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Evolutionary biology

Temperature-related birth sex ratio bias in historical Sami: warm years bring more sons

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The birth sex ratio of vertebrates with chromosomal sex determination has been shown to respond to environmental variability, such as temperature. However, in humans the few previous studies on environmental temperature and birth sex ratios have produced mixed results. We examined whether reconstructed annual mean temperatures were associated with annual offspring sex ratio at birth in the eighteenth to nineteenth century Sami from northern Finland. We found that warm years correlated with a male-biased sex ratio, whereas a warm previous year skewed sex ratio towards females. The net effect of one degree Celsius increase in mean temperature during these 2 years corresponded to approximately 1% more sons born annually. Although the physiological and ecological mechanisms mediating these effects and their evolutionary consequences on parental fitness remain unknown, our results show that environmental temperature may affect human birth sex ratio.

1. INTRODUCTION

Temperature-mediated variation of birth sex ratios has been reported in vertebrates with chromosomal sex determination. Recently, human sex ratios at birth have been proposed to be affected by environmental temperature (McLachlan & Storey 2003). In contemporary Germany, conceptions during warm months resulted in a male-biased birth sex ratio (Lerchl 1999). Furthermore, in the late twentieth century Europe, more males were born in southern latitudes than in northern latitudes, whereas the opposite was found in North America (Grech *et al.* 2002). Temperature-related effects on human birth sex ratio thus remain poorly known and controversial.

We examined whether offspring sex ratio at birth was related to environmental temperature in historical Sami populations from northern Finland, using a 145-year-long annual time series. Because conceptions taking place approximately from May onwards probably resulted in births in the next calendar year, we examined the effects of both concurrent and previous year's temperature on annual birth sex ratio simultaneously.

2. MATERIAL AND METHODS

Demographic data on three Sami populations (Utsjoki, Inari and Enontekiö) for the years 1745–1890 were extracted from historical parish registers kept by the Lutheran church, consisting of continuous baptism, burial and marital records. These Sami populations practised reindeer herding, fishing and hunting for their livelihood, occupied large, partially overlapping geographical areas and experienced natural fertility and mortality due to the lack of any advanced medical care or birth control methods (Itkonen 1948).

We recorded annual sex ratio at birth (i.e. the proportion of males born) and mean age for those parents who reproduced that year. Mean (± 1 s.d.) offspring birth sex ratio was 0.52 (± 0.14), 0.50 (± 0.12) and 0.51 (± 0.10) in Utsjoki, Inari and Enontekiö, respectively. Because birth sex ratio did not differ between populations ($\chi^2_2 = 1.48$, $p = 0.48$), we analysed pooled data. While our data include virtually all births (including stillbirths), temporal variation in the total number of annual births (mean $= 45.8$, range 21–70) may have produced some stochasticity on annual birth sex ratio. However, there was no correlation between annual birth rate and sex ratio ($r_{\text{pearson}} = -0.054$, $p = 0.52$). We are not aware of any sex-dependent infanticide that would confound our results.

(a) Environmental data

Because meteorological records in northern Finland start in the early twentieth century, we had to rely on reconstructed climatic records, of which the most frequently used are tree rings for annual summer temperatures (Briffa *et al.* 1990; Esper *et al.* 2002). Moreover, NAO-index, which describes the oscillation of atmospheric mass between the Arctic (Iceland) and the subtropical Atlantic (Azores), was used because it markedly dictates winter climate in northwest Europe (Hurrell *et al.* 2001). The reconstructed NAO-index of Luterbacher *et al.* (2002) since 1659 and two types of tree-ring chronologies of Scots pine (*Pinus sylvestris* L.) from northern Fennoscandia were used: tree-ring width chronology of Helama *et al.* (2005) and maximum density chronology of Briffa *et al.* (1990). These three datasets were integrated into one palaeoclimatic model using a linear regression to reconstruct annual mean temperature (in Celsius) in the study region (Helle & Helama 2007). The reconstructed annual mean temperature is in good agreement with the observed annual temperature variability in nearby Karasjok weather station in northern Norway between the years 1890–1978 ($r_{\text{Pearson}} = 0.72$, 95% CIs $= 0.61$, 0.80, $p < 0.0001$; Mudelsee 2003), indicating a high reliability of the reconstruction. However, some uncertainty originating from potential non-climatic variability may be incorporated into the reconstruction. Regarding NAO-index, temporal instability of NAO-climate associations may introduce some noisiness into the series (Luterbacher *et al.* 2002). Regarding tree rings, unwanted variability can arise due to the age of trees and inter-tree competition (Helama *et al.* 2005). These factors were, however, taken into account in the standard tree-ring procedures used (Helama *et al.* 2005).

(b) Statistical analysis

Association between annual birth sex ratio and concurrent and a previous year's mean temperature, while controlling for parental age at reproduction (Lazarus 2002), was examined using dynamic regression with maximum-likelihood estimation (Yaffee & McGee 2000). Prior to analysis, the response series was centred by subtracting its mean, and hence the intercept was omitted from the model (Yaffee & McGee 2000). The autocorrelation structure of the residuals of the fitted model was evaluated by autocorrelation and partial autocorrelation function plots. If significant autocorrelation was found, it was removed by using a proper autoregressive integrated moving average process (Yaffee & McGee 2000). Before accepting the model, all the estimated model parameters, including the non-autocorrelated residuals, were confirmed to be uncorrelated, and the residuals normally distributed (Shapiro–Wilk's test, $p = 0.13$). Analysis was conducted with SAS v. 9.1 (SAS Institute Inc., Cary, NC, USA).

3. RESULTS

The temporal variation of annual birth sex ratio and reconstructed mean temperature is shown in figure 1. We found that high mean temperature at the same and at the previous year were associated with a male- and female-biased annual sex ratio at birth,
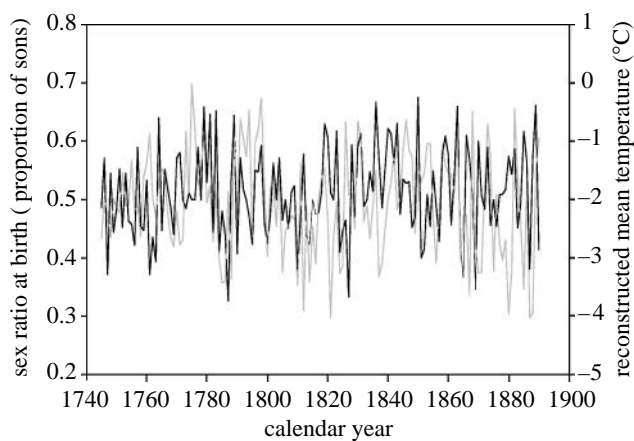
Figure 1. Temporal variation of annual offspring birth sex ratio (black line) and reconstructed mean temperature (grey line).

Table 1. Effects of mean temperature at the same and a previous year and parental age at reproduction on annual offspring birth sex ratio, while accounting for the autocorrelation of residuals by third-order moving-average (MA) term. (Model $R^2 = 0.1$.)

	$\beta(\pm s.e.)$	t	p
temperature	0.023 ($\pm$0.007)	3.23	0.001
temperature $_{t-1}$	-0.014 ($\pm$0.007)	-2.00	0.045
parental age at reproduction	0.006 ($\pm$0.005)	1.23	0.22
MA(3)	-0.189 ($\pm$0.084)	-2.25	0.025

respectively (table 1; figure 2). The magnitude of these effects corresponded to a 2.3% increase and 1.4% decrease in annual birth sex ratio for every 1°C increase in concurrent and previous year's mean temperature, respectively. Hence, the net effect of the increase of 1°C in mean temperature during these years was 0.9% more sons born annually.

4. DISCUSSION

Our results support those few previous reports suggesting that warm climate may bring more sons (Lerchl 1999; Grech *et al.* 2002). The phenomenon may, however, turn out to be rather complex, as we found contrasting effects of concurrent and previous year's temperature on birth sex ratio. This might be associated with the action of both pre- and post-conception mechanisms of sex ratio variation (Jimenéz *et al.* 2003). Temperature may influence primary sex determination by the variable fertilization success of X- and Y-bearing sperm (McLachlan & Storey 2003). In mammals, ambient temperature affects the steroid concentrations of ovarian follicles (Wolfenson *et al.* 2000; De Rensis & Scaramuzzi 2003) and, for example, a high follicular testosterone concentration may be associated with the fertilized ovum being a male (Grant & Irwin 2005). Stressful environmental conditions may also impair sperm motility, potentially promoting female-biased birth sex ratio (Fukuda *et al.* 1996, 1998; Gomendio *et al.* 2006). In addition, the temperature-related variation in birth sex ratio found may have resulted
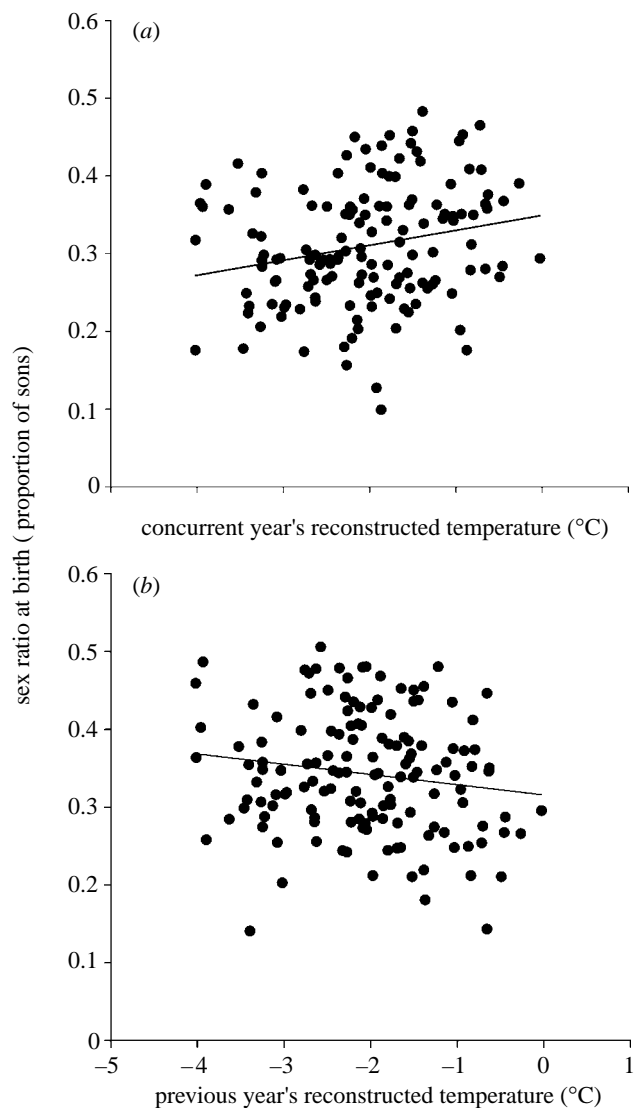

Figure 2. Association between (*a*) concurrent and (*b*) previous year's reconstructed mean temperature and birth sex ratio, after the effects of other explanatory variables on birth sex ratio are removed (table 1).

from sex-biased foetal mortality, as an increased mortality of more vulnerable male foetuses during temperature-induced stress could bias birth sex ratio towards females (Catalano *et al.* 2005). Our data cannot, unfortunately, tell what mechanism(s) was responsible for these results. It is possible that pre- and post-conception mechanisms may have responded to prevailing temperature differently. One could speculate that since most offspring born in the given year (births before September) were conceived late during the previous year (after May), cold previous year may have promoted the conception of boys and, if followed by a warm year, more boys were taken to terms, leading to an excess of sons born in that year. Monthly based data on temperature and births are however needed to shed more light into these issues.

We cannot exclude the possibility that temperature, or other temperature-related factors, affected birth sex ratio indirectly. There is some evidence that well-nourished mothers may be more prone to deliver sons than daughters (Williams & Gloster 1992; Andersson & Bergstrom 1998; Gibson & Mace 2003;

Cagnacci *et al.* 2004). Because Sami people relied on the various climate-influenced plant and animal sources of food, the physiological condition of reproducing women, and thus their offspring sex ratio, may have been related to temperature fluctuations. However, in heterogeneous populations, the adjustment of offspring sex by the relative condition of the mother is unlikely to yield any population-level patterns (West & Sheldon 2002).

Because among Sami annual mean temperature and birth rate seemed unrelated (Helle & Helama 2007), the offspring sex may be a more environment-sensitive component of female reproduction than fecundity *per se* (Cagnacci *et al.* 2005). The potential fitness consequences of climate-related skews in offspring sex ratio are unknown at present. If mothers reproducing in warm years deliver particularly successful sons, this might provide evidence for the Trivers & Willard's (1973) hypothesis. However, a temperature-dependent physiological mechanism(s) may override maternal ability to facultatively adjust offspring sex, and thus produce neutral or even maladaptive sex ratio variation (James 2006).

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