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Evolutionary ecology of human birth sex ratio under the compound influence of climate change, famine, economic crises and wars

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Summary

1. Human sex ratio at birth at the population level has been suggested to vary according to exogenous stressors such as wars, ambient temperature, ecological disasters and economic crises, but their relative effects on birth sex ratio have not been investigated. It also remains unclear whether such associations represent environmental forcing or adaptive parental response, as parents may produce the sex that has better survival prospects and fitness in a given environmental challenge.

2. We examined the simultaneous role of wars, famine, ambient temperature, economic development and total mortality rate on the annual variation of offspring birth sex ratio and whether this variation, in turn, was related to sex-specific infant mortality rate in Finland during 1865–2003.

3. Our findings show an increased excess of male births during the World War II and during warm years. Instead, economic development, famine, short-lasting Finnish civil war and total mortality rate were not related to birth sex ratio. Moreover, we found no association between annual birth sex ratio and sex-biased infant mortality rate among the concurrent cohort.

4. Our results propose that some exogenous challenges like ambient temperature and war can skew human birth sex ratio and that these deviations likely represent environmental forcing rather than adaptive parental response to such challenges.

Key-words: economics, infant mortality, natural selection, temperature, time-series analysis, war.

Introduction

In humans, several demographic, economic, environmental and physiological factors have been suggested to influence the variation of offspring sex ratio at birth (reviewed in Edwards 1962; Teitelbaum 1970; James 1987; Chahnazarian 1988; Lazarus 2002). Apart from sex-selective abortions practised in some parts of Asia and North Africa (Hesket & Xing 2006), the effects of these factors on birth sex ratio have been considered to be relatively small. The most consistent finding on the human birth sex ratio is the slight (≈ 1·4%) global excess of male births, and its post-World War II decline in industrialized countries (Møller 1996; Davis, Gottlieb & Stampnitzky 1998; Vartiainen, Kartovaara & Tuomisto 1999). The reasons for this decline and the temporal dynamics of birth sex ratio in general are currently the subject of continuing debate.

A traditional strict distinction between the genetic and environmental sex determination has recently been challenged in vertebrates (Sarre, Georges & Quinn 2004; Mittwoch 2005). In humans, much emphasis has lately been devoted to the potential role of environment-induced bias of offspring birth sex ratio. For example, stressful conditions caused by both abiotic and biotic hazards and economic deprivation have been suggested to skew human birth sex ratio towards women (Lyster 1974; Fukuda *et al*. 1998; Hansen, Møller & Olsen 1999; Catalano 2003; Stein, Zybert & Lumey 2004; Catalano & Bruckner 2005; Catalano *et al*. 2005a, b, c, 2006; Kemkes 2006; Obel *et al*. 2007; Saadat 2008). In contrast, increased man-biased birth sex ratio has been reported during and immediately after wars (reviewed in James 2009). In addition, offspring sex ratio at birth has recently been proposed to covary with ambient temperature. During the years 1946–1995 in Germany, two warm months preceding conception increased the excess of male births (Lerchl 1999). In the late twentieth-century Europe, proportionally more men were born in southern rather than in northern latitudes, whereas the opposite was found in North America (Grech, Savonna-Ventura & Vassallo-Agius 2002). Likewise, in Scandinavia during the years 1878–1914 (Catalano, Bruckner & Smith 2008) and in the nomadic Sami of northern Finland during the years 1745–1890 (Helle, Helama

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& Jokela 2008a), warm years brought proportionally more sons.

Here, our first goal was to assess the relative contributions of the aforementioned exogenous stressors on annual offspring sex ratio at birth in Finland during the years 1865–2003. We thus examined whether annual offspring birth sex ratio was related to annual change in real gross domestic product (GDP), ambient temperature anomaly, wars (World War II and Finnish civil war), the great Finnish famine of 1866–1868 and the total mortality rate. The effects of real GDP and total mortality rate were allowed to persist in the next year, as most of the conceptions resulted in births on the next calendar year. Our analysis controlled for annual average family size, as it may affect birth sex ratio variation via birth order effects (Biggar *et al.* 1999; Lazarus 2002). We did not consider the potential effect of a population's adult sex ratio on birth sex ratio (Lummaa, Merilä & Kause 1998), because national data and particularly the use of adult sex ratio are not suited to investigate the hypothesis that parents adaptively adjust their offspring sex ratio according to the operational sex ratio of a population (Helle *et al.* 2008b).

Natural selection should favour parents who adjust their offspring sex ratio according to the fitness payoffs of each sex in varying abiotic and biotic conditions (Trivers & Willard 1973). In humans, the only documented cases of adaptive sex ratio variation come from studies showing that low-status parents gained fitness benefits from the woman-biased offspring sex ratio as a result of hypergamy (Boone 1988; Bereczkei & Dunbar 1997). It is well established in humans that men are more vulnerable to the wide array of adverse environmental hazards, such as diseases and nutritional crises that cause an excess of men in pre- and post-natal mortality and morbidity (Wells 2000; Dravenstedt *et al.* 2008). Such early-life experiences have likely enduring effects on later life, affecting the reproductive success of individuals in both sexes (Lummaa & Clutton-Brock 2002). Hence, the observed reduction of the proportion of men born during the years of adverse environmental conditions may be an adaptive parental response to maximize fitness by the production of more successful daughters. We tested this idea by studying whether the years of man-biased birth sex ratio were related to decrease in the proportion of male infant mortality. Particularly in historical times, infancy was characterized by high mortality risk comparable with senescence-related mortality six to seven decades later, and men were at higher risk of death during infancy. This created important grounds for natural selection to act on (Jones, in press). However, reduction in the proportion of male births during environmental stress may also mean that, as a result of pre-natal selection, the cohort born consists of less frail men, who have decreased mortality throughout their life (Catalano & Bruckner 2006; Bruckner & Catalano 2007). This hypothesis implies a negative correlation between birth sex ratio and infant mortality rate of sons. To our knowledge, by examining the effects of several exogenous stressors simultaneously on birth sex ratio and whether birth sex ratio in turn influenced sex-specific infant mortality rates using long time series covering both historical and modern times, this study is the most comprehensive examination of the evolutionary ecology of human birth sex ratio to date.

Materials and methods

DATA

Annual offspring sex ratio at birth (the proportion of men born), estimated average family size for a woman reproducing at a given year, change in real GDP and total mortality rate (the number of deaths per annual population size) from 1865 to 2003 in Finland were obtained from Statistical Yearbook of Finland 2007 (Statistics Finland 2007). These national registers are well known for the high quality of vital statistics (Gille 1949). From 1809 to 1917, Finland was an autonomous portion of the Russian Empire and during that time Finnish language gained recognition with rapid economic and political development. After the civil war in 1918, the economy of Finland was still predominantly agrarian but despite this, it has grown from ever since, except the depressions during the 1930s–1940s and 1990s. Finland became a modern industrialized society as late as by the late-1970s (Hjerppe 1989). Our data on birth sex ratio used in the analyses exclude stillbirths, as these data are available from 1921 onwards only. At least during this period, the proportion of men among stillbirths has remained relatively constant (Vartiainen *et al.* 1999), and thus unlikely confounds the questions studied here. Racial heterogeneity is unlikely to affect our results either, because Finland has always been a racially very homogenous nation. The mean ($\pm$SD) annual birth rate was 75 551 ($\pm$12 258) births, ranging from 43 757 to 108 168. Annual birth rate and sex ratio were unrelated ($P = 0{\cdot}58$).

Annual percentage change in real GDP (i.e. corrected for purchasing power as a result of inflation) was used as a proxy of the economic state of the population, because it estimates the development of the economic well-being of a nation, was available already from the mid-nineteenth century and captures well the structural changes in national economy. Total population mortality rate was included into the model to represent unaccounted factors that caused mortality among the Finns (disease epidemics, etc.), but were not captured by the other variables included. Because conceptions taking place approximately from April likely resulted in births during the next calendar year, we also included the previous year's real GDP and total population mortality rate in our analysis.

As an estimate of the annual variation of ambient temperature (in Celsius) in Finland, we used land air temperature anomalies over the area between 70º and 60ºN, and 20º and 30ºE, extracted from the data set of Brohan *et al.* (2006). Our calculation of ambient temperature represents variation in annual temperature across the whole study area, and not from few locations only (see, e.g. Catalano *et al.* 2008), because Finnish population is, and has been, geographically rather evenly distributed across the country. To avoid biases resulting from the heterogeneity of observation sites and routines, temperatures are represented as anomalies from the base period 1961 to 1990 before averaging the estimates of regional climate variability (Brohan *et al.* 2006). The temperature fluctuations were computed over 21-month intervals to account for the conceptions taking place on the previous year (see before). That is, the value of ambient temperature was calculated as a mean anomaly over nine (April through December) and twelve (January through December) months of the previous and concurrent years, respectively.

During the study period, Finland faced a civil war and was involved in the World War II. The civil war in Finland was rather short, starting on 28 January and ending on 16 May in 1918. We thus regarded only the year 1918 to represent the effect of civil war on sex ratio, as only few pregnancies during this crisis were taken to term in the year 1919. The World War II started in Finland on 30 November 1939 and ended on 27 April 1945. The war-related birth sex ratio distortion should have thus been visible between the years 1940 and 1945. Consequently, the World War II was modelled to influence sex ratio at birth during 1940–1945. Because of the different nature of these two wars (e.g. duration, national vs. international conflict), their effect on birth sex ratio was examined separately. The great famine during 1866–1868, 'the great hunger years', was one the largest and latest famines in European history causing a very high mortality among Finns and was also included in the analysis (Pitkänen & Mielke 1993).

To gain insight of the potential evolutionary consequences of offspring birth sex ratio fluctuations in Finland, we examined the association between annual birth sex ratio and the sex ratio of cohort infant mortality rates. The annual cohort infant mortality rates by sex from 1878 to 1977 were obtained from the Human Mortality Database (http://www.mortality.org) and from 1978 to 2003 from the Statistics Bureau of Finland.

STATISTICAL ANALYSIS

Association between annual birth sex ratio and ambient temperature anomaly, change in real GDP, wars, total mortality rate and average family size was examined using the dynamic regression model (Yaffee & McGee 2000; Brocklebank & Dickey 2003). The effects of wars and famine were modelled as intervention variables, taking a value of 1 during the events and 0 otherwise. In other words, in the case of civil war, the effect was modelled as a pulse function, lasting only one time period (1 year), whereas in the cases of World War II and the great famine, the effects were modelled as extended pulse functions, lasting for 6 and 3 years, respectively. All other variables were fitted as continuous. To examine whether the effects of continuous predictors were time dependent, we also included the interactions between these predictors and year into the model.

As suggested by Fig. 1, annual birth sex ratio does not have a stationary mean. Hence, the first difference was taken from the annual birth sex ratio, which successfully rendered the series stationary (augmented Dickey–Fuller tests, $P < 0{\cdot}0001$). Accordingly, the first difference was also taken from all the explanatory series, except the intervention variables (Yaffee & McGee 2000). The collinearity between explanatory variables was assessed with variance inflation factors and tolerance values. The largest variance inflation factor was 1·71 and the lowest tolerance value was 0·59, indicating that the standard errors of regression coefficients were unbiased. Potential feedback from birth sex ratio to predictors was examined using Granger causality test (Yaffee & McGee 2000). No evidence for such a feedback were found ($\chi^2_8 = 5{\cdot}52$, $P = 0{\cdot}70$). Prior to analysis, the response series was centred by subtracting its mean and hence the intercept was omitted from the model (Yaffee & McGee 2000). After introducing the predictors into the model, the autocorrelation structure of the model residuals was evaluated by Ljung and Box's Q-test and autocorrelation and partial autocorrelation function plots. If significant autocorrelation was found, it was removed by using a proper ARIMA model (AutoRegressive Integrated Moving Average; Yaffee & McGee 2000; Brocklebank & Dickey 2003). Before accepting the final model after backward elimination of non-significant predictors, the estimated parameters of explanatory variables were confirmed to be uncorrelated with model residuals using cross-correlation functions (Yaffee & McGee 2000). This procedure tests for the potential unaccounted delayed effects of predictors on the response. The residuals of the final model were normally distributed (Shaphiro–Wilk's test, $P = 0{\cdot}21$) and homoscedastic (LaGrange Multiplier tests for 12 orders, $P > 0{\cdot}12$).

Similar approach was used to examine whether annual offspring sex ratio at birth was related to the sex ratio of infant mortality of the born cohort. The birth sex ratio series was normalized to a previous year's level and multiplied by 100 to represent changes in percentages in birth sex ratio from the previous year. Taking the first difference from the response series rendered it stationary (augmented Dickey–Fuller tests, $P < 0{\cdot}0001$). No evidence for feedback from sex ratio of infant mortality on sex ratio at birth was found ($\chi^2_4 = 3{\cdot}69$, $P = 0{\cdot}45$). After running this model and correcting for the proper ARIMA model owing to serial autocorrelation of the response, model residuals showed significant heteroscedasticity (LaGrange Multiplier tests for 12 orders, $P > 0{\cdot}0001$). This heteroscedasticity was corrected by applying a proper Integrated Generalized Autoregressive Conditional Heteroscedasticity model (IGARCH). Residuals of this model were normally distributed (Jarque–Bera test, $P = 0{\cdot}53$). Analyses were conducted with SAS version 9·2 (SAS Institute Inc., Cary, NC, USA).

Results

EXOGENOUS STRESSORS AND BIRTH SEX RATIO

The temporal variation and descriptive statistics of the variables studied is given in Fig. 1. After controlling for the autocorrelation of annual birth sex ratio by the ARIMA(2,1,1) model, we found that an increase of 1 °C in ambient temperature anomaly was related to a 0·06% increase in annual birth sex ratio, and that this effect was not time dependent (Table 1 and Fig. 2). During the World War II, annual birth sex ratio also tended to increase by 0·04% (Table 1). Furthermore, irrespective of the study period, average family size decreased annual birth sex ratio by almost 0·14% per one additional offspring born (Table 1). Instead, total mortality rate and GDP at the concurrent or at the previous year, Finnish civil war and great Finnish famine were not associated with birth sex ratio (Table 1). The final model fitted explained 52·8% of the variation in annual birth sex ratio.

BIRTH SEX RATIO AND THE SEX RATIO OF INFANT MORTALITY

After accounting for autocorrelation with the ARIMA(4,1,0) model and heteroscedasticity with the IGARCH(1,1) model, we found no association between offspring birth sex ratio and the sex ratio of infant mortality rate among those born at the same year [β (95% CI) = −0·0016 (−0·0041, 0·0009), $t = -1{\cdot}24$, $P = 0{\cdot}22$]. Furthermore, this effect did not show time dependency ($t = -0{\cdot}04$, $P = 0{\cdot}97$). The final model

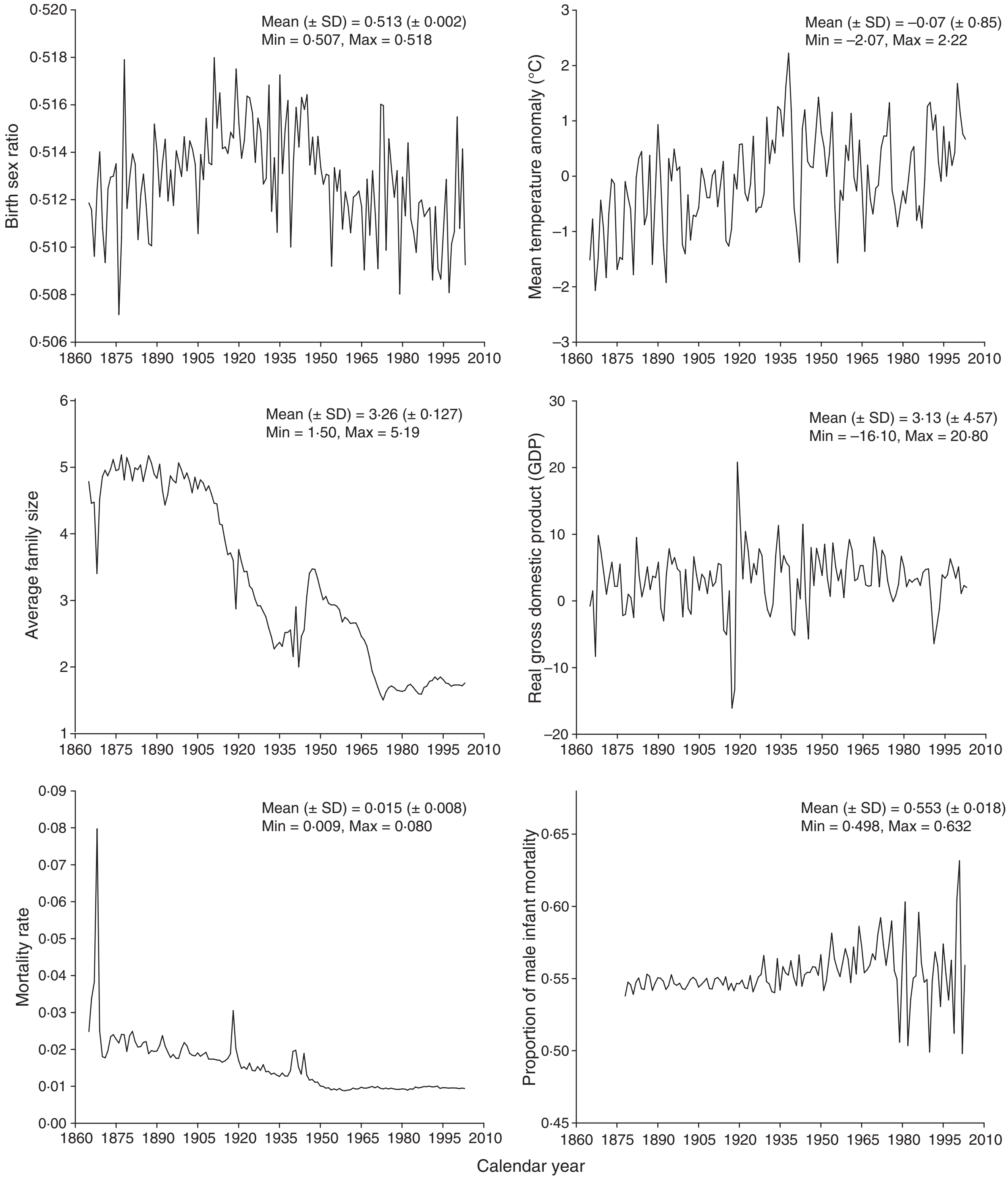

Fig. 1. Temporal variation of annual birth sex ratio, ambient temperature anomaly, average family size, real gross domestic product, total mortality rate and the sex ratio of infant mortality rates in Finland.

fitted explained 50·2% of the variation in the annual sex ratio of infant mortality.

Discussion

Our results indicate that during 1865–2003 in Finland, the annual offspring sex ratio at birth showed increased bias for men with increasing ambient temperature anomaly, whereas high average family size was related to an increase in female births. Annual birth sex ratio also tended to increase during the World War II. Instead, Finnish civil war, the great Finnish famine, total mortality rate and GDP were unrelated to fluctuations in birth sex ratio. We did not find evidence that these responses were adaptive in

Table 1. The effect of explanatory variables on annual offspring birth sex ratio in Finland, 1865–2003

Predictor	β (95% CI)	t	P
AFS	−0·0014 (−0·0024, −0·0003)	−2·58	0·0099
TA	0·00055 (0·00017, 0·0093)	2·84	0·0045
World War II	0·00043 (−0·00004, 0·00090)	1·78	0·075
GDP_{t-1}	−0·00004 (−0·00011, 0·00002)	−1·41	0·16
GDP	0·00004 (−0·00002, 0·00010)	1·32	0·19
MR_{t-1}	0·0355 (−0·0231, 0·0941)	1·19	0·24
Finnish civil war	−0·0012 (−0·0034, 0·0011)	−1·02	0·31
MR	−0·0024 (−0·0706, 0·0660)	−0·07	0·95
Great famine	0·00004 (−0·00163, 0·00171)	0·04	0·97
GDP × year	0·000002 (−0·000001, 0·000004)	1·51	0·13
MR × year	0·0017 (−0·0018, 0·0051)	0·95	0·34
AFS × year	0·00002 (−0·00003, 0·00006)	0·70	0·49
TA × year	−0·000003 (−0·000013, 0·000007)	−0·60	0·55

Explanatory variables given above the dotted line are those retained in the final model. CI, confidence interval; AFS, average family size; TA, temperature anomaly; GDP, gross domestic product; MR, mortality rate.

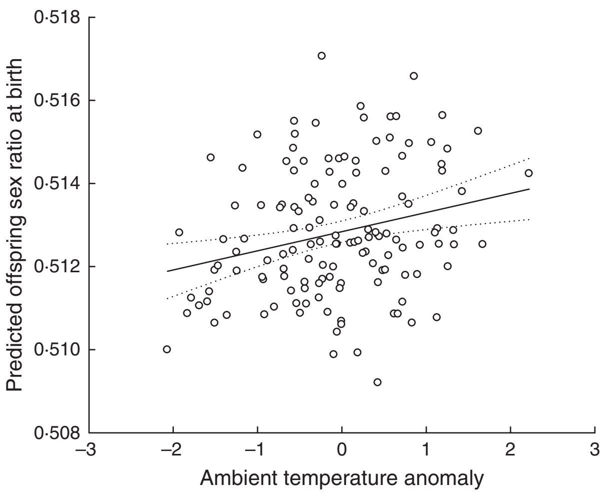

Fig. 2. Predicted offspring birth sex ratio as a function of ambient temperature anomaly. Solid line represents the fitted linear trend and dotted lines its 95% confidence intervals.

terms of offspring survival, as the years of increased bias towards sons were not associated with improved survival of male infants.

Previous studies have shown that economic regression, measured as an unemployment rate, private consumption of goods and services and collapsing economies (Catalano 2003; Catalano & Bruckner 2005; Catalano *et al.* 2005a, b, c, 2006; Kemkes 2006), and cold ambient temperature (Lerchl 1999; Grech *et al.* 2002; Catalano *et al.* 2008; Helle *et al.* 2008a) can reduce the proportion of male births. Our results provide further evidence for the temperature-related birth sex ratio variation by showing that in Finland during 1865–2003, excess of sons were born during warm periods. This finding adds to the growing body of literature in mammals suggesting a role of environmental temperature in sex ratio variation (Myers, Master & Garrett 1985; Post *et al.* 1999; Roche, Lee & Berry 2006). However, we found no association between economic development, measured here as a real GDP, and birth sex ratio.

As in the majority of the sex ratio literature, the proximate link(s) between these external stressors and offspring birth sex ratio remain unclear. At present, the most compelling proximate mechanism mediating these effects seems to be elevated maternal physiological stress that has been shown to bias offspring sex ratio towards daughters (Hansen *et al.* 1999; Obel *et al.* 2007), likely via increased mortality of more vulnerable male foetuses (Fukuda *et al.* 1996; Catalano *et al.* 2005b). A stress-related link is further supported by studies reporting woman-biased birth sex ratio after earthquakes (Fukuda *et al.* 1996; Saadat 2008) and terrorist attacks in humans (Catalano *et al.* 2005c, 2006), and experimentally elevated maternal corticosterone level in birds (Love *et al.* 2005; Pike & Petrie 2006; Bonier, Martin & Wingfield 2007). It is also possible that these kinds of external factors may affect sperm characteristics that skew offspring birth sex ratio by changing the primary sex ratio (Fukuda *et al.* 1996; Abu-Musa *et al.* 2007; Pérez-Crespo, Pintado & Gutiérrez-Adán 2008). Furthermore, in mammals ambient temperature has been shown to affect the steroidal concentrations of ovarian follicles (Wolfenson, Roth & Meidan 2000; De Rensis & Scaramuzzi 2003). High follicular testosterone concentration, for example, has in turn been shown to correlate with the increased odds of the fertilized ovum being a man (Grant & Irwin 2005; Grant *et al.* 2008). In addition, we cannot exclude the possibility that ambient temperature and economic conditions have only indirect effects on birth sex ratio. There is accumulating evidence that well-nourished mothers are more prone to deliver sons (Williams & Gloster 1992; Andersson & Bergstrom 1998; Gibson & Mace 2003; Cagnacci *et al.* 2004; Helle 2008; Mathews, Johnson & Neil 2008). Corresponding associations might have thus appeared at the population level, as both ambient temperature and economic situation might have influenced the physiological condition of the reproducing mothers, particularly in the pre-industrial era. However, several factors may confound the population-level patterns of maternal condition-dependent sex allocation (Wild & West 2007). No evidence for an effect of severe food deprivation during the great Finnish famine on birth sex ratio was found in this study, which contrasts the previous results of Stein *et al.* (2004) who reported bias for men in births during the Dutch hunger winter.

The effect of warfare on human birth sex ratio has attracted much attention for decades and the current evidence seems to suggest that wartimes are related to an increase of male births in countries where the act of war has been severe and long-lasting (James 2009). In support of this conclusion, we found an increment of 0·04% in the proportion of sons born during the World War II in Finland, whereas offspring birth sex ratio was unaffected by the Finnish civil war. This difference is most likely explained by the duration of these conflicts, as the Finnish civil war lasted only around 4 months, whereas the World War II in Finland lasted nearly 6 years. The reason(s) for the excessive increase of men in births during wars remains however unclear. It may represent an adaptive response to high mortality of breeding-age men, which might favour the overproduction of sons as a result of their increased mating success in relation to daughters (Trivers 1985; Bisioli 2004). This explanation has not received wide support, because wars do not generally last long enough to distort the human mating pool (Kanazawa 2007) and because wars skew mainly adult sex ratio that may not have relevance to the breeding population of the newborns (Helle *et al*. 2008b). Neither variation in other war-related demographic factors (maternal age, birth order, etc.) seems to provide the answer (James 2009). At the proximate level, the war phenomenon has been suggested to result from the higher rates of intercourse during the short war-time leaves, as the conception has an increased likelihood of producing a son when occurring during the either end of the cycle (James 2003). Direct evidence for this hypothesis is however lacking. Recently, Kanazawa (2007) proposed that as taller and bigger men are more likely to survive from the battle and perhaps more likely to sire sons, an increment of male births should be expected during wars and shortly after. However, it is currently unclear whether taller men do father proportionally more sons than shorter men (Denny 2008).

It is surprising that warfare, which must have imposed a tremendous stress on the nations involved, seems to generally increase the birth sex ratio whereas other stressful conditions, such as natural hazards and economic depression, seem to have just the opposite effect. Wars, when lasting for years, are also generally related to the shortage of food supply, which should bias offspring birth sex ratio towards women, not men (but, see Stein *et al*. 2004). Perhaps the most profound difference between these events is their duration. Natural hazards and economic depression, for example, can be considered mostly as rather short-term stressors, whereas wars (particularly the world wars, which have had the most marked effect on birth sex ratio) skewing birth sex ratio lasted usually for years. Moreover, wars often inflict high mortality rates also among civilians that may bear severe demographical consequences, whereas environmental stressor, excluding catastrophic earthquakes, may cause mainly psychological stress. It is also possible that these stressful events affect men and women differently or mainly one gender over another, which might, in turn, influence the relative importance of maternal vs. paternal dominance over sex ratio. The resolution to this problem may not see the daylight before we learn more on the endocrinological modulation of primary sex determination and sex-specific embryonic survival.

There is currently very little data on the evolutionary consequences of offspring sex ratio variation in humans. The only evidence for a facultative sex ratio adjustment comes from the studies showing low-status parents benefiting from the woman-biased offspring sex ratio caused by hypergamy (Boone 1988; Bereczkei & Dunbar 1997). Our results suggest that the associations found here likely represent an environmental pressure upon birth sex ratio and not an adaptive response of parents to prevailing exogenous stressors. It has been proposed that high male cohort survival may arise from the reduced proportion of male births in that cohort during adverse times, resulting from the selective mortality of frail men (Catalano & Bruckner 2006; Bruckner & Catalano 2007). This hypothesis assumes that only high-quality sons would outperform daughters at the times of scarcity, thus being a favoured strategy by natural selection. There is however a need for life-long individual-level data to investigate whether the interplay between the environment and offspring birth sex ratio has evolutionary consequences in humans. More specifically, we would greatly benefit from knowing whether ecological and economical conditions experienced during pre-natal development have sex-specific effects on individual lifetime reproductive performance and fitness, as natural selection is blind to improved survival if it does not contribute to the individual's reproductive success.

In conclusion, recent years have witnessed a shift away from a strict distinction between the genetic and environmental sex determination systems in vertebrates. Several studies have now also demonstrated how various environmental stressors can bias offspring sex ratio in humans. Our study of birth sex ratio fluctuations in Finland in 1863–2003, contrasting the relative roles of the main exogenous stressors suggested to affect birth sex ratio to date, shows an increased excess of male births during the World War II and during warm years, whereas economic development, the worst famine during the study period and Finnish civil war had no influence on birth sex ratio. No evidence was found to suggest that Finns adaptively responded to these exogenous challenges by biasing their offspring sex ratio towards the sex of higher infant survival. Although our model included all the major population-level factors suggested to date, it captured only roughly half of the annual variation in birth sex ratio. Furthermore, including only the autocorrelation structure of the birth sex ratio series into the model explained 48·2% of the variation, suggesting that the significant exogenous stressors of the final model explained 4·6% of the variation only. Therefore, we do not currently know what factors were mainly responsible for the fluctuations in sex ratio in Finland. It thus remains a major challenge for future studies to unravel the causes of temporal human sex ratio variation.

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