiply each year at rate λ_1.

Now, suppose that individuals can allocate resources to reproduction, growth, or maintenance. For the present, we consider the allocation schedule shown in Fig. 2. In each year, resources are harvested (or produced, in the case of plants) in amount r_x, x being the age of the individual in question. The total amount of resources available at age x, which we will call R_x, is thus equal to r_x plus whatever has been accumulated during preceding years. Of this total, a fraction, E_x, is allocated to reproduction. The rest goes to maintenance and growth. E_x

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$$\begin{tikzcd}
R_0 = r_0 \arrow[r, "R_0(1 - E_0 - M_0)", "p_0(M_0R_0)"'] \arrow[d, "E_0"] & R_1 = r_1 + (1 - E_0 - M_0)R_0 \arrow[r, "R_1(1 - E_1 - M_1)", "p_1(M_1R_1)"'] \arrow[d, "E_1"] & {} \\
B_0(E_0R_0) & B_1(E_1R_1) &
\end{tikzcd}$$

FIG. 2. Schematic representation of age-specific availability of resources that can be allocated to reproduction, maintenance, and growth. At each age class, resources are produced in amount r_x. Of the total, R_x, available at that age, one fraction, E_xR_x, is devoted to reproduction, and another, M_xR_x, is used for maintenance. The remainder $(1 - E_x - M_x)$, is used for growth, and some of it will be available for future reproduction at ages $j > x$.

is often termed the reproductive expenditure or effort (4, 5, 8, 14–16) at age x. Notice that, under the allocation scheme shown in Fig. 2, increasing E_x will affect fecundity and survival at ages $y \geq x$ but not at younger ages. For most organisms, this assumption seems inescapable.

Charlesworth (17) and Charlesworth and Williamson (18) have pointed out that both the rate of spread of a rare mutant and its ultimate probability of fixation vary positively with λ_1. Accordingly, the question of characterizing an optimal life history becomes one of determining the set of age-specific expenditures $\hat{E} = (\hat{E}_0, \ldots, E_w)$ that maximize λ_1. This fact was first appreciated by Gadgil and Bossert (4) who explored the problem numerically. At about the same time, Hamilton (19) and Emlen (3) published results that can be used to solve the problem analytically. Specifically, these authors showed that

$$(\partial\lambda_1/\partial B_x) = l_x/\lambda_1{}^x V_T \qquad [3]$$

and

$$(\partial\lambda_1/\partial p_x) = (l_x/\lambda_1{}^x V_T)(v_{x+1}/v_0). \qquad [4]$$

Here, v_x/v_0 is the reproductive value (10) of an x-year-old individual, and V_T is the total reproductive value of the population (13).

Eqs. 3 and 4 suggest two conclusions which had been anticipated by Cole (20) and Lewontin (21). First, from Eq. 3 we note that increased reproduction at earlier ages confers greater improvements in λ_1 than do comparable increases at later ages. Second, Eq. 4 suggests that the advantages accruing from improved survivorship at a particular age depend on the following year's reproductive value. In the case of man and other vertebrates with deterministic growth, reproductive value is a unimodal function of age, peaking roughly at the first reproduction (3, 10).* This suggests that mortality is either best postponed until late in life or experienced early on, or, more precisely, that selection will most likely "tolerate" increased mortality when reproductive value is low if, in exchange, something else is gained—for example, increased survival among sibs, enhanced parental fecundity, etc. In such cases, the interests of the offspring will often be at variance with those of the parent (23).

Equivalence of Maximizing Reproductive Value and Fitness. Let us now proceed to combine the notion of trade-offs, as expressed in Fig. 2, with the sensitivity analysis of Emlen (3) and Hamilton (19). We consider the selective advantage of a mutant with increased fecundity at age x. We assume that this increase is due to an increase in the allocation, E_x, of resources to reproduction at that age. Suppose the fecundity of the mutant is $B_x + dB_x$ in which B_x is the fecundity of the rest of the population. Then the selection advantage, $s(B_x)$, of the mutant is given by the expression

$$s(B_x) = r(B_x + dB_x) - r(B_x) \qquad [5]$$

in which $r = \ln \lambda_1$. Expanding this expression about B_x, the population average, we obtain

$$s(B_x) = r(B_x) + dB_x(dr/dB_x) + \ldots - r(B_x) \doteq dB_x(dr/dB_x)$$

or, substituting $r = \ln \lambda_1$,

$$s(B_x) \doteq (dB_x/\lambda_1)\,(d\lambda_1/dB_x). \qquad [6]$$

From our model of resource allocation (Fig. 2), we note that increasing reproductive expenditure at age x affects the following entries in the life table: (*i*) B_x, which will generally increase in value; (*ii*) p_x, which will generally decline (i.e., fewer resources allocated to maintenance); and (*iii*) $B_{y>x}$ and $p_{y>x}$, which will also usually decline. Thus, we can write

$$(d\lambda_1/dB_x) = (\partial\lambda_1/\partial B_x) + (\partial\lambda_1/\partial p_x)\,(dp_x/dB_x) + \sum_{y=x+1}^{w}\left[\frac{\partial\lambda_1}{\partial B_y}\frac{dB_y}{dB_x} + \frac{\partial\lambda_1}{\partial p_y}\frac{dp_y}{dB_x}\right]. \qquad [7]$$

Substituting for $(\partial\lambda_1/\partial B_x)$, $(\partial\lambda_1/\partial p_x)$, $(\partial\lambda_1/\partial B_y)$, and $(\partial\lambda_1/\partial p_y)$ yields

$$\begin{aligned} s(B_x) = (l_x/\lambda_1{}^{x+1}V_T)\,\{&[dB_x + (v_{x+1}/v_0)dp_x] \\ &+ (px/\lambda_1)\,[dB_{x+1} + (v_{x+2}/v_0)dp_{x+1}] \\ &+ (p_xp_{x+1}/\lambda_1{}^2)[dB_{x+2} + (v_{x+3}/v_0)dp_{x+2}] \\ &+ \ldots\}. \end{aligned} \qquad [8]$$

Now, suppose that $B_x = \hat{B}_x$, a value that maximizes λ_1. In this case, it can be shown that

$$\begin{aligned} d(v_{x+1}/v_0) = (1/\lambda_1)\,\{&[dB_{x+1} + (v_{x+2}/v_0)dp_{x+1}] \\ &+ (p_{x+1}/\lambda_1)[dB_{x+2} + (v_{x+3}/v_0)dp_{x+2}] \\ &+ (p_{x+1}p_{x+2}/\lambda_1{}^2)[dB_{x+3} + (v_{x+4}/v_0)dp_{x+3}] \\ &+ \ldots\}. \end{aligned} \qquad [9]$$

If we compare this expression with Eq. 8, it is immediately obvious that

$$\begin{aligned} s(\hat{B}_x) = (l_x/\lambda_1{}^{x+1}V_T)[&dB_x + (v_{x+1}/v_0)dp_x \\ &+ p_x d(v_{x+1}/v_0)|\hat{B}_x] = 0. \end{aligned} \qquad [10]$$

In other words, a reproductive expenditure at age x, E_x, that maximizes λ_1 also maximizes the quantity $B_x + p_x(v_{x+1}/v_0)$.

This result was first offered without proof by Williams (9). Other authors (5, 8) have given alternative derivations. In particular, Schaffer (5) showed that the stable age equation can be rewritten in the form

$$\begin{aligned} \lambda^{x+1} - B_0\lambda^x - p_0B_1\lambda^{x-1} - \ldots - l_{x-1}B_{x-1}\lambda \\ - l_x[B_x + p_x(v_{x+1}/v_0)] = 0. \end{aligned} \qquad [11]$$

From this equation, it automatically follows that maximizing $B_x + p_x(v_{x+1}/v_0)$ maximizes λ_1. In a quite different vein,

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* For analysis of the consequences to life history theory when growth, and hence increases in fecundity, continues through life, see Michod (22).

Taylor and his associates (8) used the methods of control theory to reach the same conclusion. We observe further from the definition of reproductive value

$$(v_x/v_0) = (B_x/\lambda_1) + (p_x B_{x+1}/\lambda_1{}^2) + (p_x p_{x+1} B_{x+2}/\lambda_1{}^3) + \ldots,$$

that

$$\lambda_1(v_x/v_0) = B_x + p_x(v_{x+1}/v_0).$$

Then, we have

$$s(\hat{B}_x) = (1_x/\lambda_1{}^{x+1}V_T)[d(\lambda_1\, v_x/v_0)]|\hat{B}_x.$$

But, since at $B_x = \hat{B}_x$, $d\lambda_1 = 0$, the above simplifies to

$$s(\hat{B}_x) = (1_x/\lambda_1{}^x V_T)[d(v_x/v_0)] = 0. \qquad [12]$$

We have thus shown that E_x also maximizes (v_x/v_0).

Notice that Eqs. **10** and **12** characterize *conditional* optima—that is, the expenditures at other ages $E_{y \neq x}$ are considered to be fixed. To calculate the global optimum, one considers a$(w + 1)$-dimensional space whose axes are $(E_0, \ldots, E_w)$. The conditional optima, $E_x(E_y) = E_x(E_0, \ldots, E_{x-1}, E_{x+1}, \ldots, E_w)$ describe w dimensional surfaces in this space. The global optimum $\hat{E} = (\hat{E}_0, \ldots, E_w)$ is the point at which these surfaces intersect. Because for each surface (v_x/v_0) is maximal for fixed $E_{y \neq x}$, it follows that, at the point of intersection, reproductive value is simultaneously maximized for all the age classes. [Schaffer and Rosenzweig (6) examined the shapes of the conditional optima for organisms with three age classes; they pointed out that, depending on the nature of the trade-off between B_x and p_x (v_{x+1}/v_0), there can obtain one or several values of $E = (E_0, \ldots, E_w)$ corresponding to local maxima in λ_1.]

The preceding results appear to be useful on two counts: First, Eq. **10** gives a criterion for the maximization of λ_1 in terms of quantities which on biological grounds can be expected to trade off against each other. For most mutations affecting the life table, it is reasonable to suppose that an increase in fecundity at a particular age is achievable only at a cost to subsequent survival and reproduction. Eq. **10** shows exactly how the benefits and costs are assessed. Moreover, by plotting $B_x(p_x v_{x+1}/v_0)$ against $p_x(v_{x+1}/v_0)$, the circumstances favoring the evolution of semelparity, iteroparity, or some combination of the two can be described (6, 7, 24, 25).

In addition, by pointing out the equivalence of maximizing reproductive value and λ_1 for a wide class of life history problems, Eq. **12** places current theory on a conceptual footing which is in harmony with the assumptions of previous authors—for example, Fisher (10) and MacArthur (26).

Consequences of Extended Parental Care. The preceding discussion assumes that increasing reproductive expenditure at a given age has no effect on fecundity and survival at previous ages. For the majority of cases, this would appear reasonable. Consider, however, the situation in which the period of parental care extends beyond the first year of life. Then, when computing the optimal reproductive effort at age x, it must be remembered that previous years' offspring may still depend on their parents (e.g., for food and protection). As a consequence, increasing parental investment in *new* offspring can result in resources being denied their older sibs. The result will be to lower the survival of the older offspring. This is equivalent to reducing the fecundity of the parents in previous years.

To see this, consider a life history in which young do not become independent until age τ. Let $c_{\tau x}$ be the probability that the progeny of an x-year-old individual survive until age τ. Then the stable age equation becomes

$$1 = \sum_{x=\tau}^{w} \lambda^{-(x+1)} l_x B_x \qquad [13]$$

in which we define $B_x = c_{\tau x} m_x$, $l_\tau = 1$, and $l_x = \Pi_{k=\tau}^{x-1} p_x$, $x > \tau$. Clearly, increasing expenditure on young produced at age x can be viewed as reducing fecundity at ages $y < x$ through the effect on the survival of previously produced progeny.

To calculate the selective advantage accruing to a mutant with an increase dB_x in fecundity at age x, we proceed as in the preceding section. Thus,

$$s(B_x) = \frac{dB_x}{\lambda_1} \sum_{y=x-\tau}^{x-1} \left[\left(\frac{\partial\lambda_1}{\partial B_y}\frac{dB_y}{dB_x}\right)\right] + \sum_{x}^{w} \left[\frac{\partial\lambda_1}{\partial B_y}\frac{dB_y}{dB_x} + \frac{\partial\lambda_1}{\partial p_y}\frac{dp_y}{dB_x}\right]. \qquad [14]$$

Notice that the second sum (from age x to w) is the same as before. Eq. **14** thus simplifies to

$$s(\hat{B}_x) = \frac{l_x}{\lambda_1{}^x V_T}\left[d\left(\frac{v_x}{v_0}\right) + \frac{\lambda^x}{l_x} \sum_{y=x-\tau} \lambda^{-y} l_y dB_y\right] = 0. \qquad [15]$$

The implications of this result are obvious. Suppose that, in the absence of extended parental care, the optimal reproductive effort at age x is $\hat{E}_x$. If we now suppose that there is extended parental care, we find that the optimum expenditure, $\hat{E}_x{}^{v1}$, under the new conditions is less than that previously calculated. This is because current value, v_x/v_0, is now being traded off against the contributions from prior reproduction. As might be expected, the reduction in these contributions, $dB_y < 0$, is weighted by (l_y/l_x) and λ^{x-y}—the first because the parent has a greater chance of surviving to age $y < x$; the second because offspring produced one or more years ago are always worth more than today's progeny in a population with $\lambda_1 > 1$ (10).

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