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E-Article

Lifetime Reproductive Effort

Eric L. Charnov,[1,2,*] **Robin Warne,**[1,†] **and Melanie Moses**[1,3,‡]

1. Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131;
2. Department of Fisheries and Wildlife, Oregon State University, Hatfield Marine Science Center, Newport, Oregon 97365;
3. Department of Computer Science, University of New Mexico, Albuquerque, New Mexico 87131

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abstract: In a 1966 *American Naturalist* article, G. C. Williams initiated the study of reproductive effort (RE) with the prediction that longer-lived organisms ought to expend less in reproduction per unit of time. We can multiply RE, often measured in fractions of adult body mass committed to reproduction per unit time, by the average adult life span to get lifetime reproductive effort (LRE). Williams's hypothesis (across species, RE decreases as life span increases) can then be refined to read "LRE will be approximately constant for similar organisms." Here we show that LRE is a key component of fitness in nongrowing populations, and thus its value is central to understanding life-history evolution. We then develop metabolic life-history theory to predict that LRE ought to be approximately 1.4 across organisms despite extreme differences in production and growth rates. We estimate LRE for mammals and lizards that differ in growth and production by five- to tenfold. The distributions are approximately normal with means of 1.43 and 1.41 for lizards and mammals, respectively (95% confidence intervals: 1.3–1.5 and 1.2–1.6). Ultimately, therefore, a female can only produce a mass of offspring approximately equal to 1.4 times her own body mass during the course of her life.

Keywords: lizards, mammals, life-history optimization, dimensionless, Williams's hypothesis.

The optimal size of an offspring (Smith and Fretwell 1974) and the optimal schedule of allocation to reproduction (Williams 1966) are the two central issues of life-history evolution. Williams (1966) initiated the study of reproductive allocation by suggesting that longer-lived organisms ought to expend less in reproduction per unit of time. In most data sets, Williams's hypothesis is true and is predicted theoretically (at least qualitatively) by a great many formal models (reviews in Stearns 1992; Charlesworth 1994). Williams (1966) placed center stage the issue of how we conceptualize/measure the "cost of reproduction" (now often called "reproductive effort" [RE]). Generally speaking, the literature (Stearns 1992; Charlesworth 1994) is dominated by two possibilities: reproduction can decrease parental survival and/or divert parental resources from future reproduction, perhaps through slowing (or ending) growth. It is somewhat surprising that the increase in adult mortality has rarely been seen, and many models implicitly assume that the diversion of resources from parental growth is the only cost of reproduction (e.g., Kozlowski 1992). Of course, it is possible that both potential costs are present and interact in complex ways (e.g., mortality decreases with body size and reproduction results in smaller adult size [Kozlowski 1992]).

While the definition of RE is much debated (e.g., Stearns 1992), workers on many taxa have independently come to rely heavily on the idea that the mass given to reproduction per unit of time, as a proportion of the adult mass, captures much of what we mean by the concept (particularly if there is no mortality cost to reproductive allocation). This RE metric is interesting in that it has units of 1 over time (i.e., percentage of a body mass per unit of time), and so when it is multiplied by a measure of adult life span, it produces a dimensionless number that measures "lifetime reproductive effort" (LRE; Charnov 2002, 2005). Williams's hypothesis (RE goes down as life span goes up) leads naturally to the suggestion that their product might be some fixed, or at least highly bounded, value (Charnov 2005). In order for LRE to be really useful, a uniform measure of adult life span must be used, and it was proposed previously (Charnov 2002, p. 751, 2005) that the "expectation of further life at the age of first reproduction (α)," called the average adult life span (E), was the most useful metric. Charnov (2005) also suggested that body mass at first reproduction be the normalizing size (particularly with indeterminate growth).

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[*] E-mail: rlc@unm.edu.

[†] E-mail: rwarne@unm.edu.

[‡] E-mail: melaniem@unm.edu.

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This article is about various roles for LRE in the description of life histories. We show that LRE is a key component of fitness that encompasses the central core of 40 years of life-history thought—reproductive allocation, size at maturity, and adult life span. First, we define LRE for arbitrary schedules of survivorship and fecundity. Second, we show that fitness in nongrowing populations, R_0, the net reproductive rate, is quite naturally written in terms of LRE (and the size of an offspring normalized to adult size). Third, we predict LRE for an optimal life history with metabolic production constraints (Charnov 1991, 1993); this yields a surprisingly simple (and elegant) answer: LRE = 1/(metabolic exponent). Fourth, we estimate LRE for a large sample of lizards (71 populations of 54 species) and mammals (40 species). Surprisingly, the average LRE values are very close to those predicted by the optimal life history with the simplest metabolic constraints. Finally, we initiate a sensitivity analysis for the theoretical prediction, how does predicted LRE change if we alter the trade-off structure for the life history or the production function?

Lifetime Reproductive Effort Defined (Eq. [2])

To begin, we define the following symbols for an asexual population: α = age at first reproduction; $S = l_\alpha$, where l_x is the chance of survival to age x ($l_0 = 1$); m_α = adult body mass at age of first reproduction; R_x = reproductive allocation per unit of time at age x (mass per unit of time); and finally, E = average adult life span: $E = \int_\alpha^\infty (l_x/S)dx$ (this is the definition of expectation of further life at age α). Now, the average rate of mass allocated to reproduction (R_x) over the adult lifetime ($\overline{R}$) is

$$\overline{R} = \frac{\int_\alpha^\infty [(l_x \times R_x)/S]dx}{\int_\alpha^\infty (l_x/S)dx}. \tag{1}$$

The l_x/S is simply a survivorship schedule for the adults (i.e., $l_\alpha = S$, so everyone is assumed alive at age α). The $(l_x/S)/\int_\alpha^\infty (l_x/S)dx$ is a probability density function since in a stationary (nongrowing) population, it is the chance an adult is age x. Then we may write LRE simply as

$$\text{LRE} = \frac{\overline{R}}{m_\alpha} \times E. \tag{2}$$

Since $E = \int_\alpha^\infty (l_x/S)dx$, we may also write

$$\text{LRE} = \left(\frac{1}{m_\alpha \times S}\right)\left(\int_\alpha^\infty l_x \times R_x dx\right). \tag{3}$$

The LRE is the average mass per unit time to reproduction ($\overline{R}$) multiplied by E, the average adult life span, all divided by the adult size, m_α (eq. [2]), or it can simply be written as the integral in equation (3).

Fitness in Nongrowing Populations and LRE

The net reproductive rate (R_0) is the average number of offspring produced over an individual's lifetime, and it is a measure of Darwinian fitness in nongrowing populations (e.g., Charlesworth 1994). Fitness in nongrowing populations, R_0, is a dimensionless number that can be written in various ways to show how resource allocation enters into fitness; here we will show how it contains LRE. We define the following symbols for an asexual population: m_0 = size (mass) of an offspring at independence from the parent, and b_x = fecundity per unit of time at age $x(b_x = R_x/m_0)$. Then,

$$R_0 = \int_\alpha^\infty l_x \times b_x dx = \frac{1}{m_0} \times \int_\alpha^\infty l_x \times R_x dx$$

if m_0 is independent of x, parental age. We can multiply by $(S \times m_\alpha)/(S \times m_\alpha)$ to get

$$R_0 = \frac{S}{m_0/m_\alpha} \times \left(\int_\alpha^\infty \frac{l_x \times R_x}{S \times m_\alpha} dx\right).$$

Since the integral is simply LRE we have

$$R_0 = \frac{S \times \text{LRE}}{m_0/m_\alpha}. \tag{4}$$

So, provided offspring size (m_0) is independent of parental age, R_0 is survival to adulthood (S) multiplied by LRE divided by offspring size (normalized to adult size, m_0/m_α). Equation (4) suggests that LRE and m_0/m_α are the two key dimensionless numbers in the study of life histories (in nongrowing populations). Density dependence, necessary to hold $R_0 \approx 1$ to enforce the nongrowing population assumption, is probably mostly in the S term (discussion and data in Charnov 1993).

Optimal Life Histories with the Simplest Metabolic Constraints

We begin by predicting LRE for an optimal life history with allometric (metabolic) production rates, where growth is production of self and reproduction is production of offspring. Both are measured as production of mass per unit time. Suppose production follows the equation

$$\frac{dm}{dt} = am^{\delta}, \qquad (5)$$

where m is an individual's mass, a is the height of the growth curve, and δ is the production exponent (Charnov 1991, 1993). Equation (5) determines the rate of individual growth, and at the onset of reproduction at age α (size m_α), it determines the rate of offspring production (i.e., dm/dt is available to grow offspring). Equation (5) is the simplest allometric (growth and production) equation; many life-history models use a more complex growth equation:

$$\frac{dm}{dt} = am^{\delta_1} - bm^{\delta_2}, \qquad (6)$$

where $\delta_1 < \delta_2 < 1$ (reviewed in Kozlowski 1992).

For the moment we will consider only equation (5), the simplest metabolic constraint, where RE $= dm_\alpha/m_\alpha dt = am_\alpha^{\delta-1}$. We further suppose that the instantaneous mortality rate (Z) is age and body-size independent, except during a small time period early in life when density dependence operates. Thus, the average adult life span (E) is Z^{-1}. A more complex model (Charnov 1991, 1993) that allows Z to increase at the young ages gives the same answer as below.

If offspring are of some fixed size (m_0) and the population is not growing or declining, fitness is the number of offspring produced over an individual's life span (R_0):

$$R_0 = \frac{S \times E}{m_0}\frac{dm_\alpha}{dt}, \qquad (7)$$

where S is the chance of living to age α when dm_α/dt mass is given to reproduction per year for E years. We set $S = He^{-Z\alpha}$, where H is the density-dependent part of S and H is fixed independently of α. Thus, $R_0 = He^{-Z\alpha}am_\alpha^{\delta}/m_0Z$. The optimal size at first reproduction (m_α) will maximize R_0. It is found by setting $\partial R_0/\partial\alpha = 0$. This is equivalent to the more easily solved $\partial \ln(R_0)/\partial\alpha = 0$ and yields the following rule evaluated at m_α (Charnov 1991, 1993):

$$Z = a\delta m_\alpha^{\delta-1}. \qquad (8)$$

Equation (8) shows that Z equals the derivative of the production function. Since $E = 1/Z$, then we predict

$$\text{LRE} = \frac{1}{m_\alpha}\frac{dm_\alpha}{dt}E = am_\alpha^{\delta-1}\frac{m_\alpha^{1-\delta}}{a\delta} = \frac{1}{\delta}. \qquad (9)$$

Thus, by maximizing R_0 with respect to size at maturity (m_α), we find that LRE equals the inverse of mass at maturity times the production function divided by the derivative of the production function. Given equation (5), all of the terms cancel except the inverse of the production exponent ($1/\delta$).

The value of δ has been estimated and predicted to be between 2/3 and 3/4. Metabolic scaling theory predicts the metabolic exponent $\delta = 3/4$ (reviewed in Brown et al. 2004), and Charnov (1991) assumes $\delta = 3/4$. Empirically, the interspecies allometry for production in mammals gives $\delta = 0.67$ (Charnov 2001, fig. 3). In a review of over 600 growth allometries, the exponent for metabolism has a mean of value of 0.71, but it is highly variable with a standard deviation of 0.26 (data from Glazier 2005). Thus, we assume $\delta \approx 0.7$ and therefore expect the mean value of LRE to be about 1.4, although variation in δ may cause LRE to vary between approximately 1 and 2. Notice particularly that predicted LRE is independent of a, the height of the production curve; thus, endotherms may grow and produce offspring five to 10 times as fast as ectotherms (Case 1978), but that should not affect LRE.

Our model describes the simpler case of determinate growth where m_α is the final adult size, which is constant throughout the reproductive period. For indeterminate growth where not all dm/dt is given to reproduction after age α, we predict similar LRE values if m_α is used for adult size (Lester et al. 2004), given the above mortality and prereproductive growth assumptions.

Methods to Estimate LRE in Mammals and Lizards

We estimated LRE from the Purvis and Harvey (1995) mammal data compilation (40 species) and for 71 populations of 54 lizard species; our methods and data sources are in appendixes A (mammals) and B (lizards). We treated populations as independent data points, as is appropriate for our normalizing (optimizing) natural selection model of life histories (Charnov 1993).

In brief, our methods are as follows: LRE = (litters or clutches/year) × (litter or clutch size) × (average adult lifespan) × (offspring mass at independence)/(adult mass at first reproduction). The ratio (offspring mass at independence)/(adult mass at first reproduction) assumes that the energetic cost of producing a mass of adult tissue is equivalent to the energetic cost of producing the same mass of offspring tissue. For lizards, where hatching and adult size are usually reported as body length, we cubed the length ratio. For mammals, we account for mor-

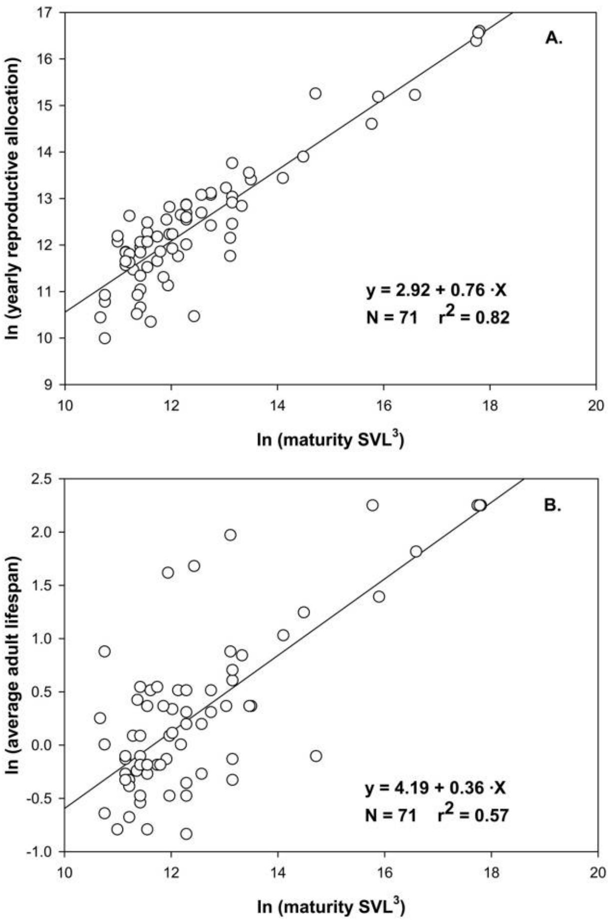

Figure 1: Life-history allometries for lizards (71 populations of 54 species). *A*, Clutch size × clutches/year × hatchling SVL^3 versus adult SVL^3. As expected, the exponent is near 0.7. *B*, Adult life span (inverse of adult instantaneous mortality rate, Z^{-1}; yearly survival $= e^{-Z}$) versus adult size. As expected, the exponent is near 0.3.

tality during the parental care period since maternal investment stops when offspring die (table A1). We use a regression between survival to weaning and litter size from empirical data to estimate the proportion of offspring that die in each litter, and we assume that they die at a mass that is the mean of mass at birth and mass at weaning. We then estimate the mass at which investment stops by averaging over the weaning mass and the mass of littermates that died (app. A).

Lifetime Reproductive Effort Results for Mammals and Lizards

Previous analyses have shown that across-species allometries for mammals satisfy equation (5) for yearly mass of offspring and equation (8) for life span versus adult mass (Charnov 1991, 1993, 2001; Charnov and Ernest 2006). In appendix B we compile the first data set to test equations (5) and (8) for lizards. Figure 1 shows that the lizard data are also closely approximated by equations (5) and (8).

Figure 2 shows the distributions of LRE for mammals (*A*) and lizards (*B*). Both distributions are approximately normal with means that are not significantly different from 1.4 (lizards = 1.43, 95% confidence interval [CI]: 1.3–1.5; mammals = 1.41, CI: 1.2–1.6). The LRE shows no significant trend with adult body mass in mammals and a slight increase in lizards (LRE $\propto m_\alpha^{0.12}$, $r^2 = 0.21$, $P < .01$). We expect, and see, broad distributions (fig. 2) for LRE because field estimates of life span and yearly offspring production generally have low precision (although not necessarily low accuracy; Krebs 1989). Our calculations combine inherently imprecise field estimates of reproductive life span, annual clutch size, and relative offspring

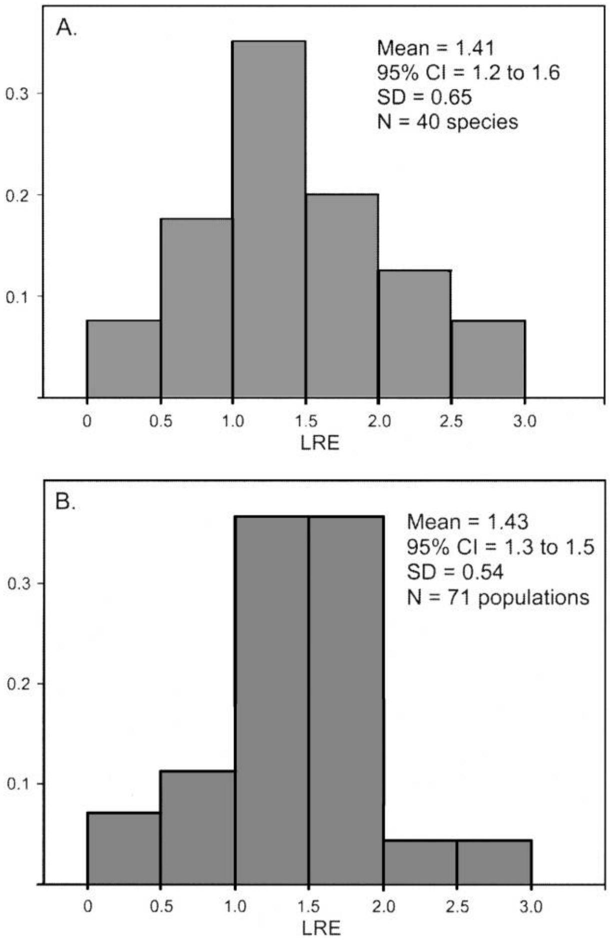

Figure 2: Frequency histogram of lifetime reproductive effort (LRE) for (*A*) mammals and (*B*) lizards. See text and appendixes for estimation procedures.

mass. If, for example, each of these three field estimates has a precision of ±20%, then compounding these errors could lead to deviations of over 70% from the actual value of LRE. There may be interesting biological meaning in the variation of LRE (tables 1, A1, A2). However, due to the inherently high measurement error, distilling such meaning from our estimates is not feasible with our current data.

In table 1 we give the mean and standard deviation for the six mammalian orders and seven lizard families for which we have LRE measurements for two or more species or populations. The mean LRE is between 1 and 2 in most taxa, indicating that LRE has similar bounds both within and between most taxonomic groups. However, LRE estimates of the Gekkonidae are consistently low, with five of six species showing values below 0.8, while LRE is consistently high for the Iguanidae (LRE > 2 for four out of six species). Environmental resource availability can dramatically affect the interannual life-history dynamics in temperate species of both taxa (Burghardt and Rand 1982; Vitt 1986). Because such interannual variation creates inaccuracy in measurements of average clutch size and number, as well as survival, LRE calculations for these taxa are inherently imprecise. Field measures of clutch number in tropical species of gecko must also come with a high degree of error. Because geckos generally lay one egg at a time, the chance of recapturing individual females that may lay more than six eggs (clutches) a year (and thus require >6 recaptures) is highly unlikely. Thus, it would not be surprising if LRE were systematically underestimated in this group. Taxonomic differences in LRE may reflect interesting ecological, evolutionary, and life-history dynamics; however, we are reluctant to speculate further on such biological meaning in LRE variation without more precise field estimates and measures of δ.

The overall patterns are as predicted by the simplest metabolic life-history theory: LRE is similar for the endothermic mammals and the ectothermic lizards, with the average predicted by a metabolic exponent of $\delta = 0.7$. We do not consider this a conclusive test of metabolic life-history theory but a hopeful beginning, given our scant knowledge of the appropriate constraints for our models (see below).

Table 1: Lifetime reproductive effort (LRE) by taxonomic group

	LRE average	Minimum LRE	Maximum LRE	SD LRE	No.
Lizard family:					
Crotaphytidae	1.49	1.32	1.65	.23	2
Gekkonidae	.71	.34	1.87	.59	6
Iguanidae	2.27	1.45	2.95	.68	6
Lacertidae	1.09	.98	1.20	.16	2
Phrynosomatidae	1.54	.93	2.45	.32	39
Scincidae	.94	.44	1.76	.46	6
Teiidae	1.10	.77	1.40	.25	6
All	1.43	.34	2.95	.54	71
Mammalian order:					
Rodentia	1.55	1.03	2.16	.42	8
Lagomorpha	1.54	.72	2.76	.93	4
Chiroptera	1.68	1.24	2.11	.61	2
Carnivora	1.50	.30	2.88	.82	10
Artiodactyla	1.34	.56	2.29	.60	10
Pinipeds	1.23	.65	1.79	.48	4
All	1.41	1.03	2.16	.42	40

Other Theoretical Models

Variations in model assumptions may change the predicted LRE. For example, suppose we make Z dependent on body size over the ontogeny, with its own power function rule (e.g., Kozlowski 1992):

$$Z_x = B_i m_x^{-P}, \tag{10}$$

where B_i means species i. Repeating the max R_0 argument leading to equation (9) predicts $Z = (\delta + P)am^{\delta-1}$, and $\mathrm{LRE} = 1/(\delta + P)$. If $P > 0$ (larger animals survive better), LRE is decreased. Since there have not been conclusive demonstrations of a mortality benefit to larger size, P is likely to be small relative to δ.

Many life-history evolution models (reviewed in Kozlowski 1992) use the more complex equation (6) as the growth equation and, depending on things such as the mortality assumptions, can generate determinate or indeterminate growth. Charnov (2001) developed a new model for mammal life histories. The model builds on a growth equation developed by West et al. (2001), which is a special version of equation (6):

$$\frac{dm}{dt} = am^{\delta} - bm. \tag{11}$$

Charnov (2001) defines a term $\mu = m_{\alpha}/M$, which is the mass at maturity relative to maximum mass, M; M is defined as the mass at which no further growth is possible ($dM/dt = 0$, so $b = aM^{\delta-1} = am^{\delta-1}\mu^{1-\delta}$). Using equation (11) for both growth and production predicts an optimal μ that is less than the inflection point in equation (11). Thus, the model predicts that determinate growers stop growing and begin reproducing before they reach the asymptotic growth phase. Therefore, Charnov suggests that equation (11) may govern growth, but reproduction (R) is governed by an equation similar to equation (5):

$$R = Cm^{\delta}, \tag{12}$$

where C is an as yet to be determined constant. According to equation (12), $\mathrm{RE} = R/M = CM^{\delta-1}$.

Now we can predict LRE, assuming that equation (10) describes mortality, equation (11) describes growth, and equation (12) describes production. Again, we find the value of Z that maximizes R_0: $Z = (\delta + P)(am_{\alpha}^{\delta-1} - b)$ (similar to eq. [10] in Charnov 2001). Substituting Z and equation (12) into equation (9) gives

$$\mathrm{LRE} = \frac{C}{a}\frac{1}{(1-\mu^{1-\delta})}\frac{1}{(\delta + P)}. \tag{13}$$

Now LRE is underdetermined until we know C/a and μ. We can make a preliminary estimate of the first two terms in equation (13) from empirical data. Charnov (2001) predicted that it requires $\mu \approx 0.7$ for this model to account for existing mammal life-history data (Charnov 1993). The proportion of adult metabolism that is allocated to reproduction is C/a, which Moses (2005, pp. 23–40) estimated as $C/a \approx 0.15$ for mammals. If we further assume that $0.6 < \delta < 0.8$, then $\mathrm{LRE} = x/(\delta + P)$, where $1 < x < 2.3$, reasonably close to our empirical estimates. Thus, we have shown that more complicated models of growth, production, and mortality (eqq. [10]–[12]) generate a prediction for LRE (eq. [13]), which can be parameterized with empirical data and also produce LRE close to our estimates. However, in this more complicated model, LRE is linearly dependent on C/a and increases with both δ and μ; thus; LRE might be expected to show much more variation than it actually does.

We think it is important to note that empirical estimates of LRE are consistent with a very simple model (eq. [5], with mortality independent of mass), and the data are consistent with the more complicated model described in this section only within a fairly narrow parameter space. It is possible that the simple model fully captures the relevant life-history parameters; alternatively, perhaps the more complicated model (eqq. [10]–[12]) is correct, but it can be collapsed to the simpler model because of trade-offs between variables in equation (13). We encourage further explorations of those trade-offs and of the sensitivity of LRE to alternative models.

Discussion

Williams's (1966) hypothesis is probably the single most influential idea in life-history studies, with about 1,200 citations (source: Web of Science http://isiknowledge.com, 2006). Its refinement in terms of LRE suggests that it is even more general than Williams originally proposed: organisms can be quite different and still have similar LRE values. Arguably, the greatest differences between various taxa lie in their production and growth rates (Case 1978), and metabolic life-history theory predicts (and our data show) LRE to be independent of those differences. Equations (5)–(8) show that maximizing R_0 results in a mortality rate (Z) that is the derivative of the production function. Using the simplest production model (eq. [5]), all of the terms cancel except the exponent on the production function.

Kozlowski (1997) criticized equation (5) because it generates exponential rather than asymptotic growth. Equation (6) (and eq. [11]) can generate asymptotic growth, but Charnov (2001) showed that if equation (11) is also used to describe reproduction, then maximizing R_0 prevents organisms from actually reaching the asymptotic growth phase described by the equation. Charnov solves this problem by using equation (11) for growth but equation (12) for production. We have shown that the predicted LRE based on the 2001 model (eq. [13]) depends on five variables (C, a, δ, P, and μ), while the 1991 model (eq. [5]) generates a much simper prediction for LRE ($1/\delta$). Our empirical estimates of LRE are quite close to $1/\delta$, suggesting that if the other four variables are part of LRE, they tend to cancel out. Parameterizing equation (13) with preliminary empirical estimates of C/a and μ do show that equation 13 collapses to something close to equation (9). We find it remarkable that species that vary widely in a, and could potentially vary widely in C, P, and μ, have very similar values of LRE. It remains an open question whether the more complicated model in equation (13) can account for some of the variation we observe in LRE or whether the simpler model captures the essence of LRE.

Estimating LRE from field data, even at the coarse level we do here, is difficult. For mammals, it required estimating mortality before weaning in the field. There is not much data on which to base this estimate, so it is necessarily a coarse estimate. For lizards, we assembled a data set with the appropriate measures, though survival measures were sometimes highly variable. We are well aware of the imprecision inherent in the estimation of LRE from field data. We simply do not know how much of the variation in figure 2 is estimation error versus biological (trade-off) differences between the species, differences in δ, or deviations from the form of the production function (eq. [5]).

The importance of LRE to understanding the evolution of life histories is evident in equation (4), which states that R_0 is the product of three dimensionless quantities: survival to reproduction, relative offspring mass, and LRE. Of these three dimensionless quantities, LRE is particularly interesting because it is the one that links the energetics of production and reproduction to life span. Previous work described R_0 as a function of other dimensionless quantities (e.g., Charnov 1997). Those remain valid quantities from which to measure R_0, but the formulation we present here is much more intuitively meaningful. In a fundamental sense, this way of rewriting R_0 says that LRE and the relative offspring size are the two key life-history variables. Though relative offspring size is taxonomically quite variable (Charnov 2002), our data suggest LRE is very similar for otherwise very different organisms. Thus, there is a trade-off between the production exponent, relative mass at independence, and survival, so that during her lifetime, a female will ultimately produce a mass of offspring approximately equal to 1.4 times her own body mass. The LRE number can easily accommodate any mortality cost to reproductive allocation, as this would simply decrease life span to increase RE; perhaps the optimum LRE would not be too different from trade-off cases without the mortality cost, like those considered here.

Finally, we note that life-history workers usually consider the age-specific schedule of reproductive allocation to be the object of interest (e.g., Kozlowski 1992; Stearns 1992; Charlesworth 1994). Our interest is in a more macro view in which we aggregate the life history by looking at the "average reproductive allocation" and the "average life span" (Charnov 1997, 2002); LRE (eq. [3]) is an aggregate number that combines reproductive allocation, adult size, and adult life span to yield a single dimensionless characterization. We consider this approach complementary to the more traditional fine-scale view of life histories. The LRE is a key component of fitness (eq. [4]) and it encompasses the central core of 40 years of life-history thought—reproductive allocation, size at maturity, and adult life span. This places it central to the study of life histories; we suggest people estimate it and theorists predict it from trade-off and production assumptions beyond ours.

Acknowledgments

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APPENDIX A

Mammals

Lifetime reproductive effort (LRE) was calculated for mammals from data in Purvis and Harvey (1995). They list life-history characteristics of 64 species in nine mammalian orders. The data are subject to reasonably stringent inclusion criteria described in their article. All of the variables required to calculate LRE are listed for 40 species. The LRE was calculated from LRE = litters/year × litter size × adult life span × mass at independence/adult mass. Litters/year, litter size, and adult mass are given in Purvis and Harvey (1995). Adult life span (average time between maturity and death) is calculated as the inverse of annual adult instantaneous mortality rate.

Purvis and Harvey list mass at weaning (m_w), and it is often assumed that mass at independence (m_i) = m_w. However, if there is mortality between birth and weaning, m_w is an overestimate of the average size that an offspring becomes independent of maternal provisioning. That is, offspring become independent either when they die or when they wean. We incorporate preweaning mortality into the estimate of m_i.

We use data from the literature (table A1) to estimate survival from birth to weaning (S_w) in the field as a function of litter size (L) and find $S_\mathrm{w} = 0.7L^{-0.35}$ ($N = 13$ species, $r^2 = 0.67$). This regression equation is used to estimate the proportion of offspring that survive to weaning (S_w), and for these offspring $m_\mathrm{i} = m_\mathrm{w}$. The proportion of offspring that die between birth and weaning is $1 - S_\mathrm{w}$, and for them we assume they die at a size that is the mean of the size at birth (m_b) and m_w; thus, $m_\mathrm{i} = 1/2(m_\mathrm{b} + m_\mathrm{w})$. Thus, we calculate an average m_i over all offspring that are born: $m_\mathrm{i} = S_\mathrm{w}m_\mathrm{w} + 1/2(1 - S_\mathrm{w})(m_\mathrm{b} + m_\mathrm{w})$.

Table A1: Litter size and rates of survival to weaning in natural populations

Species	Litter size	Preweaning survival
Ovis aries (Soay sheep)	1.14 (Gaillard et al. 2000)	.80 (Gaillard et al. 2000)
Alces alces (moose)	1.29 (Gaillard et al. 2000)	.51 (Gaillard et al. 2000)
Odocoileus virginianus (white-tailed deer)	1.54 (Gaillard et al. 2000)	.49 (Gaillard et al. 2000)
Odocoileus hemionus (mule deer)	1.64 (Gaillard et al. 2000)	.55 (Gaillard et al. 2000)
Capreolus capreolus (roe deer)	1.84 (Gaillard et al. 2000)	.57 (Gaillard et al. 2000)
Peromyscus mexicanus	2.70 (Duquette and Millar 1998)	.63 (Duquette and Millar 1998)
Microtus ochrogaster	3.50 (Innes and Millar 1994)	.44 (Millar 2007)
Peromyscus leucopus	4.58 (Millar et al. 2004)	.33 (Millar et al. 2004)
Clethrionomys gapperi	5.00 (Ernest 2003)	.46 (Millar 2007)

Table A1 (*Continued*)

Species	Litter size	Preweaning survival
Peromyscus maniculatus	5.14 (Millar and McAdam 2001)	.38 (Millar and McAdam 2001)
Microtus arvalis	5.20 (Innes and Millar 1994)	.48 (Millar 2007)
Microtus townsendii	5.30 (Innes and Millar 1994)	.37 (Millar 2007)
Microtus pennsylvanicus	6.50 (Ernest 2003)	.28 (Millar 2007)

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APPENDIX B

Lizards

Life-history data necessary for the calculation of lifetime reproductive effort (LRE) were complied from the published literature for 71 populations and 54 species of lizards of the following 11 families: Agamidae, Corytophanidae, Crotaphytidae, Gekkonidae, Iguanidae, Lacertidae, Phrynosomatidae, Polychrotidae, Scincidae, Teiidae, and Xantusiidae. The parameters of female snout-vent length (SVL) at maturity, average adult SVL, average hatchling SVL, average clutch size, average annual number of clutches, and average adult survival rate were gathered from both primary literature sources and previously published reviews of lizard life histories. These parameters were gathered from single literature sources for 60% of these 71 populations. If all of these data were not available for a single population (or from a single source), then average values for a species were derived from a number of studies.

The maturity SVL (m_α) used in our data set is either that reported by the original authors or the SVL for the smallest reproductive female reported in a study. Female SVL at maturity ranged from 35 mm to 378 mm across all species.

In our calculation of LRE and in figure 1, we used the SVL^3 of both maturity SVL and hatchling SVL as a proxy for mass. This conversion is supported by a previous study that found body mass to scale as the SVL raised to an exponent of 2.98 across 47 species of lizards (Pough 1980). Similarly, unpublished field data from one of our authors (R. Warne) shows an exponent of 3.12 across 14 species of lizards and 436 individuals ranging from hatchling to adult ($\log[\mathrm{mass}] = -10.9 + 3.12 \times \log[\mathrm{SVL}]$, 95% CI of exponent = 2.99–3.23, $r^2 = 0.87$). We did not use mass in our analyses for two reasons: first, SVL is much more commonly reported in the herpetological literature as a measure of size and age, and second, the mass of lizards of a given SVL can be highly variable due to relatively large ingested and egested meals.

We calculated adult life span as the inverse of the adult instantaneous mortality rate. We estimated the average yearly mass given to reproduction as average clutch size × clutches per year × hatchling SVL^3; again, SVL^3 is used to estimate hatchling mass.

Table B1: Lizard life-history data

Species	Female maturity SVL	Female average SVL	Hatchling SVL	Clutch size (mean)	Clutches per year (mean)	Female adult survival	LRE	Source
Agamidae:								
Japalura swinhonis	54	76.1	20	4.3	2	.82	2.39	Lin and Lu 1982
Corytophanidae:								
Basiliscus basiliscus	135	168.0	42	9.5	6	.33	1.55	Dunham et al. 1988 (appendix); Shine and Charnov 1992
Crotaphytidae:								
Crotaphytus collaris	70	85.1	40	5	1.5	.48	1.65	Turner 1977; Ballinger and Hipp 1985; Degenhardt et al. 1996
Gambelia wislizeni	90	105.0	45	7.3	1	.50	1.32	Tinkle and Hadley 1975; Degenhardt et al. 1996
Gekkonidae:								
Diplodactylus damaeus	45	52.7	22	2	2	.33	.42	Henle 1990*b*
Diplodactylus tessellatus	45	50.2	25	2	2	.18	.40	Henle 1990*b*
Gehyra variegata	48	53.7	25	1	2	.55	.47	Henle 1990*a*
Heteronotia binoei	44	46.7	21	2	2	.28	.34	Henle 1990*b*
Oedura ocellata	79	80	35	2	1.5	.87	1.87	Bustard 1971
Oedura reticulata	63	66.3	26	2	1	.83	.75	Dunham et al. 1988 (appendix); Kitchener et al. 1988
Iguanidae:								
Amblyrhynchus cristatus	252	279.0	118	2.5	1	.85	1.58	Laurie 1990; Laurie and Brown 1990
Ctenosaura similis	200	276.0	54	25	1	.78	1.98	Fitch 1970; Dunham et al. 1988 (appendix); Clobert et al. 1998 (app. I)
Cyclura carinata	192	225.0	80	4.3	1	.90	2.95	Dunham et al. 1988 (appendix); Shine and Charnov 1992
Cyclura pinguis	378	468.0	105	14	1	.90	2.85	Wiewandt 1982; Clobert et al. 1998 (app. I); Iverson et al. 2004
Cyclura stejnegeri	375	475.0	109	12	1	.90	2.80	Wiewandt 1982; Clobert et al. 1998 (app. I); Iverson et al. 2004
Dipsosaurus dorsalis	110	120.0	50	5.5	1	.70	1.45	Krekorian 1984
Lacertidae:								
Lacerta vivipara	44	57.6	21	6.0	1	.52	.98	Sorci et al. 1996; Clobert et al. 1998 (app. I)
Takydromus tachydromoides	41	45.7	22	3.6	3	.25	1.20	Telford 1969
Phrynosomatidae:								

Table B1 (*Continued*)

Species	Female maturity SVL	Female average SVL	Hatchling SVL	Clutch size (mean)	Clutches per year (mean)	Female adult survival	LRE	Source
Callisaurus draconoides	60	75.5	29	4.4	3	.20	.93	Pianka and Parker 1972
Conolophus subcristatus	370	416	99	13.5	1	.90	2.45	Werner 1982; Wiewandt 1982; Clobert et al. 1998 (app. I)
Cophosaurus texanus	50	60.0	22	6.1	3	.30	1.29	Sugg et al. 1995; Degenhardt et al. 1996
Holbrookia maculata (NM)	45	54.0	25	5	2	.20	1.07	Gennaro 1974
H. maculata (NE)	41	50.0	25	4.5	2	.27	1.56	Jones and Ballinger 1987
Phrynosoma cornutum	70	87.0	25	21.3	1.5	.48	1.98	Howard 1974; Pianka and Parker 1975; Munger 1986
Phrynosoma modestum	42	57.0	25	13	1.5	.14	2.09	Howard 1974; Munger 1986
Phrynosoma platyrhinos	70	76.5	27	8.4	1.5	.55	1.21	Medica et al. 1973; Pianka and Parker 1975
Phrynosoma solare	80		30	17	1	.58	1.65	Parker 1971; Degenhardt et al. 1996
Sauromalus ater	125	160.0	54	6.9	1	.75	1.93	Abts 1987
Sceloporus clarkii	89	100.0	34	19.6	1	.50	1.58	Tinkle and Dunham 1986; Degenhardt et al. 1996
Sceloporus graciosus (UT)	50	52.0	25	3.7	2	.56	1.60	Tinkle et al. 1993
S. graciosus (CA)	57		25	4.1	2	.55	1.16	Tinkle et al. 1993
Sceloporus jarrovii	54	77.0	29	8.4	1	.40	1.42	Ballinger 1973
Sceloporus magister	80	89.0	32	6.2	2	.61	1.19	Vitt and Ohmart 1974; Tinkle 1976; Degenhardt et al. 1996
Sceloporus merriami	43	50.2	22	4.5	2	.40	1.42	Dunham 1981
Sceloporus olivaceus	80	96.0	26	18	3	.25	1.34	Blair 1960
Sceloporus poinsetti	85	104.0	33	10.5	1	.65	1.43	Ballinger 1973
Sceloporus scalaris	41	52.0	20	8.8	1.5	.25	1.11	Ballinger and Condgon 1981; Degenhardt et al. 1996
Sceloporus u. consobrinus (NM)	54	68.4	22	9.9	3.5	.20	1.46	Vinegar 1975*b*
Sceloporus u. tristichus (NM)	53	63.3	25	7.2	2.5	.32	1.66	Vinegar 1975*b*
Sceloporus undulatus (AZ)	60	65.0	27	8.3	3.0	.24	1.59	Tinkle and Dunham 1986

Table B1 (*Continued*)

Species	Female maturity SVL	Female average SVL	Hatchling SVL	Clutch size (mean)	Clutches per year (mean)	Female adult survival	LRE	Source
S. undulatus (CO)	58	70.0	28	7.9	2.0	.37	1.79	Tinkle and Dunham 1986
S. undulatus (KA)	47	57.0	24	7.0	2.5	.27	1.78	Tinkle and Dunham 1986
S. undulatus (NE)	45	60.2	23	5.7	2.5	.30	1.58	Jones and Ballinger 1987
S. undulatus (NJ)	60	73.0	26	8.0	2.0	.44	1.59	Niewiarowski and Roosenburg 1993; Niewiarowski et al. 2004
S. undulatus (OH)	66	75.0	25	11.8	2.0	.44	1.56	Tinkle and Dunham 1986
S. undulatus (SC)	55	63.0	23	7.4	3.0	.49	1.99	Tinkle and Dunham 1986
S. undulatus (TX)	47	57.0	22	9.5	3.0	.11	1.32	Tinkle and Dunham 1986
S. undulatus (UT)	60	69.0	25	6.3	3.0	.48	1.86	Tinkle and Dunham 1986
Sceloporus virgatus	47	48.2	22	9.5	1	.50	1.41	Vinegar 1975*a*; Rose 1981
Sceloporus woodi	45		21	5	3	.40	1.66	Jackson and Telford 1974; McCoy et al. 2004
Urosaurus ornatus (NM)	41	49.0	21	7.5	2.0	.32	1.77	Ballinger 1977
U. ornatus (AZ)	45		20	7.0	1.5	.56	1.59	Smith 1977
U. ornatus (TX)	39	48.0	21	5.4	3.5	.11	1.34	Martin 1977
U. ornatus (AZ)	39	52.0	21	7.1	3.0	.11	1.51	Tinkle and Dunham 1983
U. ornatus (TX)	41	48.4	21	5.0	3.0	.33	1.82	Dunham 1981
Uta stansburiana (TX)	42	47.2	22	3.6	3.5	.25	1.31	Tinkle 1967; Tinkle and Hadley 1975
U. stansburiana (NV)	42	45.4	22	3.5	3	.23	1.03	Turner et al. 1974 (pp. 117–128)
Polychrotidae:								
Anolis acutus	36	42.2	20	1	6	.37	1.03	Ruibal et al. 1972; Ruibal and Philibosian 1974
Scincidae:								
Emoia atrocostata	80	90.0	35	2	3	.32	.44	Alcala and Howard 1967
Eulamprus tympanum	79	88.0	39	3.2	1	.66	.93	Schwarzkopf 1993; Blomberg and Shine 2001
Eumeces fasciatus	52	63.3	24	5.9	1	.50	.84	Turner 1977; Dunham et al. 1988 (appendix)
Eumeces obsoletus	77	120.0	37	11	1	.50	1.76	Hall 1971; Degenhardt et al. 1996
Morethia boulenger	36	45	19	2.7	3	.15	.63	Henle 1991

Table B1 (*Continued*)

Species	Female maturity SVL	Female average SVL	Hatchling SVL	Clutch size (mean)	Clutches per year (mean)	Female adult survival	LRE	Source
Scincella lateralis	35	42.0	19	2.5	2	.46	1.03	Brooks 1967
Teiidae:								
Aspidoscelis inornata	51	57.0	34	2.4	1.5	.30	.89	Christiansen 1971
Aspidoscelis neomexicana	47	65	37	2.3	1.5	.30	1.40	Christiansen 1971
Aspidoscelis sexlineata	55	73.0	33	2.1	2	.41	1.02	Fitch 1958; Degenhardt et al. 1996
Aspidoscelis tesselata	66	83.0	45	3.5	1.5	.27	1.27	Knopf 1966; Schall 1978; Degenhardt et al. 1996
Aspidoscelis tigris	60	82.3	38	3	1	.55	1.27	Tinkle and Hadley 1975; Degenhardt et al. 1996
Aspidoscelis uniparens	60	66.0	36	3.3	2.5	.10	.77	Hulse 1981; Degenhardt et al. 1996
Xantusiidae:								
Xantusia vigilis	36	40.0	23	1.8	1	.66	1.13	Zweifel and Lowe 1966

Note: Data from three reviews were used (Tinkle and Dunham 1986; Dunham et al. 1988; Colbert et al. 1998). SVL = snout to vent length; LRE = lifetime reproductive effort

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