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Sex difference in life span affected by female birth rate in modern humans

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Abstract

Sex differences in life span are common in different taxa, including primates, but not well understood. Theory and comparative evidence suggest that differential costs of reproduction between the sexes may explain the differences in sex-biased mortality across large taxonomic groups. The level of sex-specific reproductive effort may thus affect the difference in life span across populations. Modern humans (*Homo sapiens*), generally show the typical mammalian pattern of male-biased mortality. Here, I asked whether the differences in female birth rates between countries affect the sex difference in life span. I used the data on male and female life span and female birth rate in different countries from publicly available databases, while controlling for geographic and economic factors. The analysis suggests that female birth rate explains 17% of the variation in relative sex differences in life span across countries. Low female birth rate results in females living relatively longer than males. These data suggest that a simple biological factor—female birth rate—may explain a significant part of the variation in sex differences in life span across human populations.

Keywords: Fecundity; Life history; Longevity; Family size; Reproductive effort; Sex-specific mortality; Total fertility rate

1. Introduction

Sex differences in life span have been extensively studied in a variety of organisms using both comparative and experimental approaches (Bennett & Owens, 2002; Clutton-Brock & Isvaram, 2007; Liker & Szekely, 2005; Owens & Bennett, 1994; Promislow, 1992; Promislow, Montgomerie, & Martin, 1992). Males and females generally use different reproductive strategies and differential costs of reproduction are often put forward as potential explanations for sex bias in mortality rates (Clutton-Brock & Isvaram, 2007; Liker & Szekely, 2005; Trivers, 1972). In mammals, females usually outlive males and this pattern is often associated with costly male-male competition resulting in relatively short reproductive life span of males compared with females (Clutton-Brock & Isvaram, 2007). However, the sex difference in life span can also result from differential costs of parental care between the sexes (Bennett & Owens, 2002; Liker & Szekely, 2005). Additionally, it is often overlooked that the sex difference in any trait, including longevity, results from selection on this trait in both sexes and that the variance in the sex that lives longer needs to be taken into account. Here, I asked whether sex difference in life span in modern humans can be explained in part by differential costs of reproduction.

In humans, females live longer than males in the majority of countries and this pattern has been attributed in part to testosterone-driven mortality in males (Book, Starzyk, & Quinsey, 2001; Owens, 2002; Promislow, 2003). This includes both mortality from risky behaviours in male-male competition and the negative impact of testosterone on male immune system (Owens, 2002). These proximate explanations are in line with the more general notion that sexual competition among males may contribute to increased male mortality in mammals (Clutton-Brock & Isvaram, 2007; Trivers, 1972), including humans (Kruger & Nesse, 2006). The sex difference in life span in humans increases with total life span across countries (Teriokhin, Budilova, Thomas, & Guegan, 2004). However, the factors underlying this pattern are not well understood.

Elevated rate of reproduction reduces life span via trade-off in resource allocation between body maintenance and reproductive effort and/or via damage to soma (Barnes & Partridge, 2003; Kirkwood, 1977; Partridge, Gems, & Withers, 2005; Rose, 1991; Stearns, 1992). In line with

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this body of theory and evidence, female birth rate is negatively related to female life span in humans using both longitudinal (Doblhammer & Oeppen, 2003; Penn & Smith, 2007; Pettay, Kruuk, Jokela, & Lummaa, 2005; Westendorp & Kirkwood, 1998) and comparative (Thomas, Teriokhin, Renaud, De Meeus, & Guegan, 2000) analysis. Industrialized societies are characterized by low female birth rate and extended life span in both sexes (Borgerhoff Mulder, 1998; Finch, 2007; Mace, 2007). In this study, I asked whether the variation in sex differences in human life span across countries is explained in part by variation in female birth rate, while controlling for total life span, as well as geographic and economic factors. Controlling for total life span removes the possibility that variation in sex difference in life span is totally explained by how long the members of the particular population live (Finch, 2007), while simultaneously controlling for a large number of environmental factors, because total life span partly reflects the quality of life (e.g., health care) in the given country. Upon establishing the positive relationship between female birth rate and relative sex difference in life span [ln (male life span/female life span)], I conducted further analyses aimed at elucidating the potential effects of total life span, population density, economic condition and latitude of the country on sex difference in life span. Population density can in theory reflect the level of intrapopulation competition for resources. The economic condition of the country is likely to contribute to life expectancy of both sexes, although not necessarily in equal manner (see Results). Latitude is related to a number of environmental factors, such exposure to infections and alcohol consumption (Teriokhin et al., 2004).

2. Methods

I used publicly available databases [Population Reference Bureau (PRB), www.prb.org, and the Central Intelligence Agency World Factbook, www.cia.gov) to obtain data on life expectancy at birth for males and females, female birth rate (average number of children produced by women between ages 15–45 years assuming that current age-specific birth rate remains constant, sometimes referred to as “total female fertility rate”), population density per square kilometre, and gross national income in purchasing power parity (GNI PPP) per capita (US dollars). Sex difference in life span was defined as life expectancy at birth for females minus life expectancy at birth for males. Both data sets have been previously used in the analysis of life span and birth rates in humans [e.g., (Aarssen & Altman, 2006; Promislow 2003; Thomas et al., 2000)]. Analysis of female birth rate and sex differences in life span while controlling for total life span using both data sets produced qualitatively similar results. However, the PRB database contains more data while also being easier to use. Therefore, I used PRB data from the year 2007 in all of the analyses presented here. Not all of the data for the above variables are available for all countries. The initial analyses were conducted using data from 205 different countries and territories, using both absolute and relative [ln (male life span/female life span)] difference in life span. However, the full model controlling for GNI PPP index was performed with the data for 164 countries and territories only (see below).

The full general linear model (GLM) included the effects of female birth rate, total life span, GNI PPP index, population density and latitude. In addition, I analysed the effect of female birth rate on relative female life span (corrected for male life span) and relative male life span (corrected for female life span). The latter two models allowed for exploration of the significant effect of female birth rate on sex difference in life span revealed by the initial full model. I also reanalysed this data set using Gini index of economic inequality within countries. Gini index did not have a significant effect on any of the dependent variables (all $P>.4$) and, similarly, did not change the qualitative significance of other variables. Therefore, I did not include Gini index in the final tables because it is not available for all countries used in the original analysis and therefore would unnecessarily reduce the sample size. I chose to present the analysis conducted as a series of GLMs rather than single multivariate analysis of variance with male and female life span as repeated measures, which produced the same results, because the GLM outcome is much easier to interpret in this case and because the GLMs allowed for analysis of relative differences in life span. The data for birth rates were ln-transformed prior to the analyses. Normality was checked using normal quantile plots of predicted versus observed values for model residuals. The data were also analysed using relative sex difference [ln (male life span/female life span)] and produced qualitatively similar results. I present the outcome of the models based on the absolute difference corrected for total life span because using ratios is likely to increase the variance at low total life span due to measurement error.

3. Results

Linear regression analysis suggests that female birth rate explains 33% of variance in sex differences in life span across 205 countries (slope=−2.873, $F(1,204)=101.8302$, $p<.0001$, adjusted $r^2=0.331$; Fig. 1) and 17% of variance in relative sex difference [ln (male life span/female life span)]: [slope=0.029, $F(1,204)=43.2992$, $p<.0001$, adjusted $r^2=0.172$; Fig. 2]. Total life span was positively related to sex difference in life span [slope=0.117, $F(1,204)=73.1923$, $p<.0001$, adjusted $r^2=0.261$] and negatively to relative sex difference [slope=−0.001, $F(1,204)=26.7672$, $p<.0001$, adjusted $r^2=0.112$]. When the effects of latitude, population size, GNI PPP index, and total life span were incorporated in a general linear model, female birth rate remained a significant negative predictor of sex difference in life span