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.
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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
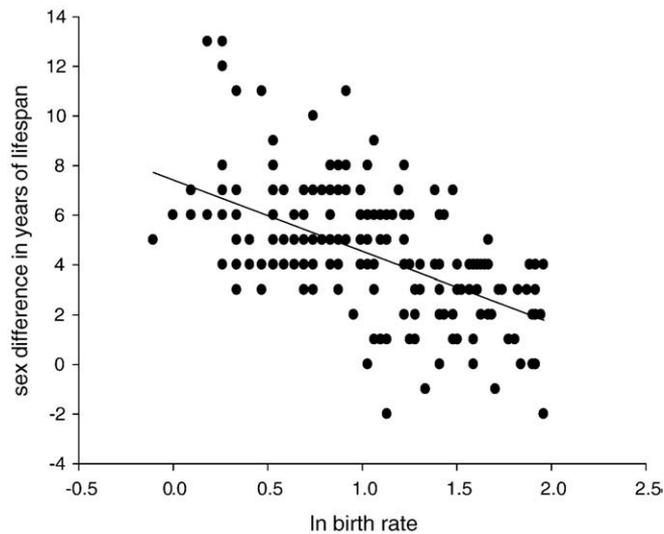
Fig. 1. The relationship between ln female birth rate (average number of children produced by women between ages 15 and 45 years assuming that current age-specific birth rate remains constant) and sex difference in life span (female life span minus male life span) for 205 different countries and territories.

(Table 1a). Moreover, while the exclusion of total life span from the model reduces the model fit from 42.2% to 40.1.2% only, the exclusion of female birth rate results in 33.9% fit.

I then analysed a second set of models with the aim of elucidating the effect of female birth rate on female and male life span, while controlling for intersexual correlation and geographic and economic factors. As predicted, female birth
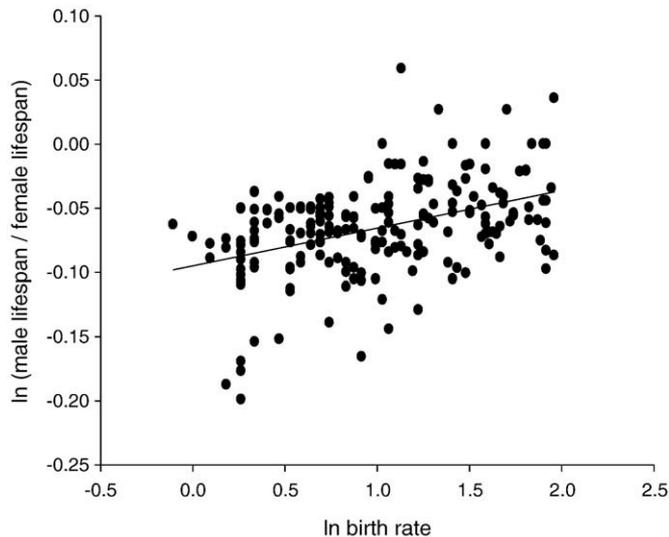

Fig. 2. The relationship between ln female birth rate (average number of children produced by women between ages 15-45 assuming that current age-specific birth rate remains constant) and relative sex difference in life span [ln (male life span/female life span)] for 205 different countries and territories. High female birth rate is associated with high values of male/female life expectancy ratio. In some countries with ln birth rate >1 (~2.72 births per female), males actually outlive females [ln (male life span/female life span) >0].

Table 1

Source	Estimate	S.E.	t Ratio	Prob>|t|
a. Sex difference in life span:				
ln birth rate	−2.8238	0.5771	−4.89	<.0001
Latitude	0.0171	0.0123	1.39	.1674
Total life span	0.0616	0.0236	2.61	.0100
Population density	−0.0003	0.0002	−1.31	.1932
GNI PPP	-6.785^{-5}	-2.072^{-5}	−3.27	.0013
b. Female life span:				
ln birth rate	−3.5658	0.5649	−6.31	<.0001
Latitude	0.0105	0.0126	0.84	.4044
Male life span	1.0164	0.0245	41.39	<.0001
Population density	−0.0004	0.0002	−1.58	.1166
GNI PPP	-5.117^{-5}	2.145^{-5}	−2.41	.0170
c. Male life span:				
ln birth rate	2.0361	0.5726	3.56	.0005
Latitude	−0.0224	0.0118	−1.90	.0587
Female life span	0.9008	0.0218	41.39	<.0001
Population density	0.0002	0.0002	1.05	.2967
GNI PPP	7.943^{-5}	1.957^{-5}	4.06	<.0001

rate was negatively correlated with relative female life span (Table 1b). However, female birth rate was positively related to relative male life span across countries (Table 1c). Notably, GNI PPP index was positively related to relative male life span (Table 1c), while it was negatively related to relative female life span (Table 1b).

4. Discussion

Female birth rate in modern humans is negatively correlated with the magnitude of male-biased mortality and explains a significant proportion of variance in sex difference in life span across different countries. Importantly, this relationship is significant while correcting for several other potentially important variables, such as population density, latitude, economic condition, and total life span.

The positive relationship between average life span and sex difference in life span across countries is well known (Finch, 2007; Teriokhin et al., 2004), suggesting that the gap between male and female life expectancy is larger in developed countries. Similarly, developed countries are characterised by reduced female birth rate compared to developing countries (Aarssen, 2005; Borgerhoff Mulder, 1998; Mace, 1998; Mace, 2007). Therefore, it was plausible to hypothesise that a negative relationship between female birth rate and sex difference in life span is a result of the confounding effect of the increase in total life span in developed countries. However, the analyses suggest that this is not the case. When total life span was included as a predictor together with female birth rate in the general linear model, the latter effect remained significant.

The economic condition of the country is accounted for in two different ways in the present analysis: first, as the function of GNI PPP index, and second, as the function of total life span in the country. The total life span is an

important predictor but explains less variation in sex difference in life span than female birth rate in this model. The significant effect of total life span and GNI PPP index on sex differences in life span supports the importance of country's economic condition.

The present data suggest that the effect of socioeconomic factors on human life span is sex-specific. Thus, relative female life span is negatively affected by female birth rate and by GNI PPP index. In sharp contrast, relative male life span is positively affected by both female birth rate and GNI PPP index. This result indicates that males are more likely to benefit from improved economic conditions in terms of increased life span than females. Additionally, it suggests that the cost of reproduction may be relatively higher for females than for males. These results are in line with the study by Penn & Smith (2007) who showed that cost of reproduction in preindustrial North American population in Utah was significantly higher and increased with age more rapidly for females than for males. The factors contributing to reduced female birth rate in industrialised countries are widely covered in the literature (Aarssen, 2005; Borgerhoff Mulder, 1998; Mace, 1998; Mace, 2007; Penn & Smith, 2007) and remain beyond the scope of this article, which focuses on the consequences of differential reproductive investment for sex differences in human life span. However, the sex-specific difference in life history tradeoffs combined with economic and reproductive autonomy of women in developed countries is one likely explanation for reduced family size in modern humans (Penn & Smith, 2007).

It would be informative to compare these results with the data from small hunter–gatherer and horticulture societies. For example, a recently published demographic data set of the contemporary hunter–gatherer community (Headland & Headland, 2007) suggests that while total birth rate was very high (6.73 births per female); there was apparently no difference in average life span between males and females (25 years [based on the data from 1950 until 2007]). Note, however, that median life span differs significantly between the sexes (19 years for males and 24 years for females), suggesting that males that survive past the early years live on average longer than females. These data are generally in line with the analysis presented here but certainly a systematic approach is needed. However, very few studies collected appropriate demographic data on hunter–gatherer societies (Gurven & Kaplan, 2007; Hill, Hurtado, & Walker, 2007; Walker et al., 2006), and there are intrinsic methodological problems associated with collecting precise information about the exact ages of death of the individual humans in such communities. Walker et al. (2006) provide data on life expectancy at age 15 years (adulthood) for males and females from another two societies where females live longer than males by 0.1 and 1.7 years. The data on sex-specific survival until 15 years of age that are available for 12 different small-scale societies (Walker et al., 2006) seem

to vary little with males having slightly higher chance of survival in several societies. The latter could be in some cases related to female infanticide (Hill & Hurtado, 1996). The data on birth rates available for four of such societies (Ache, Hadza, !Kung, Agta) suggest that they range between 4.7 and 8.2 (6.46 births on average) (Blurton Jones, Hawkes, & O'Connell, 2002; Headland & Headland, 2007). Collectively, these data suggest that small-scale societies might be characterised by relatively weak male bias in mortality, which, in theory, could be attributed in part to relatively high birth rates in these societies. We need much more data on sex-specific demographic patterns and birth rates from different small-scale societies before a comparative analysis similar to the one presented here can be performed.

In a previous study of the relationship between female birth rate and sex difference in life span in modern humans, Teriokhin et al. (2004) found the relationship between sex differences in mortality rates and birth rate to be curvilinear. However, their analysis was based only on sex differences in the age-independent parameter of the Gompertz-Makeham model of mortality rate. Unfortunately, this parameter captures only part of the variation in life span between the sexes (Pletcher, 1999). Additionally, while this term of the Gompertz-Makeham model is sometimes used to delineate environmentally caused mortality, it is problematic to attribute biological properties to the arbitrary parameters of descriptive demographic models (Williams, Day, Fletcher, & Rowe, 2006). The raw difference in life expectancy encapsulates all of the variation in sex-specific life spans, thereby providing less biased foundation for cross-country comparison.

The results of this study do not contradict the potentially important role of sexual selection in generating the pattern of male-biased mortality in humans (Kruger & Nesse, 2006; Owens, 2002). Rather, they point to the fact that the sexual dimorphism in any trait, including life span, is best approached by studying the life history trade-offs in both sexes. Sex-specific selection is likely to contribute to sexual dimorphism in human life span in different ways beyond selection on female reproductive investment in terms of fecundity. One potentially important factor is selection on postreproductive life span in humans. For example, grandparenting by females increased grand-offspring fitness in historical Finnish populations (Lahdenpera, Lummaa, Helle, Tremblay, & Russell, 2004; Lummaa, 2007), while no such benefit was associated with male grandparents (Lahdenpera, Russell, & Lummaa, 2007).

The difference between the sexes in reproductive schedule is likely to be important in the evolution of sex-specific life span (Bonduriansky, Maklakov, Zajitschek, & Brooks, 2008; Graves, 2007; Graves, Strand, & Lindsay, 2006). Timing of reproduction can affect female survival beyond the total number of offspring produced in a lifetime (Lummaa, 2007), and the role of this trait in sex difference in life span requires further investigation. On the other hand,

while it is often the case that males adopt "live fast die young" reproductive strategies, the difference in reproductive potential of males and females late in life is often overlooked (Graves, 2007; Graves et al., 2006). In humans, males but not females have the physiological ability to reproduce until very advanced age and this can, in theory, have consequences for the evolution of life span (Graves, 2007; Tuljapurkar, Puleston, & Gurven, 2007).

The sex difference in life span across taxa is likely to be a product of a suite of environmental and genetic factors. In modern humans, various socioeconomic factors have been linked to the general phenomenon of male-biased mortality (Finch, 2007) and the present analysis further confirms the importance of such factors in generating the gap between male and female longevities. Nevertheless, one important factor that affects female life span and is therefore likely to contribute significantly to sex differences in life span is female reproductive performance. The finding that sex difference in human life span is affected by female birth rate is in line with life-history theory and supports the central role of differential costs of reproduction in generating the gap in longevity between the sexes.

The data suggest that, in modern humans, females outlive males in part because females in developed countries invest less in reproduction compared to females from developing countries. As more and more countries are gradually entering the demographic transition to low fertility (Mace, 2007), we may witness an overall increase in sex difference in life span in humans.

Acknowledgments

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