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The optimal balance between growth rate and survival in mammals

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ABSTRACT

Evolutionary theory for life-history allometry in mammals is extended to include a trade-off between growth rate (or offspring production rate) and life span. The optimal balance between the two maximizes the product of the 'height of the growth curve' multiplied by the 'average adult life span'. This product rule implies that longer-lived organisms are more efficient at using resources to prolong life.

Keywords: allometry, life histories, life span, product rule, reproductive effort.

INTRODUCTION

Average adult life span (E) and age-at-maturity (α) show quarter-power allometries with female body mass (m) across typical mammal species; primates also show quarter-power scalings, but the log–log lines are displaced upwards compared with typical mammals (Millar and Zammuto, 1983; Charnov, 1991, 1993, 2001; Charnov and Berrigan, 1993; Purvis and Harvey, 1995). So both groups show E and α proportional to $m^{0.25}$, while they differ in the proportionality constant, which is bigger for primates. Both groups also show approximately −0.25 scaling for the number of offspring produced per year (b) and the primate line is displaced downwards (Charnov, 1993; Charnov and Berrigan, 1993; Alvarez, 2000). Over the last dozen years, beginning with Charnov (1991), evolutionary life-history theory (Stearns, 1992; Charlesworth, 1994) has been asked to reproduce these (and other) scaling rules, under the assumption that each species in the data set is at an optimum of fitness in the face of *specified* trade-offs (Charnov, 1993; Kozlowski and Weiner, 1997). While life-history theory admits a vast array of *possible* trade-offs (Stearns, 1989, 1992), only some forms may produce the appropriate quarter-power scalings across species.

In the original 1991 theory, the size of an offspring (m_0) at independence from the mother and the 'height' (A) of the maternal growth/offspring-production curve (see equation 1 below) were assumed not to be adjusted by natural selection, and empirical values were simply 'plugged in'. In this paper, I model the evolutionary adjustment of A. It is assumed widely by life-history workers that individual production rates (body size growth and offspring production) and mortality rates are positively related in a within-species trade-off (e.g. Williams, 1966; reviewed in Stearns, 1992); mortality can be lowered by the diversion of resources that otherwise could fuel greater personal production/reproduction. In this paper, I ask how this trade-off can be added to existing evolutionary life-history theory in a way that preserves the allometry across species.

Assume that individual production of mass (m) follows the differential equation:

$$\frac{\mathrm{d}m}{\mathrm{d}t} = A \cdot m^{0.75} \tag{1}$$

If growth ceases at adulthood and time zero is at independence from the mother (size m_0), the size reached at the age of first breeding (α) is found by integrating equation (1) from zero to α. This yields:

$$m(\alpha)^{0.25} = 0.25 \cdot A \cdot \alpha + m_0^{0.25} \tag{2}$$

If we set $\delta = m_0/m(\alpha)$, equation (2) can be written as

$$\alpha = \frac{(1 - \delta^{0.25})}{0.25 \cdot A} \cdot m(\alpha)^{0.25} \tag{3}$$

a quarter-power allometry of α versus $m(\alpha)$ for a group of species with the same (similar) A and δ. Indeed, δ is known to be approximately constant ($\approx 1/3$) across mammal species (body sizes) (Charnov, 1991), while A is likewise constant; of course, A is much larger for typical mammals than primates (about 2–3 times), which causes *upward* adjustment in the primate line (Charnov and Berrigan, 1993).

WHAT SETS A (AND α)?

What would happen if we allow a female to lower production at any size (lower A in equation 1) to achieve a lower yearly mortality rate? Note that we are not allowing the female to change A on an age-by-age (size) basis; we still require her to use equation (1) over her entire life history, and thus we enforce the quarter-power allometry of equation (3). Let Z be the adult instantaneous mortality rate, so survival for one year is e^{-Z}, and the average adult life span E is $1/Z$. Consider the following principle: at any single size, all mammal species are allowed the same maximum production rate (i.e. $\mathrm{d}m/\mathrm{d}t = A_{\max} \cdot m^{0.75}$). The species differ from each other in how A declines with declining Z. In Fig. 1, the two species have the same $\mathrm{d}m/\mathrm{d}t = A \cdot m^{0.75}$ at high Z, because here they both have $A = A_{\max}$, but at lower Z species 1 can maintain the higher A values. Both can lower mortality (make Z smaller) by allocating away from growth (lower A), but they are on different trade-off curves; species 1 could achieve the much longer life span by allocating almost all resources to mortality reduction ($Z_1 \rightarrow Z_{01}$ as $A \rightarrow 0$ versus $Z_2 \rightarrow Z_{02}$ here). I suggest that Fig. 1 represents a very natural way to implement a growth rate/mortality rate trade-off. Growth rate at any size ($\mathrm{d}m/\mathrm{d}t = A \cdot m^{0.75}$) can be lowered to decrease mortality (Z), with the various species differing in the shape of this relation (1 *vs* 2 in Fig. 1). To determine the *optimal balance* between growth rate (A) and mortality rate (Z), we now cast fitness optimization in terms of the joint evolution of A versus Z, and the age-of-first-reproduction, α.

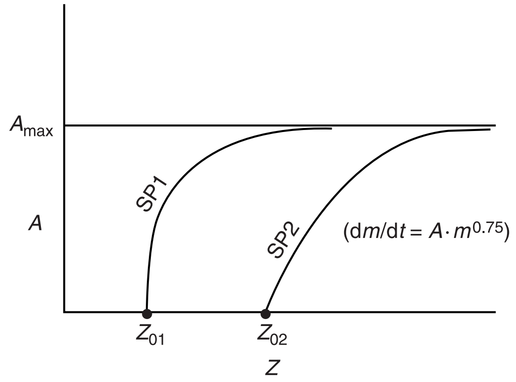

Fig. 1. Mortality rate (Z) can be lowered by allocating resources away from personal production (i.e. lowering $dm/dt = A \cdot m^{0.75}$ by lowering A). Two species are illustrated here, with different trade-off curves; however, the species are assumed to have the same *maximum* production (i.e. the same A_{max}). This figure shows adult mortality; lowering A will be assumed to lower $Z(x)$ also at earlier ages.

OPTIMAL α (m_α)

For a non-growing population, the average number of offspring (daughters, with a 1 : 1 sex ratio) produced over a female's life span, the net reproductive rate (R_0), is a measure of her lifetime fitness (Charnov, 1993). R_0 can be written as (Charnov, 1993, 1997)

$$R_0 = \frac{S \cdot b}{Z} \tag{4}$$

where S = chances of surviving to age α and b = yearly offspring production (to weaning, size m_0). We may write S as

$$S = e^{-\int_0^\alpha Z(x)dx} \tag{5}$$

where $Z(x)$ is the age (x) specific instantaneous mortality rate (see Fig. 2). Since the use of R_0 as a fitness measure requires a non-growing population, $R_0 \approx 1$ and this is enforced by

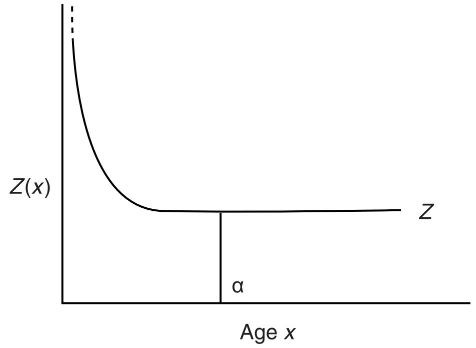

Fig. 2. A mortality rate assumption. $Z(x)$ is the instantaneous mortality rate at age x, and is assumed to reach a low and constant value (Z) prior to α, the age at first reproduction. Density dependence, necessary to make $R_0 = 1$, affects $Z(x)$ for only small x (dashed line).

Fig. 2, making very early mortality ($x \to 0$) density-dependent. Note further (see Fig. 2) that $Z(x)$ is assumed to be high at first, but to bottom out prior to feasible α.

Assuming offspring at independence are of some fixed size (m_0), $b \propto \mathrm{d}m/\mathrm{d}t$, since offspring production is simply diverted self-growth by the mother ($\mathrm{d}m/\mathrm{d}t$; Charnov, 1991, 1993). Thus, $b = Q \cdot A \cdot m(\alpha)^{0.75}$, where Q is a proportionality constant. Using equation (2), b may thus be written as:

$$b = Q \cdot A\,[0.25 \cdot A \cdot \alpha + m_0^{0.25}]^3 \tag{6}$$

Using equations (5) and (6), R_0 (equation 4) may be written as:

$$\ln R_0 = -\int_0^{\alpha} Z\,(x)\,\mathrm{d}x - \ln Z + \ln Q + \ln A + 3\ln(0.25 \cdot A \cdot \alpha + m_0^{0.25}) \tag{7}$$

The optimal life history sets $\partial \ln R_0/\partial\alpha = 0$ and $\partial \ln R_0/\partial A = 0$. Consider the first (recall Fig. 2 and equation 2):

$$0 = \frac{\partial \ln R_0}{\partial \alpha} = -Z(\alpha) + \frac{3(0.25 \cdot A)}{0.25 \cdot A \cdot \alpha + m_0^{0.25}} \tag{8a}$$

$$(\text{adult } Z =)\ Z(\alpha) = 0.75 \cdot A \cdot m\,(\alpha)^{-0.25}$$

or

$$\frac{1}{Z} = E = 1.33 \cdot \frac{1}{A} \cdot m(\alpha)^{0.25} \tag{8b}$$

Equation (8) means that average adult life span (E) will scale with $m^{0.25}$ among species with the same (similar) A value. So we need the same A for *this* allometry to hold also (recall the α allometry requires the same A *and* δ). This is the same result as in the 1991 theory. Note that the optimal $m(\alpha)$ is independent of m_0, and only dependent upon Z near α.

OPTIMAL *A* (OR *Z*)

So, what about $\partial \ln R_0/\partial A = 0$? Return to equation (7) and assume that $Z(x)$ is really $Z(x, A)$ and thus changing A also changes the immature Zs. Our assumption is shown schematically in Fig. 3. From equation (7), with $Z(x) = Z(x, A)$, we have:

$$\frac{\partial \ln R_0}{\partial A} = 0 = -\int_0^{\alpha} \frac{\mathrm{d}Z(x)}{\mathrm{d}A}\,\mathrm{d}x - \frac{\mathrm{d}Z}{\mathrm{d}A}\frac{1}{Z} + \frac{1}{A} + \frac{0.75 \cdot \alpha}{0.25 \cdot A \cdot \alpha + m_0^{0.25}}$$

The simplest assumption for $\mathrm{d}Z(x)/\mathrm{d}A$ is that they are constant with respect to x ($= \mathrm{d}Z/\mathrm{d}A$), as shown in Fig. 3; I use that assumption here (but see Discussion). Thus:

$$\frac{\mathrm{d}Z}{\mathrm{d}A}\left[\alpha + \frac{1}{Z}\right] = \frac{1}{A}\left[1 + \frac{0.75 \cdot \alpha \cdot A}{m^{0.25}}\right]$$

Recall from equation (3) that

$$\alpha \cdot A = 4(1 - \delta^{0.25})m^{0.25}$$

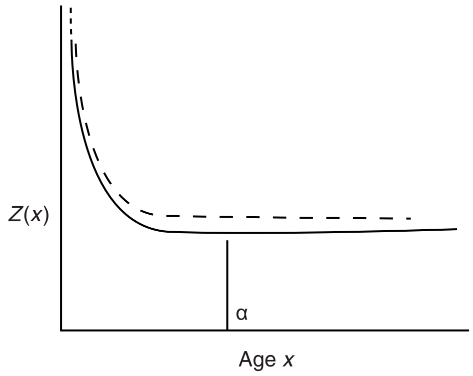

Fig. 3. Changing A is assumed to change Z at all ages (except near $x = 0$); the dashed $Z(x)$ curve is the Z curve associated with a slightly higher A value (higher production increases mortality). The assumption used here is that $\mathrm{d}Z(x)/\mathrm{d}A$ is a constant all along the $Z(x)$ curve.

so the above becomes, after multiplying by Z:

$$\frac{\mathrm{d}Z}{\mathrm{d}A}[\alpha \cdot Z + 1] = \frac{Z}{A}[1 + 3(1 - \delta^{0.25})]$$

Finally, note that equations (3) and (8) together imply that $\alpha \cdot Z = 3(1 - \delta^{0.25})$. Thus, the above becomes:

$$\frac{\mathrm{d}A}{\mathrm{d}Z} = \frac{A}{Z} \tag{9}$$

Equation (9) finds the optimal balance between A and Z; *it is the maximum of* A/Z. For this optimization to result in the same A value for a collection of species with the same $A_{\max}$, trade-off curves further out on the z axis must have *lower slopes*, illustrated in Fig. 4. The caption to Fig. 4 discusses this slope requirement in terms of a useful parametric form for the trade-offs, the negative exponential.

OPTIMAL *A*, ANOTHER WAY

Note that $1/Z = E$, the average adult life span, so maximizing A/Z is equivalent to *maximizing the product* $A \cdot E$, or $\ln A + \ln E = P$ and

$$0 = \frac{\mathrm{d}P}{\mathrm{d}A} = \frac{1}{A} + \frac{1}{E}\frac{\mathrm{d}E}{\mathrm{d}A} \qquad \text{or} \qquad \frac{-\,\mathrm{d}E}{\mathrm{d}A} = \frac{E}{A} \tag{10}$$

$-\,\mathrm{d}E/\mathrm{d}A$ is the marginal increase in life span (E) achieved by investing in life-sustaining, as opposed to growth, activities. Equation (10) says that, at the optimal A, this marginal gain will be proportional (A^{-1} times . . .) to life span (E) itself, so that longer-lived organisms are more efficient at prolonging life. Since primates have A values half or less the A value for typical mammals (Charnov and Berrigan, 1993), they are roughly twice as efficient at prolonging life in the sense of equation (10).

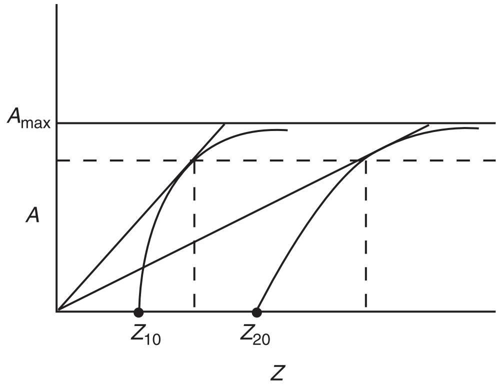

Fig. 4. The optimal balance between A and Z is where $dA/dZ = A/Z$, the maximum of A/Z (or $A \cdot E$). For this maximum to result in the same A value for a collection of species with different trade-off curves (i.e. different Z_0 values, but the same A_{max} value), the curves further out on the Z axis must have lower slopes; here I show this for two species.

One useful parametric form for these trade-off curves is a negative exponential:

$$A = A_{max}\,[1 - e^{-K[Z - Z_0]}] \tag{10}$$

where the coefficient K controls the rise to the A_{max} value; smaller K gives a smaller slope. The optimal (A, Z_{opt}) is where $A/Z = dA/dZ$ or:

$$(1 - e^{-K(Z - Z_0)}) = Z \cdot K \cdot e^{-K(Z - Z_0)}$$

Note that a collection of species with the same dimensionless number $K \cdot Z_0$ will share the same dimensionless $Z_{opt} \cdot K$ value, thus the same $1 - e^{-K \cdot Z_{opt} + K \cdot Z_0}$, and thus *the same A value*. The trade-off shape parameter $K \cdot Z_0$ is thus predicted to be the same (similar) for all typical mammals.

There is one sense in which equation (10) implies that all mammals have about the same efficiency in extending life. Rewrite equation (10) as

$$-\frac{dE/E}{dA/A} = 1 \qquad \text{or} \qquad \frac{d\ln E}{-\,d\ln A} = 1$$

Note that this means (Charnov, 1997) a 1% *decrease* in A results in a 1% *increase* in E for any E and A values.

DISCUSSION

In the Introduction, I noted that A for primates was only about half the value of A for more typical mammals. With reference to Fig. 4, this could be achieved in one of two ways. First, primates could have a lower A_{max} value, perhaps because their larger brains imply a greater diversion from personal growth (Charnov and Berrigan, 1993). Alternatively, primates could have the same A_{max} as other mammals, but have trade-off curves with shallower slopes. I am unsure which of these is more likely.

Nothing in the formalism indicates where the trade-off curves come from; why species 1 versus species 2 in Fig. 1? In the 1991 theory, I put Z (there called M) and A in the model from outside; the present effort puts the *A–Z function* in from outside. The advantage of the present approach is that we can predict something about the *shapes* of the trade-off curves under the requirement that the optimal balance result is the same (similar) A for all species (Fig. 4).

In one sense, the trade-off assumed here is the classic reproductive effort trade-off (e.g. Stearns, 1992), since mortality decreases if less is given to reproduction. Note, however, that the trade-off is better described as a production rate trade-off (self *and* offspring).

Finally, the derivation leading to equation (9), the result in Fig. 4 (max A/Z), assumes that $dZ(x)/dA$ is the same value at all x ($= dZ/dA$, the adult derivative); this allows us to work with the adult Z versus A trade-off curve (Figs 1 and 4). Of course, other assumptions are possible for how changing A impacts $Z(x)$ before adulthood. It would be worthwhile to study them to see how robust the maximization principle proposed here is (max $A \cdot E$).

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