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Reproductive effort is inversely proportional to average adult life span

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ABSTRACT

Background: Forty years ago, G.C. Williams predicted that reproductive effort should be inversely related to the average adult life span across species.

Aim: Use allometric life-history theory to refine that prediction.

Result: Reproductive effort should be inversely proportional to average adult life span, a −1 scaling rule.

Keywords: allometry, life history, optimization, trade-offs, Williams' hypothesis.

Forty years ago, Williams (1966), in a seminal paper that initiated life-history theory, proposed that a female's reproductive effort ought to decrease with average adult life span in across-species comparisons. The most accepted (Roff, 1992; Stearns, 1992) measure of reproductive effort is the fraction of a body mass expended in reproduction per year, and the hypothesis is clearly correct for this measure (Roff, 1992; Stearns, 1992; Gunderson, 1997). Allometric theory (Charnov, 1993) refines Williams' hypothesis by suggesting a special decreasing relation: reproductive effort should be *inversely proportional* to average adult life span, a −1 scaling.

If m is adult body mass, E is average adult life span and R is the average mass given to reproduction per year, many across-species plots for similar taxa (e.g. Roff, 1992; Charnov, 1993, 2001; Charnov *et al.*, 2001) have $E = A_1 \cdot m^{0.25}$ and $R = A_2 \cdot m^{0.75}$, so that $E \cdot R = A_1 \cdot A_2 \cdot m$, resulting in $R/m = (A_1 \cdot A_2)/E$: inverse proportionality of reproductive effort (R/m) and life span (E) for a collection of species with the same $A_1 \cdot A_2$ number. And the product of $A_1 \cdot A_2$ may well be quite constrained since taxa with high A_1 usually have low A_2 (Charnov, 1993).

Note that $A_1 \cdot A_2$, the proportionality constant, is a dimensionless number equal to $(R \cdot E)/m$, the fraction of a body mass given to reproduction (R/m) over an average adult life span (E), or a 'lifetime relative reproduction allocation' (LRRA). Preliminary estimates (Charnov, 1993, 2001, 2002; Gunderson, 1997; Lester *et al.*, 2004) place LRRA at about 1.5 for mammals and fish (where m is size at first reproduction for indeterminate growers like fish); although LRRA is not estimated with great precision, values of about 1–2 are typical. Standard life-history

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evolution theory (e.g. Charnov, 1993; Lester *et al.*, 2004) with allometric production/growth functions predicts LRRA values of this magnitude.

Fitness within non-growing populations (the 'net reproductive rate', R_0) can always be written as LRRA divided by the relative size of an offspring multiplied by the survival chances to adulthood (Charnov, 1997, 2002). It would be interesting to predict LRRA for a variety of life-history trade-off assumptions, in addition to the allometric production rules assumed here.

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