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Evolution of life-history variation among species of altricial birds

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ABSTRACT

A unified approach is developed for the comparative structure of bird life histories. It combines four basic components (individual production rate as a function of adult body size, stable demography, inter-generational competition for breeding sites, and natural selection for an optimal size) to predict both the powers and intercepts of the interspecific allometries of life-history variables to adult size. The theory also predicts when a taxon should deviate from the interspecific scaling lines. Finally, the theory predicts (or makes use of) several dimensionless numbers, particularly the ratio of non-breeders to breeders.

Keywords: allometry, birds, density dependence, dimensional analysis, life-history allometry, population regulation, production.

INTRODUCTION

Birds and mammals are similar in having a fixed adult size (determinate growth); they differ in that mammals usually begin reproducing upon reaching adult size, whereas altricial birds are reared to adult size by their parents, much in advance of their age of first reproduction (Williams, 1992; Charnov, 1993). A female mammal stops growing because she diverts her production, her growth, to the production of offspring (Charnov, 1993; Kozlowski and Weiner, 1997). Most life-history evolution models treat adult body size and age of first reproduction as resulting from this decision. Since altricial birds are adult size at the termination of parental care, what then determines their adult size and age of first reproduction? G.C. Williams (1992) recently posed this as an unsolved puzzle for evolutionists: Why do birds typically wait one or more years after reaching adult size to begin reproducing? The puzzle is even greater since birds and mammals show many *similarities* in their comparative life histories. To mention three: (1) Birds and mammals are similar in the exponents for the body size scaling rules for various life-history and physiological variables (Calder, 1984; Charnov, 1993; West *et al.*, 1997); for example, production or metabolism ($\approx\frac{3}{4}$) (Nagy, 1987), yearly offspring production and yearly mortality rate ($\approx-\frac{1}{5}$ to $-\frac{1}{3}$) (Gaillard *et al.*, 1989). (2) Birds and mammals also share the attribute that deviations from various interspecific scaling lines are inter-correlated (Charnov, 1993; Saether, 1988); for example, long lifespans go together with small yearly clutch size and high age at maturity at a fixed

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body size. (3) Birds and mammals share a number of invariant dimensionless relations (Charnov, 1993). For example, the ratio of the average adult lifespan to the age of first reproduction is ≈2.0–2.5 for birds and ≈1.3 for mammals (Charnov, 1993). The ratio is (approximately) invariant within each taxon, while the numerical value differs between taxons. A fourth comparison, a *difference* worthy of note, is their lifespans: at a fixed body size, birds generally have the longer average adult lifespans (Calder 1984; Gaillard *et al.*, 1989), typically several times longer.

The aim of this paper is to predict between-species life-history allometries and several dimensionless invariants for altricial birds; the theory will use many of the same elements as my previous work on mammal life histories (Charnov, 1993), but the causality will be somewhat different. The theory is mostly stimulated by the first observation in the previous paragraph – altricial birds grow to adult size much in advance of the age of first reproduction. I attack the question of what sets the age of first reproduction by suggesting a new demographic invariant for birds: birds begin changing from non-breeder to breeder when the ratio of numbers of non-breeder to breeder reaches a critical value, a competition-for-breeding-sites threshold. I will show how this (combined with one other plausible assumption) is perhaps a key to several other features of bird life histories.

STABLE DEMOGRAPHY

Consider a life history where growth ceases before or at adulthood, which is also characterized by constant fecundity and constant adult mortality. Let b be the offspring production in daughters per unit time, $S(\alpha)$ the survival fraction of daughters to the age of first breeding (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 (Charnov, 1997)

$$R_0 = \frac{b \cdot S(\alpha)}{M} \tag{1}$$

where $1/M$ is the average length of the adult lifespan during which a female produces b daughters per unit time, a proportion S of whom survive. In a non-growing (stationary) population, $R_0 = 1$. I assume that $b \cdot S/M \approx 1$ as a consequence of density dependence somewhere in the life cycle.

What sets *b*?

Suppose (Nagy, 1987) that an adult of body mass W has a production rate ($\mathrm{d}P/\mathrm{d}t$) of

$$\frac{\mathrm{d}P}{\mathrm{d}t} = A \cdot W^{0.75} \tag{2}$$

Further suppose that the offspring are of mass W_0 at independence from the parents, and that each costs $C \cdot W_0$, in units of P, to produce. Then the offspring reared to independence per unit time will be the inverse of the time to rear one offspring (t), or $(\mathrm{d}P/\mathrm{d}t) \cdot t = W_0 \cdot C$. Since half the offspring are daughters, $1/(2 \cdot t)$ is b, or

$$b = \frac{\mathrm{d}P}{\mathrm{d}t} \cdot \frac{1}{2 \cdot W_0 \cdot \mathrm{C}} = \frac{A \cdot W^{0.75}}{2 \cdot W_0 \cdot \mathrm{C}} \tag{3}$$

Collect together taxa where $W_0/W = \delta$ (size at independence is a constant proportion, δ, of adult size) and we get

$$b = \frac{A}{2} \cdot \frac{W^{0.75}}{C \cdot \delta \cdot W^1} = \frac{A}{2 \cdot C \cdot \delta} \cdot W^{-0.25} \tag{4a}$$

Thus, b scales with the –0.25 power of adult body size among species with similar A, δ and C values (Fig. 1). This is the same offspring production model as previously developed for mammals (Charnov, 1991). If production scales with an exponent different from 0.75, the scaling exponent will equal one minus the production exponent. If we plot loge b versus loge W for a collection of taxa ranging in A, δ or C, the scatter will reflect that variation (Fig. 1). If loge $(A/(2 \cdot C \cdot \delta))$ is not correlated with W, the fitted log line will pass through the mean of loge $(A/(2 \cdot C \cdot \delta))$ with a slope of –0.25; individual taxa will fall above or below the fitted line depending upon their own values of loge $(A/(2 \cdot C \cdot \delta))$ compared to the average value (Fig. 1). A typical mammal (Charnov, 1993) has $\delta \approx 0.3$. For altricial birds, we set $\delta = 1$, so

$$b = \frac{A}{2 \cdot C} W^{-0.25} \tag{4b}$$

The time to rear one offspring to independence is $1/(2 \cdot b)$, and components of this clearly scale with exponents of $\approx$ 0.20–0.25 in various data sets (Saether, 1987). $\delta \ll 1$ for precocial species, which is why I restrict attention to altricial species.

While this offspring production model for b is simple, it appears to capture the basic reasons why a collection of taxa fit a –0.25 scaling line, and why individual taxa deviate. Furthermore, equations (2) and (4) may well be the main way in which body size (i.e. allometry) enters life-history evolution (Charnov, 1993).

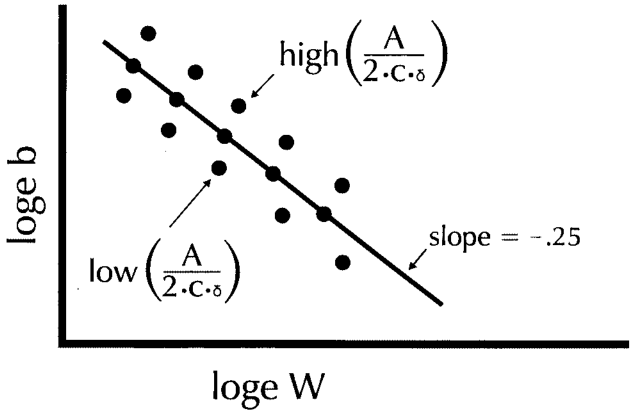

Fig. 1. Yearly production of offspring (b) will scale as –0.25 with adult body mass (W) for a collection of taxa with similar $A/(2 \cdot C \cdot \delta)$ values. See text for derivation.

What sets M^{-1}?

Let us return to equation (1) and rewrite it as $1/M = 1/(b \cdot S)$. Or, from equation (4),

$$M^{-1} = \frac{1}{S} \cdot \frac{2 \cdot C}{A} \cdot W^{0.25} \tag{5}$$

The average adult lifespan (M^{-1}) will scale with the 0.25 power of adult body size for species with similar C, A and S values. As just discussed for the b scaling, variation around the typical interspecific line will be most controlled by loge (C/A) and (here) variation in –loge S. Note that taxa with high b^s for their body size will almost automatically have low adult lifespans, as seen in the data (Saether, 1988). So a 0.25 allometry for adult lifespan goes together with a good b allometry *and an invariant S value*. It has long been realized that S is (approximately) an invariant with respect to body size, and many other features of bird lifestyles (Ricklefs, 1969, 1977); Table 1.1 in Charnov (1993) shows Ricklef's original data compilation, which puts $b/M \approx 5$, making $S \approx 0.2$. While other data sets yield different S values (B.-E. Saether, personal communication), this paper will use 0.2 as a point of illustration.

Note that I have not claimed that the invariance in S *causes* the M^{-1} allometry. Previous work on mammal life histories (Charnov, 1991) derived the M^{-1} allometry from an evolutionary model setting the age of first reproduction (α). Given a production relation for individual growth ($\mathrm{d}W/\mathrm{d}t = A \cdot W^{0.75}$), this model has adult body size as a function of the 'adult' mortality rate (M), or

$$M^{-1} \approx \frac{1.33}{A} \cdot W^{0.25} \tag{6}$$

The mammal model then derived S = 'a constant' by assuming density-dependent mortality in the very young, setting $R_0 = 1$, and so solving for S. For the mammal model (Charnov, 1993), the ESS W plus $R_0 = 1$ *causes the invariance in S*.

But, since birds reach W often long before the age of first reproduction, the argument leading to equation (6) probably does not hold. So, why is S an invariant for birds? And what links adult lifespan (M^{-1}) to W?

What sets α?

To get at α we must ask what an individual of adult size is waiting for. It is obvious that as α goes up, a non-growing population will have a greater ratio of non-breeders ($<\alpha$) to breeders ($>\alpha$), as illustrated in Fig. 2. Divide the pre-reproductive period into two parts. In a very short period at the beginning, mortality is assumed to be density-dependent and I proportion of the offspring survive it. After this period, immature mortality is assumed to be a constant (q). Of course, the adult instantaneous mortality rate is fixed at M. What is the ratio of the numbers of individuals $<\alpha$ in age to individuals $>\alpha$ in age (N_J/N_A)? If n individuals are reared per unit time,

$$N_J = n \cdot I \int_0^{\alpha} e^{-q \cdot x} \mathrm{d}x \tag{7a}$$

and

$$N_A = n \cdot I \cdot e^{-q \cdot \alpha} \int_0^{\infty} e^{-M \cdot y} \mathrm{d}y \tag{7b}$$

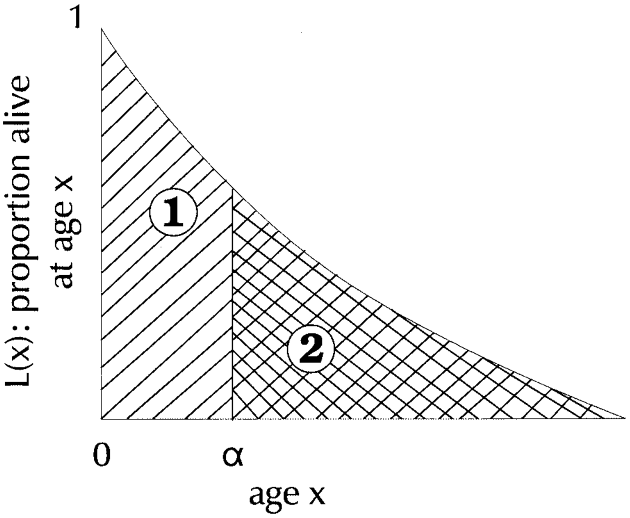

Fig. 2. In a non-growing population, the ratio of the number of individuals younger than age α to the number older than age α is the ratio of the respective areas under the $L(x)$ curve, or ① divided by ②. The text uses this rule to develop a model for α taken to be the age at first reproduction.

Equations (7a) and (7b) assume the time period during the I mortality is very small relative to α (and may be ignored). Their ratio is:

$$\frac{N_J}{N_A} = \frac{(1/q)(1 - e^{-q \cdot \alpha})}{e^{-q \cdot \alpha}/M} \tag{8}$$

Equation (8) tells us how many juveniles are clamouring to become reproductives to replace each current reproductive adult. Suppose this *competitive pressure* to gain reproductive status builds up, and the age α individuals are able to begin reproducing when the ratio reaches some *fixed value* (R) *is the same for all altricial bird species*. R is a new invariant postulated for birds. Now write $q = p \cdot M$, the immature instantaneous mortality rate q is a multiplier of the adult rate M.

Equation (8) now becomes:

$$R = \frac{(1/p)(1 - e^{-p \cdot M \cdot \alpha})}{e^{-p \cdot M \cdot \alpha}} \qquad \text{or} \qquad R \cdot p = e^{p \cdot M \cdot \alpha} - 1 \tag{9}$$

Species with the same R and p are predicted to have the same $p \cdot M \cdot \alpha$. *Thus, they will have the same* $\alpha \cdot M$; $(\alpha \cdot M)^{-1} = (1/M)/\alpha$, the ratio of average adult lifespan ($1/M$) to age of first reproduction (α) is known to equal ≈ 2.0–2.5 for birds (Charnov, 1993).

Equation (9) has one other interesting implication. Add 1 to each side, invert, and multiply by I to yield

$$\frac{I}{R \cdot p + 1} = I \cdot e^{-p \cdot M \cdot \alpha} = S(\alpha) \tag{10}$$

$S(\alpha)$ *will become the same for species with the same I, R and p values*. So the argument leading to equation (9) gives us a theory for $S(\alpha)$ and $\alpha \cdot M$.

To illustrate the utility of equations (9) and (10), set $I = 0.50$ and assume $S = 0.2$, the Ricklefs value. Then, from equation (10), we get $R \cdot p + 1 = 2.5$. This value of $R \cdot p + 1$ may now be used to predict $\alpha \cdot M$ for birds. Rewrite equation (9) as $\alpha \cdot M = 1/p$ [loge $(1 + R \cdot p)] = 1/p$ loge $2.5 = 0.92/p$. $\alpha \cdot M$ in the bird range (≈ 0.45) thus requires $p \approx 2$ (if $I \approx 0.5$). These seem quite plausible, and make estimates of I, p and R of particular value.

What sets *W*?

The last section used an 'equalization of reproductive competitive pressure (R)' to produce a theory for S:

$$S = \frac{I}{R \cdot p + 1}$$

We know from equation (5) that S invariance implies a 0.25 allometry with W for species with similar C and A values.

Rewrite equation (1) for R_0, putting in equation (4b) for b and equation (10) for S; set it equal to 1 to get a non-growing population.

$$R_0 = 1 = \left(\frac{1}{M}\right) \cdot \left(\frac{I}{R \cdot p + 1}\right)\left(\frac{A}{2 \cdot C}\right) W^{-0.25} \tag{11}$$

Suppose A, C, M and p are fixed and R is set by competition for breeding. Any body size (W) that makes $I \leq 1$ and satisfies equation (11) is alright. Indeed, if we put in W, A, C, R, p and M, density-dependent mortality will adjust I to make $R_0 = 1$. This is similar to my previous assumption on mammal life histories (Charnov, 1991); $R_0 = 1$ through density-dependent survival of the very young.

Equation (11) may be used to build a theory for natural selection on W. Suppose we introduce into this population a mutant with a different W $(= \hat{W})$ and that this mutant causes its own I $(= \hat{I})$ to be different from the typical I. For example, larger $\hat{W}$ yields relatively greater immature survival.

$$\hat{W} = W + \partial W \Rightarrow \hat{I} = I + \partial I \qquad (\partial W \text{ and } \partial I > 0) \tag{12}$$

$\hat{R}_0$ for the mutant is equation (11) with $\hat{W}$ and $\hat{I}$, or

$$\hat{R}_0 = \left(\frac{1}{M}\right)\left(\frac{\hat{I}}{R \cdot p + 1}\right)\left(\frac{A}{2 \cdot C}\right) \hat{W}^{-0.25} \tag{13}$$

The mutant will be favoured if $\hat{R}_0 > R_0 = 1$, or equation (13) > equation (11). This yields the rule

$$\frac{\hat{I}}{I} > \frac{\hat{W}^{0.25}}{W^{0.25}} \Rightarrow \frac{I + \partial I}{I} > \left(\frac{W + \partial W}{W}\right)^{0.25} \Rightarrow \text{loge}\left(1 + \frac{\partial I}{I}\right) > 0.25 \text{ loge}\left(1 + \frac{\partial W}{W}\right)$$

If we make $\partial Z/Z$ small, then loge $(1 + \partial Z/Z) \approx \partial Z/Z$, and the larger body size ($\hat{W}$) is favoured if $\partial I/I > 0.25$ $(\partial W/W)$. So long as the percent change in I is greater than one-quarter of the percent change in W, natural selection will favour a larger W. I can think of two possibilities here. The first is that successive changes in W generally satisfy the inequality and W will increase until I gets near its maximum of 1. If I is anywhere above, say, 0.85, we will have, from equation (10), $S \approx 1/(R \cdot p + 1)$, an invariant.

The second possibility is that, as W increases, the percent gain possible in I goes down so that W reaches an intermediate ESS value where $\partial I/I = 0.25\ \partial W/W$. If S (equation 10) is to be an invariant here, I must come to take on similar values for all species with the same R and p values. Variation in I will lead to scatter around the M^{-1} allometry line. I can probably be identified with the survival rate of nestlings and fledglings, the 'wastage' of parental production ($W^{0.75}$); it seems likely that $I \ll 1$.

The argument of this section can be made more general. So long as the mortality rates q and M do not change with $\hat{W}$, a mutant individual can alter S by changing its α ($=\hat{\alpha}$) in addition to changing I to $\hat{I}$. The mutant can affect its chance of becoming a breeder (relative to a wild-type individual); but, as the mutant spreads, $\hat{\alpha} \rightarrow \alpha$, since R will be the same for a population of all $\hat{W}$.

An allometry for α?

Since $\alpha \cdot M$ (equation 9) $= 1/p$ [loge $(1 + R \cdot p)$],

$$\alpha = \frac{1}{M} \cdot \frac{1}{p} \text{ loge } (1 + R \cdot p)$$

and α will scale as $W^{0.25}$, just as M^{-1} does. Furthermore, taxa with high α for their body size will also have high $1/M$ for their body size. Deviations of α and $1/M$ from the respective allometries are predicted to be positively correlated, as shown by the data (Saether, 1988).

Adult lifespans (1/*M*): Why birds > mammals?

Suppose birds and mammals have the same production curve (same A in equation 2), then the ratio of equation (5) to equation (6) gives their relative adult lifespans at fixed body weight:

$$\frac{\text{birds}}{\text{mammals}} \approx \frac{(1.5)}{S} \cdot C = 7.5 \cdot C \text{ if } S \approx 0.2 \tag{14}$$

Recall the argument leading to equation (3):

$$\frac{W_0}{t} = \frac{A \cdot W^{0.75}}{C}$$

For the mammal and bird A to be compared, they must refer to production of 'self'; then C converts self-production per unit time ($A \cdot W^{0.75}$) to offspring production per unit time (W_0/t). If $C \approx 1$, the conversion is 1 : 1; if $C > 1$, offspring are less efficient to grow than self. If $C < 1$, they are more efficient to grow. Estimates (Charnov, 1993) of the mammal C put it a bit below 1. Even if birds are as efficient as mammals, the ratio in equation (14) yields avian adult lifespans several times those of mammals. This result holds even if the bird and mammal As differ by, say, a multiplier of 2.

CONCLUSIONS

If birds cannot grow and fly at the same time, it is clear why adults rear copies of themselves, and why adult size is reached by the end of parental care (G.H. Orians, personal communication). But what, then, determines the age of first reproduction? What are they waiting for (Williams, 1992)? This paper suggests an answer (equation 9): when combined with 0.75 production allometry ($\propto W^{0.75}$), we get ($\approx$) ±0.25 allometries for the age of first breeding, yearly offspring production and adult lifespan. Bird life-history allometries are notoriously imprecise (Saether, 1987, 1989; Western and Ssemakula, 1982), but deviations around them are strongly inter-correlated (Saether, 1988). The signs of these correlations are as predicted by the theory of this paper. The theory thus makes predictions as to *what* (e.g. variation in A) causes taxa to deviate from an allometry; in doing so, the theory suggests reasons why the fitted allometries are often imprecise (or have slopes different from ±0.25).

The theory also gives a plausible numerical prediction for the ratio of adult lifespan to age α; this is the first prediction ever for the value of the $\alpha \cdot M$ number for birds.

The argument here makes use of two new dimensionless numbers for birds: the ratio of non-breeders to breeders, and the ratio of juvenile to adult instantaneous mortality rates. These numbers are assigned key roles in the theory and their measurement now becomes important.

The argument of this paper shares much with my previous work on mammals (Charnov, 1991, 1993). Both use production allometries ($W^{0.75}$) and have determinate growth; both have mortality rates fixed external to the individual organism. And, finally, both have survival of the very young density-dependent to make $R_0 = 1$. They differ in how natural selection sets adult size. For mammals, it is when self-growth ceases and production is diverted to offspring. For (altricial) birds, it is when the early survival benefits ($\uparrow I$) of being bigger balance the cost in time to rear the bigger self; the other way to view this cost is as the classic size–number trade-off (Smith and Fretwell, 1974; Charnov and Downhower, 1995).

Of course, birds with precocial offspring are much more like mammals, and bats with the need to fly at independence are much more like altricial birds. Comparisons of altricial and precocial birds seem particularly useful. For example, are adult lifespans of precocial species (M^{-1}) particularly short for their body mass or age of first reproduction?

Here, I propose a *general* answer to G.C. William's (1992) puzzle as to why birds wait to begin reproducing. If competition for breeding places does indeed equalize the ratio of breeders to non-breeders across species, a sort of equalization of 'reproductive competitive pressure', then several interesting results follow. This invariance assumption probably only needs to be approximately true to be useful.

Finally, while the model developed here owes much to the empirical allometric and dimensionless rules known (or *suspected*) for birds, it is more general than these rules. For example, I suspect that A, the height of the production function (equation 2), will correlate with phylogeny and/or aspects of the habitat, just as it does in mammals (Charnov and Berrigan, 1993); A will probably correlate with the presence or absence of paternal care, food type, and factors such as length of the breeding season. Although we can always view this variation as scatter around, or deviation from, an allometry, more useful insights may follow from simply asking what causes A to differ, and what does a higher (lower) A imply for other aspects of the life history. While invariance arguments motivated the model, the model may be useful even when the invariance is badly violated; the demographic and production mechanisms developed here seem less likely to imply precise allometries than, say, the mechanisms suggested for mammals (Charnov, 1993; Kozlowski and Weiner, 1997).

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