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# Trade-off-invariant rules for evolutionarily stable life histories

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Optimization models have been widely and successfully used in evolutionary ecology to predict the attributes of organisms<sup>1-8</sup>. Most such models maximize darwinian fitness in the face of trade-offs and constraints; the numerical results usually depend on the exact form of the trade-offs or constraints. But not always<sup>9</sup>: for example, earlier work<sup>9</sup> predicted that the optimal range in offspring size ought to show a  $-1$  scaling with small litter size, independent of most details of the underlying offspring-survival/offspring-size trade-off relation. Here I report that in non-growing (stationary), age-structured populations, three major life-history attributes (age at first breeding, size of an offspring in large litters, and reproductive effort) are likely to evolve to equilibrium values that satisfy a universal numerical rule; the underlying trade-off will have a slope of  $-1$  at the optimum, independent of most other aspects of the trade-off. Each of these three attributes can be viewed as an allocation problem between just two alternatives; the trade-off is then between having more of one alternative and less of the other. The slope of the trade-off is simply the slope of the curve of allowed combinations of the two alternatives. The theory predicts that natural selection will push to an equilibrium where the slope is always  $-1$ . The economic structure is the same as that which underlies evolution of the sex ratio where the two alternatives are sons and daughters<sup>2,10</sup>.

Consider an economic problem in the allocation between two alternatives  $X_1$  and  $X_2$  in which allowed values must fall on (or within) a constraint or trade-off curve, as shown in Fig. 1. Further suppose that the utility function (fitness) maximized is the simple product  $X_1 \cdot X_2$ , which is equivalent to maximizing  $\ln X_1 + \ln X_2$ . Figure 1 is the standard graphical solution from economics, which plots curves of equal utility, or in our case fitness ( $\ln X_1 + \ln X_2$  is constant). The optimum is where the highest equal-fitness curve just touches the trade-off curve. If  $\ln(\text{fitness})$  equals  $\ln X_1 + \ln X_2$ , the optimum will always be where the trade-off curve has a slope of  $-1$ , for any smooth trade-off curve. This is, of course, where the percentage increase in  $X_1$  is just matched by the percentage decrease in  $X_2$  (refs 2 and 10).

With fairly elementary economics, some evolutionary allocation problems can indeed be studied as two-dimensional ( $X_1, X_2$ ) and yield darwinian fitness to be a simple product. The classic example is evolution of sex allocation<sup>2</sup> (sex ratio, sperm versus eggs for hermaphrodites, time as a male (female) for a sex changer), where autosomal inheritance makes fitness a simple product<sup>2,10</sup>: gain-via-male times gain-via-female. It is this product structure for fitness combined with the two-dimensional allocation that makes sex allocation the most successful ESS (optimization) theory in evolutionary ecology<sup>2-6</sup>.

Are any other life-history problems naturally two-dimensional with fitness a product? Box 1 displays a surprisingly simple answer.  $R_0$ , the 'net reproductive rate' for age-structured life histories, can always be written as a product of three demographic averages, aggregated variables, which neatly summarize the life history:

$$R_0 = S(\alpha) \cdot \bar{b} \cdot E(\alpha) \quad (1)$$

where  $S$  is the probability of surviving to the age of first breeding ( $\alpha$ ),  $\bar{b}$  is the average rate of offspring production over the adult lifespan, and  $E(\alpha)$  is the average length of the adult lifespan (that is,

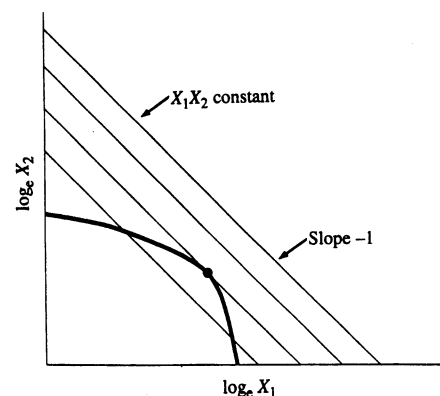
beginning at age  $\alpha$ ).  $R_0$  is a measure of darwinian fitness appropriate within stationary (non-growing) populations<sup>6</sup>.  $R_0 \approx 1$ , owing to density dependence for typical individuals, so the trade-offs are viewed as existing for individuals who deviate from the typical<sup>6</sup>. Thus, it is  $R_0$  for a mutant which is the fitness measure of interest.

Because equation (1) holds for any age-structured life history, evolutionary rules that follow from it should be quite general; the trick is to make predictions in terms of the three aggregate variables:  $S$ ,  $E$  and  $\bar{b}$ . I consider here three classic allocation problems in the evolution of life histories.

First, consider 'reproductive effort'.  $S \cdot \bar{b}$  is the rate of production of female babies (alive at age  $\alpha$ );  $E$  is the mother's reproductive lifespan. Denote  $S \cdot \bar{b}$  as  $B$ . Beginning with Williams<sup>11</sup>, it has been widely postulated that  $B$  should generally trade-off against  $E$  (refs 7, 8); effort devoted to offspring production ( $B$ ) should decrease the mother's own reproductive lifespan. Although there are life-history models<sup>12</sup> that do not make this 'reproductive effort' trade-off assumption, it is a widely held idea<sup>7,8</sup>. Usually the trade-off assumption is implemented on an age-by-age basis (following ref. 11), but nothing precludes working in terms of the aggregate variables  $B$  and  $E$ . Indeed, many existing models<sup>7,8</sup> can be alternatively viewed in terms of these averages. Assume it is generally true that natural selection sets an optimal balance between  $B$  and  $E$ . As fitness (equation (1)) is the product of  $B$  and  $E$ , Fig. 1 tells us that the optimum will be the place on the  $\ln B, \ln E$  trade-off surface where the slope is  $-1$ :  $\partial \ln B / \partial \ln E = -1$ , for all age-structured life histories where  $R_0$  can be used for fitness.

Second, suppose adult lifespan,  $E(\alpha)$ , is unrelated to how reproductive resources are divided among offspring; then  $R_0 \propto S \cdot \bar{b}$ , a product, and we have a classic offspring quality ( $S$ ) versus number ( $\bar{b}$ ) tradeoff (ch. 7 in ref. 7; refs 9, 13). At the optimum allocation  $\partial \ln \bar{b} / \partial \ln S = -1$  on the  $\ln S, \ln \bar{b}$  trade-off surface<sup>13</sup>. This  $-1$  rule also follows for many other size-versus-number allocations<sup>13</sup>, where fitness is naturally expressed as gain per unit multiplied by the number of units. This  $-1$  rule assumes maternal control over the allocation process. The rule will not hold if optimal investment per offspring is under offspring control; deviations from  $-1$  may well be a useful signature of offspring control<sup>14</sup>.

Third, write equation (1) as  $R_0 = S(\alpha) \cdot V(\alpha)$ , where  $V(\alpha)$  is  $\bar{b} \cdot E(\alpha)$ , the average production of offspring over the adult lifespan<sup>6</sup>. This is the classic trade-off with respect to age at maturity ( $\alpha$ ; ref. 7, ch. 6);  $S$  goes down with  $\alpha$ , while  $V$  goes up. As fitness is a product



**Figure 1** Economic optimization in two dimensions. Allowed combinations of two alternatives ( $X_1, X_2$ ) are on (or within) the trade-off curve, here plotted for  $\ln X_2$  versus  $\ln X_1$  and as a thick curve. If fitness is the simple product  $X_1 \cdot X_2$ , the optimum (or ESS) is found by plotting isofitness ( $\ln X_1 + \ln X_2 = C$ , a constant) curves and finding where the highest one just touches the trade-off curve. For all possible smooth trade-off curves, this yields a slope of  $-1$  at the ESS because  $-1$  is the slope of any isofitness curve:  $\partial \ln X_2 / \partial \ln X_1 = -1$  always, for a function  $\ln X_2 = C - \ln X_1$ .

( $S \cdot V$ ), the optimum is (again) where  $\partial \ln S / \partial \ln V = -1$  on the  $\ln S$ ,  $\ln V$  trade-off surface. This result is derived, but not really understood, in ref. 6.

It seems that several classic problems in life-history evolution yield a universal trade-off slope of  $-1$  at the optimum because aggregated fitness (Box 1) is naturally expressed as a product of two allocation alternatives ( $E$  versus  $B$ ,  $\bar{b}$  versus  $S$ ,  $S$  versus  $V$ ). Life histories are often treated as complex objects, with numerous possible age-dependent trade-offs<sup>7,8,15</sup>. The approach here reduces them to just a few aggregate variables ( $S$ ,  $\bar{b}$ ,  $E$ )<sup>6</sup>. Although we sacrifice all information about age-dependent allocation decisions<sup>7,8</sup>, we gain in finding general rules (hypotheses) about the shape of aggregate (average) trade-off surfaces at the equilibrium. I do not know of any data on trade-offs precise enough to test these differential-invariant predictions, particularly for the size/number or reproductive effort problems<sup>7</sup>. Theory for the optimal age at first reproduction using  $R_0$  as a fitness measure often implicitly invokes the minus-one rule as an intermediate step in the prediction of attributes such as optimal adult body mass<sup>6,7,12</sup>. Thus the minus-one rule is tested, at least qualitatively, whenever

these predictions work out. See, for example, the successful prediction of the heights and slopes of the between-species lifespan allometries for various mammal groups (ref. 6, p. 96; ref. 16). Of course, there are many qualitative (and a few quantitative) tests of product maximization for evolution of sex allocation<sup>2,6</sup>.

The procedure described here is to reduce darwinian fitness to a function of a few aggregate variables, hoping to find a general form for fitness (here a product) which then yields general rules for the equilibrium. The trick is worth trying for other problems in phenotypic evolution. Economists often use this procedure and, indeed, production or utility function in the form of products are common;  $X_1 \cdot X_2$ , or more generally  $X_1^A \cdot X_2^D$  (see any advanced text on price theory;  $A$  and  $D$  are  $> 0$  and scale the relative productive value of inputs to  $X_1$  and  $X_2$ , respectively). Then products like that of equation (1) may often characterize fitness in non-growing populations with reproductive structure even more complex than simply age. □

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## Molecular basis of symbiosis between *Rhizobium* and legumes

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Access to mineral nitrogen often limits plant growth, and so symbiotic relationships have evolved between plants and a variety of nitrogen-fixing organisms. These associations are responsible for reducing 120 million tonnes of atmospheric nitrogen to ammonia each year. In agriculture, independence from nitrogenous fertilizers expands crop production and minimizes pollution of water tables, lakes and rivers. Here we present the complete nucleotide sequence and gene complement of the plasmid from *Rhizobium* sp. NGR234 that endows the bacterium with the ability to associate symbiotically with leguminous plants. In conjunction

### Box 1: Fitness is a product

The net reproductive rate  $R_0$  is defined as  $R_0 = \int_0^{\infty} l(x)b(x)dx$ , which calculates the average number of daughters produced over a female's lifespan.  $l(x)$  is the probability of being alive at age  $x$ ,  $b(x)$  is the daughters produced at age  $x$  who are alive at independence from mother  $b > 0$  only if  $x > a$ , the age at first birth, measured from independence. Now write  $b(x) = b(y)$  for  $y = x - a$  and denote  $l(x)$  for  $x > a$  as  $S(x) = S(y + a)$ . (Notice that  $l(y)$  is zero at  $y = 0$  and is increasing with  $y$ ,  $l' = -\log'(l)/y = -m/y$ , so  $m/y$  is the instantaneous mortality rate at age  $y$ ,  $b(y)$  is the chance of living from independence to age  $y$ ,  $S(y)$  is the chance of living from independence to age  $y + a$ , which is the general life history.

$$R_0 = S(a) \int_0^{\infty} b(y) e^{-my} dy$$

Recall from the stable age distribution theory that the proportion of a breeding lifespan spent between ages  $y$  and  $y + dy$  (the probability density function for the adult ages) is given by

$$\frac{e^{-my} dy}{\int_0^{\infty} e^{-my} dy}$$

Now multiply equation (2) by (1), written as

$$\frac{\int_0^{\infty} e^{-my} dy}{\int_0^{\infty} e^{-my} dy}$$

to yield

$$R_0 = S(a) \left[ \int_0^{\infty} b(y) \frac{e^{-my}}{\int_0^{\infty} e^{-my} dy} dy \right] \left( \int_0^{\infty} e^{-my} dy \right) \quad (3)$$

$S(a)$  is the chance of living to reproduce at age  $a$ , while the term in square brackets is simply  $\bar{b}$ , the average rate of production of offspring over the reproductive adult life, and the term in curved brackets is simply  $E(a)$ , the expectation of further life at age  $a$ , the average length of the adult lifespan. So equation (3) is really

$$R_0 = S(a) \bar{b} E(a) \quad (4)$$

Equation (4) applies to any age structured life history.  $R_0$  is the simple product of three aggregated terms, each an average. For equation (4) to be used as a fitness measure, the population must not be growing. This makes  $R_0 \sim 1$  for typical individuals owing to density dependence. But mutant individuals may have their own  $R_0 > 1$ , and it is fitness and trade-offs for mutants which are discussed here. Thus we use  $R_0$  as a fitness measure, with the condition that it must equal unity at the optimum, when mutants are the same as typical.