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## Evolution of mammal life histories

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### ABSTRACT

If we assume that adult life span and age-at-maturity are described correctly by quarter power allometries across (typical) mammal species, we are tempted to look for some fundamental explanation. The explanation must acknowledge that within-species growth is sigmoid and not a power function at all, and that natural selection probably sets the age at maturity in the face of externally imposed mortality, while also allowing some mortality adjustment due to internal factors. This paper develops hypotheses to account for the above scaling rules and it predicts the numeric values of several new dimensionless numbers that interrelate growth, mortality and investment in cellular maintenance.

*Keywords:* allometry, dimensionless life histories, scaling rules, stationary populations.

### INTRODUCTION

It is widely accepted that across-species plots of life-history variables, such as adult life span ( $Z^{-1}$ ), age-of-first birth ( $a$ ) and yearly mass devoted to reproduction versus adult female mass ( $m$ ), are *linear* on a log/log scale with slopes of  $\approx 1/4$  (life span, maturation age) or  $\approx 3/4$  (mass to reproduction). The best data set for  $a$  and  $Z$  is that of Purvis and Harvey (1995); Fig. 1 shows the results. Body mass is measured with much less error than either life span or maturation age, so type I regression is used with species treated as data points. With both variables ( $y_i$ ) scaling as  $m^{0.25}$ , their ratio is, of course, invariant, as shown in Fig. 1c. (These plots exclude known atypical mammals – bats and primates – although Fig. 1c would be the same with them included.)

This paper extends my earlier work (Charnov, 1991, 1993) to again ask what meaning can be attached to the existence of quarter power allometries (Fig. 1a,b) across mammals species. Kozlowski and Weiner (1997) suggested that the plots of Fig. 1 contain no particularly basic information about the forces that structure mammal life histories and that, indeed, the 0.25 exponent has no fundamental meaning. Kozlowski's own approach to plots like Fig. 1 involves life-history evolution modelling with a large number of adjustable parameters. While I appreciate Kozlowski's thoughtful criticism of my original, perhaps overly simplistic, mammal life-history model, his own strikes me as both too complex and

arbitrary; I think we must take seriously the quarter power allometries and invariance in  $a \cdot Z$  (Fig. 1), and we must examine more deeply the structure of body size growth, mortality and other aspects of physiology in the hope that good biological reasons exist for *greatly limiting* our choice of functional forms.

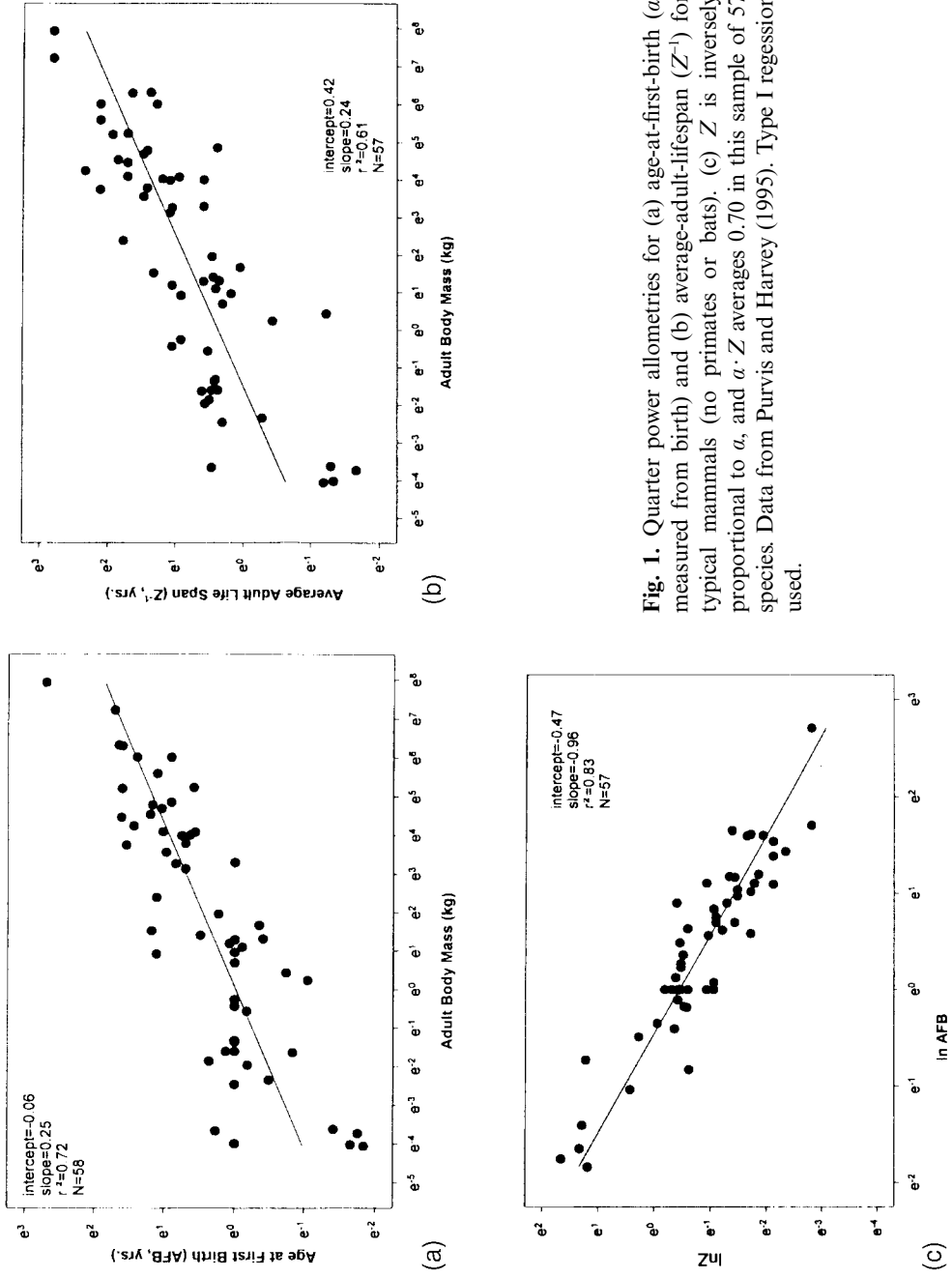
This paper develops a new model for evolution of life histories for female mammals, in the spirit of the previous two paragraphs. The development will be to contrast Charnov (1991, 1993) (CH) and Kozlowski and Weiner (1997) (KW) to the new model; the comparison is briefly summarized in Table 1.

### INDIVIDUAL PRODUCTION AND GROWTH

CH assumed that individual growth (production) follows a 0.75 power function,  $dm/dt = am^{0.75}$  (equation 1a), where  $m$  = body mass and  $a$  is similar among various mammals species. This equation integrates ( $m \approx 0$  at  $t = 0$ ) to yield  $t = [4/a]m^{0.25}$  (equation 1b), an automatic 0.25 allometry for  $t$  within a collection of species with similar  $a$  values. KW pointed out that this equation has no fastest growth rate prior to adult size, and that sigmoid growth better characterizes body size growth in mammals (Purvis and Harvey, 1997). While many sigmoid equations have been used to describe body size growth (Reiss, 1989), KW choose  $dm/dt = a \cdot m^{\delta_1} - b \cdot m^{\delta_2}$  (equation 2), with  $a$ ,  $b$ ,  $\delta_1$  and  $\delta_2$  relatively arbitrary in numeric value (constrained only by  $\delta_1 < \delta_2 \leq 1$ );  $a \cdot m^{\delta_1}$  is assimilation of food, while  $b \cdot m^{\delta_2}$  is the respiration cost. The equation has an inflection point (max  $dm/dt$ ) always less than about 35% of the asymptote ( $m$  at  $dm/dt = 0$ ), but adult size is at a size less than the asymptote, too, since initiation of reproduction diverts self-growth to offspring production; adult size in CH follows the same diversion of growth-to-reproduction idea. Since equation (2) is not a power function, across-species plots of time to maturation ( $a$ ) will look like power functions only for some distributions of parameter values and evolutionary rules for the onset of production. Furthermore, the exponent of a between-species plot has no particular basic meaning.

Accepting that growth is sigmoid (Purvis and Harvey, 1997), is it really true that we can place no constraints on growth equations like equation (2)? West *et al.* (in press) 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 cost. Their argument, developed here in an appendix, leads to an equation for change-in-mass (prior to reproduction) of the form  $dm/dt = a \cdot m^{0.75} - b \cdot m$  (equation 3), where  $a$  is expected to be *similar* for species with similar metabolic scaling (and body temperature, 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. Equation (3) excludes reproductive allocation and would result in sigmoid growth to an asymptotic size ( $M = (a/b)^4$ ), as shown in Fig. 2. There is a fastest growth rate, an inflection point, at  $0.316 \cdot M$  (which is  $(0.75)^4$ ). As noted before, 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 at  $m_i = 0.316 \cdot M = 0.316 \cdot (m_a/\mu)$  or  $m_i/m_a = 0.316/\mu$  [example  $\mu = 0.7$ ;  $m_i/m_a \approx 0.45$ ].

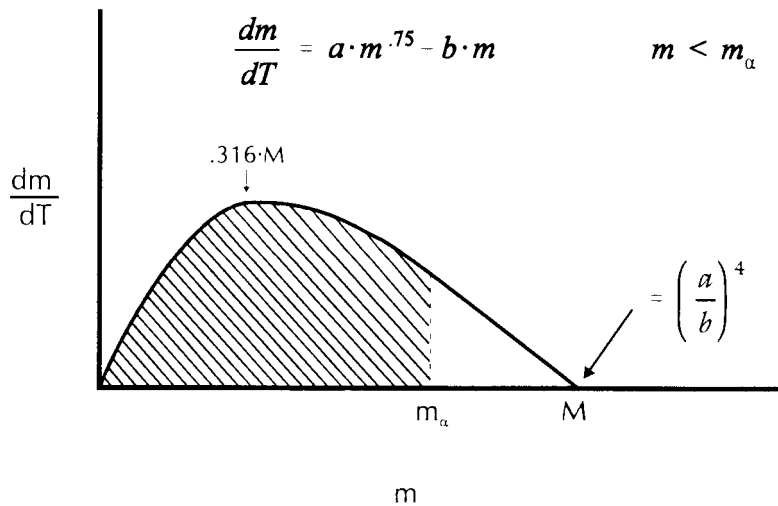
Equation (3) is like equation (2), except we have good biological reasons (derivation in Appendix) to constrain the parameters (i.e.  $\delta_1 = 0.75$ ,  $\delta_2 = 1$ ,  $a \approx$  similar among species). Equation (3) may be integrated to yield ( $m \approx 0$  at  $t = 0$ ):



**Fig. 1.** Quarter power allometries for (a) age-at-first-birth ( $a$ ), measured from birth) and (b) average-adult-lifespan ( $Z^{-1}$ ) for typical mammals (no primates or bats). (c)  $Z$  is inversely proportional to  $a$ , and  $a \cdot Z$  averages 0.70 in this sample of 57 species. Data from Purvis and Harvey (1995). Type I regression used.

**Table 1.** Comparison of three life-history models

	Charnov (1991)	Kozłowski and Weiner (1997)	This paper
Body size growth law	$dm/dt = a \cdot m^{0.75}$ , $a \approx$ constant between species	$dm/dt = a \cdot m^{\delta_1} - b \cdot m^{\delta_2}$ , $\delta_1 < \delta_2 \leq 1$ , otherwise $a, b, \delta_1, \delta_2$ show relatively arbitrary distributions. $a \cdot m^{\delta_1}$ = assimilation of food, $b \cdot m^{\delta_2}$ = respiration (whole-body loss)	$dm/dt = a \cdot m^{0.75} - b \cdot m$ ; $a \approx$ constant between species; $b$ is the cellular maintenance rate and is adjusted by natural selection. See Fig. 2 and Appendix
Offspring production relation	$\propto a \cdot m_a^{0.75}$ , where $m_a$ is size at maturity	$\propto dm_a/dt$	$\propto a \cdot m_a^{0.75}$ , resource for offspring production is not the same as resource for personal growth
Mortality	Constant over feasible ages-at-maturity; no body size effect	Generally decreases with increasing body size over ontogeny	Constant over feasible ages-at-maturity; no body size effect (see Fig. 4). Mortality inversely related to $b$ within a species (see Fig. 6)
Fitness measure	Maximize $R_0$ by choice of $m_a$	Maximize $R_0$ by choice of $m_a$	Maximize $R_0$ by choice of $m_a$ and $b$ (see above)



**Fig. 2.** Schematic diagram of the growth model ( $dm/dt$ ,  $m$  = mass) from the Appendix. 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.

$$\left(\frac{m_t}{M}\right)^{0.25} = 1 - e^{(-a \cdot t/4) \cdot M^{0.25}} \quad (4)$$

Since  $\mu = m_t/M$ , equation (4) may be rewritten (setting  $t = a$ ) as:

$$\mu^{0.25} = 1 - e^{(-a \cdot a/4)(\mu/m_a)^{0.25}}$$

or

$$a = \left[ \frac{-\ln(1 - \mu^{0.25})}{\mu^{0.25}} \right] \left[ \frac{4}{a} \right] m_a^{0.25} \quad (5)$$

Equation (5) looks just like equation (1b), with an additional term in  $\mu$ . Thus, species with similar  $a$  (as is expected) will show a 0.25 allometry for  $a$  if they also have similar  $\mu$  values. Under the West *et al.* (in press) growth model, the 0.25 allometry for  $a$ , as shown in Fig. 1a, points to a new invariance rule for mammals; they are similar in  $\mu$ . As also just noted, similarity (invariance) in  $\mu$  will show up as similarity (invariance) in  $m_t/m_a$ , the size at the fastest growth rate ( $m_t$ ) relative to adult size ( $m_a$ ). A slightly different form of equation (4) is displayed in equation (5) of the Appendix.

Since I believe that the growth model of equation (3) is based on much deeper principles than the arbitrary form of equation (2), I suggest we (tentatively) accept it and base a life-history model on it. To foreshadow the rest of this paper: invariance in  $\mu$ , suggested by equation (5) and Fig. 1a, is a key result.

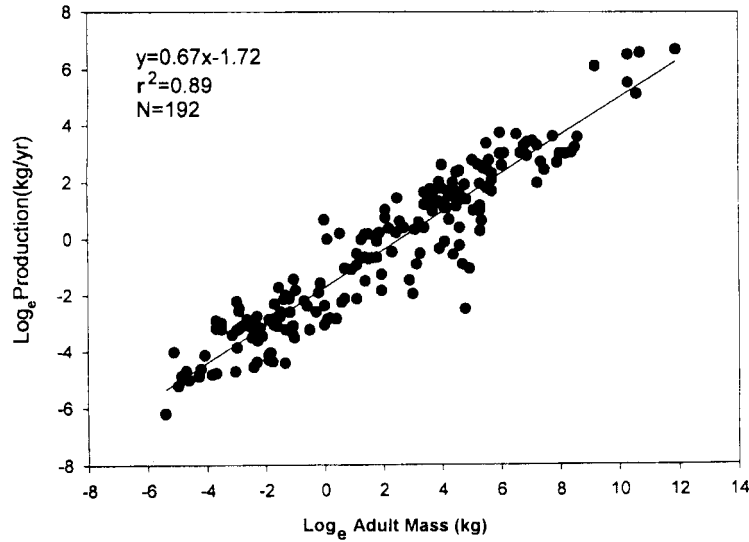
### YEARLY OFFSPRING PRODUCTION

Estimates of the biomass devoted to offspring production are usually rather imprecise, commonly measured as litter size times litters per year times offspring size. Since offspring size at weaning is proportional (across species) to birth size, consistent use of one or the other in the above plot yields a rough measure of (or proportional to) yearly mass devoted to reproduction. Across-species plots of this versus adult female mass are usually log/log linear with a slope near 0.7; Fig. 3 shows one such plot. It is easy to see how CH would produce this relation, since at adult size ( $m_a$ ) self-production ( $dm/dt$ ) is simply diverted to offspring production; thus offspring production is proportional to  $a \cdot m_a^{0.75}$ , a 0.75 scaling for species having similar  $a$  values. Since KW also have offspring production being diverted to self-growth, offspring production is likewise  $\propto dm/dt = a \cdot m^{\delta_1} - b \cdot m^{\delta_2}$  (evaluated at  $m_a$ ); it is more difficult to see how this necessarily yields an across-species scaling rule with a ( $\approx$ ) 0.75 exponent. At first sight, the growth model adopted here ( $dm/dt = a \cdot m^{0.75} - b \cdot m$ ) may not appear to be much better, but, surprisingly, it can be rewritten as:

$$\frac{dm}{dt} = a \cdot m^{0.75} [1 - \mu^{0.25}] \quad (6)$$

If offspring production is simply diverted self-growth ( $\propto dm/dt$ ), the species with similar  $a$  and  $\mu$  values will show a 0.75 allometry of offspring production across species, since equation (6) is to be evaluated at  $m_a$ .

This argument again suggests a role for invariance in  $\mu$  leading to an allometry across species. Later in this paper I provide a numerical argument for why I think equation (6)



**Fig. 3.** Yearly production (mass) of offspring estimated as (litter size) · (litters per year) · (birth weight of an offspring) scales as  $\approx 0.7$  with adult female mass for a sample of 192 mammal species (excluding, as usual, primates and bats). Data from Nowak (1991); figure courtesy of Dr Sarah Morgan Ernest.

is not correct for getting at offspring production. Although it seems logical to assume that resource for offspring is simply resource diverted from self-growth, growing one's self *may not be* the same thing as growing offspring. To grow self, one delivers resources to all body cells via the fractal branching network of the vascular systems (West *et al.*, 1997, in press); offspring are grown by handing them food or by delivery of resources to a specialized location (breasts, teats) that turns it into milk. It is quite possible that the use of adult activity to gather and deliver resources to offspring allows greater yield than is apparent in the  $\infty dm/dt$  idea; West *et al.* (in press) suggest something like this, as they propose that offspring production is not self-growth, but relies on a *scope for activity (to gather and process) resource* that lies at least partly outside the  $dm/dt$  calculation. If equation (6) is not the source of resource for growing offspring, where does the offspring production allometry (Fig. 3) come from? For this paper, offspring production will shut down personal growth *but is assumed proportional to*  $a \cdot m^{0.75}$ . Since  $a \cdot m^{0.75}$  is itself proportional to total metabolic rate (see Appendix), this offspring production assumption is that resources for offspring are a multiplier of total metabolic rate.

### STRUCTURE OF MORTALITY

Evolutionary models for  $a$  (or  $m_a$ ) typically assume that the capacity to reproduce increases within a species as maturation is delayed, but with a mortality cost (i.e. the greater the delay, the greater the chance of dying before adulthood is reached) (Stearns, 1992). The optimal  $a$  ( $m_a$ ) balances these two. Let  $Z(x)$  be the instantaneous mortality rate at age  $x$ . CH assumes that  $Z(x)$  is high (and most likely density-dependent) at small  $x$ , and that  $Z(x)$  drops to some constant value prior to feasible ages of maturity. (It may go up again late in

life.) KW believe that  $Z(x)$  is unlikely to be size- ( $m$ ) or age-independent within an ontogeny and they suggest a general form  $Z(m) = v \cdot m^\lambda$ , where  $\lambda < 0$  is about the only constraint assumed. This size dependence of mortality has a plausible ring to it, although other assumptions also seem plausible (e.g.  $Z$  increases as  $dm/dt$  increases; Stearns and Crandall, 1981). Neither CH nor KW allow mortality to go up after the onset of reproduction (but see Charnov, 1993, p. 95), a concession to the idea that mortality ought not to change just because production is reallocated from self to offspring.

Is there evidence to support the assumption of KW that  $Z$  is size-dependent within an ontogeny? The only broad-scale comparison I know of is for fish, which show indeterminate growth; they typically initiate reproduction and then keep growing. Typical data put  $m_a$  at 25% or less of some asymptotic size; do fish show  $Z(m)$  to decrease with increasing size (or age) within an ontogeny? For the vast majority of species examined, the answer surprisingly is *no* (e.g. Gunderson, 1997); mortality is independent of size/age over the post- $m_a$  growth. Of course, egg, larval and juvenile mortality are higher, and mortality typically increases late in life. What I conclude from the fish data is that mortality may not decline with increasing size within an ontogeny. Perhaps mammals are like fish in this way and I suggest that size independence for  $Z$  may not be an unrealistic assumption. The  $Z$  assumption adopted here is shown in Fig. 4. Since time ( $x$ ) begins at conception, the early parental care period should have lower  $Z$ .  $Z$  should show a spike after weaning and I assume that  $Z(x)$  decreases to some fixed value prior to feasible ages of maturity ( $a$ ).

### FITNESS MAXIMIZATION

CH and KW both assume that natural selection maximizes  $R_0$ , the net reproductive rate. Both models thus assume non-growing populations; CH is specific in putting density dependence into survival of the young shortly after independence from the mother. With age independence of adult mortality and fecundity,  $R_0$  can be written as (Charnov, 1993, 1997):

$$R_0 = \frac{S_a \cdot f(a)}{Z} \tag{7}$$

where  $S_a$  = the survival chance to age of first reproduction ( $a$ ),  $f$  = fecundity in daughters per unit of time,  $Z^{-1}$  = the average adult life span ( $Z$  is the adult instantaneous mortality rate). Recalling Fig. 4 for  $Z(x)$ ,  $S_a$  can be written as

$$S_a = e^{-\int_0^a Z(x)dx}$$

and  $R_0$  expressed as:

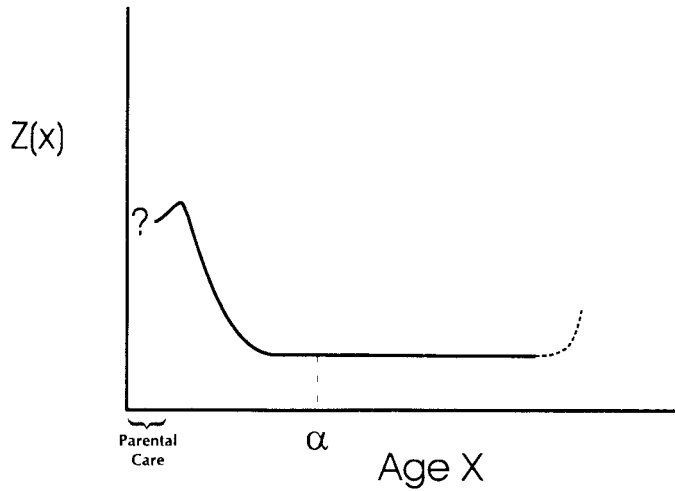
$$\ln R_0 = -\int_0^a Z(x)dx + \ln f(a) - \ln(Z) \tag{8}$$

Since  $\ln(Z)$  is a constant with respect to  $a$  (Fig. 4),

$$\frac{\partial \ln R_0}{\partial a} = -Z(a) + \frac{\partial \ln f(x)}{\partial a}$$

$Z(a)$  is the adult  $Z$ , and  $a$  and  $x$  in  $\partial \ln f(x)/\partial a$  are simply both time; so  $\partial \ln R_0/\partial a = 0$  when:





**Fig. 4.** The instantaneous mortality rate  $Z(x)$  is externally imposed (*but* see Fig. 6) and is assumed age- and size-independent over most of the life span. See the text for justification and a detailed discussion.

$$Z = \frac{\partial \ln f}{\partial a} \tag{9}$$

Now, for the sake of argument, suppose  $f \propto dm/dt = a \cdot m^{0.75} - b \cdot m$ , the resource for personal growth is also the resource for growing offspring. (Recall that CH simply puts  $b = 0$ .) Write  $f = C(a \cdot m^{0.75} - b \cdot m)$ ; then  $\ln f = \ln C + \ln(a \cdot m^{0.75} - b \cdot m)$  and

$$\frac{\partial \ln f}{\partial t} = \frac{a \cdot 0.75 \cdot m^{-0.25} (dm/dt) - b(dm/dt)}{a \cdot m^{0.75} - b \cdot m} = a \cdot 0.75 \cdot m^{-0.25} - b$$

Thus, equation (9) becomes (where  $m$  is  $m_a$ ):

$$Z = a \cdot 0.75 \cdot m_a^{-0.25} - b \tag{10}$$

This equation has an interesting form. Divide both sides by  $b$  to yield  $Z/b = (a/b) \cdot 0.75 \cdot m_a^{-0.25} - 1$ ; recall that  $a/b = M^{0.25}$  ( $M$  = the asymptote in Fig. 2), so the equation becomes  $Z/b = 0.75 (M/m_a)^{0.25} - 1$ , or  $Z/b = 0.75/\mu^{0.25} - 1$ . As  $Z/b$  is a positive number,  $0.75/\mu^{0.25} > 1$  or  $\mu^{0.25} < 0.75$ ; or  $\mu < 0.316$ , the inflection point on Fig. 2. This, of course, implies that all species begin reproduction *before*  $0.316M$ , which is clearly not true, since if they did individual growth would show no inflection point, a major fact KW criticized CH for ignoring.

This result strongly suggests that either: (1)  $f$  is not proportional to  $dm/dt$  or (2) (maybe) mortality decreases with increasing  $m$ , which would push  $m_a$  to a value higher than implied by equation (9). As noted earlier, with reference to data on fish, (2) appears less likely; this paper proposes that  $f \propto a \cdot m^{0.75}$ , a new offspring production model for mammals.

If  $f = C \cdot m^{0.75}$ ,

$$\frac{\partial \ln f}{\partial t} = \frac{0.75}{m} \frac{dm}{dt} = \frac{0.75}{m} [a \cdot m^{0.75} - b \cdot m] = 0.75[a \cdot m^{-0.25} - b]$$

Putting this into equation (9) (and setting time to age  $a$ ) yields the rule:

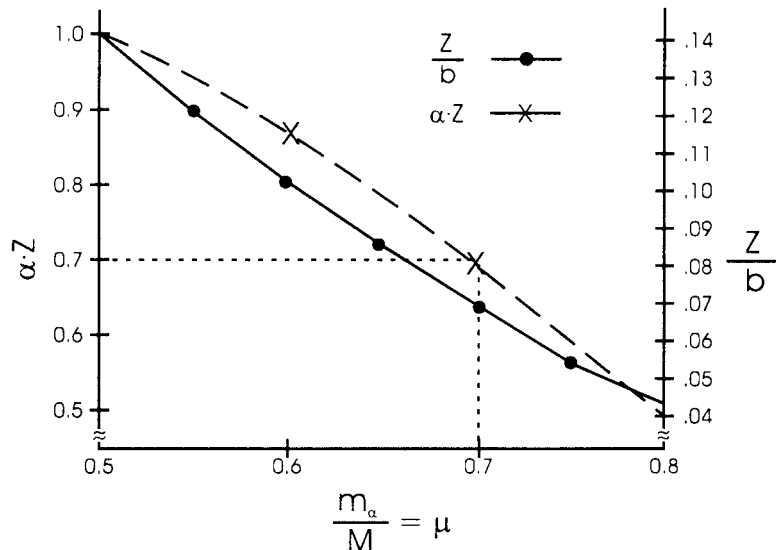
$$Z = 0.75 \cdot a \cdot m_a^{-0.25} - 0.75b \tag{11}$$

If we set  $b = K \cdot Z$ , equation (11) can be rewritten as:

$$Z^{-1} = \left[ \frac{1 + 0.75K}{0.75 \cdot a} \right] m_a^{0.25} \tag{12}$$

It is clear that species with similar  $a$  values will have  $Z^{-1} \propto m_a^{0.25}$  (as shown in Fig. 1b) only if  $b = K \cdot Z$  among the species.

But there is more here, since it is straightforward to estimate  $K$ : rewrite equation (11) as  $Z/b = (0.75 \cdot m_a^{-0.25})(a/b) - 0.75$  and recall again that  $a/b = M^{0.25}$ ; thus equation (13)  $Z/b = 0.75[\mu^{-0.25} - 1]$  and so the predicted  $Z/b$  is solely a function of  $\mu$ , the size at maturity ( $m_a$ ) relative to the asymptotic size ( $M$ ) of Fig. 2. Figure 5 plots  $Z/b$  versus  $\mu$  ( $= m_a/M$ ). To summarize to this point: a 0.25 allometry for adult life span ( $Z^{-1}$ ) requires that  $Z/b$  be an invariant across species, which proves to be equivalent to  $\mu$  being an invariant (all under the optimization argument and its assumptions); this is, of course, the same requirement needed for  $a$  to show a 0.25 allometry (Fig. 1a and equation 5). Equation (12) and equation (5) together show that  $a \cdot Z$  is solely a function of  $\mu$  (since  $Z/b$  [or  $K$ ] is solely a function of  $\mu$ ). Figure 5 also plots  $a \cdot Z$  as a function of  $\mu$ ; thus, a fixed  $a \cdot Z$  follows from a fixed  $Z/b$ .



**Fig. 5.** Optimization of the age-at-first-birth ( $a$ , or  $m_a$ ; equation 11) says that, for a fixed  $Z/b$  ratio,  $a \cdot Z$  will take on a fixed value, and so will the relative size at maturity ( $\mu = m_a/M$ ). Since  $a \cdot Z$  is known to be  $\approx 0.7$ , we can predict  $\mu \approx 0.7$  and  $Z/b \approx 0.07$ .

As first noted by Charnov (1991), the 'height of the growth curve' (here  $a$  of equations 3 and 5) drops out of the equation predicting  $a \cdot Z$ ; this is probably why the  $r^2$  is higher in Fig. 1c than in Figs 1a,b (where between-species variation in  $a$  will cause variation around the allometry).

We can now use the observed  $a \cdot Z$  to predict  $\mu$  and  $Z/b$ . Figure 1c is a loge/loge plot of  $Z$  versus  $a$  for the mammal data, and shows a  $-1$  slope, indicating that  $a \cdot Z$  is indeed an invariant across species. The average  $a \cdot Z$  for the 57 species of mammals is 0.70. Figure 5 shows that  $a \cdot Z = 0.7$  is predicted to correspond to  $\mu \approx 0.7$  and  $Z/b \approx 0.07$ . Thus, the life-history model may be combined with the observed  $a \cdot Z$  value to predict the numeric values of two new dimensionless invariants for mammals. Of course, the other way to say this is that, if  $Z/b$  is an invariant, the optimal life history (equation 12) makes  $\mu$  and  $a \cdot Z$  invariants; this makes both  $a$  and  $Z^{-1}$  show a 0.25 allometry for species with similar  $a$  values. Note that I have imposed  $Z/b = \text{constant}$  as a side condition; why might  $Z/b$  be an invariant across species?

### EVOLUTION OF $Z$ AND $b$ ?

KW and CH, as well as many other life-history evolution models, take the production function (equation 2 or 3) as given and only allow processes like the shunting of production from personal growth to reproduction. But the condition  $Z/b = \text{constant}$  is a strong hint that somehow  $b$ , and thus the production function, must also be adjusted by natural selection in relation to mortality,  $Z$ .  $b$  is the maintenance cost per unit of time of a cell divided by the cost of a new cell; it is the investment per unit of time in a cell *before that cell yields any net production*. So why would any organism build cells that are expensive to maintain (high  $b$ )? I suggest that, within a species, the individual can decrease its death rate ( $Z$ ) by increasing investment in cellular maintenance; increasing  $b$  lowers  $Z$ . Figure 6 shows this trade-off assumption, illustrated for species 1 and species 2. Note that the species fall on different trade-off curves, with species 2 having higher  $Z$  at any  $b$  value; external sources of mortality set the *height* of the trade-off curves, while (internal) adjustment of  $b$  allows the species to change  $Z$  along a trade-off curve. Recall that what we are looking for *between* species is  $Z = K^{-1} \cdot b$ , a positive relation, so we wish to ask what would force the various species to move to positions on their respective *negative* trade-off relations so that  $Z = K^{-1} \cdot b$  between trade-off relations. I have no particular intuition as to the shape of these  $Z$  versus  $b$  trade-offs within species, except to note that an interior solution for the optimization problem probably requires they be bowed down as in Fig. 6. Fitness ( $R_0$ ) can be written as:

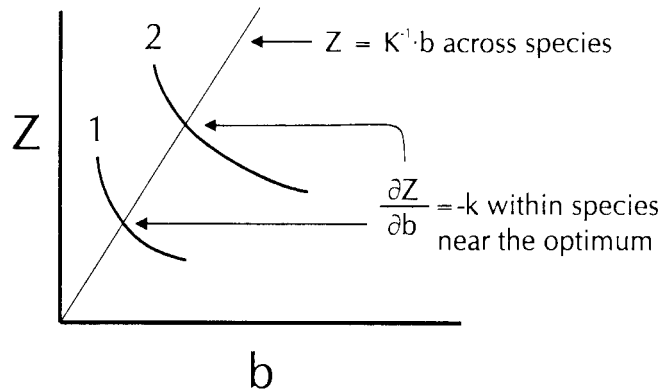
$$R_0 = \frac{e^{-\int_0^a Z(x)dx} \cdot C \cdot m^{0.75}}{Z} \quad (\text{where } f = C \cdot m^{0.75}) \quad (14)$$

or

$$\ln R_0 = -\int_0^a Z(x)dx + \ln C + 0.75 \ln m - \ln Z \quad (15)$$

Setting  $\partial \ln R_0 / \partial b = 0$  (with  $a$  held constant) yields:

$$0 = -\int_0^a \frac{\partial Z(x)}{\partial b} dx + 0.75 \frac{\partial \ln m}{\partial b} - \frac{1}{Z} \frac{\partial Z}{\partial b} \quad (16)$$



**Fig. 6.**  $b$  is the maintenance metabolic rate per cell (divided by the cost of a new cell) and so is the investment per time per cell before that cell yields any net production. We assume here that, within a species, higher  $b$  leads to lower  $Z$ . Various species (here 1 and 2) differ in the height of the trade-off curves, and so natural selection can lower  $Z$  by more investment in cellular maintenance (i.e. higher  $b$ ). The slope of the trade-off curve ( $-k$ ) is a dimensionless number, and the life-history model done here requires that  $k$  be similar at similar  $Z/b$  ratios across species. The text discusses this and provides a numerical estimate for  $k$  ( $\approx 0.1$ ).

The first term in equation (16) could be very complicated, since it asks how changing  $b$  alters  $Z(x)$  at every age, and then requires that we integrate over them. I will (*first*) make the simplest assumption and assume no age effect:  $\partial Z(x)/\partial b = \partial Z/\partial b = -k$  (equation 17), where  $-k$  is the slope of the trade-off near the optimum (see Fig. 6). Thus, the first term of equation (16) becomes  $\int_0^a k dx = k \cdot a$  (equation 18). Equation 4 allows us to write:

$$m^{0.25} = \frac{a}{b} [1 - e^{(-b/4) \cdot a}]$$

or

$$\ln m = 4 \ln a - 4 \ln b + 4 \ln (1 - e^{(-b/4) \cdot a})$$

and

$$\frac{\partial \ln m}{\partial b} = -\frac{4}{b} + \frac{a e^{(-b/4) \cdot a}}{1 - e^{(-b/4) \cdot a}} \tag{19}$$

Using equations (17), (18) and (19), condition (16) may be written as:

$$0 = k(a \cdot b) + k \frac{b \cdot a}{Z \cdot a} + 0.75 \left[ -4 + \frac{a \cdot b e^{(-b/4) \cdot a}}{1 - e^{(-b/4) \cdot a}} \right] \tag{20}$$

Equation (20) must be satisfied for  $\partial \ln R_0 / \partial b = 0$ ; it is a function of three dimensionless numbers:  $k$ ,  $a \cdot b$ , and  $a \cdot Z$ . Recall that  $-k$  is the slope of the  $Z - b$  trade-off in the neighbourhood of the optimum, and so  $k$  will probably change as  $Z/b$  changes. For the optimal life history ( $\partial \ln R_0 / \partial a = 0$  and  $\partial \ln R_0 / \partial b = 0$ ) to make  $Z/b$  an invariant (the condition for  $a \cdot Z$  to be invariant),  $k$  must take on a similar value near the same  $Z/b$  value across species. Equation (9) for  $\partial \ln R_0 / \partial a = 0$ , with  $f \propto m^{0.75}$ , can be written as:

$$a \cdot Z = \frac{0.75 \cdot a \cdot b \cdot e^{(-b \cdot a)/4}}{1 - e^{-a \cdot (b/4)}} \quad (21)$$

which gives a second function relating  $a \cdot Z$  to  $b \cdot a$ . Since we know the value of  $a \cdot Z$  is  $\approx 0.7$  (Fig. 1c), equation (21) allows us to solve for  $a \cdot b$ , and then use the  $a \cdot b$  and  $a \cdot Z$  values in equation (20) to solve for  $k$ , which is predicted to equal  $\approx 0.1$ , a new dimensionless invariant for mammals, and one which relates how internal investment in cellular maintenance ( $b$ ) results in adjustment of the adult death rate ( $Z$ ) within a species.

The assumption  $\partial Z/\partial b = -k$ , independent of age, may well be too simple; of course, it also does not explain *why* the separate trade-off curves illustrated in Fig. 6 should show similar  $k$  values near the same  $Z/b$  values. We could study various parametric forms for the trade-offs. Consider a power function  $Z = A \cdot b^{-h}$ , which has  $\partial Z/\partial b = -h[Z/b]$  and so automatically yields the same slope at the same  $Z/b$  for species with the same exponent,  $h$ . But  $\partial Z/\partial b$  is now no longer age-independent, since (Fig. 4)  $Z$  changes with age while  $b$  does not. However, all is not lost since the first term of equation (16) contains the only age-dependence and it now becomes:

$$-\int_0^a \frac{\partial Z(x)}{\partial b} dx = \frac{h}{b} \int_0^a Z(x) dx = (-\ln S_a) \left( \frac{h}{b} \right)$$

(Recall equation 7 for  $S_a$ .) Straightforward enumeration of the other terms in equations (16) and (21) (with  $a \cdot Z = 0.7$ ) shows that for the adult  $Z$ ,  $\partial Z/\partial b$  equals  $\approx -0.085$  (if  $S_a \approx 0.4$ , as is known for mammals; Charnov, 1993). Thus, a power function for the trade-offs yields similar slopes at similar  $Z/b$  values and predicts that  $k = -\partial Z/\partial b \approx 0.1$ , just as in our much more simplified model for  $k$  (equation 17).

## TWO PRODUCTION INVARIANTS: $G/Z$ and $(G - b)/Z$

The ‘height of the production curve’ – the total metabolism fuelling growth and maintenance – is  $a \cdot m^{0.75}$  (from equation 3). If we express this as a per-unit-mass measure ( $G$ ), it will have units of (time)<sup>-1</sup>:  $G_a = a/m_a^{0.25}$ . We can multiply  $G$  by the average adult life span ( $Z^{-1}$ ) as given by equation (12) to form the dimensionless number  $G/Z$ , which equals:

$$\frac{G_a}{Z} = \frac{1 + 0.75(b/Z)}{0.75} \quad (22)$$

This makes the average adult life span ( $Z^{-1}$ ) inversely proportional to  $G_a$ , the mass-specific metabolism fuelling growth at maturity.

The growth rate at maturity is  $dm/dt = a \cdot m_a^{0.75} - b \cdot m_a$ , so the mass-specific growth rate is  $dm/(m \cdot dt) = G_a - b$ . Multiplied by the adult life span ( $Z^{-1}$ ), this gives  $G/Z - b/Z$ , a dimensionless invariant that relates the growth rate per unit mass just at adulthood to the adult life span.

## ONE SPECIAL PREDICTION: $a \cdot Z$ versus $\mu$

While it seems sensible to treat  $a \cdot Z$  as an approximate invariant ( $\approx 0.7$ ), the number does vary somewhat among species. The previous mammal model (Charnov, 1991, 1993) at first seemed to predict this variation, but later analysis (Purvis and Harvey, 1995) failed to

support it. The model developed here predicts (Fig. 5) that  $a \cdot Z$  will be negatively related to  $\mu$ , which makes  $a \cdot Z$  positively related to  $m_i/m_a$ ; the theory makes an exact numeric prediction. It may be possible to test this if  $m_i/m_a$  can be estimated for the species which also have estimated  $a \cdot Z$  values (Purvis and Harvey, 1995, 1997).

## DISCUSSION

Perhaps the most observable and straightforward prediction is that  $\mu \approx 0.7$  (Fig. 5); this, of course, puts the inflection point ( $m_i$ ) at about 45% of the adult size ( $m_a$ ), since  $m_i/m_a = 0.316/\mu = 0.45$ . Most sigmoid growth curves fit to data are *parametric* (Reiss, 1989) and *thus* assume some fixed  $m_i/m_a$  value. So testing the  $\mu \approx 0.7$  prediction will require data fitting that allows  $m_i/m_a$  to take on arbitrary values. It is also unclear how unique this prediction is. (I suspect that the predicted values of  $Z/b$ ,  $(G - b)/Z$  and the  $Z - b$  trade-off slope are more powerful predictions. Perhaps someone can suggest how to measure them.)

## CONCLUSION

The model developed here takes seriously the 0.25 allometries for  $a$  and  $Z^{-1}$ , and tries to justify limitations on the functional forms (for growth,  $Z(x)$ , offspring production) put into the life-history evolution scheme. (It may be wrong; for example, perhaps we should retain  $f \propto dm/dt$  and force  $m_a$  beyond  $0.316M$  by a mortality advantage to size; of course, this must yield  $Z^{-1} \propto m_a^{0.25}$  across species to give  $a \cdot Z$  invariance.) What I like about the new model is that it tells us to pay attention to a whole new suite of dimensionless numbers (e.g.  $Z/b$ ,  $(G - b)/Z$ ,  $m_i/m_a$ ,  $k$ ) that characterize growth, mortality and, even, investment in cellular maintenance. The relative size at the fastest growth rate  $m_i/m_a$  is assigned a very special meaning in this conceptual scheme. Only time (and data analysis) will tell if this is the light and the way, or a temporarily well-lit alley.

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### APPENDIX: THE PRODUCTION/GROWTH MODEL

West *et al.* (in press) expand their previous work (1997) on whole-organism metabolic rate to encompass growth; their argument follows. Their basic starting point is the balance of energy flow within an organism. Incoming energy and materials from the environment are transported via hierarchical branching network systems to supply all cells. In general, these resources are transformed into metabolic energy, which is utilized for life-sustaining activities such as maintenance of existing biomass. During ontogeny, however, some fraction of the total metabolic energy is allocated to the production of new tissue. In general, then, the rate of energy transformation is the sum of two terms, one representing the maintenance of existing tissue, the other the creation of new tissue. This can be expressed by the dynamic conservation of energy equation:

$$B = N_c B_c + E_c \frac{dN_c}{dt} \quad (2)$$

where the incoming rate of energy flow,  $B$ , is the average metabolic rate of the whole organism at some time  $t$ . The whole organism is composed of fundamental units, cells, subscripted  $c$ . The metabolic rate of a single cell is denoted by  $B_c$  and the metabolic energy required to create such a cell by  $E_c$ .  $N_c$  is the total number of cells; here we consider some average, typical cell as the fundamental unit. The first term of equation (2),  $N_c \cdot B_c$ , is simply the power needed to sustain the organism in all of its activities, whereas the second term is the power allocated to the production of new cells and therefore to growth.  $E_c$ ,  $B_c$  and the mass of the cell,  $m_c$ , are assumed to remain constant throughout growth and development.

At any time,  $t$ , the total body mass  $m = m_c \cdot N_c$ , so equation (2) can be written as:

$$\frac{dm}{dt} = \left(\frac{m_c}{E_c}\right)B - \left(\frac{B_c}{E_c}\right)m \quad (3)$$

Now, the whole-organism metabolic rate scales (West *et al.*, 1997) as  $B = B_0 m^{3/4}$ , where  $B_0$  is constant for a given taxon. This immediately leads to the general growth/production equation:

$$\frac{dm}{dt} = a \cdot m^{3/4} - b \cdot m \quad (4)$$

The argument leading to equation (4) is *similar* to the original argument for the classic Bertalanffy growth equation, which differs in having a  $\frac{2}{3}$  rather than a  $\frac{3}{4}$  exponent. Whereas Bertalanffy had absorption of food by the gut (assumed a  $\frac{2}{3}$  scaling) limit material (energy) delivery to cells, West *et al.* (1997, in press) put the delivery limit in the functioning of the hierarchal branching networks (e.g. blood) that supply cells (hence, a  $\frac{3}{4}$  scaling).

Equation (4) may be integrated ( $m \approx 0$  at  $t = 0$ ) to give:

$$m_a = \left[ \frac{a}{b} \right]^4 \cdot \left[ 1 - e^{(-a \cdot b)t/4} \right]^4 \quad (5)$$

which is equivalent to equation (4) in the text.



