Humans at tropical latitudes produce more females

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Skews in the human sex ratio at birth have captivated scientists for over a century. The accepted average human natal sex ratio is slightly male biased, at 106 males per 100 females or 51.5 per cent males. Studies conducted on a localized scale show that sex ratios deviate from this average in response to a staggering number of social, economical and physiological variables. However, these patterns often prove inconsistent when expanded to other human populations, perhaps because the nature of the influences themselves exhibit substantial cultural variation. Here, data collected from 202 countries over a decade show that latitude is a primary factor influencing the ratio of males and females produced at birth; countries at tropical latitudes produced significantly fewer boys (51.1% males) annually than those at temperate and subarctic latitudes (51.3%). This pattern remained strong despite enormous continental variation in lifestyle and socio-economic status, suggesting that latitudinal variables may act as overarching cues on which sex ratio variation in humans is based.

Keywords: sex ratio; photoperiod; temperature; sex allocation

1. INTRODUCTION

Since Dssing (1884) and Fisher (1930) first provided a theoretical framework explaining sex ratio patterns, scientists have struggled to understand variation in natal sex ratios among human populations. Correlations between the human sex ratio at birth and a wide range of socio-economic factors and population-dependent variables such as war, economic stress, maternal and parental diets and age (reviewed in Jacobsen *et al.* 1999; Jongbloet *et al.* 2001) have been documented. However, understanding the functions of cultural and socio-economic variables as potential driving factors in human sex ratio manipulation is infinitely complicated, because in addition to the cultural variation in the factors themselves, the behavioural and physiological responses of humans to these variables differ among individuals and populations as well. Thus, cues of a more natural origin, which are pervasive throughout human and animal populations, may better predict sex ratio variation in humans across the globe.

From an adaptive standpoint, animals must optimize reproductive strategies, and often adjust sex ratios, according to fluctuating environmental

conditions that signal changes in resource availability (Trivers & Willard 1973; Ricklefs 2000, reviewed in Cockburn *et al.* 2001). This is because each sex comes with its own set of fitness costs and benefits, and selectively thrives in environments where, for example, resources are abundant and/or competition for those resources is low. In a geographical sense, tropical and temperate environments present very different challenges in terms of resource availability and consumer density (Ricklefs 2000). Environmental factors that underlie such latitudinal variation—day length and ambient temperature—are used by animals in both a geographical and a seasonal context to time and optimize daily activities (Bartness *et al.* 2002). Humans continue to respond behaviourally and physiologically to photoperiod and temperature despite enormous variation in productivity and cultural variables (Rojansky *et al.* 1992). Because latitudinal cues remain stable, despite economic and cultural fluctuations, they may serve as good candidates on which sex allocation patterns in humans may be based.

Taking a global perspective when analysing a phenomenon such as sex ratio adjustment and examining cues that affect a majority of humans in a similar manner can reveal general patterns onto which detailed local responses are superimposed. Here, human natal sex ratios were examined on a global scale, in relation to latitude and associated climatic variables as well as with socio-economic status (SS) for each country, to determine the factors that contribute most to the variation in human natal sex ratios on a global scale.

2. MATERIAL AND METHODS

Counts of the sex ratio at birth (reported as the ratio indicating the number of males per 100 females) for 202 countries spanning the years of 1997–2006 were obtained from the Central Intelligence Agency (CIA) World Factbook (CIA 1997–2006), which is published annually. The average proportion of male offspring was calculated for each country from which all 10 consecutive years of sex ratio data were available. This 10-year timespan was long enough to ensure that short-term socio-economic changes did not drive observed patterns, but short enough to ensure that the time scale accurately reflected the stability and status of each country.

Latitude was collected for the capital city for each country and the numerical latitude value was used, regardless of direction. Average annual temperatures from 2001 to 2008 were also obtained for each country from the Countries of the World website (Students of the World 2008), and the longest and shortest day lengths in 2006 were obtained from the US Naval Observatory Astronomical Applications Department. The annual variation in day length was calculated by subtracting the shortest from the longest annual day length. Latitude, average temperature and the annual day length variation were analysed using a principal components analysis (PCA) that produced a single component (LAT) with a variance proportion of 0.908 ($p < 0.0001$). Latitude and day length variation loaded positively, each accounting for 97 per cent of variation while average temperature loaded negatively, accounting for 92 per cent. These variables could not be used in analyses separately due to collinearity among all three (variance inflation factor = 3.33).

SS was assessed using the average gross domestic product (GDP) and unemployment rates over the same 10-year period (CIA 1997–2006). Additionally, an instability index, representative of state failure and conflict, was calculated for each country using the sum of 12 instability indicators published in the 2007 Failed State Index (Fund For Peace 2007). An overall indicator of SS was calculated using a PCA incorporating GDP, unemployment rate and the instability index for each country. This analysis produced one component with a variance proportion of 0.523 ($p < 0.0001$). Unemployment rate and instability index loaded positively, accounting for 82 and 80 per cent of the variation, respectively. GDP loaded negatively, accounting for 51 per cent of the variation.

Figure 1. (a) Visual depiction of average annual proportions of males at birth for individual countries around the globe from 1997 to 2006. (b) Colour-coded average proportion of male offspring for each five degrees of global latitude, for 202 countries ranging from 0° to 65°. (c) Mean (+s.e.) percentages of males at birth for countries categorized according to continental location. Human sex ratios showed significant continental variation. (d) Mean proportion of males at birth (s.e.s and s.d.s were too small to plot) for countries located in tropical, temperate and subarctic latitudes. Countries at tropical latitudes produced significantly less males compared with temperate and subarctic latitudes ($F=11.07$, $p<0.0001$, tropical–temperate and tropical–subtropical comparisons, $p<0.01$). All sex ratios were calculated using the average for 1997–2006. All figure segments are colour-coded (blue, more than 51.7% males; yellow, 51.2–51.7% males; orange, 50.7–51.2% males; red, 50.7% or less males). In (c) and (d), significant differences are indicated by different capital letters.

The relationships between LAT, SS and natal sex ratio were analysed using a nested multiple logistic regression and a nested logistic regression was used to determine which latitudinal segment drives variation in sex ratios (temperate, tropical or subarctic). Continent of origin was included as the nested variable in each case. These analyses allowed each country to be considered as an independent data point, and controlled for continental variation that may otherwise drive sex ratio trends. Individual effects were determined using effect likelihood ratio tests. Latitude segments were labelled according to classic definitions based on latitude (tropical = 0–32°, temperate = 32–50° and subarctic = 50–65°). Analyses were carried out using JMP v. 8 statistical software (SAS Institute, Inc., Cary, NC, USA).

3. RESULTS

Globally, human sex ratios were significantly and positively correlated with latitude and its related climatic variables, but not with SS (overall model: $R^2=0.19$, $\chi^2=88.65$, $p<0.0001$; LAT: $\chi^2=14.29$, $p<0.03$; s.d.: $\chi^2=4.54$, $p<0.60$). The latitudinal segment driving sex ratio variation is the tropical segment, where significantly more females were produced compared with the temperate and subtropical segments ($p<0.001$; figure 1). Continental variation contributed significantly ($\chi^2=26.38$, $p<0.0001$), with African countries producing the lowest sex ratios (average = 50.7% males) and European and Asian countries producing the highest (average = 51.4% males for both; figure 1).

Because Asia and Africa each lie at opposite extremes for both natal sex ratios and latitude, it is important to consider the possibility that the trends seen here were driven by pre-partum gender selection through preferential induced abortions of males or females, which has been reported in many Asian and African countries (Sen 2003). When these skewed data were excluded from the analyses, LAT remained positively correlated with natal sex ratios while SS still showed no relationship (overall model: $R^2=0.17$, $\chi^2=38.73$, $p<0.0001$; LAT: $\chi^2=13.17$, $p=0.01$; s.d.: $\chi^2=3.75$, $p<0.44$).

4. DISCUSSION

Results described above show a strong and persistent relationship between natal sex ratios and latitude across the world—significantly more females were produced at tropical latitudes, and this relationship emerged despite enormous lifestyle and socio-economic variation among countries and continents. Two previous studies have examined natal sex ratios in relation to latitude on a local scale. One study of only European countries showed the opposite pattern, where sex ratio was negatively related to latitude (Grech *et al.* 2000), while another study incorporating data from Mexico, the United States and Canada

showed a positive relationship with latitude (Grech *et al.* 2002). If only European countries were considered in the current analyses, an inverse pattern between sex ratios and latitude also emerged ($p=0.003$). However, European countries only cover 15° of global latitude, and contain no tropical countries, in contrast to the latitudinal ranges within Grech *et al.* (2002) and the current global analyses that contained both tropical and temperate countries, both of which showed a positive relationship between sex ratio and latitude. Indeed, the greatest differences in sex ratios in the current analyses are found between tropical and temperate countries, while there is no difference between temperate and subarctic countries. A global perspective containing countries representative of the full latitudinal spectrum is optimal for revealing the full extent of sex ratio variation in relation to latitude.

Previous studies have shown similar continental variation in the human natal sex ratio. African countries consistently report fewer male births compared with all other continents (Gerenne 2002), and Asian countries consistently report more male births (Hull 1990). These patterns could simply reflect sex-selective induced abortion, or an inherent genetic or racial difference in the ability to produce male versus female offspring (James 1984; Khoury *et al.* 1984). However, while genetic and artificial influences on the human sex ratio cannot be discounted, studies show that natal sex ratios among African countries are as diverse as in other parts of the world (Gerenne 2002) and show a positive correlation with latitude and its associated climatic variables just as we see globally ($p<0.01$). Thus, it is likely that other natural, non-genetic factors may contribute to human sex ratio manipulation. Additionally, the latitudinal patterns shown here are not solely driven by the extreme sex ratios in African and Asian countries, given that the latitudinal variation remains when these countries are removed from the analyses.

The relationship between natal sex ratios and latitudes may represent the vestiges of prior selection based on latitude-dependent factors such as day length and ambient temperature. Indeed both variables related significantly to natal sex ratios, but it is currently impossible to tease out the effects of these related variables. There is evidence that human natal sex ratios vary with temperature (Lerchl 1999; Catalano *et al.* 2008; Helle *et al.* 2008) and in relation to seasonal variables (Lerchl 1998); however, these results conflict and/or remain hard to interpret, potentially because they were conducted on a small scale. Regardless, these studies indicate a role for temperature and potentially day length in patterns of sex allocation. Here, more females were produced in tropical environments, which have the highest average ambient temperatures, the lowest annual variation in day length and the highest annual levels of environmental resource abundance. The results shown here mirror findings of an experimental study in Siberian hamsters where more males were produced in short day lengths (Navara *et al.* in press), as well as studies in house mice (Drickamer 1990) and meadow voles

(McShea & Madison 1986), where more males were produced during the winter months.

Clearly, a relationship exists between human natal sex ratios and latitudinal variables on a global scale. Whether human sex ratios are skewed before or after fertilization remains to be determined. Perhaps male ejaculate quality or miscarriage rates vary on a latitudinal scale, indirectly affecting sex ratio. Indeed, ejaculate quality and fertility rate in humans vary with day length (Rojansky *et al.* 1992). The results shown here could indicate an adaptive strategy employed by humans, or there may be another non-adaptive explanation. More work is needed to tease apart the genetic, socio-economic and climatic influences on sex ratio adjustment and to determine whether adaptive strategies explain latitudinal variation in human natal sex ratios.

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