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ABSTRACT

Darwinian fitness in non-growing populations is expressed as the product of two benefit–cost ratios. Several implications of this product-ratio form are developed for life-history evolution.

Keywords: offspring size, reproductive effort, stationary populations.

Natural selection is thought to favour an optimal offspring size that maximizes a benefit–cost ratio, an efficiency, of the form survival of the offspring to adulthood divided by offspring size (Smith and Fretwell, 1974; Stearns, 1992; Charnov and Downhower, 1995). Most theory for life-history evolution maximizes this efficiency independently of the total reproductive allocation, which itself is assumed to negatively impact the parent's own survival (Williams, 1966; Stearns, 1992; Charlesworth, 1994; Charnov, 1997). Here I show that, in non-growing (stationary) age-structured populations, Darwinian fitness (R_0) can always be written as the product of the offspring size efficiency times an efficiency of the form total reproductive allocation divided by parental mortality. Maximization of Darwinian fitness thus often leads to the independent maximization of each efficiency, a surprisingly general rule for life histories. Several implications of this rule are developed.

Evolutionary life-history theory is based on the assumption that a measure of Darwinian fitness is maximized in the face of trade-offs and constraints among demographic and reproductive allocation parameters (Stearns, 1992; Charlesworth, 1994). Assuming that the population is not growing in size, the 'average number of surviving offspring produced over a mother's reproductive life' (called the 'net reproductive rate', R_0) is a measure of her Darwinian fitness (Charnov, 1993; Charlesworth, 1994). R_0 is both a measure of fitness from an individual's perspective, and a population parameter with a value of about 1, due to density dependence holding the population size approximately stable (Charnov, 1993, 1997).

Previous work (Charnov, 1997) has shown that, for non-growing populations, R_0 can *always* be written as:

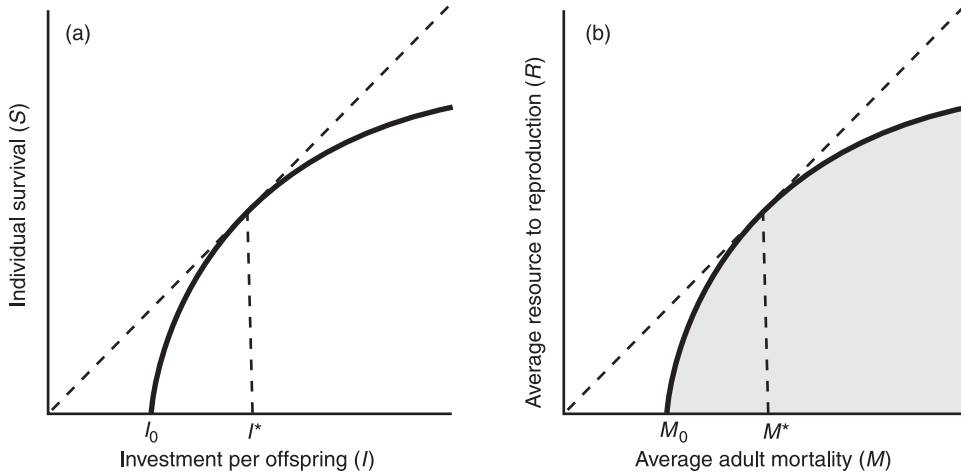$$R_0 = S \cdot b \cdot E \qquad (1)$$

Fig. 1. Two basic trade-offs in life histories. (a) Survival of an offspring to adulthood (*S*) increases with the resource invested in the offspring (*I*). (b) Average rate of resource allocated to reproduction (*R*) versus the average adult instantaneous mortality rate (*M*). The shaded area shows all possible (feasible) *R*, *M* values and the dark curve is the outer bound (highest *R* at a fixed *M*), here represented as a smooth curve. The optimal *R*, *M* pair will be on the outer bound, here called 'trade-off curve'. According to equation (3), the optimal life history maximizes *S/I and R/M* independently; the respective optima (I^*, M^*) can be found by seeing where a ray from the origin is just tangent to the trade-off curve ($\partial Y/\partial X = Y/X$).

where *S* = survival chances to the age of first breeding, *b* = average fecundity (per unit time) for the adults and *E* = average length of the adult life span. Equation (1) holds for *any* age-structured life history, so life-history rules that follow from it should be quite general (some are discussed in Charnov, 1997).

There is one disadvantage in the form of equation (1); it is written in terms of only demographic parameters. Life-history theorists (e.g. Stearns, 1992) often wish to make predictions in terms of resource (e.g. calories) allocation (and its impact on *b*, *S* and *E*). We can remedy this deficiency by assuming that, at each adult age *i*, the mother has R_i units of resource (calories) that will be expended in reproduction, resulting in fecundity at that age of $b_i = R_i/I$, where *I* is the investment per offspring (assumed to be independent of parental age). If *R* is the average of R_i for the adults, the average of b_i (*b*) equals *R/I*, and R_0 can be rewritten as:

$$R_0 = \left(\frac{R}{I}\right) \cdot S \cdot E \tag{2}$$

But note that 1/*E* may be interpreted as an average adult instantaneous mortality rate. Label *M* = 1/*E*, then R_0 can be written as:

$$R_0 = \frac{R}{I} \cdot \frac{S}{M} = \left(\frac{S}{I}\right)\left(\frac{R}{M}\right) \tag{3}$$

It is commonly assumed in life-history theory (e.g. Smith and Fretwell, 1974; Stearns, 1992) that S is solely a function of I, and adult mortality (M) is solely a function of the rate of resource allocation by adults (R). Equation (3) is now the product of two efficiencies (benefit–cost ratios: S/I and R/M) that are, at the optimal life history, *maximized independently of each other*. Figure 1 displays S as an increasing function of I, and mortality (M) as increasing with reproductive allocation (R). Note again that M and R are *averages* for the adults (Charnov, 1997); the trade-off curve is the curve made by the outer bound of the feasible M, R points (Fig. 1b). The respective optima ($\partial R_0/\partial I = 0$ and $\partial R_0/\partial M = 0$) are at I^* and M^* and are found where rays from the origin are just tangent to the trade-off curves. Such tangent arguments are ubiquitous for the maximization of benefit–cost ratios (e.g. Parker, 1974; Smith and Fretwell, 1974) and in economic jargon mean that the optimum (I^*, M^*) is where the *marginal gain* (e.g. $\partial S/\partial I$) equals the *average gain* (S/I). It is also clear that the model may fail if offspring size (I) impacts the individual's performance as an adult (e.g. R and/or M); here, I is only allowed to affect S (but see below).

Let us note a few implications of (the form of) equation (3) and its evolutionary optimization. First, the optimal efficiency rule for R/M (Fig. 1b) holds for R and M viewed as averages for the adults; most life-history theory views reproductive allocation and its impact on mortality (or growth) on an age-by-age basis (Stearns, 1992; Charlesworth, 1994). The general rule discussed here holds only for the aggregated (or average) values [but recall that earlier work (Charnov, 1997) showed that R_0 can *always* be written as a function of these averages]. Second, since we assume non-growing populations, $R_0 \approx 1$, the product of the average efficiencies (equation 3) equals 1. So, a species high in one average efficiency (say, offspring quality, S/I) *must be low* in the other efficiency (here, reproductive gains, R/M). Third, the evolutionary optimization displayed in Fig. 1 has $\partial S/\partial I = S/I$ and $\partial R/\partial M = R/M$, so that population and evolutionary stability together make $\partial S/\partial I \cdot \partial R/\partial M \approx 1$; marginal gain for investment in a single offspring ($\partial S/\partial I$) must be inversely related to marginal gain for investment in reproduction overall ($\partial R/\partial M$). The product of the two marginal gains is a conserved quantity equal to unity. Fourth, the age of first reproduction (α) may affect both trade-off curves of Fig. 1 (Charnov, 1993). To accommodate the joint evolution of I^*, M^* and α^* simply requires we view Fig. 1a,b for possible alternative α values; the evolutionarily stable strategy (ESS) still maximizes equation (3) (but this may require a formal ESS analysis to find the equilibrium).

The results discussed in the last two paragraphs suggest a new one-dimensional surface on which to plot life-history variation. Some species will fall near the high-quality offspring end (high S/I^*, $\partial S/\partial I$), others towards the high-quality adult end (high R/M^*, $\partial R/\partial M$). And the shapes of the two trade-offs (Fig. 1) theoretically control the position along the surface. I am unaware of data sets complete enough to test these ideas, although average adult body mass (W) for a species may be a useful variable here. Within many taxa, the following are *approximately* true between species (Charnov, 1993): $R \propto W^{0.75}$ and $M \propto W^{-0.25}$, making $R/M \propto W$. Since evolutionary and demographic equilibrium (Fig. 1) makes $R/M \cdot \partial S/\partial I \approx 1$, we predict that $\partial S/\partial I \propto W^{-1}$ between species. Unfortunately, there are no estimates for the $S(I)$ functions.

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