Evolution of life history variation among female mammals

(life history allometry/body size scaling/evolution of maturation/dimensional analysis/stable demography)

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ABSTRACT   A unified approach is developed for the evolutionary structure of mammalian life histories; it blends together three basic components (individual growth or production rate as a function of body size, natural selection on age of maturity, and stable demography) to predict both the powers and the intercepts of the scaling allometry of life history variables to adult size. The theory also predicts the signs (+, −) of the correlations between life history variables when body size is held constant. Finally, the approach allows us to eliminate body size to predict the dimensionless relationships between the life history variables themselves.

Two major approaches have dominated recent thinking about variation in mammalian life histories. The first sees variation as simply reflecting allometric or scaling consequences of adult body size (1–4), whereas the second sees natural selection as molding the life history fairly independent of body size (5–8). Both approaches recognize that "to grow big takes time" so that larger adults must have longer immature periods; they differ in that the first assumes that demographic and birth rates are also mainly determined by adult size, with a rather mysterious causal connection (at least for demography; ref. 9), whereas the second sees these rates as free to evolve within broad limits, independent of adult size. A major finding supporting the second position is that life-history variables, such as birth rates, death rates, and age of maturity, are highly correlated with each other even when adult body size is held constant (5–8).

This paper develops a unification of the two approaches. It assigns a central, yet well-defined, role to body size. It also invokes natural selection, primarily on the age of maturity, to link adult demography to adult body size, through the effects of size on individual productivity (or growth potential). Finally, the approach makes use of a demographic identity appropriate for a nongrowing population; the net reproductive rate (R_0) must equal 1 in such a population so that not all variables in R_0 can vary independently (4, 10, 11).

The model developed here makes four types of predictions: (i) the allometric or scaling relations of life-history variables with adult body size, including the intercepts of the $\log_e$ lines; (ii) the correlations between life-history variables with body size held constant (5–8); (iii) the assignment of ecological reasons for why species differ in their assemblage of life-history variables, with or without consideration of body size (this latter sort of prediction follows from the fact that only a few major parameters are shown to influence the "permitted combinations" of life-history variables); and (iv) numeric values of the dimensionless relationships between the life history variables themselves (12).

Empirical Patterns

Several life-history variables scale as power functions of adult body size. In particular, age at maturity (by several

definitions), life expectancy at birth, life expectancy at maturity, and annual fecundity all scale with exponents [a; where $Y = \propto(\text{weight})^a$] near $\pm 1/4$ (fecundity is negative) (4, 5–9, 12–14). The extensive analyses are at a variety of taxonomic levels and degrees of precision. The exponents invariably fall in the range of magnitude 0.2–0.3. Using the life table data set compiled by Millar and Zammuto (13), I estimated average instantaneous mortality rates for both the juvenile and adult periods of life; both scaled with exponents near −0.25 (adult, −0.21; $r = 0.83$; $n = 26$; juvenile, −0.27; $r = 0.89$; $n = 26$). The definitions of these rates are given later in this paper. This scaling is expected because life expectancy is a direct function of the inverse of the mortality rates (and it scales with a +0.25 power).

Harvey and colleagues (5–8) have also shown that these life-history variables (age at maturity, adult and juvenile mortality rates, and annual fecundity) are correlated with each other, even when adult body size is held constant. Table 1 shows the results of the following analyses. The authors fit lines of the form $\log_e(\text{variable})$ vs. $\log_e(\text{adult weight})$. Since some taxa fall above or below the line, one can then extract the deviation of the particular $\log_e(\text{variable})$ from the line. These deviations are highly correlated with each other (Table 1). For example, taxa with relatively high ages of maturity also have relatively low adult mortalities.

Theory: The Basic 0.25 Scaling

Stable demography. Consider a life history where growth ceases at adulthood, which is also characterized by constant fecundity and constant adult mortality. Let b be the birthrate in daughters per unit time, $S(\alpha)$ the survival fraction of daughters to maturity (age α), and M the adult instantaneous mortality rate (i.e., survival for one time period $= e^{-M}$). R_0 is the average number of daughters produced over a female's lifetime. For this life history R_0 is given by (10)

$$R_0 = \frac{b \cdot S(\alpha)}{M},\qquad [1]$$

where $1/M$ is the average length of the adult life-span during which a female produces b daughters per unit time, S proportion of whom survive. In a nongrowing (stationary) population $R_0 = 1$ so that any two of the variables set the value of the third (4, 10, 11). Sometimes it will be more useful to write $S(\alpha)$ as

$$e^{-\int_0^\alpha Z(x)dx},\qquad [2]$$

where $Z(x)$ is an immature instantaneous mortality rate appropriate for age x. In general, $Z(x)$ decreases with x but it may well reach its lowest value prior to age α.

Growth versus body size. Several authors (14–16) have noted that the adult-body-size/age-of-maturity scaling (a 0.25 power) follows directly from a growth relation, provided the growth rate (individual productivity) scales with the 0.75 power of body size, after independence from the parent.

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Table 1.   Signs of correlations between life-history variables, with adult body size held constant (from refs. 5–8)

Variable pair	Sign of correlation
Adult mortality rate–age of maturity	Negative
Juvenile mortality rate–age of maturity	Negative
Juvenile mortality rate–adult mortality rate	Positive
Annual fecundity–age of maturity	Negative
Annual fecundity–adult mortality rate	Positive
Annual fecundity–juvenile mortality rate	Positive

Each pair is expressed in $\log_e$(variable) form; the correlation is between respective deviations of the variables from their means, derived as the deviations (or residuals) from the $\log_e$(variable) vs. $\log_e$(adult body size) regressions. The exact measures of adult and juvenile mortality rates used in ref. 6 differ from the instantaneous rates developed in the theory of this paper. To determine whether these somewhat different measures affected the signs of the correlations, I repeated the $\log_e$ deviation analysis by using the appropriate instantaneous rates calculated for the life table data compilation of Millar and Zammuto (13). In terms of the signs of the correlations, my more precise analysis gave the same answers.

There is abundant evidence that individual productivity does indeed scale in this way within many animal groups (17). If W is body size, we have

$$\frac{dW}{dT} = A \cdot W^{0.75}. \qquad [3]$$

The growth coefficient A differs between taxa (17) but the power coefficient, here shown as 0.75, is generally between 0.7 and 0.8. In what follows, I use 0.75; alteration of it to another value is straightforward. If we take time 0 as the point of independence from the parent (approximately the time of weaning) and let W_0 be the corresponding offspring size, Eq. 3 may be integrated to give

$$W(T)^{0.25} = 0.25 \cdot A \cdot T + W_0^{0.25}.$$

If α is the age of maturity (measured from independence) when growth ceases, and if $W_0/W(\alpha)$ is defined as δ, the above may be written as

$$W(\alpha)^{0.25} = \frac{0.25 \cdot A}{(1 - \delta^{0.25})} \cdot \alpha. \qquad [4]$$

Thus, the age of maturity (α) will scale with the 0.25 power of adult body size among species with similar A and δ values.

Offspring production versus adult body size. Although a fair amount is known about offspring growth and energetics during the period of parental care (4, 14, 18), I use a very simple aggregated model for this process. We want b the clutch size in daughters per unit time. Note that b is the ratio of the brood size to the average time between broods, so that neither appears alone in the theory. Read and Harvey (5) label b "annual fecundity." Suppose at independence each offspring is of size W_0 and that rearing an offspring to W_0 size requires $(C/2) \cdot W_0$ energy, where C is in units of parental growth (Eq. 3). (Later I shall discuss a slightly more general model, where a W_0 sized offspring requires $(C/2) \cdot W_0^{1+k}$ energy.) If τ is the time to rear one offspring to independence, then $1/\tau$ is the clutch size per unit time (or $1/2\tau = b$). In τ units of time, an adult of size $W(\alpha)$ can deliver $A \cdot W(\alpha)^{0.75} \cdot \tau$ units of energy (from Eq. 3). Note that the cost of an offspring is entirely given by the diversion of parental potential growth (Eq. 3) to offspring. To get b, we set $A \cdot W(\alpha)^{0.75} \cdot \tau = (C/2) \cdot W_0$,

write $W_0/W(\alpha) = \delta$, and solve for $1/2\tau$. This gives

$$b = \frac{A}{C \cdot \delta} \cdot W(\alpha)^{-0.25}. \qquad [5]$$

Thus, b scales with the -0.25 power of adult body size among species with similar A, δ, and C values. {If a W_0 sized offspring costs $(C/2) \cdot W_0^{1+k}$ units of energy, the power in Eq. 5 is larger in magnitude by an additive amount k [i.e., $-(0.25 + k)$ instead of -0.25].}

Natural selection on the age of maturity (α). The mortality rate of immatures is generally high; suppose that it drops with age but reaches its minimum, and adult value, prior to maturation and then remains relatively constant until it begins to increase late in life (19). R_0, a Darwinian fitness measure appropriate for a nongrowing population (10), can be written as

$$R_0 = \frac{b \cdot e^{-\int_0^\alpha Z(x)dx}}{M}. \qquad [6]$$

But if the instantaneous mortality rate bottoms out prior to α, only b and $e^{-\int_0^\alpha Z(x)dx}$ are functions of α in Eq. 6. The optimal or ESS (20) α may be found (21) by setting $\partial \log_e R_0/\partial\alpha = 0$. We have (21)

$$\frac{\partial \log_e b}{\partial\alpha} = Z(\alpha), \qquad [7]$$

but $Z(\alpha)$ is M, the adult mortality rate.

Since reproduction is assumed to be simply energy diverted from personal growth, $\partial \log_e b/\partial\alpha$ should be equal to $\partial \log_e(dW/dT)/\partial\alpha$ [as first noted by Kozlowski and Wiegert (15, 16)]. Notice that the use of b in this relation is not the same as the b of Eq. 5. There we solved for b vs. $W(\alpha)$, setting $\delta = W_0/W(\alpha)$; here we are after $\partial \log_e b/\partial\alpha$ in the absence of W_0 changing with α so we set $b = (A \cdot W^{0.75})/(C \cdot W_0)$. Direct support of this assumption is provided by the fact that total biomass of offspring per year is a power function of adult weight with an exponent of 0.69, rather near 0.75 (see ref. 5).

This leads directly (through Eqs. 3 and 7) to a scaling of the adult instantaneous mortality rate, M, on adult body size, or

$$M = 0.75 \cdot A \cdot W(\alpha)^{-0.25}. \qquad [8]$$

Note that the causal connection of M to $W(\alpha)$ is via natural selection on the age of maturity (i.e., when one stops growing and diverts all production to offspring); unlike the argument of Reiss (14) for the evolution of α, which assumes mortality to be related to adult body size, this argument has adult body size determined by mortality through the evolution of α. A special case of Eq. 8 is developed in refs. 15 and 16.

Average immature mortality ($\bar{Z}$) follows directly from $R_0 = 1$. Define $\bar{Z}$ as follows: $e^{-\int_0^\alpha Z(x)dx} = e^{-\bar{Z}\cdot\alpha}$; thus $\bar{Z}$ is the temporal average of $Z(x)$ over the immature period. Since $R_0 = (b/M) e^{-\bar{Z}\cdot\alpha}$ equals 1 in population equilibrium, and since M, b, and α are given by Eqs. 8, 5, and 4, respectively, we may solve the relation for $\bar{Z}$ as a function of adult body size

$$\bar{Z} = \left[\log_e\left(\frac{1}{C \cdot \delta \cdot 0.75}\right)\right]\left(\frac{0.25 \cdot A}{1 - \delta^{0.25}}\right)W(\alpha)^{-0.25}. \qquad [9]$$

Average immature mortality ($\bar{Z}$) will scale with the -0.25 power of adult body size among species with similar C, δ, and A values.

Further Theoretical Interpretations

Eliminate adult body size. We may use the growth relation (Eq. 4) to eliminate adult body size from the equations for b, M, and $\bar{Z}$ (Eqs. 5, 8, and 9) and thus express b, M, and $\bar{Z}$ as functions of the age of maturity (α). Note that $\alpha \cdot M$, $\alpha \cdot b$, and $\alpha \cdot \bar{Z}$ are dimensionless numbers (4, 12, 22), which express the relation between maturation (α) and mortality (M, $\bar{Z}$) and/or offspring production (b). $e^{-\alpha \cdot \bar{Z}}$ is the proportion of offspring surviving to maturity. The present theory says that these dimensionless numbers take on fixed (or constant) values for species with the same δ and C values. The productivity parameter, A, does not appear in these relations. We have

$$\alpha \cdot \bar{Z} = -\log_e(0.75 \cdot C \cdot \delta) \quad \text{(or } e^{-\alpha \cdot \bar{Z}} = 0.75 \cdot C \cdot \delta) \quad \text{[10a]}$$

$$\alpha \cdot M = 3(1 - \delta^{0.25}) \quad \text{[10b]}$$

$$\alpha \cdot b = 4\left(\frac{1 - \delta^{0.25}}{C \cdot \delta}\right). \quad \text{[10c]}$$

What if adult body size is held constant? We rewrite Eqs. 4, 5, 8, and 9 in the $\log_e$ form

$$\log_e \alpha = -\log_e\left[\frac{0.25 \cdot A}{(1 - \delta^{0.25})}\right] + 0.25 \log_e W(\alpha) \quad \text{[11]}$$

$$\log_e M = (\log_e 0.75 \cdot A) - 0.25 \log_e W(\alpha) \quad \text{[12]}$$

$$\log_e b = \log_e\left(\frac{A}{C \cdot \delta}\right) - 0.25 \log_e W(\alpha) \quad \text{[13]}$$

$$\log_e \bar{Z} = \log_e(-\log_e(C \cdot \delta \cdot 0.75)) + \log_e\left(\frac{0.25 \cdot A}{1 - \delta^{0.25}}\right)$$
$$- 0.25 \log_e W(\alpha). \quad \text{[14]}$$

To illustrate my proposed use of these four equations, focus first on Eqs. 11 and 12. Suppose a group of species with similar, but not identical A, C, and δ values are plotted versus $\log_e W(\alpha)$. If the A, C, and δ values do not correlate with $W(\alpha)$, then the plots of $\log_e \alpha$ and $\log_e M$ will be power functions of $W(\alpha)$, with the exponents of $+0.25$ and -0.25, respectively. The intercepts will be through the average values of $-\log_e[(0.25 \cdot A)/(1 - \delta^{0.25})]$ and $\log_e(0.75 \cdot A)$, respectively. Notice, however, that individual species will fall above or below the scaling relation based on how their particular $-\log_e[(0.25 \cdot A)/(1 - \delta^{0.25})]$ and $\log_e(0.75 \cdot A)$ values differ from the respective average values. If we hold adult body size constant in Eq. 12, then a species i with $\log_e A_i >$ (average $\log_e A$) will have $\log_e M_i >$ (average $\log_e M$) and will fall above the fitted line. But $\log_e A_i >$ (average $\log_e A$) will cause the same species to fall on average below the fitted line of $\log_e \alpha$: thus, a correlation calculated between [$\log_e \alpha$ − (average $\log_e \alpha$)] and [$\log_e M$ − (average $\log_e M$)] will be negative. Since the $\log_e$ scaling relations for α, M, $\bar{Z}$, and b all contain combinations of the same three parameters (A, δ, C), deviations from the average scaling relations are necessarily correlated with each other. Eqs. 11–14 may thus be used to study the correlations between $\log_e(\alpha, M, b, \bar{Z})$ expressed as deviations from their average $\log_e$ values, with body size held constant. (Notice that these deviations are also dimensionless numbers.) As shown in Table 2, five of the six correlation coefficients are given unambiguously with respect to sign, while one (α, b) depends on just why a species deviates from the average (i.e., does it differ in δ, or in A, from the average species?). Interestingly, all four $\log_e$ lines share the A parameter; if variation in it is the main cause of species deviating from the average, then even the sign of (α, b) is

Table 2. Theoretically expected correlations between life-history variables, with adult body size held constant (derived from Eqs. 11–14 under the assumption that A, δ, and C are uncorrelated with each other)

Variable pair	Sign of correlation
$\log_e M$, $\log_e \alpha$	Negative
$\log_e \bar{Z}$, $\log_e \alpha$	Negative
$\log_e \bar{Z}$, $\log_e M$	Positive
$\log_e b$, $\log_e \alpha$	?*
$\log_e b$, $\log_e M$	Positive
$\log_e b$, $\log_e \bar{Z}$	Positive

Each variable is expressed as the deviation from its mean value, as given by the scaling Eqs. 11–14, with adult body size (the $\log_e W$ term) held constant.

*This pair (Eqs. 11 and 13) has two parameters in common (A, δ). Eq. 11 has the term $\log_e(1 - \delta^{0.25})$, while Eq. 13 has $-\log_e \delta$; these two are positively related to each other. Eq. 11 has the term $-\log_e A$, while Eq. 12 has $\log_e A$: these two are, of course, negatively related. Thus, variation in δ generates a positive (b, α) correlation, while variation in A generates a negative correlation.

given; it's negative. With respect to sign ($-$, $+$), all of these predicted correlations (Table 2) are as shown in the data (Table 1). And $r(\alpha, b)$ is negative.

General theoretical interpretations. The approach developed here takes A, δ, and C as given parameters and uses them to predict the other variables; of course, we would also like to know just what determines the A, δ, and C values, as well as why the production relation (Eq. 3) is a power function with exponent ≈ 0.75. Although the discussion has been couched in terms of between-species scaling, the entire formalism really refers to predictions for any combinations of A, δ, and C. Although the between-species scaling suggests similarities in these, the real power in the approach may well lie in its freedom from any particular assumptions about them. It is probably worth noting that while A appears in the body size relations (and may greatly influence deviation from the average scaling line), A does not appear in the relations (Eq. 10) for $\bar{Z}$, b, and M vs. α. Of course, equations such as Eq. 10, which predict the values of dimensionless numbers (e.g., $\alpha \cdot M$), can only be in terms of other dimensionless numbers; thus, for A to remain in such an equation would require it to appear with another factor to cancel the dimensions (δ and C are already dimensionless).

Perhaps the most speculative part of the argument is the derivation of b in Eq. 5; for example, if the more complex production model is needed (cost scales with W_0^{1+k}) this will alter the body size scaling of both b and $\bar{Z}$. $\bar{Z}$ will not be exactly a power function of body size at all; however, $S(\alpha)$ from Eq. 1 will be and it will scale with $W(\alpha)$ to the k power. Interestingly, this will also alter the scaling of b and $\bar{Z}$ with α; both will now scale very closely (b identically) with $\alpha^{-(1+4k)}$. Thus, the $\alpha \cdot \bar{Z}$ and $\alpha \cdot b$ numbers of Eq. 10 will now alter with α. None of the alterations discussed in this paragraph will affect the qualitative results of the correlations between residuals (Table 2).

The equations derived here (Eqs. 11–14) are probably the simplest that give the 0.25 scaling and the correct correlations between residuals (Tables 1 and 2); more complex formulations might attempt to recover 0.25 scaling (and the correct correlations between residuals) while allowing, for example, nonzero correlations between A, δ, and C, or more complex offspring production relations.

One special hypothesis: $\alpha \cdot M$. From Eq. 10b we have that $\alpha \cdot M$ depends only on δ. From a sample of 26 mammal species (6, 13), I estimated M and α (time from independence to maturation). A $\log_e$ plot has a slope of -0.98 (and $r = -0.88$) and the average $\alpha \cdot M$ equal to 0.72. Millar (1) gives relative

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size at weaning (δ) for 100 mammalian species (mostly <1 kg), with an average ($\bar{\delta}$) equal to 0.37. Since $1 - \delta^{0.25}$ is almost linear in δ over the range 0.15–0.65, we may use $3(1 - \bar{\delta}^{0.25})$ (Eq. **10b**) to predict the average $\alpha \cdot M$ for mammals; with $\bar{\delta} = 0.37$, we get $\alpha \cdot M = 0.66$. David Berrigan (personal communication) was able to use the literature to estimate δ for 23 of the 26 species (13) with estimated $\alpha \cdot M$ values. His sample had $\bar{\delta} = 0.33$, so average $\alpha \cdot M$ is here predicted to be 0.73. More interesting however is that $M \cdot \alpha$ is inversely related to δ, just as Eq. **10b** predicts; a linear regression has $r = -0.67$, significant at the >0.01 level. His detailed analysis will be published elsewhere.

Conclusion

Time will tell if the approach begun here continues to be a fruitful direction (or simply a temporally well-lit alley). Of course, there are additional life-history variables that show intercorrelations after adult body size is held constant (5–8); some of these relate to components of b. My present focus on b, $\bar{Z}$, M, and α is simply that they are the major variables in the demographic and life-history evolution equations and thus are easier to work with directly.

In the larger context of life-history evolution, one point is worthy of note. The only cost of reproduction allowed in the present theory is the diversion of energy from growth to offspring production; adult mortality is assumed to be fixed independent of reproduction, so that increased mortality is not a cost of reproduction. Many life-history models have increased adult mortality as a cost of reproduction (10, 23–26); the assumption may simply be wrong for female mammals, or such cost may affect their life histories in ways too small to disrupt the larger patterns.

1. Millar, J. S. (1977) *Evolution* **31**, 370–386.
2. Western, D. & Ssemakula, J. (1982) *Oecologia* **54**, 281–290.
3. Peters, R. H. (1983) *The Ecological Implications of Body Size* (Cambridge Univ. Press, Cambridge, U.K.).
4. Calder, W. A. (1984) *Size, Function and Life History* (Harvard Univ. Press, Cambridge, MA).
5. Read, A. F. & Harvey, P. H. (1989) *J. Zool.* **219**, 329–353.
6. Promislow, D. E. L. & Harvey, P. H. (1990) *J. Zool.* **220**, 417–437.
7. Harvey, P. H., Read, A. F. & Promislow, D. E. L. (1989) *Oxford Surv. Evol. Biol.* **6**, 13–31.
8. Harvey, P. H. & Zammuto, R. M. (1985) *Nature (London)* **315**, 319–320.
9. Linstedt, S. L. & Calder, W. A. (1981) *Q. Rev. Biol.* **56**, 1–16.
10. Charnov, E. L. (1986) *Oikos* **47**, 129–134.
11. Sutherland, W. J., Grafen, A. & Harvey, P. H. (1986) *Nature (London)* **320**, 88.
12. Stahl, W. R. (1962) *Science* **137**, 205–212.
13. Millar, J. S. & Zammuto, R. M. (1983) *Ecology* **64**, 631–635.
14. Reiss, M. J. (1989) *The Allometry of Growth and Reproduction* (Cambridge Univ. Press, Cambridge, U.K.).
15. Kozlowski, J. & Wiegert, R. G. (1987) *Evol. Ecol.* **1**, 231–244.
16. Kozlowski, J. & Wiegert, R. G. (1986) *Theor. Popul. Biol.* **29**, 16–37.
17. Lavigne, D. M. (1982) *J. Anim. Ecol.* **51**, 195–206.
18. Case, T. (1978) *Q. Rev. Biol.* **53**, 243–282.
19. Keyfitz, N. (1968) *Introduction to the Mathematics of Population* (Addison-Wesley, Reading, MA).
20. Maynard Smith, J. (1982) *Evolution and the Theory of Games* (Cambridge Univ. Press, Cambridge, U.K.).
21. Charnov, E. L. (1990) *J. Evol. Biol.* **3**, 139–144.
22. Charnov, E. L. & Berrigan, D. (1990) *Evol. Ecol.* **4**, 273–275.
23. Charnov, E. L. & Krebs, J. R. (1974) *Ibis* **116**, 217–219.
24. Bell, G. (1980) *Am. Nat.* **109**, 453–464.
25. Charlesworth, B. (1980) *Evolution in Age Structured Populations* (Cambridge Univ. Press, Cambridge, U.K.).
26. Williams, G. C. (1966) *Am. Nat.* **100**, 687–690.