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Eric Charnov

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Optimal (plastic) life histories in growing versus stable populations

Eric L. Charnov

Department of Biology, The University of New Mexico, Albuquerque, New Mexico, USA

ABSTRACT

Question: What is the effect of population dynamics on the evolutionarily optimal life history with metabolic (allometric) production constraints?

Mathematical methods: Optimization of a phenotype's intrinsic rate of increase r with respect to adult mass, m_a.

Results: The change in optimal adult size (m_a) between growing ($r > 0$) and stable ($r = 0$) populations is hard to predict, but reproductive effort (and lifetime reproductive effort) in the growing population is predicted to be $1 + r \cdot E$ times larger, where E is the average adult life span.

Keywords: allometry, dimensionless, metabolic ecology, norm-of-reaction, r/k-selection.

MATHEMATICAL METHODS AND RESULTS

Natural selection usually favours earlier reproduction and greater reproductive allocation in growing versus stable populations (Lewontin, 1965; reviewed in Roff, 1992; Stearns, 1992), because with population growth an individual's reproductive future is worth relatively less. If the up-phase lasts several generations, the door opens for an individual growing up during it to adjust facultatively its life history (adult size, reproductive allocation) to match the optimum for the increasing population conditions. Reproductive effort (R), the mass given to reproduction per unit of time divided by the adult's size (Charnov *et al.*, 2007), is predicted to increase during the up-phase; maximization of the intrinsic rate of increase (r) in the face of metabolic production constraints leads to a remarkable prediction: R will increase in the up-phase compared with the value selected-for in a stable population by the multiplier $1 + r \cdot E$, where E is the average adult life span. Larger-bodied species generally have smaller R, but are predicted to have a similar $r \cdot E$ multiplier (Charnov, 1993, Ch. 6).

Consider a mammal whose population undergoes occasional bouts of increase, lasting several generations, followed by more or less stable numbers for several generations (periods of decrease may lead to lower population size followed by a low stable phase . . . I ignore these times here). This is illustrated in Fig. 1. I show that the optimal (or evolutionarily
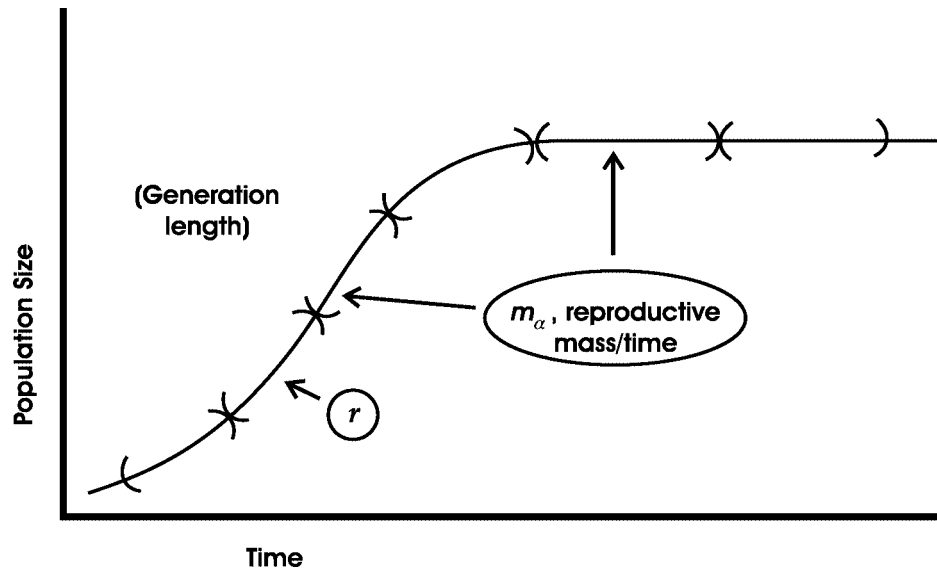

Fig. 1. Data to test theory (circled): each (—) interval refers to a single generation, and during the up-phase and the stable phase, we need estimates of the intrinsic rate of increase (r), adult size (m_a), and reproductive allocation. Also needed is an estimate of E, the average adult life span.

stable strategy, ESS) life history during the up-phase differs from that during the stationary phase; if we consider these two options to be plastic responses (e.g. Stearns, 1989) by individuals growing up in the two phases, we can predict, for example, the optimal body size or reproductive allocation for individuals in one phase relative to the other phase. If we believe that a plastic response is unlikely, then the results for the up-phase probably apply only to populations that often are on the increase from a catastrophic decline, where the down-phases are really non-selective with respect to life history [see, for example, discussion of 'r-selection' in Roff (1992)]. I think it more interesting to interpret the predictions as implying plastic responses in body size and reproductive allocation to different demographics.

One referee noted that, in this paper, 'All individuals are assumed identical in their capability to develop and implement the same appropriate plastic phenotype. From a population standpoint, two other outcomes to environmental change are possible. One is to create a polymorphic population and the other is to have one all-purpose phenotype whose value is some sort of weighted average of the two adapted phenotypes, where the weighting depends at least on the relative proportions and autocorrelations of the two environment types'. I leave it to the reader to consider these possibilities.

The life history assumed (Charnov, 1991, 1993) approximates that of a mammal with deter-minate growth; adult mass (m_a) follows the allometric (metabolic) growth rate $dm/dt = A \cdot m^\delta$ (where $\delta \approx 0.7$). Reproductive allocation is simply diverted personal growth ($= A \cdot m_a^\delta$). Reproductive effort (R) is simply this divided by adult mass, or $R = m_a^{\delta-1}$. Note that for fixed A, R decreases with m_a as a power function with exponent $\delta - 1$. In this life history, proportion S_a of the offspring survive to breed at age α (size m_a), and the instantaneous mortality rate (Z_x) as a function of age is high at young ages and decreases to some fixed

value (Z_a) prior to feasible ages of maturation (Charnov, 1991, 1993); note that $S_a = e^{-\int_0^a Z(x)dx}$ and that the average adult life span (E) is simply $1/Z_a$. Density-dependent mortality is assumed to be on Z_x at small x. To allow this population to grow, I relax the density dependence on Z_x and assume that A in $dm/dt = A \cdot m^\delta$ is increased because the low population numbers allow individuals greater access to resources. E is assumed not to change with population size. The number of offspring born per year is b $[= (dm_a/dt)\,(1/m_0)]$, where m_0 is the size of each offspring. The Appendix shows that this demography will lead to an intrinsic rate of increase (r) that satisfies $e^{r \cdot a}\,[Z_a + r] = b \cdot S$. The Appendix also shows that the optimal α (or m_a if we specify A) is found easily by setting $dr/d\alpha = 0$ (equations A4 and A8 in Appendix). If A_s and A_g refer to the dm/dt A's in the stationary ($r = 0$) versus the growth phase ($r > 0$), the ratio of optimal adult body size (m_s, m_g) in the two phases is:

$$\frac{m_s}{m_g} = \left[\left(\frac{A_s}{A_g} \right)(1 + r \cdot E) \right]^{\frac{1}{1-\delta}} \tag{1}$$

The ratio of optimal reproductive effort, R_g/R_s ($R_s = A_s \cdot m_s^{\delta-1}$, $R_g = A_g \cdot m_g^{\delta-1}$), is much simpler:

$$R_g/R_s = 1 + r \cdot E \tag{2}$$

because $R = (Z_a + r)/\delta$ in each phase.

It is hard to know if predicted adult mass (m_a) will be increased or decreased during the up-phase. If $A_g > A_s$, the body growth part of equation (1) pushes for larger size, while the population dynamic part $(1 + r \cdot E)$ pushes for smaller size. Reproductive effort (equation 2), however, should always increase by a $1 + r \cdot E$ multiplier. $E \cdot r$ should be similar for species with different body sizes (mouse vs. deer); rewrite it as $(\alpha \cdot r)(E/\alpha)$ and note that, in mammals, both $\alpha \cdot r_{max}$ and E/α are independent of body size (Charnov, 1993, Chs. 5 and 6). I also suspect that the $1 + r \cdot E$ multiplier applies to life histories more complicated than that modelled here (i.e. indeterminate growth, as in fish), because rules for optimal life histories with metabolic growth/offspring-production constraints often generalize (Charnov, 2001; Charnov *et al.*, 2001). Finally, lifetime reproductive effort (Charnov *et al.*, 2007) is $(dm_a)/(m_a \cdot dt) \cdot (E)$, and equals $(1/\delta)(1 + r \cdot E)$; here, again, it is increased in the up-phase by the $1 + r \cdot E$ multiplier. Obviously, this predicted plastic response to altered r assumes that the individual has knowledge of the population phase, as well as the physiological ability to respond appropriately. I illustrate the data required in Fig. 1; I am unaware of any species that meets this requirement.

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APPENDIX: OPTIMAL BODY SIZE AND REPRODUCTIVE EFFORT

Assuming asexual reproduction (a two-sex model gives the same answer), the intrinsic rate of increase (r) associated with a particular life table (lx, bx schedule) is given by

$$1 = \int_0^\infty \frac{lx \cdot bx}{e^{r \cdot x}}\, dx,$$

where lx is the chance of living to age x ($l_0 = 1$) and bx is the number of offspring born to an individual of age x.

For the life history laid out in the text:

$$1 = \frac{S_\alpha \cdot b}{e^{r \cdot \alpha}} \int_\alpha^\infty \frac{e^{-z_\alpha(x-\alpha)}}{e^{r(x-\alpha)}}\, dx.$$

Thus, $1 = \dfrac{S_\alpha \cdot b}{e^{r \cdot \alpha}(r + Z_\alpha)}$, leading to [dropping the α subscript (see also Charnov, 1993, p. 118)]:

$$e^{r \cdot \alpha}[r + Z] - S \cdot b = 0 \tag{A1}$$

or

$$r \cdot \alpha + \log_e[Z + r] = \log_e b + \log_e S. \tag{A2}$$

We need $dr/d\alpha = 0$ and can implicitly differentiate equation (A2):

$$\frac{dr}{d\alpha} \cdot \alpha + r + \left(\frac{1}{Z + r}\right)\frac{dr}{d\alpha} = \frac{d \log_e b}{d\alpha} + \frac{d \log_e S}{d\alpha} \qquad \text{if } \frac{dZ}{d\alpha} = 0. \tag{A3}$$

Setting $dr/d\alpha = 0$ yields:

$$\frac{d \log_e b}{d\alpha} + \frac{d \log_e S}{d\alpha} - r = 0. \tag{A4}$$

Assume:

$$\frac{dm}{dt} = A \cdot m^\delta \tag{A5}$$

and

$$b \propto m_a^\delta.$$ (A6)

Thus,

$$\frac{d \log_e b}{d\alpha} = \frac{\delta}{m_a} \cdot \frac{dm}{dt} = \delta \cdot A m_a^{\delta-1}.$$

Let $S = e^{-\int_0^a Z(x)dx}$, so

$$\frac{d \log_e S}{d\alpha} = -Z(\alpha).$$ (A7)

Putting (A6) and (A7) into (A4) gives

$$\delta \cdot A \cdot m_a^{\delta-1} - (Z(\alpha) + r) = 0.$$ (A8)

With equation (A8), it is straightforward to show that if m_s is m_a in a stationary population ($r = 0$) and m_g is m_a in a growing population ($r > 0$), the adult-size ratio is

$$\frac{m_s}{m_g} = \left[\left(\frac{A_s}{A_g} \right)(1 + r \cdot E) \right]^{\frac{1}{1-\delta}},$$

where A_s and A_g refer to the mass production function A's for stationary and growing populations, respectively, and $E = 1/Z_a$, the average life span.

Reproductive effort is $R = \dfrac{dm_a}{m_a \cdot dt} = A \cdot m_a^{\delta-1} \left(= \dfrac{Z_a + r}{\delta} \right.$ by equation A8$\left. \right)$. The ratio of reproductive efforts for the two kinds of populations R_g/R_s is simply $R_g/R_s = 1 + r \cdot E$.