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# A trade-off-invariant life-history rule for optimal offspring size

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OPTIMIZATION models have been widely and successfully used in evolutionary ecology to predict the attributes of organisms<sup>1-6</sup>. Most such models maximize darwinian fitness (or a component of fitness) in the face of trade-offs and constraints; the numerical results usually depend on the exact form of the trade-offs/constraints. Here we report the first (to our knowledge) numerical optimum for life-history evolution which is independent of the details of the underlying trade-off, for a large array for trade-off forms. The rule is that at small litter sizes, the range in offspring size is inversely proportional to the size of the litter. Details of the offspring-survival/offspring-size trade-off<sup>7-10</sup> set the value of the proportionality constant, but the -1 exponent, the inverse proportionality itself, is universal. Studies of life histories have yielded many empirical examples of universality for various scaling exponents<sup>6</sup> (for example, adult lifespan scales as  $\approx 0.25$  with adult body mass within many taxa); this is an example of the numerical value of an exponent (here -1) emerging from a life-history model as independent of all but a few general features of the underlying economic structure.

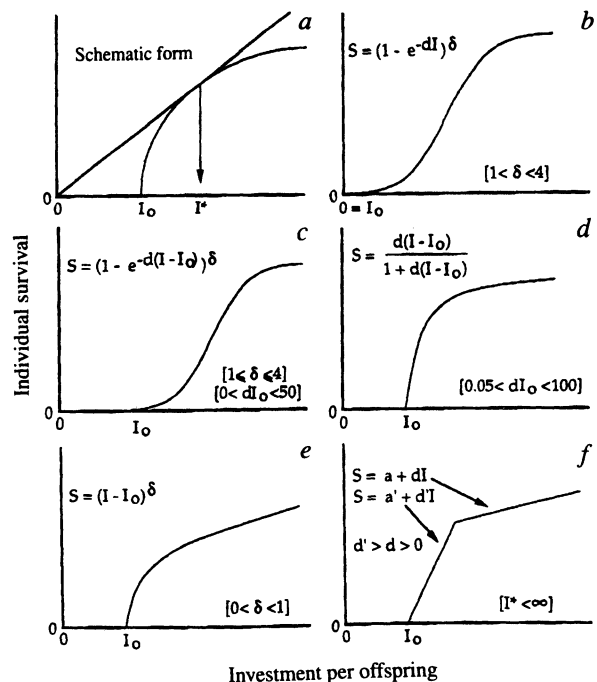
Most evolutionary models for the optimal investment per offspring<sup>7-12</sup> begin with a trade-off structure (Fig. 1a). Individual offspring survival to adulthood ( $S$ ) is solely a function of the amount of resource given to the offspring ( $I$ ). A female with an amount,  $R$ , of reproductive resource can produce  $R/I$  offspring in a litter, each of which survives with probability  $S(I)$ . Thus,

the parent will produce  $(R/I) S(I)$  surviving offspring. Provided that the parent controls  $I$ , natural selection ought to favour the maximization of  $RS/I$  through choice of  $I$  (called  $I^*$  at the maximum); this solution also assumes that the parent's own survival and growth are uncorrelated with  $I$  (although they may be related to  $R$ ). For fixed  $R$ , this is equivalent to maximizing  $S/I$ ; this optimal  $I$  satisfies  $\partial S/\partial I = S/I$  and may be found by the tangent argument illustrated in Fig. 1a. We will refer to  $I$  as 'offspring size' which is taken to be proportional to investment per offspring (but see below).

This answer for the optimal  $I$  assumes  $R$  is large relative to  $I^*$  so that  $R/I^*$  is (effectively) an integer, a necessary condition for real litters. When litter sizes are small (1-6),  $R/I^*$  may differ significantly from an integer, and a female may gain more by increasing the size of her  $C$  offspring than by producing  $C+1$  smaller offspring. Thus there is a range of 'optimal' offspring sizes ( $I$ ) at each litter size<sup>7</sup>. Suppose that the offspring produced by members of a particular population face the trade-off illustrated in Fig. 1a. Each female ( $i$ ) has  $R_i$  resources to divide up;  $R_i$  may differ among females but the  $S(I)$  curve does not. Provided that a female does not produce offspring of variable size within her litter, she will have  $R_i/I_i$  offspring in each litter with a per-offspring survival of  $S(I_i)$ . If  $R$  is great enough to produce one viable offspring (above  $I_0$  on Fig. 1a),  $C=1$  and  $I=R$ . As  $R$  increases, so will  $I$ , as long as one offspring of size  $R$  will be better than two of size  $R/2$ . At higher values of  $R$ ,  $C$  will equal 2 and  $I=R/2$ ; still higher values of  $R$  yield  $C=3$  (and  $I=R/3$ ) and so forth. Each  $C$  will be associated with a maximum ( $I_{max}$ ) and a minimum ( $I_{min}$ ) offspring size, and resource ( $R$ ) amounts. The litter size  $C$  should change from one to two when the fitness gain from one offspring of size  $I$  equals the fitness gain from two offspring of size  $I/2$  or  $S(I) = 2S(I/2)$ . The change from two to three offspring should be at size  $I$  where  $2S(I) = 3S(I/3)$ . The total resource amount ( $R_2$ ) at this switch point is the value of  $R$  where  $2S(R_2/2) = 3S(R_2/3)$ . When continued to even larger litter sizes, this argument yields successive resource

FIG. 1 Various trade-off functions for offspring survival ( $S$ ) as a function of investment in each offspring ( $I$ ). Each equation (in panels a-f) may be multiplied by any positive number without altering any of the results reported here. The trade-off assumed in the classic model<sup>10,11</sup> is that individual offspring survival to adulthood is solely a function of the resource given to each offspring. A female has some fixed amount of resource ( $R$ ) to allocate among offspring, so the number of offspring in any litter ( $C$ ) is  $R/I$ . The optimal  $I$  maximizes the number of surviving offspring ( $RS/I$ ). For any fixed  $R$ , this is equivalent to choosing  $I^*$  to maximize  $S/I$  and may be found by the tangent argument illustrated in a. This  $I^*$  answer requires that the resulting litter size  $R/I^*$  be an integer; this requirement is not well approximated at small litter or clutch sizes (1-6) which are common in many animals. b-f, The invariance/scaling rules discussed in the text hold (to within 5%) for these trade-off curves, over a large range of parameter values (given in brackets) which yield the finite equilibrium  $I^*$  in a. Notice that the parameter value ranges refer only to the dimensionless numbers  $dI_0$  and  $\delta$ ; it is straightforward to show that the rules discussed here only depend on these dimensionless numbers (see below).

**METHODS.** Let  $R_i$  be the total resource level at the change-over from litter size  $i$  to  $i+1$ . Then  $R_1$  is where  $S(R_1) = 2S(R_1/2)$ ,  $R_2$  is where  $2S(R_2/2) = 3S(R_2/3)$ , and so forth. Let  $\bar{R} = \text{mean } R$  to within 5%; then  $R_{i+2} - R_{i+1} = R_{i+1} - R_i$ . Because the dimensionless ratio between successive  $R$  intervals is only dependent upon the dimensionless numbers in each parametric form ( $dI_0, \delta$ ), calculations are greatly simplified. Dividing by the respective litter sizes yields rule (1). The resource interval  $(R_{i+1} - R_i)$  is the constant of proportionality (equation (2) in text). Some parametric forms lead to strict equality (for example, f, e with  $\delta = 0.5$ ); other show convergence to equality for large  $i$  with the '5% or better' rule applicable for small (2-6) litters. The convergence of  $R_{i+1} - R_i$  to a fixed value at large  $i$  may be developed as follows. The largest (smallest) offspring size is converging to  $I^*$  (Fig. 2); for large  $i$  we have  $R_i/i \approx I^*$  and  $(R_{i+1})/(i+1) \approx I^*$ . This immediately implies  $R_{i+1} - R_i \approx I^*$ . Interestingly this is also approximately true for  $R$  values yielding clutch sizes of 2-6, although the error here may be up to 10%. Curves e and f are



non-asymptotic, but may usefully represent  $S$  over a reasonable  $I$  range, particularly as the calculated answers are independent of any positive multiplier of the  $S$  function.

amounts ( $R$ ) at the switch points, and the rule that the largest offspring associated with litters of size  $C$  ought to be  $(C+1)/C$  times as large as the smallest offspring associated with the next largest litter size,  $C+1$ . The maximum and minimum offspring sizes converge from above and below to the optimal size  $I^*$ , as given in the classic model<sup>9,10</sup> (Fig. 1a). When offspring size is measured relative to  $I^*$  the convergence is then to 1.0 (Fig. 2). We note two limitations to this argument. First, if the parent can easily control  $R$  it may well pay simply to accumulate resource until an (or a few)  $I^*$ -sized offspring can be produced. Second, the argument assumes that the conversion of  $R$  into offspring is linear; significant nonlinearity would distort the observed sizes (investment per offspring) at the switch points. Even given these caveats ( $R$  fixed, proportional conversion), the rules discussed here should be broadly applicable.

Our previous work<sup>7</sup> suggested the theoretical convergence to be more or less symmetric around  $I^*$ ; new calculations have proved this to be often not true, but these calculations showed the convergence to have one, unexpected, universal feature; the size range is proportional to  $C^{-1}$  (Fig. 2). Except for  $C_1$ , the ratio of the ranges of offspring size at litter sizes  $i$  and  $j$  are inversely proportional to the ratio of the litter sizes ( $C_i, C_j$ ); or

$$(I_{\max_i} - I_{\min_i}) / (I_{\max_j} - I_{\min_j}) = C_j / C_i \quad (1)$$

Thus the size range for  $C_3$  is predicted to be 2/3 that at  $C_2$ , and so on; the rule often fails (up to 20–35% off the mark) at  $C_1$ , although it works even here for the parameter values of Fig. 2. This rule is correct to within 5% (often less, even exact) for  $2 < C < 6$  for a remarkable variety of trade-off functions, illustrated in Fig. 1. Whereas specific functions and parameter values yield specific values of  $I^*$ ,  $I_{\max}$ ,  $I_{\min}$ , and proportionality constant, each  $S(I)$  combined with various and increasing  $R$  values yields rule (1). It seems to follow from the economic rule of when a female should switch from a litter size of  $C$  to  $C+1$  with consequently smaller offspring (compare discussion above and Fig. 1 legend). Rule (1) holds mathematically even for large  $C$  values, but is biologically less plausible here.

Writing rule (1) as  $OSR \propto C^{-1}$  (where  $OSR$  is offspring size range) implies a proportionality constant (that is,  $OSR = H/C$ ) and  $H$  may be developed as follows. The range in resource values at any litter size  $k$  may be written as  $R_{\max_k} - R_{\min_k}$ . The maximum

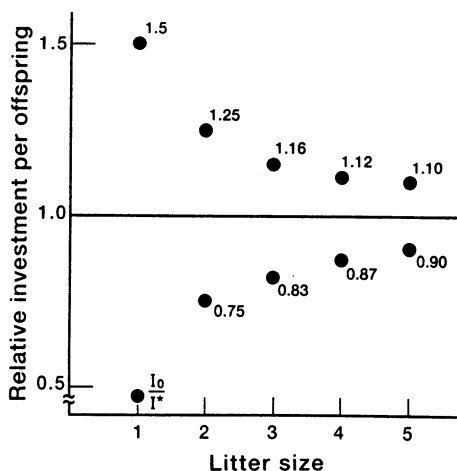


FIG. 2 Maximum and minimum offspring sizes, measured relative to  $I^*$ , at different litter sizes for the parametric model  $S = (1 - e^{-d(I - I_0)})$  (Fig. 1c with  $\delta = 1$ ). The maximum and minimum values converge on 1.0 from above and below. Here  $d$  and  $I_0$  were chosen to make  $I_{\max_i}/I^* \approx 1.5$  and the convergence is nearly symmetric. Note that the range of offspring sizes at any litter size ( $C$ ) is  $C^{-1}$ , hence the ratio of ranges at any two litter sizes is the inverse of the ratio of the litter sizes. This scaling rule holds true for a wide range of values of  $d$  and  $I_0$  in this model, and for many shapes for the  $S(I)$  curve (Fig. 1).

( $I_{\max}$ ) and minimum ( $I_{\min}$ ) sized offspring at this litter size are given by  $R_{\max_k}/C_k = I_{\max_k}$  and  $R_{\min_k}/C_k = I_{\min_k}$ . Thus we have

$$OSR_k = H/C_k = (R_{\max_k}/C_k) - (R_{\min_k}/C_k) \quad (2)$$

and see immediately that the proportionality constant  $H$  is simply the resource range at any litter size,  $H = R_{\max_k} - R_{\min_k}$ . Or said slightly differently, the range of resources yielding any single litter size will be the same for all litter sizes.

There is one other interpretation of  $H$ . In Fig. 1 legend we show that, as  $k$  gets large,  $R_{\max_k} - R_{\min_k} \rightarrow I^*$ ; as the  $R$  intervals are not too different from this even at small  $C$ , we have to a good approximation,  $H \approx I^*$ . If offspring size is measured relative to  $I^*$ , as in Fig. 2, then  $H \approx 1$  and the intervals are equal to  $C^{-1}$ . Notice that this means the entire convergence illustrated in Fig. 2 can be reconstructed approximately from any single point (except  $I_0/I^*$ ). For example, each  $I_{\max_i}/I^*$  will be associated with a convergence, independent of trade-off details. Notice also that this allows an estimate of  $I^*$  from two boundary points; that is,  $I^* = 2$  ( $OSR$  at  $C_2$ ), and so forth.

Our previous work<sup>7</sup> estimated the largest egg size (the 90th percentile in volume of a single egg) for litters of 1–5 in the poeciliid fish *Gambusia hubbsi*, and showed a close correspondence to the decline predicted in Fig. 2. This decline is predicted to hold, as a good approximation, for models (Fig. 1) yielding  $I_{\max_i}/I^*$  near 1.5. Unfortunately, it proved impossible to estimate the smallest egg size at each litter size so we were (are) unable to estimate the ranges in egg size. We are not aware of any existing data that would allow such estimates in other species.

It has proven exceedingly difficult to get detailed information about the shapes of life-history trade-offs<sup>11</sup>, and two decades of research (beginning with refs 9 and 10) have yielded very few examples<sup>8,12</sup> for the estimation of the shape of the trade-off illustrated in Fig. 1. This makes theoretical predictions that are independent of the exact form of trade-offs, like the ones developed here, of particular interest. It is surprising that the numerical prediction of  $-1$  scaling holds for such a large and diverse class of  $S(I)$  trade-offs (Fig. 1). This universality makes empirical studies of offspring size ratios especially worthwhile. Size/number trade-offs characterize many other evolutionary problems with similar economic structure<sup>13</sup>, and these may be expected to show similar scaling rules for the size ratios. In addition, the theoretical existence of trade-off invariance for this problem should point theorists to search for numeric universality in other life-history evolution problems<sup>6</sup>. Finally (and empirically), scaling exponents of  $\pm 1$  are ubiquitous between timing (size) variables for life histories, and for inter-species (population) comparisons<sup>6,14–16</sup>; the proportionality constant differs between higher taxa (for example, mammals<sup>6</sup> versus reptiles<sup>16</sup>) but, again, not the exponent. These seem sensible candidates for trade-off-invariance rules. □

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