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Dimensionless Numbers and the Assembly Rules for Life Histories [and Discussion]

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Dimensionless numbers and the assembly rules for life histories

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SUMMARY

This paper reviews recent efforts to use certain dimensionless numbers (DLNs) to classify life histories in plants and animals. These DLNs summarize the relation between growth, mortality and maturation, and several groups of animals show interesting patterns with respect to their numeric values. Finally we focus on one DLN, the product of the age of maturity and the adult instantaneous mortality, to show how evolutionary life history theory may be used to predict the value of the DLN, which differs greatly between major groups of animals.

1. INTRODUCTION

This paper is about the use of dimensionless numbers (DLNs) to characterize and classify life histories in animals and plants. DLNs are widely used in dynamical and mechanical problems where the behaviour of the system of interest often depends on the ratio or product of parameters and not the values of each alone. A simple example from theoretical biology is the equation for change in gene frequencies for a single diallelic locus under natural selection. Under the usual assumptions, the dynamics are entirely given by the relative fitnesses of the three genotypes. While actual Darwinian fitness is the product of survival and fertility (and has units of 'numbers'), relative fitness is constructed by dividing the three genotype fitnesses by the fitness of the heterozygote (and is dimensionless); thus, we get, for the genotypes AA : Aa : aa, the relative fitnesses $1\text{-}s:1:1\text{-}t$.

Mathematical functions between dimensional variables can always be rewritten in dimensionless forms by using formal techniques from so-called 'dimensional analysis' (see, for example, Giordano *et al.* (1987); Stephens (1991), for applications to behavioural ecology; or Stahl (1962) and Calder (1984) for body size and physiology). Dimensionless variables have a number of useful properties; for example, (i) they reduce the number of variables in the problem (e.g. three fitnesses reduced to two numbers, s and t; (ii) they express the *relation* between variables; (iii) the DLNs, being unit-free, have magnitudes that have absolute meaning from case to case ($s = 0.2$, $t = 0.5$ means the same thing with respect to genotype dynamics, independent of the actual survival times fertility values).

DLNs have sometimes been used to characterize life histories. Five examples will show this: (i) sex ratio (proportion males) in a brood (Charnov 1982); (ii) reproductive effort (Williams 1966) loosely defined as the proportion of available resources devoted to reproduction, as opposed to growth or maintenance; (iii) scaling allometry of life-history variables with body size (Harvey *et al.* 1989; Calder 1984; Millar & Zammuto 1983), the exponents are DLNs (indeed, deviations from log-scaling relations are also DLNs; Harvey *et al.* 1989); (iv) the dimensionless form of age-of-sex-change in a sequential hermaphrodite (Charnov & Bull 1989); and finally (v) the total force of mortality over some life-history phase, such as birth to adulthood (Ricklefs 1969; Charnov 1991). In each of these cases, empiricists have noted some general patterns (e.g. mortality rates scale with the -0.25 power of body size in mammals, or the first sex is always more abundant among the breeders under sex change) and life-history theorists have attempted general explanations as to why natural selection in the face of trade-offs has produced the patterns.

This paper reviews recent efforts to apply some other DLNs to characterize animal (and plant) life histories, in particular some numbers developed in the context of fishery science, which summarize relations between growth, mortality, and maturation (Beverton & Holt 1959). We review the Beverton–Holt patterns for fish, and extend the results to sea urchins, shrimp, snakes, and lizards. In the process we propose a new DLN related to theirs (Charnov & Berrigan 1990), and use this one to look additionally at birds and mammals. Finally, we show how evolutionary life-history theory may be used to answer why some of the patterns exist. Our claim is that the 'aggregate' characterization of life histories through these DLNs leads us to see new patterns in the data and to develop evolutionary life-history theory in novel ways.

2. LIFE HISTORIES WITH DETERMINATE AND INDETERMINATE GROWTH

Birds, mammals, insects (and a few other animals) have determinate growth where adult size does not alter. By contrast most other animals have inde-

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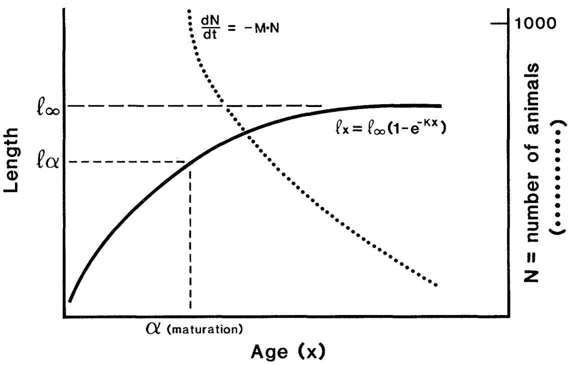

Figure 1. A life history under indeterminate growth. Growth in length (l_x) follows the Bertalanffy equation, $l_x = l_\infty(1-e^{-Kx})$, mass follows length to a power near 3. Maturation is at age α, length l_α, while l_∞ is the asymptotic length; thus l_α/l_∞ is the relative size at maturity. The adult instantaneous mortality rate is M. In practice M is a weighted average over the adult lifespan, weighted towards the younger adults (see Beverton (1963) for the specific statistic).

terminate growth where body size continues to increase after maturation. Figure 1 shows a typical life history. Body length (l) increases with age and is often usefully described by the Bertalanffy equation; in its simplest form the growth equation has two parameters, l_∞, the asymptotic length, and K, the growth coefficient. Maturation is at age α, corresponding to size l_α. In this simple example (figure 1) the adult instantaneous mortality rate (M) is shown as a constant, resulting in exponential decline for the cohort reaching the age of maturity. In actual practice M may increase over the adult life time; here we will be led to define an average M (Beverton 1963). K and M both have dimensions of 1/time, l_∞ and l_α have dimensions of length, and α has the dimension of time. From these we can construct three DLNs:

l_α/l_∞ = relative size at maturity (1)

$\alpha \cdot M$ = relation between maturation and adult mortality (ratio of age at maturity (α) to the average adult lifespan ($1/M$) (Charnov & Berrigan 1990)) (2)

K/M = relation between relative growth (K) and mortality (M). (3)

The number $K \cdot \alpha$ is related to l_α/l_∞ through the Bertalanffy equation of figure 1; or

$$\frac{l_\alpha}{l_\infty} = 1 - e^{-K \cdot \alpha}. \tag{4}$$

Notice also that equation (4) implies that any two of DLNs ($l_\alpha/l_\infty, K/M$ or $M \cdot \alpha$) suffice to determine the third.

The suggestion that we view life histories under indeterminate growth in terms of the two DLNs K/M and l_α/l_∞ goes back 30 years and is owing to Beverton & Holt (1959) and Beverton (1963), who developed the notion in relation to fish; they were motivated by the fact that in fisheries the steady-state equation for annual catch per recruit (a dimensionless equation) could be written in a form that included only three parameters, all of which were DLNs, two of which were K/M and l_α/l_∞. (Our use of M here differs slightly from theirs but the point here is simply to acknowledge their priority.) They were thus led to ask if various fish groups showed any patterns in the values of K/M and/or l_α/l_∞.

Determinate growers, like birds, mammals, and insects have l_α/l_∞ near 1; the $\alpha \cdot M$ number is useful to characterize them. There are, however, additional possibilities. With a clutch size per unit time per mother of b, independent of age, and survival to adulthood (age α) written as S, the average number of offspring produced over an individual's life is $b \cdot S/M$. Since b has units of 1/time, this equation is dimensionless and with a 1:1 secondary sex ratio will equal 2 in a non-growing population (Charnov 1986; Sutherland *et al.* 1986). We can rewrite it as $(\alpha \cdot b)/(\alpha \cdot M)\,S = 2$, which give a relation between three DLNs ($S, \alpha \cdot b, \alpha \cdot M$) imposed by the condition of population stability. This paper will only deal with the $\alpha \cdot M$ number for the determinate growers. Charnov (1991) discusses the other two for female mammals.

This paper will review some of the empirical patterns relating to the above DLNs, and will develop evolutionary life-history theory about the $\alpha \cdot M$ number. We begin with the classical Beverton–Holt patterns for indeterminate growers.

3. BEVERTON–HOLT: FISH

Thirty years ago Beverton & Holt (1959) and Beverton (1963) pioneered the comparative study of fish life histories by showing that within limited taxonomic boundaries (such as within the cod, salmon or herring family), there existed certain across species (or populations within a species) patterns in growth and mortality. These patterns, reviewed in Cushing (1968) and Pauly (1980) are two in number. (A third pattern, not developed here, is discussed in Charnov & Berrigan (1991).) Within each taxon the adult instantaneous mortality rate, M, and the Bertalanffy growth coefficient, K, are positively related to each other so that the ratio K:M tends to be relatively constant; and the K:M ratio differs between taxa. The second pattern is that the length at maturity (l_α) is positively related to the Bertalanffy asymptotic length (l_∞) so that the relative length at maturity, l_α/l_∞, tends to be a constant value within a taxon. Of course, as shown with equation (4), these two imply the constancy of $\alpha \cdot M$ within a taxon. Figure 2 shows an example of the data, here for the Clupeomorph fishes of the families Clupeidae and Engraulidae. Figure 2*a* shows a plot of $1/T_{\max}$ versus K, where $T_{\max}$ is the age of the oldest individual observed in a large sample. Beverton (1963) showed that, at least for large samples, many fish species or populations have maximum age ($T_{\max}$) that is highly correlated with the adult mortality rate M, so that $M = g/T_{\max}$ with $g \simeq 6$. In a much larger and taxonomically diverse sample of animal species, Hoenig (1983) confirmed Beverton's relation, with a similar g value. Applied to figure 2, this relation has

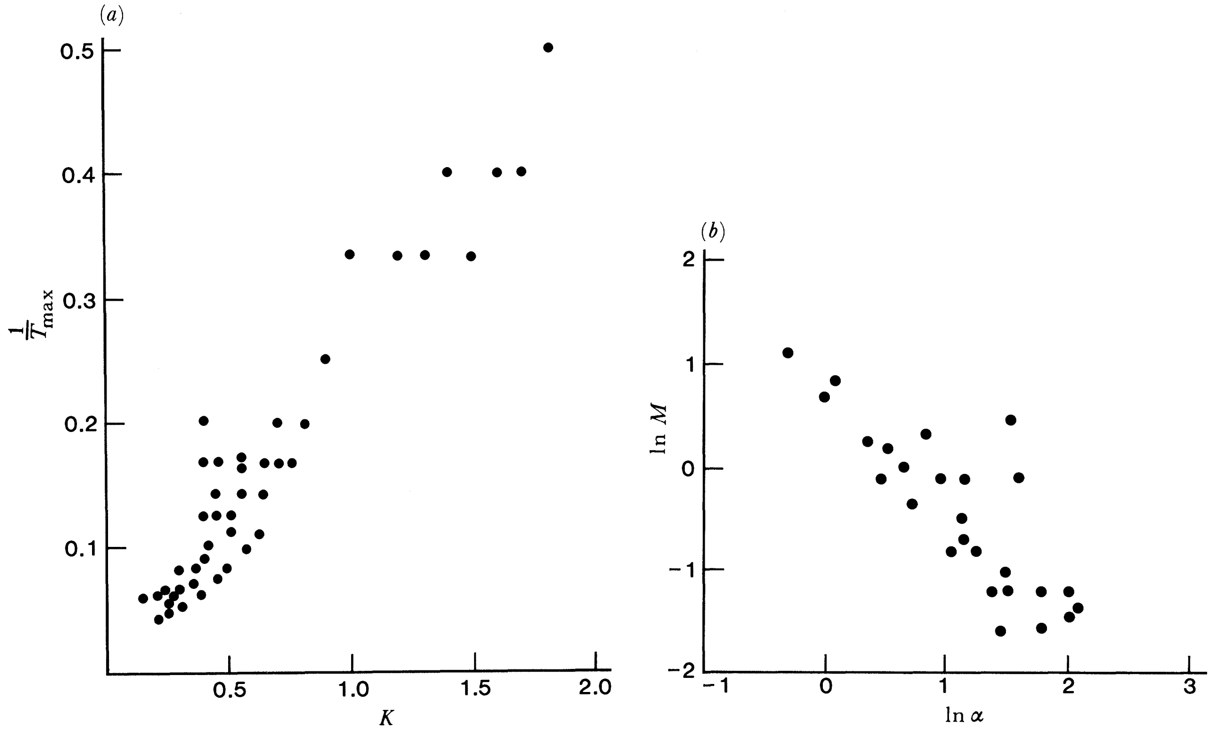

Figure 2. (*a*) Growth coefficient, K, against the inverse of the maximum lifespan ($1/T_{\max}$) for 45 populations of ten species of fish in the families Engraulidae and Clupeidae. Because the adult instantaneous mortality rate, M, is proportional to $1/T_{\max}$ (or $M \simeq 6/T_{\max}$), we have that $M \simeq 1.5$ K for these fish. Figure redrawn from Beverton (1963). (*b*) The adult instantaneous mortality rate, M, is inversely proportional to the age of maturity, α, for fish in the families Clupeidae and Engraulidae, or $\ln M = C - \ln \alpha$. Data from Beverton (1963) and only includes populations with direct estimates of M (which is why there are fewer data points here compared with figure 2*a*). ($y = 0.69 - 1.04x$; $r = -0.84$; $n = 26$; s.t.d. errors; slope $= 0.14$; intercept $= 0.17$.) Time in years.

$M \simeq 1.5 \cdot K$ for the Clupeomorpha. Figure 2*b* shows that M and α are inversely proportional, making $M \cdot \alpha \simeq e^{0.69} = 2$. These two make $l_\alpha / l_\infty \simeq 0.75$, a number confirmed by the length data. While Beverton (1963) discusses some between-species differences in these numbers, the overall pattern is near constancy.

4. OTHER INDETERMINATE GROWERS

K/M, l_α / l_∞ and $\alpha \cdot M$ may also be approximately constant within other taxa showing indeterminate growth. Ebert (1975) showed K/M near 1 in a sample of over a dozen species of sea urchin ($r = 0.91$, sample size = 15, line through the origin). He provided no data on $\alpha \cdot M$ or l_α / l_∞. Charnov (1979, 1989) showed all the Beverton–Holt patterns to hold within the shrimp family Pandalidae in a sample that included 27 populations of five species and spanned the Northern latitudes from California to the subarctic. The data have $K/M \simeq 0.37$, $l_\alpha / l_\infty \simeq 0.56$, and $\alpha \cdot M \simeq 2.2$.

The above indeterminate growers are aquatic ectotherms. Shine & Charnov (1991) asked if the Beverton–Holt patterns also held for terrestrial ectotherms. They assembled data for 16 species of snakes and 20 species of lizards. l_α / l_∞ is near a constant for both snakes ($\simeq 0.64$) and lizards ($\simeq 0.73$). M and α are also inversely proportional in these groups, with $\alpha \cdot M \simeq 1.3$ for lizards and a bit higher ($\simeq 1.5$) for snakes.

It appears that the Beverton–Holt fish patterns (the approximate constancy of $\alpha \cdot M$, l_α / l_∞ and K/M 'within a kind-of-animal') hold for several other groups with indeterminate growth; *the life-history rules are about the allowed values for certain dimensionless numbers*. Now we turn to the determinate growers, birds and mammals.

5. $\alpha \cdot M$ IN BIRDS, MAMMALS (AND THE OTHERS)

Bird and mammals both have determinate growth but with one key difference. Mammals begin reproducing at near 90% their adult mass while birds with altricial young usually reach their adult mass near the time of independence from the parents. Most birds reach adult size long before α while mammals reach it near α.

They also differ in the $\alpha \cdot M$ number. Figure 3 shows a plot of $1/M$ (average adult lifespan) versus α for 66 bird species and 26 mammal species; the birds have adult lifetimes about double a mammal with the same age of maturity (recall that $1/M$ divided by α is $1/(\alpha \cdot M)$). $\alpha \cdot M$ is $\simeq 0.70$ for mammals, $\simeq 0.40$ for birds. A plot of $\ln M$ versus $\ln \alpha$ shows a slope of -1 for the mammals, but a somewhat steeper slope (-1.2) for the birds; thus $1/M$ is proportional to α in mammals but only approximately so for the birds. Birds with higher α^s have slightly higher $1/M^s$ than expected by strict proportionality (table 1).

Of course, the other way to summarize these relations is to plot the average length of the adult lifespan (expectation of further life at age α) ($\simeq 1/M$) versus the age at maturity (α). We summarize these

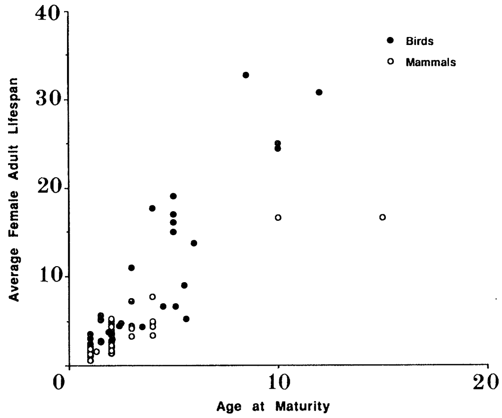

Figure 3. Average female adult lifespan ($1/M$) plotted against age of maturity (α) for 26 mammal species (data from Millar & Zammuto (1983) and Promislow & Harvey (1990)) and 66 bird species (data from many sources). Statistics as follows: mammals: $y = 0.27 + 1.25x$ ($r = 0.95$, $n = 26$); birds; $y = -1.32 + 2.75x$ ($r = 0.91$, $n = 66$). For a given α, birds have adult lifespans near double a comparable mammal. See also figure 4.

Table 1. *A summary of* $\alpha \cdot M$ *for all the groups*

group	$\alpha \cdot M$
birds	$\simeq 0.40$
mammals	$\simeq 0.70$
snakes and lizards	$\simeq 1.40$
fish and shrimp	$\simeq 2.00$

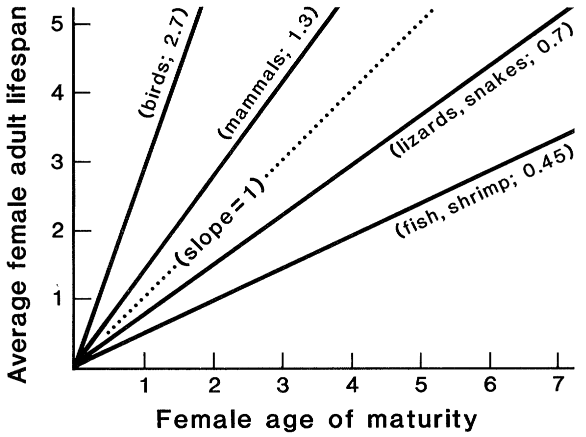

Figure 4. Average adult lifespan ($1/M$) versus α for all groups. For contrast I treat the birds as having a proportional relation (see text for qualifications). I also pool lizards and snakes. Shrimp data are for both sexes. Number on each line refers to estimated slope, the number $1/(\alpha \cdot M)$. (After Charnov & Berrigan 1990.)

data in figure 4. Notice that birds have adult lifetimes, for a given age of maturity, about 2 × mammals, 3 × snakes and lizards, and 5 × fish and shrimp. Notice also that figure 4 says nothing about the actual values of α or M; indeed, there are fish (Beverton 1963; Beverton & Holt 1959) with ages of maturation of 10–20 years, the same magnitude as elephants and well beyond most birds. It is the *relation* between α and M which differs between groups; upon reaching the maturation age of 10 years, a bird has an average of about 25 years to live, a fish has 5 years. These differences are so striking that they demand explanation in terms of some fundamental differences between the groups (Charnov & Berrigan 1990).

6. WHAT SETS $\alpha \cdot M$?

The above heading could well expand to include K/M and l_α/l_∞, but this paper will only deal with $\alpha \cdot M$. Charnov & Berrigan (1991) have begun a life-history evolution theory aimed at predicting all three DLNs under indeterminate growth. Our aims are more modest here ($\alpha \cdot M$ alone) and we ignore the added complications of indeterminate growth.

We believe that the answer to why $\alpha \cdot M$ takes on particular values lies in how natural selection acts to set the maturation time itself. In what follows we will construct a theory for evolution of the age of maturity and require as its output the $\alpha \cdot M$ number. The broad brush approach to the theory will be in three phases: first, a general evolutionary theory for α; second, a phenomenological approach to predicting the $\alpha \cdot M$ number; and finally an 'individual growth or productivity' approach specifically designed for determinate growers like mammals.

The model

Consider a newborn female and define l_x as the probability she is alive at age x, and b_x as her birth rate, in daughters, at age x. Her lifetime production of daughters is:

$$R_o = \int_\alpha^\infty l_x\, b_x\, \mathrm{d}x. \tag{5}$$

We can rewrite R_o as follows:

$$R_o = l_\alpha \left[\frac{\int_\alpha^\infty l_x\, b_x\, \mathrm{d}x}{l_\alpha} \right]. \tag{6}$$

The term in brackets is the average number of daughters born over a female's adult lifespan, the 'reproductive value' (Fisher 1930) of an age α (a just mature) female, and will therefore be labelled $V(\alpha)$.

Now, write l_α as $\mathrm{e}^{-\phi(\alpha)}$. R_o can now be written as:

$$R_o = \mathrm{e}^{-\phi(\alpha)} \cdot V(\alpha). \tag{7}$$

For R_o to be a valid fitness measure, the population must not be growing, or $R_o \approx 1$. This is a population dynamic side condition on an optimization-of-R_o problem (Charnov 1986) and is discussed in great detail in Charnov (1990). We wish to maximize R_o with respect to α, which is the same as maximizing:

$$\ln R_o = \ln V(\alpha) - \phi(\alpha).$$

In equilibrium (at the ESS α, Maynard Smith (1982)), we require

$$\frac{\partial \ln V(\alpha)}{\partial \alpha} = \frac{\partial \phi(\alpha)}{\partial \alpha}. \tag{8}$$

Now, suppose that $Z(x)$ is the instantaneous mortality rate at age x; in general $Z(x)$ will decrease with x (and for many species will reach some low and near constant value before maturation; it may go up again late in life). We may thus write

$$\phi(\alpha) = \int_0^\alpha Z(x)\,\mathrm{d}x$$

and

$$\frac{\mathrm{d}\phi(\alpha)}{\partial\alpha} = Z(\alpha).$$

But if mortality does not change much after maturation $Z(\alpha)$ is the adult mortality rate, called M earlier in this paper. The ESS equation (8) may now be written as

$$\frac{\partial \ln V(\alpha)}{\partial\alpha} = M. \tag{9}$$

This equation for the ESS age of maturity is the first step towards getting a value for the $\alpha\cdot M$ number. The key apparently lies in the $V(\alpha)$ function; notice that equation (9) does not require that we know the actual $V(\alpha)$ function, only its proportional change with α, its shape (Charnov 1990). For example, suppose that we guess that $V(\alpha) \propto \alpha^d$; $V(\alpha)$ is a power function in α with exponent (a DLN!) d. $\ln V(\alpha) = \text{constant} + d \ln \alpha$, and

$$\frac{\partial \ln V(\alpha)}{\partial\alpha} = d/\alpha.$$

If we put this into equation (9), a rather interesting thing happens; the ESS is where $\alpha\cdot M = d$. All life histories where $V(\alpha)$ can be treated as a power function in α have the property that '$\alpha\cdot M$ = the exponent' at the ESS. Here is a theory for the $\alpha\cdot M$ number; it suggests that fish have quite high exponents and that birds have quite small ones. Better still, we know the values of d (at least approximately) to be searched for. This is a phenomenological model as nothing really informs us as to what determines the d coefficient, only that whatever it is is similar within fish, birds, etc. It seems clear that to go further we must tie d (or something like it) back to general models of growth, or other developmental processes.

7. $\alpha\cdot M$ IN MAMMALS

In this section we model $V(\alpha)$ as a function of individual productivity; the approach makes two new assumptions, in addition to those leading to equation (9). These are that growth depends on body size (W) and can be described as $\mathrm{d}W/\mathrm{d}T = AW^c$ (equation 10), and that growth is determinate and ceases at reproductive maturity when energy is simply diverted from growth to offspring production. The derivation in Appendix 1 shows that these assumptions and equation (9) lead to the prediction that $\alpha\cdot M = (c/1-c)\,(1-\delta^{1-c})$ (equation 11), where c is the exponent describing the size dependence of energy acquisition for growth and reproduction (equation 10) and δ is the offspring's relative size at independence, its mass at independence divided by its mother's mass. Direct measurements of animal production rates put c near 0.75 within many taxa (Lavigne 1982). Note that if $c = 0.75$, equation (11) reduces to $3(1-\delta^{0.25})$ (equation 12). The relative size at independence (δ) is the point at which an animal moves from a potential growth trajectory determined by its primary care giver to one determined by its own size. Thus we are assuming that a mammal grows during two periods; one from birth to independence where its mother controls its growth rate and a second from independence to maturity, where its own size determines its growth rate. The size at maturity is assumed to be the final adult size and this size in turn determines the offspring production rate through equation (10). The age at maturity (α) is the interval between independence (estimated here as weaning) and first reproduction.

Equation (12) is almost linear in δ for $0.2 < \delta < 0.6$, a range that includes most mammals (Millar 1977). This means that to predict the average $\alpha\cdot M$, it is sufficient to substitute the average $\delta\ (=\bar{\delta})$ for mammals. Millar (1977) estimated $\bar{\delta}$ (weaning mass/adult female mass) for 100 species, mostly < 1 kg in mass, and got $\bar{\delta} = 0.37$. We have an additional sample of 23 species (Appendix 2), mostly of body size > 1 kg and get $\bar{\delta} = 0.33$. These numbers inserted into equation (12) predict $\alpha\cdot M$ to be ≈ 0.7, right at the observed average value.

We have also tested the prediction that $\alpha\cdot M = 3(1-\delta^{0.25})$ by comparing the values of $\alpha\cdot M$ with the ratio of mass at weaning to the average adult female mass (δ) for 23 species of mammals (figure 5; data sources and species listed in Appendix 2). The data strongly support the predicted relation. Notice that the r value of the linear regression between observed and predicted values of $\alpha\cdot M$ increases from 0.71 to 0.93 when we fit averages (figure 5*b*) over even intervals of δ rather than all 23 points (figure 5*a*). We cannot distinguish between a linear regression of $\alpha\cdot M$ versus δ ($r = -0.67$, $p < 0.001$) and this slightly curvilinear relation ($r = 0.71$, $p < 0.001$). In these tests we assume that $c = 0.75$. We also used nonlinear regression to fit the one parameter model for c (equation 11). The solution from fitting all 23 points, plus or minus one standard error, gives a value of $c = 0.74 \pm 0.03$ ($r = -0.71$, $p < 0.001$) and the solution for the five average values gives $c = 0.75 \pm 0.04$ ($r = -0.93$, $p < 0.03$). Because the production relation of equation (10) appears to be an important component of mammalian life histories, it is particularly significant that at evolutionary equilibrium, the 0.75 exponent appears in the relation between $\alpha\cdot M$ and δ (equation 12). Our analysis (figure 5) is the first indirect determination of this exponent and gives virtually the same answer as direct measurements of individual or offspring production (Lavigne 1982).

The ecological correlates of differences in $\alpha\cdot M$ and δ within the mammals are not obvious. The three largest values of δ in this study are those of the impala, wildebeest, and zebra, and the three lowest those of the rabbit, otter, and boar; squirrels and elephants have similar and intermediate values of δ and $\alpha\cdot M$. Body size is also not responsible for the observed correlation between $\alpha\cdot M$ and δ because $\alpha\cdot M$ is not correlated with adult mass ($r < 0.001$, $p > 0.05$) or mass at

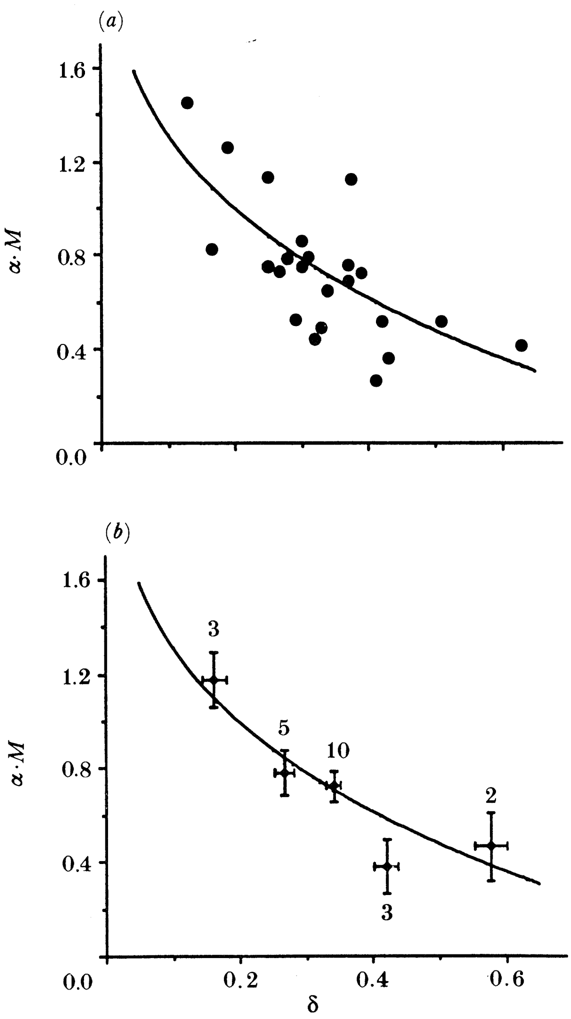

Figure 5. We plot the value of $\alpha \cdot M$ versus δ for females of 23 mammal species (see Appendix 2). α is the age at first reproduction adjusted for the parental care period. M is the average adult instantaneous mortality rate (Beverton 1963) and δ is the ratio of mass at weaning to adult female mass. (*a*) We show the observed values of $\alpha \cdot M$ (●) and the predicted values (equation 12) (—). We tested the fit with a linear regression of observed against predicted values ($r = 0.71$, $p < 0.001$). (*b*) Here we averaged the values of δ and $\alpha \cdot M$ over the intervals $\delta = 0.1$–0.2, 0.2–0.3, 0.3–0.4, 0.4–0.5, and > 0.5. The error bars are one standard error, the numbers are the sample size, and the line is the predicted value ($r = 0.93$, $p < 0.03$). The statistical tests are one-tailed.

weaning ($r < 0.003$, $p > 0.05$). Considering the uncertainties involved in field estimates of life-table parameters and the estimation of δ by weaning mass, the observed fit of the data to the predicted line is encouraging.

8. DISCUSSION AND CONCLUSION

Perhaps the most appealing aspect of a dimensionless approach to life histories is its focus on general patterns, in terms of relations between vital rates (growth, mortality, maturity, fecundity); and the data do show patterns (even for some plant groups, see, for example, Loehle (1988) and figure 2 therein), begging for explanation in terms of evolutionary life-history theory (which itself must be made dimensionless). The exploration of these patterns, in both theory and data, has really just begun. Life-history theory is almost always based on the assumption of fitness maximization in the face of trade-offs (= constraints). If the fitness function (e.g. R_0) does not differ between species, then species differ in life history only because they differ in trade-offs. However, similarities of DLNs (within a taxon) strongly suggest similarities in the trade-off functions. Indeed, several modelling efforts (Charnov 1990, 1991; Charnov & Berrigan 1991) say that similarities of the DLNs point to similarities of the shapes of the trade-offs (e.g. $\alpha \cdot M \approx 1$ implies $d \approx 1$, under the assumption $V(\alpha) \propto \alpha^d$). Another way to say this is that the various DLNs show *conservation principles* (i.e. they are fairly invariant within a taxon) and that the existence of such conserved quantities points to deeper underlying symmetries (Watson 1990) in the transitions allowed for trade-offs; the allowed trade-offs may differ in height but not in shape.

We would like to conclude this paper with a brief and final illustration of the above points, chosen from the theory of sex change. Sex change exists in two forms: protandry, male first and protogyny, female first. The usual evolutionary theory aims to predict the order and time of sex change (Charnov 1982). The dimensionless version of sex-change theory aims to predict the breeding sex ratio. Under quite broad conditions, the theory says that the first sex will be more abundant among the breeders, and that the extent of bias depends upon just how fast (= shape) each sex gains reproductive ability with age or size (Charnov 1982; Charnov & Bull 1989). Indeed, the first sex is almost always more abundant, and the skew is greater under protogyny (Charnov & Bull 1989). The dimensionless view of sex change provides us with some broad empirical rules, and some general theoretical reasons (hypotheses) as to why the data patterns exist.

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APPENDIX 1 $\alpha \cdot M$ FOR MAMMALS

The growth and production model developed here is strictly applicable only to determinate growers like female mammals who cease growing at age α. The argument is from Kozlowski & Wiegert (1986, 1987), and Charnov (1990, 1991).

Let W stand for body mass; then a great many groups of animals show the following growth relation (before maturation but after independence from parental feeding):

$$\frac{\mathrm{d}W}{\mathrm{d}T} = AW^{c}, \tag{1}$$

where c is near 0.75 and A varies between taxonomic groups; see Lavigne (1982) and review by Reiss (1989). Set $c = 0.75$; then we have

$$\int_{W_0}^{W(\alpha)} \frac{\mathrm{d}W}{W^{0.75}} = \int_{0}^{\alpha} AT, \tag{2}$$

where W_0 is the size at the end of parental feeding, called time zero. The change of variable $Y = W^{0.25}$ leads to $(\mathrm{d}Y = [0.25]/[W^{0.75}]\,\mathrm{d}W)$ and the general solution of equation (2):

$$W(\alpha)^{0.25} - W_0^{0.25} = \frac{A\alpha}{4}.$$

Now, write W_0 as $\delta \cdot W(\alpha)$; we have finally

$$W(\alpha)^{0.25} = \frac{0.25 \cdot A}{1-\delta^{0.25}} \cdot \alpha \quad (\delta \text{ is of course a DLN}). \tag{3}$$

Notice that α in equation (3) is measured from some time called zero when we assign the individual some starting size W_0 which is taken to be δ proportion of the adult size.

Equation (3) is simply a growth relation. Kozlowski & Wiegert (1986, 1987) noted that equation (1) is also an offspring production relation if offspring are simply the result of shifting resources, primarily energy, from self-growth to offspring-production. Let $b =$ offspring production (per female) per unit time, then for a determinate grower $V(\alpha) = b/M$ (see equation (7) in text for $V(\alpha)$). Provided M does not increase with a delay in maturation (the mortality rate reaches its minimum value prior to age α) then $V(\alpha) \propto b$. But if $b \propto \mathrm{d}W/\mathrm{d}T \propto AW^{0.75}$, then $V(\alpha) \propto AW^{0.75}$, $\ln V(\alpha) = \text{Constant} + 0.75 \log W$ and

$$\frac{\partial \ln V(\alpha)}{\partial \alpha} = \frac{0.75}{W}\frac{\mathrm{d}W}{\mathrm{d}T} = 0.75\,AW^{-0.25}.$$

From equation (9) in the text we have the ESS result

$$M = \frac{\partial \ln V(\alpha)}{\partial \alpha} = 0.75AW^{-0.25}. \tag{4}$$

If we use the growth equation (3) to eliminate W from (4), the following results:

$$\alpha \cdot M = 3(1-\delta^{0.25}). \tag{5}$$

For an arbitrary exponent c in equation (1), we have in general

$$\alpha \cdot M = \frac{c}{1-c}[1-\delta^{1-c}]. \tag{6}$$

Notice that this argument (equations 3 and 4) also gives the known ± 0.25 scaling of age at maturity (α) and mortality (M) with adult body size (Harvey *et al.* 1989).

APPENDIX 2

Table 1. *Data on $\alpha \cdot M$, and δ for 23 species of mammals*

(The adult mortality rate (M) and age at first reproduction (α) (from estimated age at independence) were obtained from Millar & Zammuto (1983). The ratio of mass at weaning to adult mass (δ) was obtained from the sources listed below.)

species	$\alpha \cdot M$	δ	source for δ
Castor canadensis	1.13	0.25	Aleksiuk & Cowan (1969)
Sciurus carolinensis	0.52	0.29	Horwich (1972)
Spermophilus armatus[a]	0.78	0.28	Slade & Balph (1974)
S. beldingi	0.75	0.30	Morton & Tung (1971)
S. lateralis	0.76	0.37	Millar (1977)
S. parryi	0.79	0.31	Armitage (1981)
Tamias striatus	0.86	0.30	Wishner (1982)
Tamiascurus hudsonicus	0.44	0.32	Millar (1977)
Ochotona princeps	0.52	0.42	Millar (1977)
Sylvilagus floridanus	1.45	0.13	Millar (1977)
Lutra canadensis	0.82	0.17	Mason & Macdonald (1986)
Lynx rufus	0.73	0.27	Crowe (1975)
Mephitis mephitis	0.65	0.34	Casey & Webster (1975)
Taxidea taxus	0.49	0.33	Neal (1986)
Equus burchelli	0.42	0.63	Wackernagel (1965)
Aepyceros melampus	0.36	0.43	Howells & Hanks (1975)
Cervus elaphus	1.13	0.37	Clutton-Brock *et al.* (1982)
Connochaetes taurinus	0.52	0.51	Talbot & Talbot (1963)
Kobus defassa	0.27	0.41	Spinage (1982)
Ovis canadensis	0.72	0.39	Hansen & Deming (1980)
Sus scrofa	1.26	0.19	Myrcha & Jezierski (1972)
Syncerus caffer	0.69	0.37	Sinclair (1977)
Loxodonta africana	0.75	0.25	Laws (1966)

[a] Averaging the four values for the *Spermophilus* spp did not significantly affect the results of the analysis shown in the text.

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Discussion

R. J. H. Beverton (*Montana, Old Roman Road, Langstone, Gwent NP62JU, U.K.*). It is intriguing to see how Professor Charnov has been able to extend the early explorations by Holt and myself into dimensionless indices of life-history characteristics to a wide range of animal groups. Perhaps I could add two comments as a postscript. One concerns Professor Stearn's question (not printed) about the reality of the results. It is true that there is strong covariation in certain of the underlying parameters and it would certainly be unwise, for example, to attempt to apply detailed statistical tests of linearity to some of the relations. Nevertheless, the broad patterns of the basic ratios which Professor Charnov is comparing – such as that between age at maturity and longevity – are not artefacts; and his finding that they take clearly different characteristic values for the major animal groups – fish, reptiles, birds and mammals – opens up further rewarding avenues of study.

My other comment concerns the variation of these ratios within the environmental range of one species. The North American fish *Stizostedion vitreum* (walleye) provides a good example. At the southern end of its range, in Texas and Colorado, it matures (with difficulty) at 2 years and none live longer than 4 years, whereas in northern Canada it does not mature until it is about 7 or 8 years and lives to about 20; but the *size* at maturity and the total lifetime fecundity per maturing recruit is nearly the same throughout the environmental range. It is as if temperature is determining the 'rate of living' – manifest both in the time it takes to reach a threshold size at maturity and the subsequent lifespan, with growth and fecundity adjusted to achieve nearly the same overall 'fitness'. As John Thorpe pointed out at this meeting, there is much still to be learned about the physiological basis of the attainment of maturity.