

Allometry of human fertility and energy use

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Abstract

The flux of energy and materials constrains all organisms, and allometric relationships between rates of energy consumption and other biological rates are manifest at many levels of biological organization. Although human ecology is unusual in many respects, human populations also face energetic constraints. Here we present a model relating fertility rates to per capita energy consumption rates in contemporary human nations. Fertility declines as energy consumption increases with a scaling exponent of $-1/3$ as predicted by allometric theory. The decline may be explained by parental trade-offs between the number of children and the energetic investment in each child. We hypothesize that the $-1/3$ exponent results from the scaling properties of the networked infrastructure that delivers energy to consumers. This allometric analysis of human fertility offers a framework for understanding the demographic transition to smaller family sizes, with implications for human population growth, resource use and sustainability.

Keywords

Allometry, demographic transition, human ecology, human life history.

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INTRODUCTION

Relationships between body size, metabolism, and biological rates and times result from fundamental allometric constraints on the structure and function of individual organisms (Peters 1983; West *et al.* 2000). Recent theory proposes that these ubiquitous empirical patterns occur because organisms have been selected to simultaneously maximize metabolic capacity and the efficiency of internal energy transport (West *et al.* 1999).

Modern humans are unique in that energy consumption is not limited by body mass and metabolic rate, but by the ability to harness non-metabolic energy such as gas, oil, coal, and nuclear, solar and hydroelectric power. Here we examine how modern human fertility varies with per capita energy consumption. Interestingly, modern fertility rates are largely a matter of choice, and like energy consumption, are not solely determined by human physiology. Still, human fertility varies with energy consumption in accordance with allometric predictions. This raises the possibilities that allometry may describe non-biological energy distribution networks and that human reproductive choices may ultimately be guided by that allometry.

Allometric scaling relationships are described by power functions that relate dependent variables to body mass.

Whole-organism metabolic rate, or the rate of energy consumption, scales as mass to the $3/4$ power (Peters 1983; West *et al.* 1999):

$$B = B_0 \times M^{3/4} \quad (1)$$

where B is the metabolic rate, M is body mass and B_0 is a scaling constant.

Most other biological rates, R , such as heart rate, reproductive rate or cellular metabolic rate, are predicted and observed to scale as mass to the $-1/4$ power (Peters 1983; West *et al.* 1999, 2000):

$$R \propto M^{-1/4} \quad (2)$$

These scaling laws follow from allometric theory in which metabolism is limited by an energetically efficient, space-filling, fractal-like resource distribution network such as the circulatory system of mammals or the vascular system of plants (West *et al.* 1999, 2000). Biological rates are ultimately limited not by mass, *per se*, but by rates of energy and material turnover. Re-arranging eqns 1 and 2 shows the predicted relationship between metabolic rate and other biological rates:

$$R \propto B^{-1/3} \quad (3)$$

Life is constrained by these fundamental allometric relationships at many levels of biological organization including the level of mitochondrial activity within cells (West *et al.* 2002), the fertility rates of mammals and growth rates of populations (Charnov 1993), and the population density of mammals and trees (Damuth 1981; Enquist *et al.* 1998). Scaling exponents are predictable despite extraordinary differences among these systems in network size and architecture, suggesting that there are fundamental trade-offs between biological rates and power consumption. We suggest that these trade-offs constrain human fertility as well.

Although humans are highly unusual organisms in many respects, most characteristics of human physiology are predictable from scaling relationships observed in other mammals, particularly primates. For example, human metabolic rate can be predicted by allometric equations. By using the empirically determined $B_0 = 5.66$ for higher primates (Peters 1983), eqn 1 predicts that the metabolic rate of a 60-kilogram human is 120 watts or 2500 calories per day. However, humans differ from other organisms in their social organization and ecology. The exploitation of supplemental energy sources has fuelled 10 000 years of exponential human population growth (Cipolla 1972), the development of modern industrial–technological societies, and the rise of *Homo sapiens* to become the dominant species on earth, with major impacts on global biodiversity, biogeochemical cycles and climate (Vitousek *et al.* 1986, 1997).

Biological metabolism is a small fraction of the total energy consumed by modern humans who utilize vast distribution networks to extract and deliver oil, gas, coal, electricity and other resources. Per capita consumption of this extra-metabolic energy varies from a few hundred watts in the poorest nations, to many thousands of watts in more industrial countries, which rely predominantly on fossil fuels (World Resources Institute 2000). The per capita energy consumption rate in the United States is 11 000 W (World Resources Institute 2000) which is approximately 100 times the rate of biological metabolism and, from eqn 1, is the estimated rate of energy consumption of a 30,000-kg primate.

METHODS

We used data from over 100 nations from 1970 to 1997 (World Resources Institute 2000) to test the hypothesis that human energy consumption and fertility rates are related by eqn 3. Demographic data consist of total fertility rates (projected lifetime births per woman based on age specific annual fertility), crude fertility rates (births per 1000 population per year) and infant mortality rates (deaths per 1000 live births) for each nation. Per capita energy

consumption rates describe the per capita share of the total energy consumed by each nation. These values were converted into watts and averaged to correspond with 5-year averages of demographic data. Additional data covering the period 1850–2000 were obtained for USA fertility (Coal 1963), and per capita energy consumption (Schurr & Netschert 1960; US Department of Energy 2002).

Mammal masses and annual birth rates were obtained from Ernest (in press). Mammal metabolic rates were estimated from mass using allometric equations for the different orders (Peters 1983). In humans, annual births per woman were calculated by dividing lifetime fertility by an assumed average 20-year reproductive period.

The relationship between fertility and per capita energy consumption was determined using ordinary least squares regression of log transformed variables to be consistent with other allometric calculations. Ten oil-producing nations with extremely high per capita energy production (Oman, Qatar, Saudi Arabia, United Arab Emirates, Bahrain, Kuwait, Netherlands Antilles, Brunei, Libya and Turkmenistan) are significant outliers in most years and are excluded from regression equations.

RESULTS

Of interest here is the extent to which extra-metabolic energy consumption constrains human life history and demography. A well-known feature of human ecology is the demographic transition, the tendency of fertility to decline as economic development increases. This phenomenon appears to challenge life-history theory because individuals with greater access to resources have fewer children and apparently reduced biological fitness (Hill & Kaplan 1999; Borgerhoff Mulder 2001). Here we show that per capita fertility is closely correlated to per capita rates of extra-metabolic energy use (E), where E is the individual share of total national energy consumption and includes end consumer uses (heating houses, driving cars, running refrigerators) and per capita contributions to infrastructure (building and maintaining roads, airlines, communications networks and national defence systems).

Figure 1 shows that human fertility declines with $E^{-1/3}$ in each time period from 1970 to 1997. Each data point represents the average fertility and per capita power consumption of a nation over the indicated time interval. The qualitative trend in Fig. 1 is consistent with what is known about the demographic transition: fertility is lower in wealthier nations which have high energy consumption. More compelling is the fact that the allometric exponent (slope of the log–log plot) is statistically indistinguishable from $-1/3$, as predicted by eqn 3. The same scaling relationship is seen whether fertility is measured as total fertility or crude fertility rate. Although several nations have

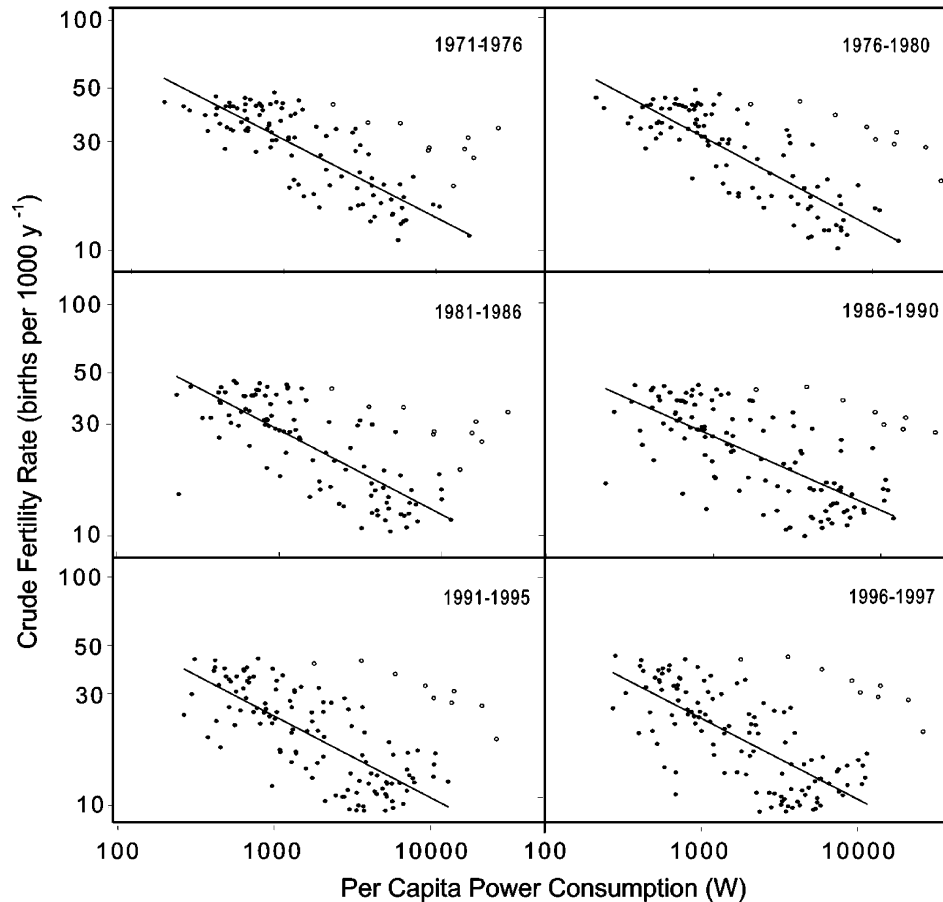


Figure 1 Annual human fertility rates (births per 1000 per year) plotted on logarithmic axes as a function of extra-metabolic energy consumption (E) for 98–116 nations in 6 periods from 1971 to 1997. Here infant mortality is subtracted from fertility to more accurately estimate the number of children actually raised by parents. Empty circles represent outliers (all of these nations were major oil producers) not included in the regression. The outliers in the lower left of the middle two panels are Latvia and Bosnia. The slopes of the 6 regressions are between -0.33 and -0.37 . These values are statistically indistinguishable from the predicted value of $-1/3$ ($P > 0.10$ in all cases). The intercepts range from 2.43 to 2.59, with an average r^2 of 61%. Inclusion of outliers, excluding the effect of infant mortality, and considering total fertility rather than annual fertility have little effect on the slope of the relationship.

undergone significant shifts in fertility and energy consumption, the same pattern is apparent in every 5-year time interval since 1970.

A similar dynamic relationship exists across time in the USA from 1850 through 2000, as shown in Fig. 2. Each data point represents the average fertility rate and per capita consumption for the USA in 5-year intervals. As energy consumption increases over time, fertility decreases. Again the slope of the regression is statistically indistinguishable from $-1/3$.

Allometric relationships accurately describe the broad scale pattern of change from pre-industrial averages of 6.5 births per woman and power consumption of 600 W (Livi-Bacci 1997) to the modern levels of fertility and energy consumption. However, given the short period

of available data, the dynamic relationship in most nations is difficult to assess. A 50% decrease in fertility in South Korea is accompanied by a 6-fold increase in E (consistent with allometric predictions) while a similar fertility reduction in Cuba occurs with stagnant E . Once the allometric relationship is identified, social and economic conditions may explain the residual variation or systematic deviations from the regression line in particular regions, i.e. low fertility in many former Soviet states and high fertility in many oil producing nations in the Middle East.

Figure 3 shows fertility rate as a function of power consumption for modern humans compared with other mammals. The same scaling law with the predicted exponent of $-1/3$ can account for variation of fertility rate

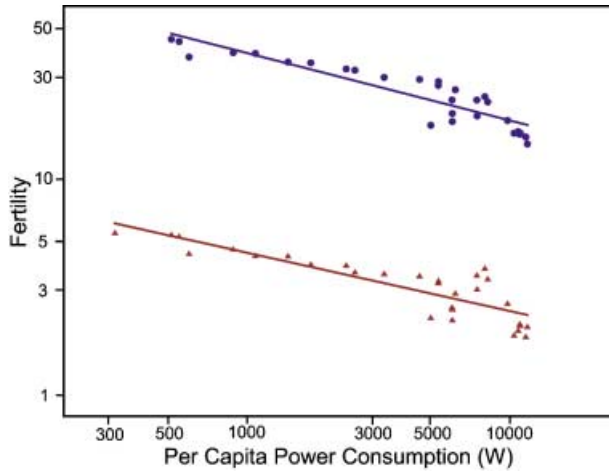


Figure 2 Human fertility in the USA as a function of extra-metabolic energy consumption (E) plotted on logarithmic axes. Data represent five-year intervals from 1850 through 2000. Circles represent crude fertility rate (births per thousand population) and triangles represent lifetime births per woman. The slope for crude fertility is -0.31 ($r^2 = 0.83$) and for total fertility is -0.27 ($r^2 = 0.76$).

with power consumption, estimated as whole-organism metabolic rate for species of mammals, and nations of humans, where power consumption is estimated as the per capita share of national consumption (E). Fertility rates of primates are known to be lower than other mammals (Charnov 1993), and fertility rates of modern humans have decreased from this 'ancestral' primate rate just as predicted by increased power consumption. Figure 3 shows that the decline in human birth rates is quantitatively consistent with the life-history patterns of other mammals.

DISCUSSION

Why should human fertility decisions be guided by extra-metabolic energy consumption, and why are these patterns quantitatively similar to those observed in primates and other mammals? We hypothesize that parents face a trade off between the number of offspring and the energetic investment in each offspring. Such trade-off decisions have been well explored by biologists, human behavioural ecologists and economists (Smith & Fretwell 1974; Becker & Barro 1988; Kaplan 1996; Mace 1998).

Here we additionally propose that the perceived energetic investment (including material goods and education) required for a child to be competitive in a given society is greater in more consumptive societies. We assume that the cost of a raising a child increases in direct proportion to E. Our assumption is similar to the mammal reproductive allocation assumption made by Charnov (1993). In that

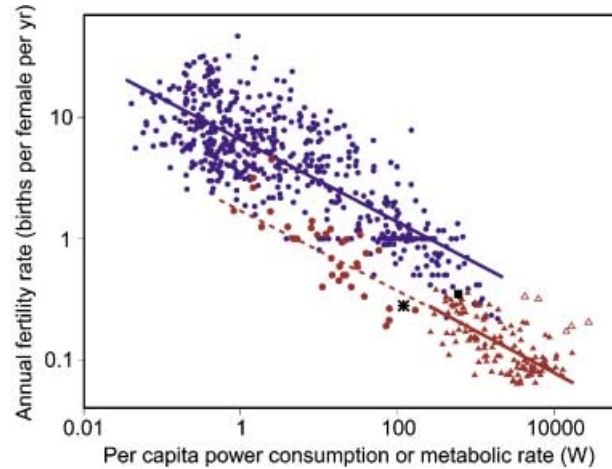


Figure 3 Fertility rate of humans and other mammals plotted as a function of power consumption. Power consumption is estimated as metabolic rate for mammals and extra-metabolic energy consumption for humans. Circles represent mammals, with primates in red. Red triangles represent nations and empty triangles are outliers. The black star and box represent human hunter-gatherers and pre-industrial agriculturalists, respectively. Fertility was measured as average number of births per female per year of reproductive life for species of mammals and nations of humans using data from 1990 to 1995. Metabolic power (B) of mammals was estimated from body mass using the allometric regression equations for different orders of mammals (Peters 1983). Hunter-gatherer and agriculturalist fertility rates and metabolic consumption are estimated population averages (Livi-Bacci 1997). The blue line shows the regression equation for annual fertility of non-primate mammals, $6.54 \times B^{-0.339}$ ($r^2 = 0.68$, $P < 0.001$). The red line shows the regression for humans, $1.89 \times E^{-0.346}$ ($r^2 = 0.47$, $P < 0.001$). The dashed line is extended to show the fit through the primate data. The exponent values of -0.339 and 0.346 are well within the 95% confidence intervals for the predicted value of $-1/3$.

model, the observed $-1/4$ power scaling of reproductive rate with mass results from investing a constant proportion of energetic resources in each offspring.

Finally, we hypothesize that the scaling properties of extra-metabolic networks are similar to biological networks. The scaling of energy delivery rate with network size has been derived for biological networks in terms of mass (West *et al.* 1999), but mass scales linearly with the volume (V) of the metabolic network, i.e. total blood volume (Banavar *et al.* 1999; West *et al.* 1999). Substituting V for mass in the West *et al.* model, the distance (l) and time (t) it takes for a resource to travel from uptake to consumption (i.e. the distance from the heart to a capillary) scale as $V^{1/4}$ and total energetic rate (E) scales as $V^{3/4}$. Thus,

$$l \propto t \propto E^{1/3} \quad (4)$$

Thus, biological rates are slowed by the increased time it takes to move energetic resources through greater lengths of network in larger organisms. These scaling relationships can be generalized to describe the constraints on the efficiency of any three dimensional transportation network (Banavar *et al.* 1999).

We suggest that in human societies, as in the bodies of organisms, larger networks deliver more energy, but with increased total transport time and infrastructure cost. Some components of this infrastructure are visible networks: oil pipelines, power grids, and rail and highway systems; while other components such as banking systems, governments and research programs may function as virtual networks to develop and spread energy, information and products. If this infrastructure is described by eqn 4, the time required to gain energetic resources, E , increases as $E^{1/3}$. Additionally, as E increases, each unit of energy must pass through greater network length, l , incurring increased infrastructure costs.

In our analysis, parents have as many children as they can afford to provision with the energetic resources expected in their society. As the cost and time to obtain these resources increases in more industrialized nations, the number of children parents can support decreases. We propose that the $-1/3$ power scaling of birth rate reflects the increasing cost of infrastructure and the increasing time and energy required to collect and distribute greater quantities of resources to children in more industrialized nations. Given the complexity of the networks supplying E , it may be difficult to determine empirically whether the time and cost of obtaining E increase with $E^{1/3}$ or even to determine the geometry and dimensions of the networks supplying E ; however, we suggest that further tests of these hypotheses may be fruitful.

The data show that variation in human fertility rate across nations, through time, and in relation to other mammals, is quantitatively consistent with allometric theory. The cross-national comparison has remained consistent for 30 years, and the dynamic changes in fertility match expectations based on energetic changes in the USA for 150 years. Allometric theory may provide a fruitful framework to link biological and ecological approaches with sociological and economic considerations that may jointly influence human reproduction.

We see our analysis as complementary to other explanations of the demographic transition as the result of ecological and evolutionary processes (Kaplan *et al.* 2002). After socio-economic variables are considered, fertility has been shown to be influenced by population density (Lutz & Qiang 2002) and the diversity of human diseases (Guegan *et al.* 2001). Other social factors – the availability of family planning choices, economic conditions, the unusually high energetic reserves of some nations – may also help to explain the residual variation

around the regression lines in Fig. 1. This analysis is also complementary to other work which seeks to understand the ecological forces which shape human cultures, for example Collard & Foley (2002).

The products of agriculture, industry and technology are commonly thought to have freed modern humans from energetic and biological constraints. In fact, the limits to human population density, historically imposed by food availability and disease, have greatly increased from less than 1 km^{-2} in pre-agricultural societies to $5\text{--}25 \text{ km}^{-2}$ in pre-industrial societies (Cipolla 1972; Livi-Bacci 1997). The present densities of 30 km^{-2} in the USA and 140 km^{-2} in China far exceed the 4 km^{-2} predicted for a 65-kg mammal (Damuth 1981; Peters 1983). However, limits have been raised, but not removed, and through reliance on new sources of energy and systems of energy acquisition and distribution, humans remain organisms constrained by energy. Per capita energy consumption strongly influences the behavioural and economic decisions that ultimately limit the sizes of families and the investment in rearing children. Recent evidence suggests that the current human population is utilizing natural and industrial systems at levels that are not biologically or energetically sustainable (Wackernagel *et al.* 2002), even as the global population continues to increase in size and resource consumption. Understanding the energetic constraints to population growth and consumption is vital to attaining a globally sustainable human population.

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