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Lifetime reproductive effort in humans

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Lifetime reproductive effort (LRE) measures the total amount of metabolized energy diverted to reproduction during the lifespan. LRE captures key components of the life history and is particularly useful for describing and comparing the life histories of different organisms. Given a simple energetic production constraint, LRE is predicted to be similar in value for very different life histories. However, humans have some unique ecological characteristics that may alter LRE, such as the long post-reproductive lifespan, lengthy juvenile period and the cooperative nature of human foraging and reproduction. We calculate LRE for natural fertility human populations, compare the findings to other mammals and discuss the implications for human life-history evolution. We find that human life-history traits combine to yield the theoretically predicted value (approx. 1.4). Thus, even with the subsidized energy budget and uniqueness of the adult lifespan, human reproductive strategies converge on the same optimal value of LRE. This suggests that the fundamental demographic variables contained in LRE trade-off against one another in a predictable and highly constrained manner.

Keywords: life-history theory; reproductive effort; human reproduction

1. INTRODUCTION

Lifetime reproductive effort (LRE) estimates a mother's total reproductive output across her lifespan (Charnov *et al*. 2007). LRE is a central life-history metric and key component of fitness because it captures the two fundamental life-history trade-offs, that between survival and reproduction (Williams 1966) and that between the quantity and quality of offspring (Smith & Fretwell 1974). Biomass production is a metabolic process ultimately constrained by body size, and so for demographically stable populations, reproductive-aged females must replace themselves with a predictable amount of biomass over their lifetimes. LRE is expected to be a constant or highly bounded value because larger organisms generally live longer than smaller ones (Calder 1984), and because of the Williams' (1966) hypothesis that reproductive effort should decrease with increasing lifespan. Recently, Charnov *et al*. (2007) derived and tested the hypothesis that LRE should be the same across organisms that have very different life histories. Indeed, across a wide diversity of mammals and lizards, LRE was theoretically predicted, and empirically shown to be about 1.4; meaning that, at replacement levels, the average female produced 1.4 times her own mass during her lifespan.

Here we test the null hypothesis that human LRE is statistically equivalent to the predicted value by using life-history data from 17 populations of natural fertility humans. We are interested in whether or not humans have departed from the generalized mammalian life history or if they are subject to the evolutionary constraints postulated by Charnov (Charnov & Berrigan 1993; Charnov 2002; Charnov *et al*. 2007), Williams (1966) and others (e.g. Fowler 1981). LRE is an ideal measure

for investigating the potential uniqueness of the overall human life-history strategy because it compresses the key features of a species' life history into a single dimensionless quantity that can be compared across species. Placing human life history in this broad comparative context is essential for understanding the generality of ecological constraints and the structure of life-history trade-offs.

There are reasons to suspect either outcome for the hypothesis that human LRE is the same as other animals. On the one hand, primate (human) life histories are distinctively slow (Charnov & Berrigan 1993), exhibiting slow relative growth rates (Walker *et al*. 2006*a*), late ages at maturity (Kaplan *et al*. 2000; Hawkes 2006) and long lifespans (Gurven & Kaplan 2007) when compared to other mammals. In addition, human traits such as food-sharing and cooperation result in offspring that typically receive substantial energy shares not only from parents, but from non-related members of the broader social network (Hawkes *et al*. 2001; Marlowe 2001; Gurven 2004).

On the other hand, humans are subject to the same ecological constraints as other organisms. We already know, for example, that humans are subject to the same basic trade-off between offspring size and number as other mammals (Walker *et al*. 2008). Hawkes *et al*. (1998) found that humans fit the predicted value for the product of adult mortality rate and age at maturity, but differed in the product of birth rate and age at maturity. Furthermore, comparative studies frequently find that substantial regularity exists in the basic structure of life histories (Purvis & Harvey 1995; Charnov 2002). As a result, life-history traits tend to be correlated, and deviations from the average mammal trend in one respect are likely to be offset by a complimentary deviation in another (Purvis & Harvey 1995).

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2. THE DEFINITION OF LRE

LRE is the product of adult reproductive lifespan E, annual birth rate b and offspring mass at weaning m_w, normalized to adult size, m_a (Charnov *et al.* 2007):

$$\text{LRE} = E \times b \times m_w/m_a.$$

Average reproductive lifespan, E, captures the expected number of years a female invests energy towards the direct production of offspring. Birth rate, b, is the average number of live births per year (during the reproductive lifespan). Weaning mass, m_w, is the mass at which an offspring no longer depends directly on its mother's metabolized energy for growth and survival. For mammals (including humans) this is the size at which the offspring is weaned from mother's metabolic production (i.e. lactation). Note, however, that this is not equivalent to the age of full nutritional independence, which may occur at a later age (as it does in humans). We discuss the implications of this point in more detail below. When an offspring is weaned, the mother has the option of diverting energy toward the production of future offspring. It is the trade-off between investing in present reproduction and the ability to start producing future offspring that weaning size is designed to capture (Charnov 1991). Weaning size captures this trade-off as long as the time to wean a child (plus gestation time) is similar to the time between births. The time to wean a child, then, represents the optimal time to switch from present to future reproduction given ecological constraints. Reproductive effort per unit time, then, is the rate that offspring mass is produced normalized by adult size ($b \times m_w/m_\alpha$) and LRE is this value multiplied by E.

The energy available for reproduction during adulthood results from diverting the energy that was invested in growth (during the juvenile phase) to reproduction (Charnov 2001; Roff 2002). The relationship between energy available for reproduction and body size is described by the production function:

$$\frac{dm}{dt} = Am^\delta, \tag{1.1}$$

where m is the mass in kg, A the height of the function and δ the metabolic exponent describing the constraint of body size on the energy (the dm/dt) that can be allocated toward growth (during the juvenile phase) or reproduction (during adulthood). LRE is predicted to equal the inverse of the metabolic exponent, $1/\delta$ (Charnov *et al.* 2007) given the simplest constraints on mortality and the production constrain specified by equation (1.1). See appendix A for the derivation of this prediction. Empirically, δ has been shown to be near 0.7 (approx. 0.67–0.75) in cross-species analyses and hence LRE is predicted to equal 1.4, meaning that in a non-growing population, a female can only produce 1.4 times herself in her lifetime. Or, put another way, LRE captures a female's metabolic investment to produce a lifetime's worth of offspring. It focuses specifically on the amount of her metabolized energy that is channelled directly to offspring growth and captures the trade-off between the quantity and quality of offspring by considering the size at which it is optimal for a mother to switch from metabolically supporting and growing one offspring

to the production of another. Likewise, it captures the trade-off between mortality and reproduction because it contains the optimal product of birth rate and lifespan and arises from selecting the age at maturity that maximizes the net reproductive rate (appendix A).

3. MATERIAL AND METHODS

To calculate LRE for humans, data were gathered for the parameters in the model: size at weaning, reproductive lifespan, birth rate and adult size. Weaning size captures the mass of the offspring when it becomes independent of a mother's direct investments of metabolized energy to reproduction. However, offspring that die before weaning also represent a form of reproductive investment and the energy lost in pre-weaning mortality needs to be accounted for in order to obtain an accurate understanding of the reproductive energy budget (Charnov *et al.* 2007). Consequently, pre-weaning mortality is included in the calculation of m_w. Charnov *et al.* (2007) provide an equation for survivorship to weaning S_w as a function of litter size L based on a review of the literature which gives:

$$S_w = 0.7L^{-0.35}.$$

This equation estimates survivorship to weaning among natural fertility humans at about 0.70 and the empirical estimate from our sample is 0.72. Offspring that die between birth and weaning are assumed to die at the average size between the two ages. The final expression for size at weaning adjusted for pre-weaning mortality, $\hat{m}_w$, is (Charnov *et al.* 2007)

$$\hat{m}_w = S_w \times m_w + 0.5 \times (1 - S_w)(m_b + m_w),$$

where m_b is the mass at birth and m_w the mass at weaning.

Values for m_b were not available for all societies in our dataset and when missing, the average birth mass of the sample was used (2.8 kg; see also Hawkes *et al.* 1998). The sample average was used for reproductive lifespan as well ($E = 19$), which was calculated empirically as the difference between the first and last average ages at reproduction using a sample of 16 populations (unpublished dataset compiled by R. Walker, 2008). We do not extend the reproductive lifespan to later ages to account for the post-reproductive lifespan as it is the productivity of females at these later ages that make possible (at least in part) the birth rates and lower mortality rates at younger ages (Alvarez 2000; Hawkes *et al.* 2000). To assume that post-reproductive women were directly reproducing their own offspring while also subsidizing their daughters would essentially measure their productivity twice. Data were tabulated for natural fertility human groups (table 1), a sample that consisted largely of foraging populations. This is desirable because of the common assumption that foragers and forager–horticulturalists more closely approximate our evolutionary past than do agricultural or industrial societies.

4. RESULTS

Natural fertility humans have an average LRE of 1.45 ± 0.12 (95% CI, $n = 17$) (table 1), statistically indistinguishable from the average mammalian value of 1.41 ± 0.21 (95% CI, $n = 40$; figure 1). Humans appear to fall in the midst of the range of values calculated for mammals (figure 2). Thus, our results cannot falsify

Table 1. LRE data for human populations used in this study. For original sources see Walker *et al.* (2006*b*). m_a = adult size; b = birth rate; m_w = weaning size.

population	m_a	b	m_w	LRE
Ache res.	53.7	0.38	11.7	1.4
Agta	40.3	0.33	10.1	1.42
Arnhem land	41.3	0.27	11.5	1.27
Baka	44.4	0.33	12.4	1.56
Gainj & Asai	38	0.32	9.5	1.34
Gambian villages	52.1	0.38	11.9	1.46
Guaja	50.4	0.35	13.8	1.62
Hiwi	49.7	0.27	12.2	1.1
Ju'/hoansi	42.2	0.29	11.4	1.32
Maku-Nadeb	49.7	0.38	10.8	1.4
Maya	51.3	0.45	11.5	1.72
Pygmy (W. Af.)	42.7	0.28	9.8	1.08
Toba	64.2	0.42	12.7	1.41
Tsimane	51	0.36	12.4	1.46
Turkana	48.9	0.41	12.2	1.70
Wichi	62.3	0.56	13.2	2
Yanomamo	45.4	0.3	12.5	1.39
average	48.3	0.35	11.7	1.45

Figure 1. LRE as a function of log mass for mammals (open circles, $n = 40$) and human populations (shaded circles, $n = 17$); 95% CI are shown for the mean (dotted line) and the sample prediction (dashed line), for the mammal data (excluding the human data points).

the null hypothesis that natural fertility humans have the same LRE as other animals. Despite having an unusual life history, humans have an LRE predicted for an optimal life history with the simplest mortality and production constraints.

5. DISCUSSION

Our findings show that despite their unique life histories, social structures and ecologies, human LRE does not differ significantly from that of other animals, suggesting that similar underlying constraints are at work. We consider the implications of this finding for two broad issues of human life history, the evolution of the post-reproductive lifespan and the role of cooperative breeding. We consider each in turn after a general discussion of the production constraint (equation (1.1)).

The predicted value of LRE comes from the function describing the constraint of body size on productivity (equation (1.1)). Production can be thought of as respired energy available to grow one's self or one's offspring after accounting for the energy needed for maintenance (Kleiber 1961; Kuzawa 2007). The production function captures the direct costs of growing an offspring with energy metabolized by the mother (Charnov 1991). As such, metabolized energy is limited by resources and body size. Hence, lactation is a process linked directly to the physiology of metabolism and production. At weaning, a mother shifts her body-sized constrained production (metabolized energy) from growing the present offspring to growing a future one. LRE captures the sum of these metabolic investments toward offspring production.

There are, of course, other costs associated with successfully rearing an offspring to adulthood. Weaned offspring continue growing for several years and the costs of this growth in humans seem to be met largely by the productivity of group members other than the parents, pointing to the important coevolution of social networks and the lengthy juvenile period (Hawkes *et al.*
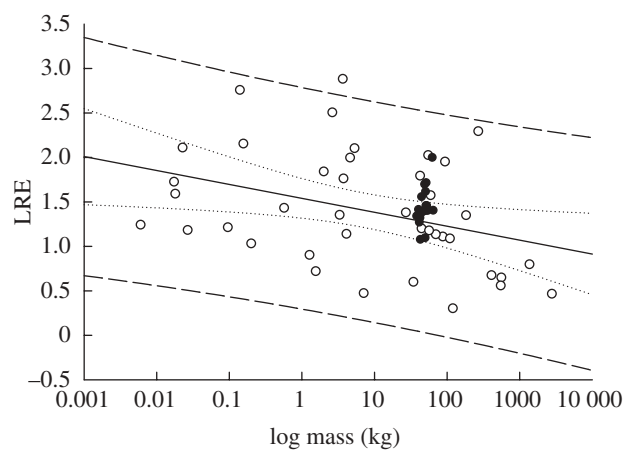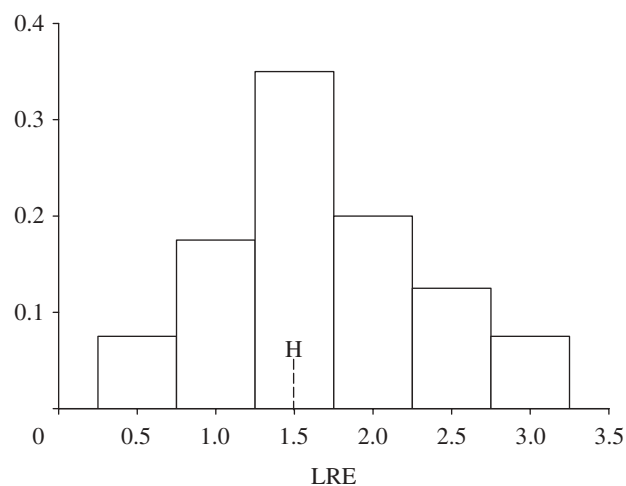

Figure 2. Histogram of LRE values for mammals (open bars, data from Purvis & Harvey 1995), with the estimate of LRE for human foragers indicated by an 'H' (redrawn from Charnov *et al.* 2007).

1998; Kaplan *et al.* 2000; Marlowe 2001; Hrdy 2006). However, the costs of rearing a child after weaning are not constrained by the production function, which only describes the somatic energy budget. The energy derived from the cooperative social network can be considered extra-somatic because it is external to the physiology of metabolism and production of the mother. As a result, the upfront metabolic costs of growing offspring are highly constrained and these costs are captured by LRE, but the remaining costs of the juvenile period seem largely made possible by cooperative human social networks (Hrdy 2006).

The observation that human LRE does not differ from other mammals suggests that reproductive effort probably changed predictably with reproductive lifespan during hominid evolution. Assume that some human ancestor was the first to develop a post-reproductive lifespan and that this period of the lifespan increased in each subsequent ancestor. The length of the reproductive period could shorten by delaying the age of first birth or by
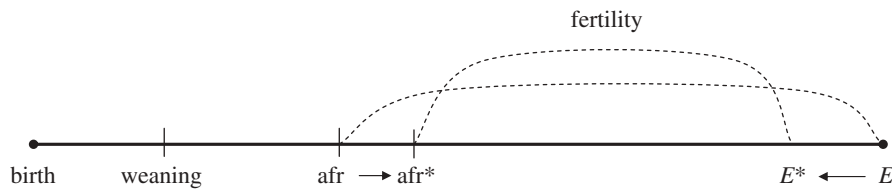
Figure 3. Hypothesized relationship between age-specific fertility and a re-organized lifespan that exhibits a significant post-reproductive period. A hypothetical human ancestor has lifespan E, and some subsequent ancestor has a shortened reproductive lifespan due to the lengthening of the juvenile period (a shift from afr to afr*) and/or a reduction in the age of last birth (a shift from E to E*), such that reproduction ceases before death. Such shifts represent significant reorganizations of the mammalian lifespan. If LRE is the same for some ancestor exhibiting either or both of these possible adjustments, then the area under each fertility curve should be the same as a reduction in the reproductive lifespan should be offset by a proportional increase in age-specific fertility.

lowering the age of last birth (the former perhaps being more probable). Regardless of the specific evolutionary scenario, an equilibrium LRE of approximately 1.4 for this string of hypothetical hominids requires that age-specific reproductive effort during the lifetime must have traded off predictably with each adjustment to the age of first reproduction or the lengthening of the post-reproductive period (figure 3). If so, then the area under each curve of age-specific fertility rate in figure 3 should be roughly equal for hominids at different points in their evolutionary history. As humans developed post-reproductive lifespans, the *proportion* of adulthood spent reproducing shortened, but this shortening of reproductive years was offset by increases in age-specific fertility. Note that there are a suite of additional behavioural and life-history changes going on concurrently with this process and it seems probable that subsidies to the female energy budget derive from multiple sources.

The finding that human LRE converges on the predicted value demonstrates the fundamental role of stabilizing selection and the strength of the underlying trade-offs shaping the structure of life histories. Despite the fact that derived components of the human life history are probably affected by the complex socio-ecology of humans, our results show that each adjustment trades-off against a complementary variable, resulting in an LRE that is not fundamentally different from other organisms.

APPENDIX A. PREDICTING THE VALUE OF LRE

The sources for deriving LRE and its associated predictions are presented in Charnov *et al.* (2007) and in Charnov (1991). In this appendix we summarize this derivation in condensed form and briefly comment on its connection to the human lifespan.

To arrive at the general prediction that LRE should equal 1/(the metabolic exponent), one only needs the simplest production constraint, the conventional definition of the net reproductive rate and the definition that the reproductive lifespan is the inverse of the adult mortality rate.

The production function is given by

$$\frac{\mathrm{d}m}{\mathrm{d}t} = Am^{\delta}, \tag{A 1}$$

where $\mathrm{d}m/\mathrm{d}t$ is mass per unit time, δ the exponent describing the relationship between mass and production (e.g. the metabolic exponent) and A the height of the function. Equation (A 1) determines the rate of biomass production during growth and the rate that energy is diverted to reproduction during adulthood. More elaborate production functions could be examined (and are by Charnov *et al.* 2007), but equation (A 1) captures the basic constraint for many organisms and fits the growth of Ache foragers (Hill & Hurtado 1996). The net reproductive rate, R_0, is given by

$$R_0 = S * b * E, \tag{A 2}$$

where S is the probability an offspring will reach reproductive age (juvenile survival), b the birth rate and E the reproductive lifespan. Juvenile survival can also be written as $S = He^{-Z\alpha}$ where H gives the strength of juvenile mortality early in the lifespan, Z is the adult mortality rate and α is the age at first reproduction. Substituting this expression for juvenile mortality into equation (A 2) gives

$$R_0 = He^{-Z\alpha} * b * E, \tag{A 3}$$

which can be used to find the optimal α, and hence the optimal life history subject to the given constraints, by solving

$$\frac{\partial \ln R_0}{\partial \alpha} = 0,$$

which gives

$$\frac{\partial \ln b}{\partial \alpha} = Z \tag{A 4}$$

but because the production function describes the energy that can be allocated to reproduction, the birthrate b can be written as

$$b = \frac{1}{m_0}\frac{\mathrm{d}m}{\mathrm{d}t} = \frac{1}{m_0}Am^{\delta},$$

which we substitute into equation (A 4) to get

$$\frac{\partial \ln b}{\partial \alpha} = Z = \frac{\delta}{m}\frac{\mathrm{d}m}{\mathrm{d}t} = \frac{\delta}{m}Am^{\delta} = \frac{1}{E}.$$

And since LRE is reproductive effort across the lifespan and reproductive effort is energy devoted to reproduction normalized by adult size we have

$$\text{LRE} = \frac{dm/dt\,E}{m_\alpha} = Am^{\delta-1}E = Am^{\delta-1} * \frac{1}{A\delta m^{\delta-1}} = \frac{1}{\delta}.$$

Because of the simple production constraint and the fact that E is the inverse of the adult mortality rate we get a convenient series of cancellations that results in the prediction that $\text{LRE} = 1/\delta$.

Importantly, for most organisms $E = 1/Z$ and E can be taken to mean *both* the reproductive lifespan and the average adult lifespan. This has been shown empirically via the study of mammalian life tables, but has to be true simply because of the units of E and Z. If Z is deaths per year then the inverse of Z is years per death, or average adult lifespan. However, due to the post-reproductive lifespan in humans, the reproductive lifespan E is shorter for females than would be predicted by the inverse of the adult mortality rate ($1/Z$). So $1/Z$ is the average adult lifespan in humans, as it is in other organisms, but is not equivalent to average female reproductive lifespan E. This is why we calculate E as the average time between first and last age at reproduction (which is also equivalent to E in animals without a post-reproductive lifespan) and is part of the deeper life-history insight obtained from calculating human LRE directly. In this regard the finding that humans have the predicted value of LRE without the strictly imposed mortality constraint that $E = 1/Z$ is all the more interesting. This may mean that the mortality constraint is not ultimately important for determining the value of LRE or it may mean that the constraint on years spent living is more important than the constraint on years spent reproducing (or it may mean something else entirely). Future investigations could consider more complex functional forms for the relationship between E and Z.

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