Reproductive effort, offspring size and benefit–cost ratios in the classification of life histories

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ABSTRACT

There have been many attempts to document links between reproductive allocation and factors such as adult body size and demography. This paper suggests that among closely related taxa, two dimensionless numbers, each a benefit–cost ratio summarizing reproductive timing, allocation and demography, are invariants and thus are useful to classify life histories. The two numbers are E/α and $C \cdot E$, where E is average adult life span, α is age-at-first-reproduction and C is average mass (per adult) devoted to reproduction per unit of time, divided by the average adult body mass (m); C is usually called 'reproductive effort'. Since E^{-1} is the average adult mortality rate, C/E^{-1} is the reproductive effort (benefit) per unit death (cost). Similarly, E/α is the amount of time for reproduction (E) divided by the time cost to get there (α). Combining these two numbers with the relative size (I) of an offspring (I/m) yields a new classification scheme for life histories; this is contrasted with other classification schemes (e.g. r and K).

Keywords: classification of life histories, dimensionless numbers, life-history cube, r and K selection, Smith–Fretwell.

INTRODUCTION

This paper develops a new way to classify or organize life histories, one which removes the units of mass and time and views a life history in terms of a handful of dimensionless variables. The variables with units that make up the dimensionless numbers are, I claim, a very natural set of reproductive–demographic averages, at least for non-growing populations. The new scheme expands on one published a dozen years ago (Charnov and Berrigan, 1990). This approach to life histories raises many issues about natural selection in the face of constraints (Charnov, 1993), but this aspect is downplayed here as I mostly wish to argue for the usefulness of the classification scheme itself.

Organisms exist to reproduce and the rules governing reproductive allocations (timing, mass to offspring, etc.) are usually viewed in a cost–benefit framework (e.g. Williams, 1966; Stearns, 1992). Figure 1 is a very simple life history. α time is spent preparing to reproduce and the average adult life span (E) is spent in reproduction; E is the benefit, α the cost. Thus,

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E/α is a benefit–cost ratio for the time made available to reproduce. After initiation of reproduction at age α, a mass of R per unit time is devoted to reproduction. This is a benefit, but what is the cost? Most people would argue that mortality is the cost, since after age α resources are devoted to either reproduction (R) or keeping one's self alive, ultimately reflected in E. $1/E$ is an adult mortality rate, thus R/E^{-1} is another benefit–cost ratio (Charnov, 2001b). But this ratio has units of mass (R = mass/time, E^{-1} = 1/time), while E/α is dimensionless. Organisms with larger body size almost always have larger R and E, which is why many authors have proposed that a natural measure of 'reproductive effort' be something like R/(adult mass), the fraction of a body mass devoted to reproduction per unit of time; call this ratio C. Now C/E^{-1} is a dimensionless benefit–cost ratio; the fraction of a body mass given to reproduction per unit of adult death (E^{-1}).

   The life history shown in Fig. 1 is very (too) simple; neither R nor adult body mass (m) change with adult age, which allows adult demography to be summarized in E. However, the life history points towards two dimensionless benefit–cost ratios (E/α, C/E^{-1}) that may be useful in classifying life histories among various species. For the scheme to be useful, however, the two numbers must somehow apply to much more complex life histories. Surprisingly, they do. However, they are not the only dimensionless numbers needed to characterize life histories; at least three more are needed, as I now show.

GENERAL AGE-STRUCTURED LIFE HISTORIES

Understanding age-specific life histories can be difficult because life tables, body-size growth rules and age- (size)-specific reproductive allocations add up to a pretty long and complicated list. However, we can reduce this seeming complexity somewhat by calculating averages over the age distribution (Charnov, 1997), and get even more reduction if we use
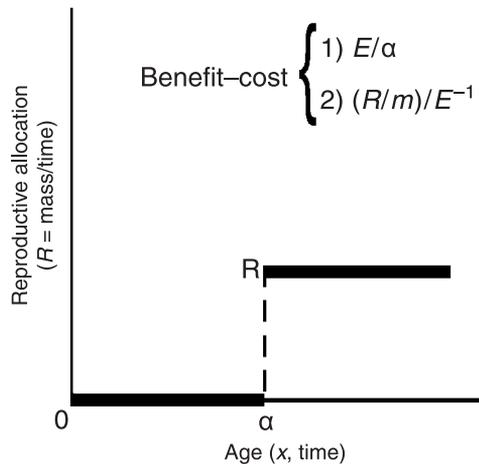
Fig. 1. A simple life history. Reproduction begins at age α and size m. R resources are given to reproduction per unit of time and the average reproductive interval, the average adult life span, is E. Two dimensionless benefit–cost ratios are defined for this life history. E/α is reproductive time (E) over preparation time (α), and $(R/m)/E^{-1}$ is the relative reproductive rate (R/m) over the mortality rate (E^{-1}).

the averages to make up dimensionless variables (Charnov, 1993). Seven numbers, five of them averages, neatly summarize any age-structured life history. They are:

(1) α = age-at-first-reproduction (equation 1).
(2) $S = l_\alpha$, where l_x is the chance of surviving to age x ($l_0 = 1$). We can rewrite this as:

$$S = e^{-\int_0^\alpha Z(x)\mathrm{d}x} = e^{-\bar{Z}\cdot\alpha} \tag{2}$$

where $Z(x)$ is the instantaneous mortality rate at age x and $\bar{Z}$ is the 'average-immature-instantaneous-mortality rate'. S is the average chance of breeding.

(3) I = size (mass) of an offspring at independence from the parent (equation 3).
(4) m = average adult body mass:

$$m = \frac{\int_\alpha^\infty l_x\cdot m_x\mathrm{d}x}{\int_\alpha^\infty l_x\mathrm{d}x} \tag{4}$$

(5) R = average reproductive allocation per unit of time:

$$R = \frac{\int_\alpha^\infty l_x\cdot R_x\mathrm{d}x}{\int_\alpha^\infty l_x\mathrm{d}x} \tag{5}$$

R and m can be related in an interesting way. Suppose $R_x = C_x\cdot m_x$, so C_x is the reproductive effort, the allocation (R_x) at age x as a fraction of the body size at that age (m_x). Define the average of C_x ($=C$) as follows:

$$C = \frac{\int_\alpha^\infty l_x\cdot m_x\cdot C_x\mathrm{d}x}{\int_\alpha^\infty l_x\cdot m_x\mathrm{d}x} \qquad \text{so } C = R/m \tag{5a}$$

and we can choose any two of the three numbers to work with. We will use C and m.

(6) E = average adult life span:

$$E = \int_\alpha^\infty \frac{l_x}{S}\,\mathrm{d}x \tag{6}$$

(7) The final useful number (already dimensionless) is R_0, the 'net reproductive rate', the average number of daughters produced over a mother's lifetime. Since here we wish to count total offspring produced, we simply assume a 1 : 1 primary sex ratio and multiply R_0 by 2. If b_x is the number of daughters produced by an age x female,

$$2\cdot R_0 = 2\int_\alpha^\infty l_x\cdot b_x\mathrm{d}x = \int_\alpha^\infty \frac{l_x R_x}{I}\,\mathrm{d}x = \frac{S}{I}\int_\alpha^\infty \frac{l_x\cdot C_x\cdot m_x}{S}\,\mathrm{d}x$$

$$2R_0 = S \cdot \left[\frac{\int_\alpha^\infty \frac{l_x}{S} \mathrm{d}x}{1} \right] \cdot \left[\frac{\int_\alpha^\infty \frac{l_x \cdot C_x \cdot m_x \mathrm{d}x}{S}}{\int_\alpha^\infty \frac{l_x}{S} \cdot m_x \mathrm{d}x} \right] \cdot \left[\frac{1}{I} \right] \cdot \left[\frac{\int_\alpha^\infty \frac{l_x \cdot m_x \mathrm{d}x}{S}}{\int_\alpha^\infty \frac{l_x}{S} \mathrm{d}x} \right]$$

Using equations (2), (4), (5a) and (6), $2R_0$ may be written as:

$$2R_0 = (\bar{e}^{\bar{z} \cdot \alpha}) \cdot [C \cdot E] \cdot \left[\frac{m}{I} \right] \tag{7}$$

SEVEN NUMBERS AND $R_0 \approx 1$

We have now reduced the age-specific life history to seven numbers, six of them with units of time or mass:

$$\underbrace{R_0}_{} \qquad \underbrace{I, m}_{} \qquad \underbrace{1/\bar{Z}, C^{-1}, E, \alpha}_{}$$

units: dimensionless   mass   time

We can further reduce the list by working only with dimensionless variables. There are four: I/m, S, E/α, $C \cdot E$.

Note that R_0 (equation 7) is itself a function of three of these numbers. Not all of the three numbers in equation (7) can vary independently; $R_0 \approx 1$ in non-growing populations, since a female just replaces herself with one daughter. This 'non-growing population constraint' means that equation (7) is held equal to ≈ 2 by density dependence (somewhere in the life history), or

$$\frac{S(E \cdot C)}{I/m} \approx 2 \tag{8}$$

So, if we know two of the numbers, the value of the third is fixed. I suspect (Charnov, 1993) that S is the most likely candidate for density dependence and I suggest that the comparative study of life histories across species should focus on the 'allowed' values for the three dimensionless numbers $E \cdot C$, I/m and E/α. $C \cdot E$ is the reproductive effort (C) per unit of adult mortality ($1/E$). As discussed in the Introduction, E/α and C/E^{-1} are *both* reproductive benefit–cost ratios, here defined for arbitrarily complex age-structured life histories. So, what do E/α, $C \cdot E$ (and I/m) look like across various taxa? Surprisingly, E/α *and* $C \cdot E$ may be invariants within some taxa (e.g. mammals, fish); I/m is sometimes an invariant.

VALUES FOR THE THREE NUMBERS: MAMMALS, BIRDS AND FISH

It has long been known that E is proportional to α within various taxa (for a summary, see Charnov and Berrigan, 1990; Charnov, 1993): $E/\alpha \approx 0.5$ for fish, ≈ 2.25 for birds and ≈ 1.35 for mammals. $I = m$ for altricial birds, which raise their offspring to adult size. $I/m \approx 0.3$ for a diverse sample of mammals (Charnov, 1993, fig. 5.4). Offspring size (egg size) appears to be unrelated to adult size across species of fish, so I/m is *clearly not an invariant for fish*. However, $I/m \approx$ a few percent, at most, for the majority of fish.

Gunderson (1997) showed that C is proportional to E^{-1} in a large and diverse sample of fish, so that $C \cdot E \approx 0.60$; he used gonad mass per year over body mass as the estimate of C. $C \cdot E$ are probably invariants within birds and mammals as well, by the following calculation, which sets $R_0 = 1$ (Charnov *et al.*, 2001). Figure 1.2 in Charnov (1993) shows that $S \approx 0.2$ for a wide variety of altricial birds. So a female bird raises $1/S = 5$ daughters over her lifetime; since each is her mass, $C \cdot E \approx 5$. Here we assume her mate rears the five sons; if she raises more than half the brood, $C \cdot E > 5$, so 5 is a minimum. Female mammals typically rear both their sons and daughters, and $S \approx 0.3$–0.4 (Charnov, 1993); $1/S \approx 2.85$ (if $S = 0.35$), so a female rears twice this in sons and daughters, or $C \cdot E = (2)\,(2.85)\,(0.3) \approx 1.7$, since each offspring is 0.3 of the mother's mass at independence. So, $C \cdot E \approx 0.6$ for fish, ≈ 5 for birds and ≈ 1.7 for mammals.

R_0 IS A FITNESS MEASURE

R_0 plays two roles in understanding life histories in non-growing populations (Charnov, 1993, 1997). $R_0 \approx 1$ (equation 7 = 2) is a population dynamic constraint and implies that not all aspects of demography are free to vary. We implicitly assume density dependence somewhere in the life history; usually, I assume it is in S, which is why the value of S is set after the other dimensionless numbers in equation (7). R_0 is also a measure of individual fitness (Charnov, 1997); here the various parameters in equation (7) are linked by trade-offs (Charnov, 1993, 1997, 2000, 2001a,b; Charnov *et al.*, 2001). Here also enters α, the age of first reproduction, since things like body size (m) depend upon α. The optimal life history adjusts some life-history variables (i.e. α) in the face of trade-offs with others (we set $\partial R_0/\partial$ [somethings] = 0). If we wish to predict dimensionless numbers such as $C \cdot E$, E/α or I/m, the resulting formulae can only contain other dimensionless numbers. *If $C \cdot E$ and E/α are invariants across species, then it is likely that the dimensionless numbers that characterize the trade-offs are also invariants.* Thus, the dimensionless approach to life histories looks for *invariants* in the *outward life history* (e.g. $C \cdot E$, E/α) and in the *trade-offs* that generate the set of optimal life histories (Charnov, 1993, 2000, 2001a,b; Charnov *et al.*, 2001).

It will be useful to illustrate this with a life-history evolution model for indeterminate growers like fish (Charnov *et al.*, 2001). Suppose (Fig. 2) body size growth follows some particular function of body mass, m_x, prior to the age (size) of first reproduction (α, m_α) when some constant fraction (C) of m_x is then given to reproduction; the growth rate follows the hatched area in Fig. 2. The average adult size (m, equation 4) will thus be a function of α (m_α), adult survivorship, and C. Suppose survivorship follows Fig. 3; $Z(x)$ is high at small x, but drops to some constant value (Z) prior to feasible ages of first reproduction. The adult Z is assumed to be independent of C; these Z and C assumptions are justified in Charnov *et al.* (2001). R_0 (equation 7) may be written as:

$$R_0 = \frac{1}{2} \cdot e^{-\int_0^\alpha Z(x)dx} \cdot C \cdot m \cdot \left[\frac{1}{I \cdot Z}\right] \qquad \text{since } E = 1/Z$$

$$\log_e R_0 = \log_e \left(\frac{1}{2 \cdot I \cdot Z}\right) + \log_e C + \log_e m - \int_0^\alpha Z(x)dx$$

The optimal α (m_α) and C are found by setting $\partial \log_e R_0/\partial \alpha = 0$ and $\partial \log_e R_0/\partial C = 0$ (in this procedure, we assume $C \cdot m_\alpha$ takes on a value less than 100% of production (Fig. 2); otherwise, growth will cease at age α and $m_\alpha = m$).
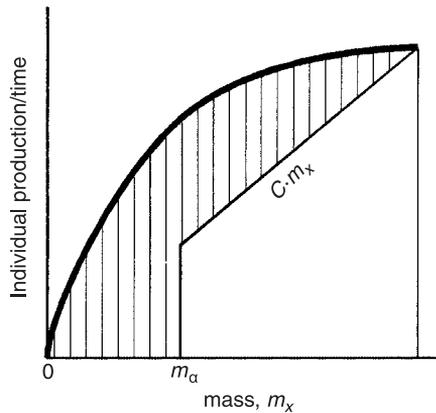
$$0 = \frac{\partial \log_e R_0}{\partial \alpha} \Rightarrow \frac{\partial \log_e m}{\partial \alpha} = Z \Rightarrow \frac{1}{Z} = E = \left(\frac{\partial \log_e m}{\partial \alpha}\right)^{-1}$$

$$0 = \frac{\partial \log_e R_0}{\partial C} = \frac{1}{C} + \frac{\partial \log_e m}{\partial C} \Rightarrow C = -\left(\frac{\partial \log_e m}{\partial C}\right)^{-1}$$

These equations allow us to solve for the optimal α (or m_α) and C, and they summarize the effects of α and C on the percent change on the average adult size, m.

We can easily write these conditions in terms of our two dimensionless benefit–cost ratios (E/α, C/E^{-1}):

$$\frac{E}{\alpha} = \left(\frac{1}{\alpha}\right)\left(\frac{1}{\frac{\partial \log_e m}{\partial \alpha}}\right) = \left(\frac{\partial \log_e m}{\partial \log_e \alpha}\right)^{-1}$$

Fig. 2. A model for indeterminate growth. Before age α, growth follows the production relation (bold line). After α, $C \cdot m_x$ of production is given to offspring, so growth rate is the hatched area. Thus the average adult size, m (equation 4), depends on α, C and the adult mortality schedule.
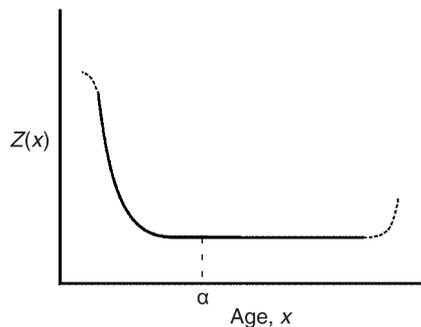
Fig. 3. The mortality rate, $Z(x)$, assumption. Early in life, $Z(x)$ is high, but it drops to some constant value (Z) prior to feasible ages of first reproduction. $Z(x)$ is also assumed to be density dependent early in life and $Z(x)$ may go up late in life, due to senescence. $Z(x)$ is also assumed to not change with C, the reproductive allocation.

$$C \cdot E = \left(\frac{\partial \log_e m}{\partial \alpha} \right)^{-1} \cdot \left(\frac{\partial \log_e m}{\partial C} \right)^{-1}$$

If E/α and $C \cdot E$ are to be invariants across absolute magnitudes in (say) fish, the underlying similarities are in how α and C impact relative growth rate in terms of the average adult size, m. Charnov *et al.* (2001) discuss a specific, and plausible, growth model (dm_i/dt) that yields invariant E/α and $C \cdot E$ values of the fish magnitude ($E/\alpha \approx 0.5$, $C \cdot E \approx 0.6$).

OPTIMAL SIZE OF AN OFFSPRING AND $C \cdot E$

I suspect that I/m is the least invariant number within taxa (excepting altricial birds) because optimal offspring size is often independent of the total resource to be divided up among offspring (Smith and Fretwell, 1974; Charnov and Downhower, 1995) and more dependent upon the survival/growth environment for the offspring, an environment that may be rather unlike that of the adult.

The classic model for optimal offspring size is that of Smith and Fretwell (1974). S is considered to be a function of I as in Fig. 4, and the optimal I ($= I^*$) is where $\partial S/\partial I = S/I$. This model is easily extended to include a density-dependent component to S (Charnov, 1993: 107; 1997) with the same result; after all, the I^* is not affected by any multiplier of the $S(I)$ function. Return to equation (7) and rewrite it as:

$$\frac{S}{I} = \left[\frac{2R_0}{C \cdot E} \right] \cdot m^{-1}$$

Set $R_0 \approx 1$ and assume I^* is the offspring size; then:

$$\frac{\partial S}{\partial I^*} = \left[\frac{2}{C \cdot E} \right] \cdot m^{-1}$$

The slope of the trade-offs function, $S(I)$ at I^*, is predicted to be inversely proportional to the average adult body mass (m) among species with the same $C \cdot E$ value; indeed, $2/C \cdot E$ is the proportionality constant. This extends a result first hinted at in Charnov (2001b) and links the $C \cdot E$ number to the classic Smith–Fretwell idea. Since $C \cdot E \approx 0.6$ for fish and ≈ 1.7 for mammals, $\partial S/\partial I \approx 3.3 \ m^{-1}$ for fish and $\approx 1.2 \ m^{-1}$ for mammals (predicted). These $\partial S/\partial I$ predictions have yet to be tested for any animals (Charnov, 2001b). Note that S/I is itself a benefit (S)/cost (I) ratio: S survival per offspring achieved at a cost of I resources per offspring. Note that, at a fixed body mass (m), fish, with tiny eggs, are predicted to be almost three times (3.3/1.2) more efficient at offspring production (S/I, $\partial S/\partial I$) than mammals with $I/m \approx 0.3$. S/I and R/E^{-1} were introduced earlier (Charnov, 2001b) as useful dimensional benefit–cost ratios.

DISCUSSION

Consider Fig. 5, where life histories are represented in an cube with edges $C \cdot E$, E/α and I/m; I have placed fish, mammals and altricial birds in their *approximate* locations, and the birds define the present limits of the $C \cdot E$ and E/α values. This visualization immediately suggests a series of questions: Are large parts of the cube unoccupied? Are only certain locations
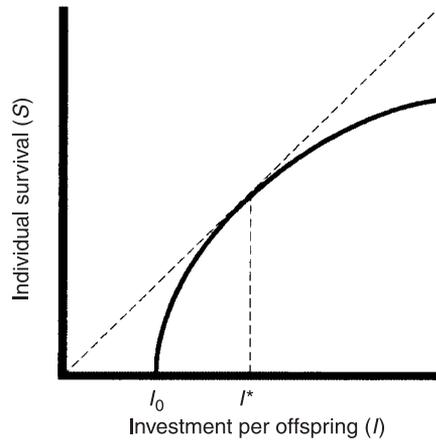
Fig. 4. Survival of an offspring to adulthood (S) increases with the resources invested in the offspring (I). The optimal offspring size is I^*, where a ray from the origin is just tangent to the trade-off curve ($\partial y/\partial x = y/x$).
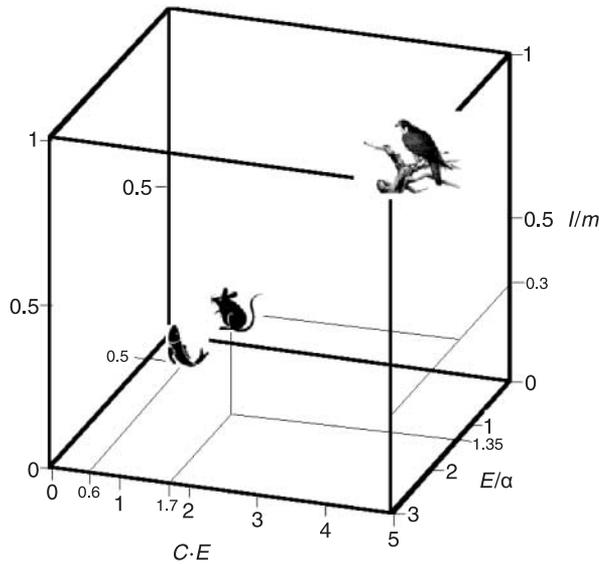
Fig. 5. The life-history cube. The dimensionless axes are (1) relative size of an offspring (I/m), (2) reproductive effort (C) per unit of adult mortality (E^{-1}), and (3) reproductive life span (E) over time to reach adulthood (α). Altricial birds, mammals and fish are placed in their approximate locations.

occupied, or is the occupied region a nearly one- or two-dimensional object? Why? One constraint here is that S is probably held < about 0.5, so $R_0 \approx 1$ places restrictions on I/m and $C \cdot E$ (equation 8). And then there are more specific questions: Where are bats, mammals with $I/m \approx 1$? Or, where are precocial birds, which have I/m very small? Where are vascular

plants, which have tiny I/m, but also may have density dependence throughout the life history (and how do we accommodate asexual reproduction or even hermaphroditism as opposed to dioecy)? And, finally, there are questions that relax the invariance notion of $C \cdot E$ or E/α; many, if not most, aspects of life history are somewhat plastic (e.g. norms of reaction for age/size at maturity; Stearns, 1992). Do plastic responses move life histories within a taxon all over the cube, or are the responses themselves confined to certain regions of the cube?

This classification scheme for life histories differs from those such as 'r- and K-selection' or the 'triangular-life-history-continuum' (both discussed in Pianka, 2000: 186–187) in that these other schemes invariably use axes with dimensional magnitudes such as time or mass. Elephants and squirrels are at opposite poles in these schemes, and the suggestion is made that natural selection operates in fundamentally different ways when we contrast them (opportunistic *vs* equilibrium, for example; many more contrasts are discussed in Pianka, 2000). But when we remove absolute magnitude for time and mass, squirrels and elephants look a lot alike, and look different from fish or altricial birds. Selection may well operate similarly on squirrel and elephant life histories in the sense that R_0 is fitness and the trade-offs have the same dimensionless features. My working hypothesis (Charnov, 1993, 2000, 2001a; Charnov *et al.*, 2001) is that the trade-off features are the same *within* (say) altricial birds, mammals or indeterminate growers like fish, with major differences *between* these groups; the 'differences between' generate the distribution shown in Fig. 5.

I assume non-growing populations (i.e. $R_0 \approx 1$) but, if one wishes, the scheme could be extended to growing populations; here the stable age distribution plays the probability density role that the l_x schedule plays for the non-growing case, and the intrinsic rate of increase, with units of 1/time, is an additional necessary number (Charnov, 1993: 137).

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