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ABSTRACT

Question: What is the effect of within-species size dependence of mortality on the between-species allometries for maturation and adult life span?

Mathematical methods: Optimization of net-reproductive rate, R_0, with respect to adult mass, m_α.

Key assumptions: Instantaneous mortality at age x, size m_x, is proportional to m_x^{-h}, and this assumption is added to the Charnov (2001) mammal life-history model.

Results: h in the range of zero to 0.20 has a very small (≈ 10–15%) effect on the heights of the allometries.

Keywords: allometry, life span, maturation, optimization, sensitivity analysis.

INTRODUCTION

It is widely accepted that for mammals across-species plots of life-history variables, such as average adult life span (E) and age-of-first-birth (α), versus adult female mass (m_α) are *linear* on a log/log scale with slopes of $\approx \frac{1}{4}$. The best data set for α and E is that compiled by Purvis and Harvey (1995), plotted in Figure 1 of Charnov (2001). With both variables scaling as $m_\alpha^{0.25}$ their ratio is, of course, invariant, and $E/\alpha \approx 1.43$ for mammals. This paper extends my earlier work (Charnov, 1991, 1993, 2001) to ask again what meaning can be attached to the existence of quarter-power allometries across mammal species. This paper allows sigmoid growth in body mass and allows mortality rates to be size dependent. Kozlowski and Weiner (1997) criticized my earlier work for ignoring sigmoid growth and the (possible) size dependence of mortality rates. The present paper looks at both of these features and asks for the resulting optimal life histories to satisfy 0.25 allometries (and invariance in the E/α number).

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INDIVIDUAL GROWTH

Accepting that growth is sigmoid, what functional form is appropriate? West *et al.* (2001) have proposed a new body-size growth equation that derives net production of mass from the first principles of energy intake minus maintenance and activity costs. Their argument leads to an equation for change-in-mass (prior to reproduction) of the form $dm/dt = a \cdot m^{0.75} - b \cdot m$, where a is expected to be *similar* for species with similar metabolic scaling (i.e. within mammals). b is equal to the maintenance metabolic rate per existing body cell divided by the cost of building a new cell. This equation excludes reproductive allocation and would result in sigmoid growth to an asymptotic size ($M = (a/b)^4$), as shown in Fig. 1. There is a fastest growth rate, an inflection point, at $0.316 \cdot M$ (which is $(0.75)^4$). Nothing precludes an adult size (m_a) well before the asymptotic size (M), so the size at the inflection point, relative to adult size, tells us where the adult size (m_a) is relative to M: if $m_a = \mu \cdot M$, then the size at fastest growth (m_i) is where $m_i/m_a = (0.316/\mu)$. μ will play a special role in the new life-history model, since 0.25 allometries will require it to be invariant across mammal species.

AVERAGE ADULT LIFE SPAN (*E*)

Average adult life span (E) often scales with the 0.25 power of adult body mass (m_a) in across-species plots. Various taxa (e.g. primates, more typical mammals) differ in the height (intercept) of the allometry, but not the slope; and the height is (roughly) inversely proportional to the height of the individual production or body-size growth relation. For example, primates grow at only about a half to a fourth the rate of typical mammals of the same body size, and their life spans are two to four times as great (Charnov, 1993). Suppose individual production follows West and colleagues' (2001) equation:

$$\frac{dm}{dt} = a \cdot m^{0.75} - b \cdot m \tag{1}$$
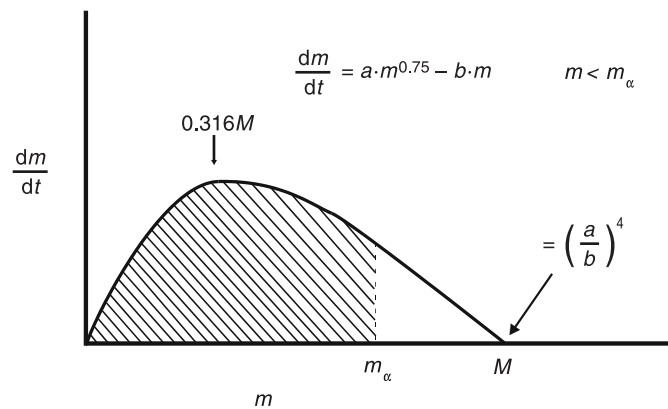
Fig. 1. Schematic diagram of the growth model (dm/dt, m = mass). Growth follows the domed curve until size-at-reproduction (m_a). Asymptotic size ($dm/dt = 0$) is at $M = (a/b)^4$, while the fastest growth rate (m_i at max dm/dt) is at $0.316M$, so that m_i relative to m_a tells us the m_a/M ratio, too. m_a/M is called μ in the text.

where a is the height of the growth curve. Equation (1) determines individual growth, and at the onset of reproduction at age α (size m_α), $c \cdot a \cdot m_\alpha^{0.75}$ determines offspring production (i.e. $c \cdot a \cdot m_\alpha^{0.75}$ is available per unit time to grow offspring); this offspring production function is developed in great detail in Charnov (2001). Growth ceases at α, so m_α is the adult size.

Further suppose that the instantaneous mortality rate (Z_x) at any age (x) is strictly a function of body mass (m_x), excepting during a small time period early in life when density dependence operates.

$$Z_x = k \cdot m_x^{-h} \qquad \text{or} \qquad E = 1/Z_\alpha = \frac{1}{k} \cdot m_\alpha^h \tag{2}$$

Let us suppose that if offspring are of some fixed size (m_0), fitness is the number produced over an individual's life span (R_0) (Charnov, 1993, 1997):

$$R_0 = \frac{S \cdot E}{m_0} \cdot c \cdot a \cdot m_\alpha^{0.75} \tag{3}$$

where S = the chance of living to age α, when $c \cdot a \cdot m_\alpha^{0.75}$ mass is given to reproduction per year, for E years.

$S = H \cdot e^{-\int_0^\alpha Z(x)dx}$, which can be expressed as $S = H \cdot e^{-\int_0^{m_\alpha} \frac{Z(m)}{a \cdot m^{0.75} - b \cdot m} dm}$. H is the probability of surviving to the end of the (short) density-dependent time interval. Thus, R_0 is equal to:

$$R_0 = H \cdot e^{-\int_0^{m_\alpha} \frac{k}{a \cdot m^{(0.75+h)} - b \cdot m^{(1+h)}} dm} \cdot \left(\frac{c \cdot a \cdot m_\alpha^{0.75}}{k \cdot m_\alpha^{-h} \cdot m_0} \right)$$

The optimal m satisfies $\partial \ln R_0 / \partial m_\alpha = 0$ and yields the rule (evaluated at m_α):

$$Z_\alpha + (0.75 + h)b = \alpha(0.75 + h)m_\alpha^{-0.25} \tag{4}$$

We want E to scale with $m_\alpha^{0.25}$ (or $1/E = Z_\alpha$ to scale with $m_\alpha^{-0.25}$) *and* the height of the E versus m_α curves to be inversely proportional to a, the height of the growth curve. This will happen if all species in the data set share the same a and h values, and b is proportional to the adult mortality rate Z_α:

$$b = q \cdot Z_\alpha \tag{5}$$

Equation (4) then becomes $Z_\alpha [1 + (0.75 + h)q] = a(0.75 + h)m_\alpha^{-0.25}$.

$$E = 1/Z_\alpha = \left[\frac{1 + (0.75 + h)q}{0.75 + h} \right] \left[\frac{1}{a} \right] m_\alpha^{0.25} \tag{6}$$

[Since q will be near 15 (see below), this scaling rule is very insensitive to h values up to (say) 0.2.]

AGE-AT-FIRST-BREEDING

Age-at-maturity (α) also shows a 0.25 allometry with adult mass; the height of the allometry is again *inversely* proportional to a (Charnov, 1993). Equation (1) may be integrated from size ≈ 0 at $t = 0$ to give (integration hint: set $y = m^{0.25}$ and work in y; t and y can now be separated):

$$\alpha = \left[\frac{-\ln(1 - \mu^{0.25})}{\mu^{0.25}} \right] \left[\frac{4}{\alpha} \right] m_\alpha^{0.25} \tag{7}$$

where $\mu^{0.25} = (m_a^{0.25}/a) \cdot b$; μ is the adult size (m_a) as a proportion of the asymptotic size $[(a/b)^4]$. $\mu \approx$ constant is required for α to show a 0.25 scaling with m_a across species with the same a value.

TWO DIMENSIONLESS RULES AND A SENSITIVITY ANALYSIS

Note that since $\mu^{0.25} = \dfrac{m_a^{0.25} \cdot b}{a}$ and $b \cdot E = q$ (equation 5), equation 6 may be rewritten as:

$$\left[\frac{1 + (0.75 + h)q}{0.75 + h} \right] = \frac{q}{\mu^{0.25}} \tag{8}$$

Equations (6) and (7) may be combined to eliminate body mass and a:

$$\frac{4 \cdot E}{\alpha} = \left[\frac{1 + (0.75 + h)q}{0.75 + h} \right] \left[\frac{\mu^{0.25}}{-\ln(1 - \mu^{0.25})} \right] \tag{9}$$

Equations (8) and (9) have two very interesting implications. First, q is a unique function of μ for any E/α value; it is

$$q = \frac{4 \cdot E}{\alpha} [-\ln(1 - \mu^{0.25})] \tag{10}$$

and equation (8) may then be solved for the associated h:

$$h = \frac{\mu^{0.25} + 0.75q\mu^{0.25} - 0.75q}{q(1 - \mu^{0.25})} \tag{11}$$

$h = 0$ in the 2001 model so that equations (10) and (11) may be solved for q and μ for the observed E/α (≈ 1.43); this results in $q \approx 14.3$ and $\mu \approx 0.7$ (Figure 5 in Charnov, 2001). Obviously, a positive h will increase μ (i.e. begin reproduction at a larger relative size). Now, set $E/\alpha = 1.43$ and $\mu = 0.8$, solve equation (10) for $q = 16.65$, and then use the μ, q pair in equation (11) to solve for $h = 0.18$. Similarly, h would have to be near 0.5 to push μ up to 0.85. Recall that $\mu = 0.7$ results in the inflection point for growth being at 45% the adult mass (0.316/0.70); if $\mu = 0.8$, the inflection point is at 39.5% the adult size (0.316/0.80), a 12% drop. $\mu = 0.85$ makes the inflection point at 37% the adult size, a 17% drop; h this high (≈ 0.5) would have been observed long ago in data sets, so it is difficult to believe that h is bigger than, say, 0.2. But, this means that *size dependence of mortality ($h \leq 0.2$) would seem to have a potentially very small effect on the optimal μ*. Indeed, as noted earlier for the E scaling (equation 6), h of this magnitude should likewise have a very small ($< 10\%$) effect on the height of the E allometry. Similarly, changing h from zero to 0.2 alters the height of the α allometry (equation 7) by about 15%.

DISCUSSION

Charnov (2001) discusses why b/Z_a may be expected to be a constant across species, and develops a model for the joint evolution of b and Z_a; a similar argument may be applied to the joint evolution of b and the $Z(m)$ function here. Perhaps the most interesting aspect of adding Z as a function of m is how small the effect is on μ, or the height of E or α allometries (10–15% change as h goes from zero to 0.20).

REFERENCES

Charnov, E.L. 1991. Evolution of life history variation among female mammals. *Proc. Natl. Acad. Sci. USA*, **88**: 1134–1137.

Charnov, E.L. 1993. *Life History Invariants*. Oxford: Oxford University Press.

Charnov, E.L. 1997. Trade-off invariant rules for evolutionarily stable life histories. *Nature*, **387**: 393–394.

Charnov, E.L. 2001. Evolution of mammal life histories. *Evol. Ecol. Res.*, **3**: 521–535.

Kozlowski, J. and Weiner, J. 1997. Interspecific allometries are by-products of body size optimization. *Am. Nat.*, **149**: 352–380.

Purvis, A. and Harvey, P.H. 1995. Mammal life history evolution: a comparative test of Charnov's model. *J. Zool.*, **237**: 259–283.

West, G.B., Brown, J.H. and Enquist, B.J. 2001. A general model for ontogenetic growth. *Nature*, **413**: 628–631.