

The trade-off between number and size of offspring in humans and other primates

Journal:	<i>Proc. R. Soc. B</i>
Manuscript ID:	RSPB-2007-1511
Article Type:	Research
Date Submitted by the Author:	03-Nov-2007
Complete List of Authors:	Walker, Robert; MPI EVAN, Evolutionary Anthropology Gurven, Michael; University of California, Santa Barbara, Anthropology Burger, Oskar; University of New Mexico, Anthropology Hamilton, Marcus; University of New Mexico, Anthropology
Subject Area:	Anthropology/ Human biology & BIOLOGY, evolutionary ecology & Ecology & BIOLOGY
Keywords:	Quantity-quality trade-off, Smith-Fretwell model, number and size of offspring, natural-fertility human societies, primate life histories, quarter-power scaling
Categories:	Behavioural Ecology

Quantity-quality trade-off

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Resubmitted to *Proceedings of the Royal Society, Series B*

7 Title: The trade-off between number and size of offspring in humans and
8 other primates
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10 1st Author: Robert S. Walker ¹ (robert_walker@eva.mpg.de)
11

12 2nd Author: Michael Gurven ² (gurven@anth.ucsb.edu)
13

14 3rd Author: Oskar Burger ³ (oskar@unm.edu)
15

16 4th Author: Marcus J. Hamilton ³ (marcusj@unm.edu)
17

18 Affiliations:
19

20 ¹ Max Planck Institute for Evolutionary Anthropology
21 Deutscher Platz 6, 04103 Leipzig, GERMANY
22

23 ² Department of Anthropology,
24 University of California, Santa Barbara
25 Santa Barbara, California 93106 USA
26

27 ³ Department of Anthropology,
28 University of New Mexico
29 Albuquerque, New Mexico 87131 USA
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SUMMARY

Life-history theory posits a fundamental trade-off between number and size of offspring that structures the variability in parental investment across and within species. We investigate this “quantity-quality” trade-off across primates and present evidence that a similar trade-off is also found across natural-fertility human societies. Restating the classic Smith-Fretwell model in terms of allometric scaling of resource supply and offspring investment predicts an inverse scaling relation between birth rate and offspring size and a $-1/4$ power scaling between birth rate and body size. We show that these theoretically-predicted relationships, in particular the inverse scaling between number and size of offspring, tend to hold across increasingly finer scales of analyses (i.e., from mammals to primates to apes to humans). The advantage of this approach is that the quantity-quality trade-off in humans is placed into a general framework of parental investment that follows directly from first principles of energetic allocation.

Keywords: Quantity-quality trade-off, Smith-Fretwell model, number and size of offspring, natural-fertility human societies, primate life histories, quarter-power scaling

1. INTRODUCTION

Life-history models assume parents make investment decisions that maximize reproductive success (fitness) in the face of constraints whereby energy, effort, resources or time invested in the provisioning of offspring cannot be invested in producing more offspring (Stearns 1992). As a consequence, one of life's most fundamental trade-offs is between the number and size of offspring (Lack 1947; Roff 1992). Animal studies using experimental manipulation of offspring number or the environment generally have been successful in revealing the quantity-quality trade-off (Roff 2002).

The quantity-quality trade-off has received considerable attention in the field of human behavioral ecology (Hill & Kaplan 1999; Mace 2000; Kaplan & Lancaster 2000; Borgerhoff Mulder 2000). Blurton Jones & Sibly (1978) tested a model where a 4-year interbirth interval was fitness-maximizing in the Ju/'hoansi of Botswana and Namibia. Strassmann and Gillespie (2002) demonstrated a trade-off between female fertility and offspring survivorship for the Dogon of Mali. Hagen and colleagues (2006) showed that Shuar (Ecuador) children in families with fewer adults and more dependents have compromised growth and nutrition. Despite these and other demonstrated relationships, life-history trade-offs have been difficult to demonstrate in observational studies given the problem of unmeasured and confounding variables (Hill & Hurtado 1996). Since parental condition varies considerably within and across populations, the problem of phenotypic correlation between parental condition and reproductive effort may mask the underlying trade-off (Reznick 1985; Stearns 1992). In such cases, a typical result is that parents with a higher number of children are also able to invest more in each child, presumably because healthier, higher-status individuals are better able to monopolize resources. For example, there is a positive relationship between childhood survival and number of siblings among Ache hunter-gatherers of Paraguay (Hill & Hurtado 1996) and Kipsigis agro-pastoralists of Kenya (Borgerhoff Mulder 2000). These relationships remain positive even after statistically controlling for body size or wealth, suggesting that other intrinsic differences among individuals may be obscuring the trade-off. Similarly, lifetime reproductive success as measured by number of grandchildren has been shown to increase with higher fertility in several populations, including the Ju/'hoansi (Pennington & Harpending 1988; cf. Blurton Jones & Sibly 1978), Ache (Hill & Hurtado 1996), and New Mexico men (Kaplan et al. 1995), contrary to the expectation based on trade-offs.

While attempts have been made to examine trade-offs within human populations, to our knowledge no attempt has been made to uncover the trade-off between number and size of offspring across human societies, perhaps due to the problems described above. A comparative study with humans is important because some derived human traits, such as cultural norms, food sharing, extended provisioning, and extra-maternal care, may affect reproductive effort in ways that make the quantity-quality trade-off different than the trade-off in other animals. For example, equitable pooling of resources could hypothetically erase the trade-off within a population, though the trade-off may still be visible across populations. Moreover, given the problem of phenotypic correlation, it is likely that no quantity-quality trade-off will be visible if birth rate is not adjusted by mother's reproductive energy budget. The analytical approach we use was developed by Smith and Fretwell (1974) and Charnov and Ernest (2006) in a model that accounts

for the phenotypic correlation by controlling for mother's mass raised to the $3/4$ power, a proportionality of energy available for reproduction. An advantage of this approach is that the quantity-quality trade-off in human populations can be analyzed from the same underlying framework as other animals. We make the parsimonious prediction that a trade-off will emerge across humans that is similar to the inverse relationship between quantity and quality seen in other mammals and driven by the same first principles of energetic allocation.

Analyzing the quantity-quality trade-off

Smith and Fretwell (1974) developed a general model of the trade-off between number and size of offspring. A parent with R resources to devote to reproduction must divide them among C offspring in a clutch, creating a limited investment per offspring, I , such that

$$I = R / C . \quad (1)$$

Most primates have only one offspring per litter, but C can be interpreted as the fertility rate (births per year) and R as the flow of total resources allocated to reproduction (offspring production rate). Time then cancels out of the ratio such that I describes the energetic investment of parents to an average offspring.

The trade-off between the investment, I , and fertility rate, C , can be analyzed under the assumption that offspring production rate, R , is constant across populations or species. However, as discussed in Charnov's (1993) general life-history model, R scales approximately as the $3/4$ power of adult body mass, M , across mammals (Charnov 2001). Indeed, daily milk yield and lactational capacity, perhaps the most direct measures of mammalian R , scale as approximately the $3/4$ power of body size (Oftedahl 1984; Martin 1984). Given that $R \propto M^{3/4}$, the following equation applies (Charnov & Ernest 2006):

$$\frac{C}{M^{3/4}} \propto I^{-1} . \quad (2)$$

The left side of equation 2 is mother's-energy-adjusted fertility rate and is expected to be inversely proportional to investment per offspring, I , estimated as size at independence. The predicted inverse relationship between number and size of offspring is strong across mammals (Charnov & Ernest 2006), a remarkable result given that different species likely express a variety of relationships between offspring fitness and parental investment (Charnov & Downhower 1995).

Re-expressing the Smith-Fretwell model in terms of allometric scaling predicts the $-1/4$ power scaling of fertility rates with body size, provided resources invested per offspring is proportional to the mass of the mother. Indeed, across a wide spectrum of mammals, including primates, weaning size is approximately $1/3$ mother's size (Charnov 1993; Alvarez 2000). Given that $R \propto M^{3/4}$ and $I \propto M^1$, fertility rate, C , as a function of body mass, M , becomes

$$C = \frac{R}{I} \propto \frac{M^{3/4}}{M^1} = M^{-1/4}. \quad (3)$$

Thus offspring production increases with mass slower than offspring investment increases with mass, and fertility rate scales to the $-1/4$ power of body mass.

The elegance of the Smith-Fretwell model with the Charnov-Ernest correction is that it can be used to investigate the trade-off between offspring number and size both across and within species where phenotypic correlation is expected. Here we apply the model to study the trade-off across primate species and human societies, exposing variability in fertility decisions and shifts towards differential life-history strategies that favor more or less quantity versus quality of offspring. We have compiled a comparative database of 16 natural-fertility human societies and a primate database that we analyzed with both conventional and phylogenetically-controlled methods. Our primary hypotheses are 1) that fertility rate will scale as the $-1/4$ power of body size and 2) that fertility rate adjusted by offspring production rate will be an inverse function of offspring size in both humans and other primates.

2. METHODS

Evaluation of the Smith-Fretwell model with the Charnov-Ernest correction requires estimates of the following life-history components: 1) fertility rate, C , 2) $M^{3/4}$ to estimate a proportionality of offspring production rate, R , and 3) offspring size, I , at some age (e.g., weaning, 5 and 10). We calculated 95% confidence intervals of the trade-off exponent using ordinary least squares and reduced major axis regression. Log-log multiple regressions of C on R and I (and I on R and C) across natural-fertility societies were performed using SPSS 15.0 (SPSS, Inc., Chicago, IL).

Non-human primates and mammals

Primate data ($n=101$ species) are from Lindenfors (2002) and non-volant, eutherian mammals ($n=610$ species excluding primates) are from Ernest (2003). Fertility rate was calculated by multiplying births per year by the average number of offspring per litter. Adult body sizes for primates were taken from Smith and Jungers (1997) with an emphasis on wild weights where available. Sizes at weaning for primates ($n=5$ apes, $n=30$ other haplorhines) included estimates from growth curves (Lee 1999; Lindenfors 2002). Analyses were conducted with primate species as independent data points and using independent contrasts that adjust for phylogenetic constraints (Nunn & Barton 2001) because phylogenetically-close species may be similar only because they share a recent common ancestor (Felsenstein 1985). The independent contrasts module of PDTREE by Garland and colleagues (1993) with the phylogenetic tree and branch lengths of Bininda-Emonds and colleagues (2007) were used to construct independent contrasts. Diagnostics available in PDTREE were examined to ensure homoscedasticity in residuals and that branch lengths were statistically appropriate.

Natural-fertility human societies

The sample used here is 16 subsistence-based societies including foragers, horticulturalists, and one pastoral society. To our knowledge it is the most complete sample of human populations that have limited access to modern contraception and

health care and whose economies are primarily subsistence-based. We focus here on subsistence societies because most resources are invested as somatic capital in human bodies (i.e., body size and fertility) as opposed to stored, inherited wealth. Fertility rate was estimated as the inverse of closed interbirth intervals (IBI) for the Ache (Hurtado & Hill 1996), Aeta (Migliano 2005; Eder 1987), Agta (Early & Headland 1998), Aborigines in Arnhem land (Billington 1948; Hamilton 1981), Baka (Yamauchi et al. 2000), Gambian villagers (Billewicz & McGregor 1981; Sear et al. 2003), Guaja (Gradimir Djurovic, unpublished data), Hadza (Blurton Jones et al. 1992), Hiwi (Hurtado & Hill 1987), Ju/'hoansi (Howell 1979), Maku-Nadeb (Walker, unpublished data), Toba (Bove et al. 2002), Tsimane (Gurven, unpublished data), Turkana (Little et al. 2003), West African "Pygmies" (Cavalli-Sforza 1986), and Yanomamo (Neel & Weiss 1975). The Ache were allowed to enter the sample twice, as hunter-gatherers in earlier research and as horticulturalists on a reservation in more recent research. Female adult body sizes and average male and female sizes at ages 3, 5 and 10 were either available from the original sources above or from Walker et al. (2006). Comparative studies across societies may also suffer from problems of phylogenetic non-independence. We addressed this issue by adjusting for general geographic location (Africa, South America, Australia, and Southeast Asia) in multiple regressions.

3. Results

Fertility allometry

Fertility rates decline with body size to the $^{-1/4}$ power (-0.26 ± 0.01 , slope \pm 95% confidence interval) across mammals (Charnov 1993; Figure 1). The fertility rates of non-ape primates demonstrate an allometry steeper than $^{-1/4}$ (-0.36 ± 0.06), driven by shifts towards slower reproduction in larger species. Non-human apes ($n=8$) strongly shift towards a slower life history (i.e., lower intercept) yet also scale as $^{-1/4}$ (-0.25 ± 0.22 , Figure 1). In addition, there is approximately a $^{-1/4}$ power scaling for fertility rates across large haplorhines using data from only wild studies ($n=8$; data from Barrickman et al. in press). Using independent contrasts across primates yields a slope of -0.32 ± 0.11 ($n=95$), steeper than expected but not significantly different from the predicted value of $^{-1/4}$. Humans have reproductive rates that are faster than those of other apes, yet still considerably slower than those of other mammals. Contrary to the expectation of negative allometry, human fertility rates increase with body size in natural-fertility populations (slope = 0.55 ± 0.39 , Figure 1). Based on the ratio of scaling intercepts (ratio of geometric means assuming $^{-1/4}$ scaling), an average mammal reproduces at a rate 3.6 times faster than non-ape primates, 4.5-fold faster than humans, and 7.7-fold faster than non-human apes. Humans reproduce on average at rates about 1.7-fold faster than non-human apes and only about 19% slower than non-ape primates.

Trade-off between number and size of primate offspring

Across primates the negative relationship between \log_{10} energy-adjusted fertility ($C \cdot R^{-1}$) and \log_{10} weaning size (I) demonstrates a quantity-quality trade-off (Figure 2). The slope and 95% confidence intervals are -0.90 ± 0.43 for non-human apes and -0.89 ± 0.23 for other haplorhines. The wide confidence intervals are unavoidable in this sample but nonetheless show that the tradeoff is near the theoretically-predicted value of -1 . Non-human apes demonstrate a shift towards slower fertility for a given weaning

size at rates only 36% of an average haplorhine, yet the expected trade-off holds despite the limited number of species. It should be noted that the R^2 values for these relationships in primates (and other mammals, Charnov & Ernest 2006) are much higher, and the slope much steeper, with the adjustment for offspring production rate than they are with regressing the unadjusted fertility rate on weaning size. Correcting for the potential problem of phylogenetic non-independence gives similar results. The trade-off between energy-corrected fertility rate and weaning size using independent contrasts yields a slope of -0.71 ± 0.20 across primates, but after removing one contrast with considerable leverage the slope is -0.94 ± 0.22 (Figure 3).

Trade-off between number and size of human offspring

Humans have a higher mother's-energy-adjusted fertility rate given weaning size than do other apes. Moreover, because weaning does not mark economic independence in humans, their true "weaning size", indicative of maternal investment, should be farther to the right in Figure 2 and even more divergent from other apes. In other words, the high fertility rate for weaning size in humans is surprising because weaning size actually underestimates the energetic investment per offspring. The trade-off is not seen with size at age 3 either because the sample size is small or the long, continued investment by human parents is better indexed by size at later ages. There are more data available for sizes at age 5 and 10 and a trade-off is apparent between mother's-energy-adjusted fertility rate and size at these ages. Using ordinary least squares regression (OLS), the trade-off is shallow (-0.56 ± 0.51 , Figure 4). However, if there is error in the estimates of offspring size, OLS regression will underestimate the slope of the trade-off. The exact relationship between maternal investment and age/size of offspring is difficult to estimate for humans and may further increase uncertainty in empirical estimates of the tradeoff. Using a reduced major axis (RMA) regression that adjusts for such error yields a trade-off with an exponent of -1.15 ± 0.86 . Using size at age 10 as a measure of offspring investment, an RMA regression gives a slope of -0.87 ± 0.72 .

An alternative method to uncover the trade-off is with a multiple regression of fertility rate (C) as a power function of size at age 5 or 10 (I) and adult body mass (M), which only requires a simple re-arrangement of the variables into the form $C = I^{-1} \cdot R$. The results from this multiple regression are similar to those from the graphical method, yielding the equation $C = 0.07 \cdot I^{-0.65} \cdot M^{0.89}$. Comparable results are obtained using size at age 10 and switching the dependent and independent variables (Table 1). Switching dependent and independent variables is justifiable because a trade-off implies bi-directional causality (i.e., higher fertility leads to decreased investment and higher investment leads to decreased fertility). We find no evidence of a trade-off if fertility rate is not adjusted by female body mass because the problem of phenotypic correlation masks the trade-off. We also included an adjustment for geographic location given the potential problem of non-independence in the data, but the effects of geographic location are very weak and not significant in any of the regressions.

4. Discussion

Our results show the predicted energetic trade-off between the number and size of primate offspring using both conventional analysis and independent contrasts. Importantly, the quantity-quality trade-off in primates, and especially apes, is down-

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3 shifted in comparison to that of other mammals. That some smaller primates often
4 exhibit scaling more similar to the typical mammal pattern, whereas apes display a more
5 down-shifted trade-off, may be important for explaining why allometric slopes
6 sometimes differ from predicted values. When all primates are included in the same
7 dataset, we are lumping fast and slow life histories together. Primates, and especially
8 larger-bodied species, reproduce at slower rates for a given weaning size than most
9 other mammals likely reflecting the larger brains of primate offspring and generally
10 slower life histories.
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13 In contrast to mixed results of within-population studies mentioned in the
14 Introduction, the quantity-quality trade-off consistently emerges across human
15 populations provided an adjustment is made for mother's energy budget. Here we used
16 the same budget adjustment for both within- and across-species analyses. Our OLS
17 estimates of the trade-off exponent for humans are consistently less negative than the
18 predicted -1. However, OLS might underestimate the true slope as it is reasonable to
19 assume there is also error in the estimates of offspring size and there may be
20 considerable variation in the true caloric investment per offspring. Indeed, RMA
21 regression gives exponents that are closer to the predicted value of -1 (albeit with wide
22 confidence intervals). Alternatively, some derived human traits like extra-maternal care
23 and food sharing may compensate for the mother and adjust the trade-off. Nonetheless,
24 that a significant trade-off is found is encouraging. In fact, the approximately inverse
25 relationship between fertility rate and offspring investment appears to hold at
26 increasingly finer scales of analyses (mammals to primates to apes to humans). The
27 quantity-quality trade-off across human populations may follow the same pattern as
28 seen in other animals and suggests that reproductive variation in natural-fertility
29 societies can be understood from first principles of energetic allocation.
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32 Importantly, the $-\frac{1}{4}$ fertility allometry generally holds across eutherian mammals
33 and also suggests the existence of a fundamental trade-off between number and size of
34 offspring following directly from the Smith-Fretwell model (Equation 3). At first glance
35 the increase in fertility rate with body size observed across human societies seems to
36 contradict the $-\frac{1}{4}$ power fertility allometry seen across species. The shape of the
37 relationship between offspring quality and parental investment may be important to
38 understanding positive fertility scaling across humans. The optimal investment in
39 offspring depends on the rate at which returns to offspring quality (fitness) diminish
40 with each additional unit of investment (Kaplan et al. 1995). Natural-fertility societies
41 with large-bodied individuals and fast population growth are pushing the biological envelope
42 in terms of reproductive output with interbirth intervals as low as 20 months, but these
43 offspring are still able to grow to the size of normal adults. Most likely there are quickly
44 diminishing returns on investments to offspring quality, perhaps even a fixed threshold
45 investment, in these societies such that investment per offspring increases sublinearly
46 for larger mothers (I scales less than M^1) and surplus energy is funneled to fertility. The
47 common result of a positive effect of maternal body size on fertility rates within other
48 species (Roff 2002) and within human populations may also reflect a similar
49 phenomenon (e.g., Ache: Hill & Hurtado 1996, Gambian villagers: Sear et al. 2003, and
50 New Guinea Highlanders: Brush et al. 1983).
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53 There are high-density hunter-gatherers (near zero population growth) with large
54 offspring and low fertility (e.g., Hiwi) and other foragers, also near carrying capacity, that
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3 have small offspring and relatively high fertility (e.g., Agta and Aeta, Figure 4). Many
4 other human societies in our sample are undergoing population expansion and this may
5 affect our inter-specific comparisons. However, even the human populations that are
6 nearly stationary, including the Hiwi, reproduce at mass-adjusted rates that are faster
7 for their weaning size than those of other apes. Population expansion in the sample
8 may also affect our ability to accurately reveal the true fertility scaling within humans,
9 and it is unclear exactly how differential population growth affects the trade-off and the
10 extent to which controlling for mother's body size also adjusts for population growth.
11 The positive fertility allometry within humans may in large part reflect faster population
12 growth in relatively resource-abundant societies, in which case R scales greater than
13 $M^{3/4}$.

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16 Our primary hypothesis of an inverse relationship between fertility rate and
17 offspring size across natural-fertility human societies cannot be rejected. Controlling for
18 mother's energy availability, primate species and human societies with faster fertility
19 rates have predictably smaller offspring, and vice versa. However, humans have a
20 higher than expected fertility rate for weaning size than other apes when adjusting for
21 mother's energy budget, suggesting that energy available for human reproduction is
22 likely increased by technological advances, slow offspring growth (Gurven & Walker
23 2006), and/or extra-maternal provisioning (e.g., grandparents: Hawkes et al. 1998 and
24 husbands: Kaplan et al. 2000). Humans as large, long-lived, cooperative mammals that
25 reproduce at a fast rate create a formidable life-history combination that likely figured
26 prominently in the successful colonization of hunter-gatherers around the globe.
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30 **Acknowledgements**

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32 We thank Melanie Moses, Ric Charnov, Kim Hill, Eric Schniter, Chris Von Rueden, and
33 Charles Nunn for helpful comments that improved this paper. We also thank Gradimir
34 Djurovic for providing unpublished data for the Guaja. The National Science Foundation,
35 LSB Leakey Foundation, and Wenner-Gren Foundation provided dissertation research
36 grants to RSW that supported fieldwork with the Maku-Nadeb.
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Figure captions

Figure 1. The allometry of birth rates across eutherian mammals on \log_{10} - \log_{10} axes. In Smith-Fretwell notation this relationship is equivalent to regressing C on $R \cdot I^{-1}$ from Equation 3. Mammals and apes scale as approximately the $^{-1/4}$ power of body size. The “Other primates” include strepsirrhines and haplorhines as both clades show similar scaling. Natural-fertility human societies are the only sample here where fertility increases with body size.

Figure 2. Energy-corrected fertility rate as a function of weaning mass for primates on \log_{10} - \log_{10} axes. In Smith-Fretwell notation this relationship is $C \cdot R^{-1}$ regressed on I . The slopes are close to -1 (apes: -0.90 ± 0.43 ; other haplorhines -0.89 ± 0.23). While there is some uncertainty in the data for 5 smaller haplorhines, their removal has little effect on the scaling (-0.88 ± 0.36). These primate lines are downshifted in comparison to the trade-off in other mammals (Charnov and Ernest, 2006). Size at age 3 is shown for humans.

Figure 3. Independent contrasts ($n=32$) of the trade-off between energy-corrected fertility rate and weaning size (both on \log_{10} -scale) for primates (humans excluded and no data for strepsirrhines). In the Smith-Fretwell model this is $C \cdot R^{-1}$ regressed on I . The slope of this relationship constrained through the origin is -0.71 ± 0.20 across primates (dotted line), but one particular contrast (*Miopithecus talapoin* and *Cercopithecus*, right-most side of graph) has considerable leverage and upon removal the slope is -0.94 ± 0.22 (solid line).

Figure 4. Energy-corrected fertility rate as a function of offspring size at age 5 across natural-fertility human societies. Axes are not logged; the fits are power equations. Following the Smith-Fretwell model, this graph is $C \cdot R^{-1}$ regressed on I . Dashed line is the ordinary least squares fit with an exponent of -0.56 ± 0.51 . However, given that error is likely present in our estimates of offspring size, reduced major axis regression may be more appropriate (solid line, exponent = -1.15 ± 0.86). Similar results are found for size at age 10.

Table and caption

Table 1. Multiple regressions of the quantity-quality trade-off across natural-fertility human societies ($n=17$). The first two models correspond to C as a power function of R and I , and the second two are I as a power function of R and C (Equation 1).

Dependent variable	Independent variables	Exponent	Bootstrapped 95% confidence interval	R^2
Fertility rate	(Constant)	(0.07)		0.55
	Mother's mass	0.89	0.49, 1.29	
	Offspring size age 5	-0.65	-1.24, -0.07	
Fertility rate	(Constant)	(0.03)		0.55
	Mother's mass	1.23	0.62, 1.87	
	Offspring size age 10	-0.68	-1.40, -0.10	
Offspring size age 5	(Constant)	(1.01)		0.35
	Mother's mass	0.59	0.32, 0.86	
	Fertility rate	-0.41	-0.72, -0.09	
Offspring size age 10	(Constant)	(0.19)		0.63
	Mother's mass	1.11	0.82, 1.40	
	Fertility rate	-0.52	-0.76, -0.28	

Quantity-quality trade-off

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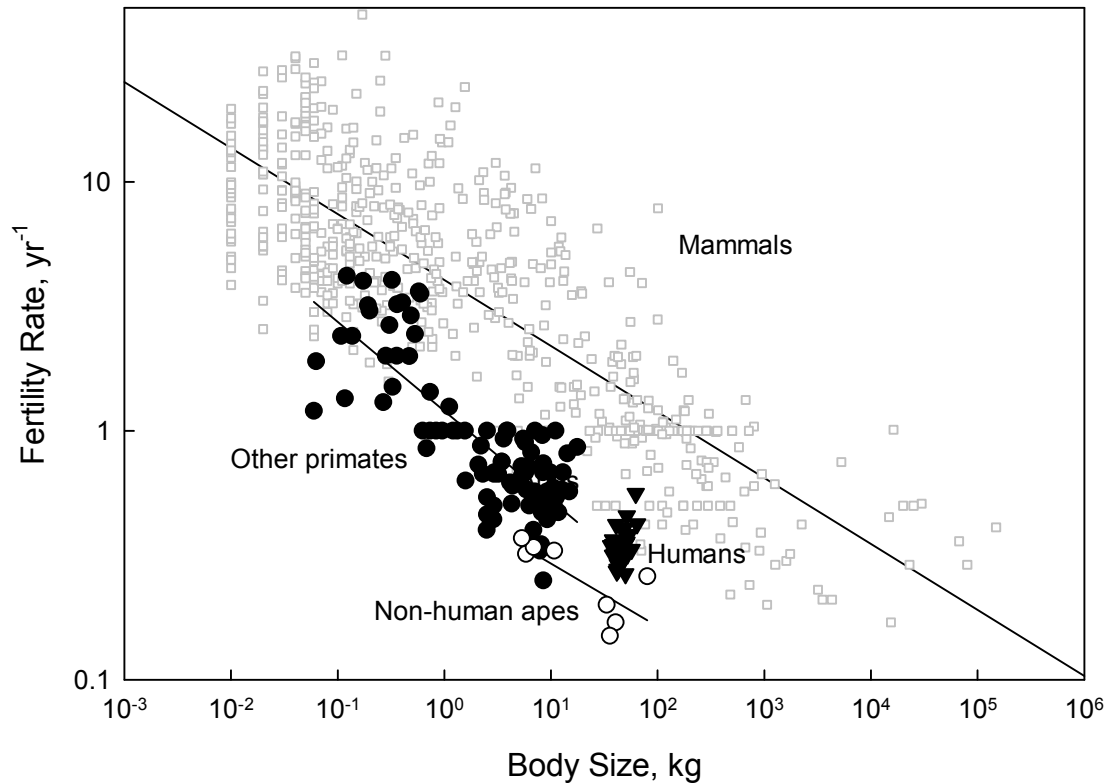


Figure 1.

Pre-proof Only

Quantity-quality trade-off

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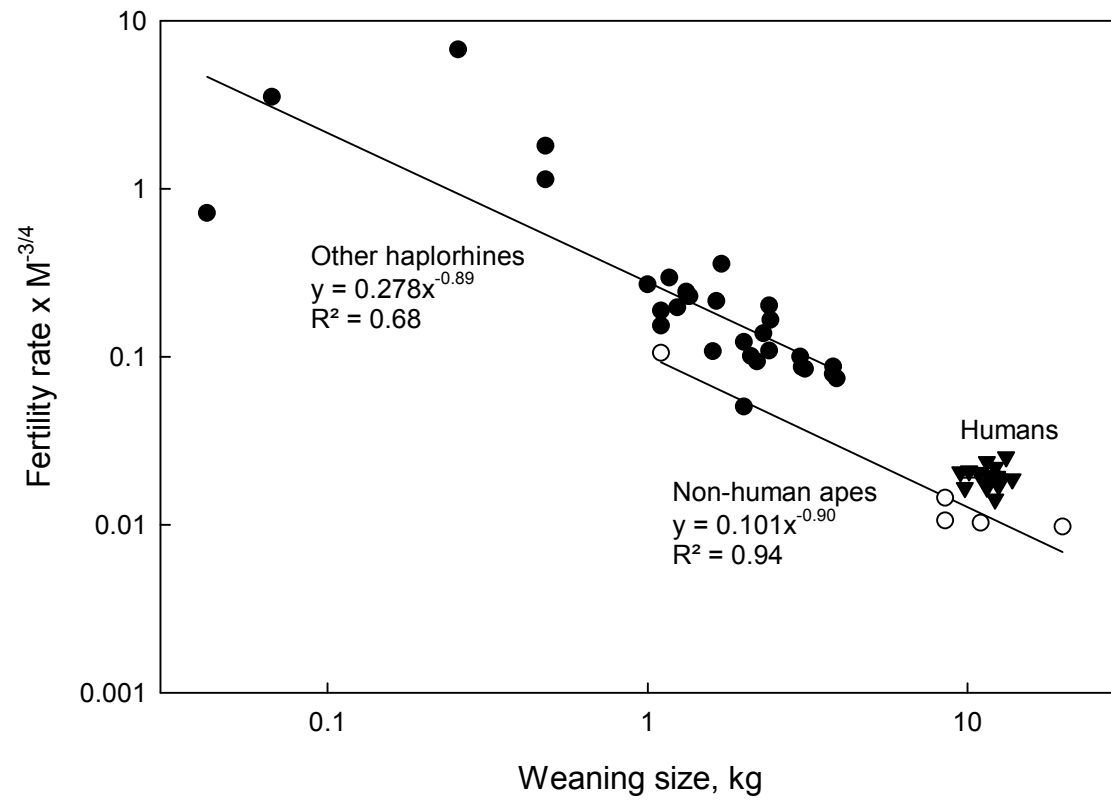


Figure 2.

Quantity-quality trade-off

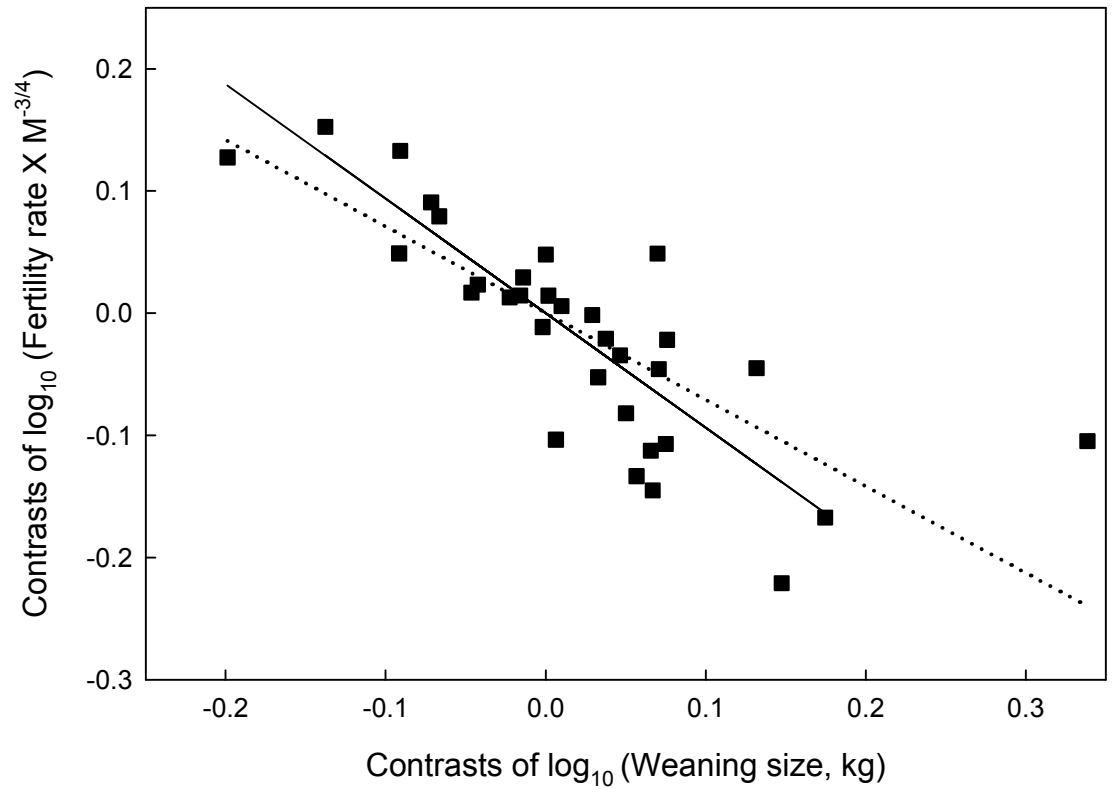


Figure 3.

Quantity-quality trade-off

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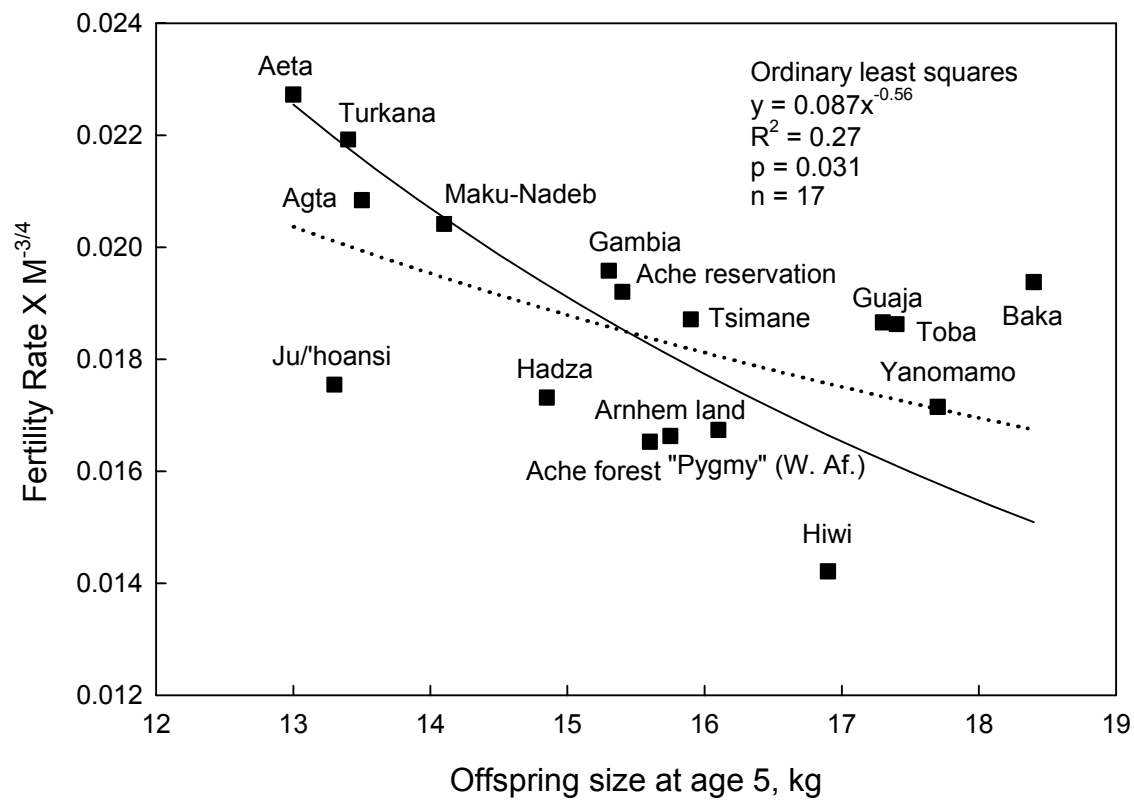


Figure 4.

Running Head: Quantity-quality trade-off