ASHDIN
PUBLISHING

Research Article

EPIDEMIOLOGY

Do Mothers from Rich and Well-Nourished Countries Bear More Sons?

Frédéric Thomas,[1] Simon P. Daoust,[1] Eric Elguero,[1] and Michel Raymond[2]

[1]*MIVEGEC, UMR CNRS-IRD-UM1 5290, 911 Avenue Agropolis, BP 64501, FR-34394 Montpellier Cedex 5, France*
[2]*Institute of Evolutionary Sciences Montpellier (UMR CNRS 5554), University of Montpellier II, Place Eugene Bataillon, CC065, 34095 Montpellier Cedex 5, France*
Address correspondence to Simon P. Daoust, daoust.simon@gmail.com

Abstract Although an increasing number of studies in mammals provide support to the Trivers-Willard prediction, evidence of this phenomenon in human remains controversial. Here, assuming that contemporary humans respond in an ancestral manner to recent improvements of lifestyle, we explored the hypothesis of a facultative adjustment of sex ratio in relation to resource availability from more than 120 countries worldwide. Although maladaptive at the population level, we found that sex ratio at birth is significantly more male-biased in nations that are rich, well nourished, and with low fertility. The tendency was weak however, suggesting that the magnitude of this effect is small and/or that other processes act to maintain sex ratio equilibrium. These results provide support to the hypothesis predicting investment in costly male offspring when resources are abundant. They also suggest that mechanisms that might have been adaptive under ancestral conditions can produce maladaptive population-level consequences in the modern world.

Keywords comparative analysis; evolutionary mismatch; resources; sex ratio; Trivers-Willard hypothesis

1 Introduction

For many species, including humans, it is predicted that natural selection should favor parental ability to manipulate offspring sex in response to environmental conditions (Trivers-Willard hypothesis, TWH) [33]. The TWH stipulates that mothers will bias their offspring sex ratio toward sons when resources are plentiful and toward daughters when resources are scarce. Sons in good condition are expected to have greater reproductive success than their female siblings because their quality allows them to outcompete potential rivals, to be more attractive to females, and, hence, to have more numerous reproductive opportunities. Conversely, when resources are scarce, the reproductive potential of females is likely to become greater because malnourished males are less competitive and/or less attractive, and are therefore often excluded from reproductive opportunities. Alternatively, it has also been suggested that sons, all things being equal, are more physiologically costly to produce than daughters, so that only mothers experiencing good conditions could bear the cost of having sons [13, 19, 20, 21, 25, 31].

While studies on mammals as a whole provide support for the hypothesis of a facultative adjustment of sex ratio in relation to resource availability [8, 15, 29], TWH in humans is more controversial. When classes of individuals from distinct socioeconomic statuses are compared, expectations of the TWH are generally found: billionaire mothers do give birth to more sons than mothers from the general population [19], lower-ranking polygynous wives in Rwanda have significantly more daughters than higher-ranking polygynous wives and monogamously married women [27], and the Hungarian gypsy population has a female-biased sex ratio compared to the male-biased sex-ratio of the co-resident Hungarians [5]. Gibson and Mace [13] and Mathews et al. [23] recently linked nutritional abundance to sex ratio biasing in humans and confirmed that maternal nutritional status is associated with a preponderance of male offspring. These examples aside, other studies (e.g., [1, 10, 19, 30, 39]) have provided at best limited support for a link between maternal resource or condition and sex ratio at birth. Proximate mechanisms for this sex-ratio adjustment remain unclear, although it could ultimately result from natural selection having favored mechanisms allowing selective mortality of male embryos (due to higher energetic requirements) when the environment is poor [35].

Testing the TWH (or other hypotheses predicting investment in costly male offspring when resources are abundant) at the population level is a priori not appropriate because other processes intervene at this scale. For instance, Fisher's model [11] predicts that individuals that respond to a sex-ratio imbalance by concentrating on the production of the rare sex enjoy a selective advantage by having

a disproportionately large number of grandchildren. As a result of this dynamic, the sex ratio should become stabilized around a 1:1 ratio, even if all individuals of the concerned population have access to plentiful resources. However, this situation is expected at equilibrium, and because of various and recent changes in human lifestyles, it is unclear for numerous resource-dependent variables if we are, or not, currently at equilibrium. For instance, the rich food environment recently created in the developed world results in a mismatch between our evolutionary heritage of food preferences and current eating habits, leading to several maladaptive consequences such as obesity and type 2 diabetes [17, 36]. For the same reason, biological maturation (e.g., age at menarche) has come to significantly precede psychosocial maturation for the first time in our evolutionary history [14]. This developmental mismatch is also maladaptive as it is disadvantageous for reproductive competence to precede the capacity to function adequately as an adult and as a parent.

Although it would appear maladaptive for a whole population to durably bias the sex ratio toward an over-production of males [11], we explored the idea that such response to resource abundance, however, exists in contemporary human populations, because they are still composed of individuals responding in an ancestral manner to the recent changes of their lifestyle. The variation in sex ratio from nation to nation provides an opportunity for a comparative study using data from populations throughout the world. More specifically, we tested the roles of two major resources on the sex ratio at birth, namely money and nutrition, predicting that they should both positively influence the production of sons. Conversely, we predicted that the mean fertility should be negatively correlated with son production because, all things being equal, successive pregnancies decrease the maternal condition (e.g., [32]) and each additional child in the household dilutes available resources.

2 Material and methods

2.1 Data sources

International statistics on sex ratio at birth (number of male births per one female birth) were from CIA World Factbooks 18 December 2003 to 28 March 2011 (www.nationmaster. com/graph/peo_sex_rat_at_bir-people-sex-ratio-at-birth). Extreme values of sex ratio were observed for six countries well known for having a very marked cultural preference for male children (Armenia: 1.15; Azerbaijan: 1.14; India: 1.12; China: 1.11; Georgia: 1.13; Albania: 1.1 (see [4, 18, 24])). These countries were excluded from the analysis. In order to assess the predictors of sex ratio values worldwide, we considered various socioeconomic parameters that could presumably exert some influence on fetal sex. We first considered variables correlated with the beginning of

reproductive life for females as well as fertility, namely the mean age at marriage and at childbearing, obtained from www.un.org/esa/population/publications/WMD2008/Main.html and www.un.org/esa/population/publications/worldfertility2009/worldfertility2009.htm, respectively. The mean level of education was taken into account by considering adult illiteracy rate available from the United Nations Development Program (hdr.undp.org/en/media/HDR_2009_EN_Complete.pdf). The level of income or wealth inequality among individuals within each country was considered through the Gini index from https://www.cia.gov/library/publications/the-world-factbook/fields/2172.html. Data on infant mortality by sex were obtained from www.who.int/whosis/whostat/EN_WHS10_Part2.pdf. This information, although postnatal, could a priori be informative on the differential vulnerability of each sex in response to environmental conditions. Finally, two resource-related variables were retained for testing TWH: the per capita GPD and the food availability (data on dietary energy consumption, kcal/person/day, from the FAO www.fao.org/economic/ess/food-security-statistics/en/). Although food availability is not equal to actual food consumption, due to losses during storage, preparation, and cooking, the former should still be considered as a proxy of the latter.

2.2 Statistical analyses

Depending on the country, estimates of sex ratios at birth were based on national censuses or on smaller samples. Because details of data collection protocols were not uniformly available, these estimates were taken as primary data and were given equal weight. Due to the fact that modern countries are generally not ethnically and culturally homogeneous (especially the Americas, Australia and New Zealand), it seemed inappropriate to use a phylogenetic comparative approach [22]. Similarly, because of recent immigrations and emigrations (e.g., Australians being derived mainly of European descent), geographic distances between countries are not necessarily correlated to proximities on other variables, limiting the need for considering spatial autocorrelations, which measures the fact that near points in space have either more similar (positive correlation) or more dissimilar values (negative correlation) than randomly selected pairs [7]. For the above reasons, different countries were therefore assumed to provide independent information (of note, the inclusion of a continent explanatory variable into the model—not shown herein—did not change the conclusions).

Linear regression was used to study the influence of several covariates on log-transformed sex ratios (see Table 1). Although the ranges in Table 1 are given in the original units of the covariates, the covariates in our models were standardized by removing their mean and dividing them by their standard deviation (z scores). Due to the

Table 1: Tested covariates, number of replicates, and observed ranges.

Covariate	Number of countries	Range
Male mortality at 1 year (per 1,000 live births)	178	2–172
Female mortality at 1 year	178	1–158
Male mortality at 5 years	178	3–258
Female mortality at 5 years	178	1–256
GDP per capita (USD)	204	300–121,500
Gini index	123	23–70.7
Mean age at childbearing	197	25.1–36.8
Women's age at marriage	187	22–35.4
Fertility (number of children per woman)	167	1.2–7.2
Literacy (%)	168	26.2–99.8
Available calories per day (calories)	163	1,590–3,770
Fat consumption per day (calories)	161	117–1476
Protein consumption per day (calories)	162	100–532

Table 2: (a) Parameters of the final model. Odds ratios are given for an increase of one standard deviation of the covariate. (b) Correlations between explanatory covariates retained in the final model.

Covariate	Odds ratio (95% CI)	P-value
Fertility	0.994 (0.991–0.998)	0.0010
Calories	1.003 (1.0001–1.006)	0.017
Log GDP	1.004 (1.001–1.006)	0.0068
Male mortality at 1 year	0.995 (0.991–0.999)	0.021
Gini index	11.0011 (0.9995–1.0028)	0.16 (NS)

(a)

	Fertility	Calories	Log GDP	Male mort.	Gini
Fertility	1				
Calories	−0.682	1			
Log GDP	−0.780	0.819	1		
Male mort.	0.881	−0.725	−0.842	1	
Gini	0.133	−0.206	−0.135	0.182	1

(b)

multiple origins of the data, not every variable was available for every country; hence, we had to employ a two-step procedure: we first screened all covariates by including them one by one in a model together with our main target covariates: GDP and food availability. This enabled us to identify a subset of potential explaining variables and left us with a subset of 109 countries where all these variables were available. We then used a stepwise regression procedure based on Akaike information criterion (AIC) to select a best model [2]. All computations were performed in R [28].

2.3 Results

In Table 2(a), we report the results of the final model fit, and Table 2(b) shows the correlations between covariates retained in the final model. Because the covariates were

Table 3: Food type with odds-ratios given for an increase of 100 calories.

Food types	Odds ratio (95% CI)	P-value
Proteins	1.002 (0.997–1.006)	0.395
Fat	1.001 (0.999–1.002)	0.087
Carbohydrates	1.0001 (0.9993–1.0009)	0.74

standardized, odds ratios are given for an increase in the covariate of one standard deviation. Food availability and GDP are shown to be positively associated with a bias of the sex ratio toward males, whereas fertility and male mortality by the age of 1 year are negatively associated with such a bias.

Given that food availability was associated with sex ratio, we tried to differentiate among three types of food: proteins, fat, and carbohydrates. We introduced protein, fat, and carbohydrate calories per day as variables in the linear model and found that none are significantly associated with sex ratio (although their sum is). Nevertheless, the estimated parameters enabled us to assess the importance of each type of food. Table 3 shows that an increase of 100 calories of protein per day is associated with twofold increase in odds of producing a male offspring as compared to an increase of 100 calories of fat. An increase of 100 calories of protein per day is associated with a 10-fold increase in the odds of producing male offspring as compared to an increase of 100 calories of carbohydrates.

2.4 Discussion

Our international comparative study indicates that sex ratio at birth is significantly more male-biased in populations that are rich, well nourished, and with low fertility. These findings, although statistically weak, provide support to hypothesis predicting investment in costly male offspring when resources are abundant. With regards to the negative effect of fertility on (male-biased) sex ratio, it is not possible from this analysis to determine if it results from the progressive reduction of maternal condition with successive pregnancies and/or from the fact that resources are diluted when family size increases. While in most situations the two effects are superimposed and therefore difficult to disentangle, the study by Pollet et al. [27] on polygynous societies allowed them to test the consequence of the effect of resource dilution due to child addition per se. This factor is apparently strong enough to induce sex ratio biasing toward daughters. In addition, our findings may also indicate that, in countries where the health women is compromised by high fertility, the biological costs of producing boys may be important as well as potentially other benefits of producing girls may be greater (e.g., helping to take care of younger siblings).

Recently, Cameron and Dalerum [9] demonstrated that humans in the highest economic bracket (billionaires)

produce more sons than the general population. The present study, although performed at another scale, comes to the same conclusion. As opposed to variables such as nutrition (see below), money is unlikely to intervene directly on sex ratio; instead its effect is mediated through the potential correlations it has with resource availability, which has a direct effect on maternal condition. These correlations are probably numerous, ranging from the quality of food, habitats, access to health care, etc. In addition, because of the link between money and these material resources, the former is usually associated to a greater attractiveness in males and, therefore, a greater reproductive success. However, it is not known if the later phenomenon intervenes in this context, given that our work is performed at the nation level from national means and not from individuals in the same geographic area.

The few studies that have linked nutritional deficiencies and sex ratio biasing in humans have not found consistent results [3, 13, 38]. It is not possible from our results to conclude that they provide support for the TWH and/or just that the physiological cost to mothers of bearing sons is greater than of bearing daughters. The reason why food availability is retained in the analysis but not the different types of food (proteins, fat and carbohydrates) is unclear. Perhaps this simply indicates that the way these categories are defined is not the most suitable for addressing the present biological question. When tendencies are considered, the fact that fat, rather than protein and sugar consumption, tends to have the most significant influence on the sex ratio variation is interesting in an adaptive context. While exclusive breastfeeding may inhibit conception for up to 4 years post partum [6], this inhibition is known to largely depend on the mother energy stores, especially body fat [12]. Abundance of dietary fat could then be perceived as a signal indicating that environmental conditions are convenient for producing competitive sons.

Our study highlighted that infant mortality, especially that of males, was strongly correlated to sex ratio variation, indicating that when male mortality increases in early life, the male bias in the sex ratio at birth decreases. A first possible explanation for this result is that poor environmental conditions that differentially eliminate males in early life are also responsible for a selective male mortality during pregnancy. In other words, males would be more fragile than females both as embryos and as infants. The greater vulnerability of males to environmental insults compared to females is a well-established phenomenon, which presumably corresponds to a mechanism selected over evolutionary time to maximize maternal reproductive success [35]. Indeed, natural selection is predicted to have favored processes that allow selective mortality of existing offspring (from conception to weaning) when investing in a new one is a better option. Investing time and energy to raise males produced in poor conditions is unlikely to be advantageous from an evolutionary perspective given their low expected reproductive success as adults. A second possible explanation is that females living in poor environmental conditions avoid, directly at conception or early in the pregnancy, the production of the sex with the lowest survival probability (i.e., males). At least on the short term, such mothers should enjoy a selective advantage as they produce offspring who will live until sexual maturity. Sex ratio adjustment would then be conditional upon the opportunities for offspring survival evaluated by the parents themselves, for instance, through observations of infant mortality around them.

According to Fisher's model [11], it is not adaptive for an entire population to bias their sex ratio toward the over-production of one sex, and compensatory responses are therefore favored by selection (but see [37] for examples of cultural selection). We do not exclude that this phenomenon applies here and may serve to explain at least partially why, although significant, the tendencies we detected are statistically weak. Interestingly, the extent to which modern societies fit with the Fisherian conditions is also questionable. In the past, human societies lived in relatively isolated communities, and as a consequence, the geographical areas where people encountered potential mates traditionally tended to be relatively small and local. In modern societies, however, social networks are known to be small worlds [34]; increasing international travel and the use of the Internet have broadened the geographical opportunity structure for potential partners. This increases the chances of meeting a partner from abroad, possibly resulting in a rise in international marriage migration (e.g., [26]). In this context, biasing the sex ratio toward sons in rich countries should not be, or is at least less maladaptive in the future than predicted by Fisher's model.

Akin to all comparative studies, our results are correlational and are therefore potentially explainable by alternative hypotheses. For instance, sex ratio at birth and nutrition could both be correlated to a third factor (e.g., coital frequency [16], economic constraints, and/or cultural heterogeneity). A sex ratio at birth bias due to cultural mechanisms (e.g., under-reporting of infanticide and use of contraception once desired sex composition of family achieved) cannot entirely be discounted in this cross-cultural sample. The direction of causation between fertility and sex ratio could be reversed in cultures where there is a strong preference for sons, as couples could have the habit to give up procreating after the birth of a son. We cannot exclude the possibility that no factor other than the condition of females at conception and during gestation intervene; resources, for instance, could also influence the balance of X and Y spermatozoa in relation to paternal condition. Finally, because of the nature of the data used here, it is not possible to test whether there is greater investment in females per

se in countries with low resources or whether skews in the sex ratio toward females are then compensated by increasing resources to the fewer men produced, leading to an equal allocation among them. Despite these limitations, we feel that our findings are sufficiently strong to conclude that resources at the international level are key players in influencing sex ratio biasing in humans.

References

[1] D. Almond and L. Edlund, *Trivers-Willard at birth and one year: evidence from US natality data 1983–2001*, Proc Biol Sci, 274 (2007), 2491–2496.

[2] D. R. Anderson, *Model Based Inference in the Life Sciences: A Primer on Evidence*, Springer-Verlag, New York, 2008.

[3] R. Andersson and S. Bergström, *Is maternal malnutrition associated with a low sex ratio at birth?*, Hum Biol, 70 (1998), 1101–1106.

[4] P. Arokiasamy, *Sex ratio at birth and excess female child mortality in India: Trends, differentials and regional patterns*, in Female Deficit in Asia: Trends and Perspectives, Singapore, 2005.

[5] T. Bereczkei and R. I. M. Dunbar, *Female-biased reproductive strategies in a Hungarian Gypsy population*, Proc R Soc Lond B Biol Sci, 264 (1997), 17–22.

[6] N. Blurton Jones, *Bushman birth spacing: A test for optimum birth intervals*, Ethol Sociobiol, 7 (1986), 91–105.

[7] D. Borcard, F. Gillet, and P. Legendre, *Numerical Ecology with R*, Springer-Verlag, New York, 2011.

[8] E. Z. Cameron, *Facultative adjustment of mammalian sex ratios in support of the Trivers-Willard hypothesis: evidence for a mechanism*, Proc R Soc Lond B Biol Sci, 271 (2004), 1723–1728.

[9] E. Z. Cameron and F. Dalerum, *A Trivers-Willard effect in contemporary humans: male-biased sex ratios among billionaires*, PLoS One, 4 (2009), e4195.

[10] G. C. Chacon-Puignau and K. Jaffe, *Sex ratio at birth deviations in modern Venezuela: the Trivers-Willard effect*, Biodemography Soc Biol, 43 (1996), 257–270.

[11] R. A. Fisher, *The Genetical Theory of Natural Selection*, Oxford University Press, Oxford, 1930.

[12] M. H. Fitzgerald, *Is lactation nature's contraceptive? Data from Samoa*, Biodemography Soc Biol, 39 (1992), 55–64.

[13] M. Gibson and R. Mace, *Strong mothers bear more sons in rural Ethiopia*, Proc R Soc Lond B Biol Sci, 270 (2003), S108–S109.

[14] P. D. Gluckman and M. A. Hanson, *Evolution, development and timing of puberty*, Trends Endocrinol Metab, 17 (2006), 7–12.

[15] A. S. Griffin, B. C. Sheldon, and S. A. West, *Cooperative breeders adjust offspring sex ratios to produce helpful helpers*, Am Nat, 166 (2005), 628–632.

[16] W. H. James, *Time of fertilization and sex of infants*, Lancet, 315 (1980), 1124–1126.

[17] J. R. Krebs, *The gourmet ape: evolution and human food preferences*, Am J Clin Nutr, 90 (2009), 707S–711S.

[18] W. Lavely, *Sex selective abortion, hidden girls, or infanticide? Explaining the female deficit in a Chinese county*, in Female Deficit in Asia: Trends and Perspectives, Singapore, 2005.

[19] J. Lazarus, *Human sex ratios: adaptations and mechanisms, problems and prospects*, in Sex Ratios: Concepts and Research Methods, I. Hardy, ed., Cambridge University Press, Cambridge, 2002, 287–311.

[20] R. J. Loos, C. Derom, R. Eeckels, R. Derom, and R. Vlietinck, *Length of gestation and birthweight in dizygotic twins*, Lancet, 358 (2001), 560–561.

[21] V. Lummaa, *Reproductive investment in pre-industrial humans: the consequences of offspring number, gender and survival*, Proc R Soc Lond B Biol Sci, 268 (2001), 1977–1983.

[22] R. Mace and F. Jordan, *The evolution of human sex ratio at birth: A bio-cultural analysis*, in The Evolution of Cultural Diversity: A Phylogenetic Approach, R. Mace, C. J. Holden, and S. Shennan, eds., UCL Press, London, 2005, 207–216.

[23] F. Mathews, P. J. Johnson, and A. Neil, *You are what your mother eats: evidence for maternal preconception diet influencing foetal sex in humans*, Proc R Soc Lond B Biol Sci, 275 (2008), 1661–1668.

[24] F. Meslé, J. Vallin, and I. Badurashvili, *A sharp increase in sex ratio at birth in the Caucasus. Why? How?*, in Female Deficit in Asia: Trends and Perspectives, Singapore, 2005.

[25] J. H. Myers, *Sex ratio adjustment under food stress: Maximization of quality or numbers of offspring?*, Am Nat, 112 (1978), 381–388.

[26] T. Niedomysl, J. Östh, and M. van Hamc, *The globalisation of marriage fields: The Swedish case*, J Ethn Migr Stud, 36 (2010), 1119–1138.

[27] T. V. Pollet, T. W. Fawcett, A. P. Buunk, and D. Nettle, *Sex-ratio biasing towards daughters among lower-ranking co-wives in Rwanda*, Biol Lett, 5 (2009), 765–768.

[28] R Development Core Team, *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna, Austria, 2009.

[29] J. R. Roche, J. M. Lee, and D. P. Berry, *Pre-conception energy balance and secondary sex ratio—partial support for the Trivers-Willard hypothesis in dairy cows*, J Dairy Sci, 89 (2006), 2119–2125.

[30] A. D. Stein, P. G. Barnett, and D. W. Sellen, *Maternal undernutrition and the sex ratio at birth in Ethiopia: evidence from a national sample*, Proc R Soc Lond B Biol Sci, 271 (2004), S37–S39.

[31] R. M. Tamimi, P. Lagiou, L. A. Mucci, C. C. Hsieh, H. O. Adami, and D. Trichopoulos, *Average energy intake among pregnant women carrying a boy compared with a girl*, BMJ, 326 (2003), 1245–1246.

[32] F. Thomas, A. T. Teriokhin, F. Renaud, T. de Meeûs, and J. F. Guégan, *Human longevity at the cost of reproductive success: evidence from global data*, J Evol Biol, 13 (2000), 409–414.

[33] R. L. Trivers and D. E. Willard, *Natural selection of parental ability to vary the sex ratio of offspring*, Science, 179 (1973), 90–92.

[34] D. J. Watts and S. H. Strogatz, *Collective dynamics of 'small-world' networks*, Nature, 393 (1998), 440–442.

[35] J. C. Wells, *Natural selection and sex differences in morbidity and mortality in early life*, J Theor Biol, 202 (2000), 65–76.

[36] J. C. Wells, *The evolution of human fatness and susceptibility to obesity: an ethological approach*, Biol Rev Camb Philos Soc, 81 (2006), 183–205.

[37] G. C. Williams, *Adaptation and Natural Selection*, Princeton University Press, Princeton, NJ, 1966.

[38] R. J. Williams and S. P. Gloster, *Human sex ratio as it relates to caloric availability*, Biodemography Soc Biol, 39 (1992), 285–291.

[39] M. E. Zaldívar, R. Lizarralde, and S. Beckerman, *Unbiased sex ratios among the Barí: An evolutionary interpretation*, Hum Ecol, 19 (1991), 469–498.