

CHAPTER 11

THE EVOLUTION OF HUMAN SEX RATIO AT BIRTH: A BIO-CULTURAL ANALYSIS

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A PHYLOGENETIC APPROACH TO TESTING EVOLUTIONARY HYPOTHESES USING CROSS-CULTURAL DATA

Physiological data from a range of human populations living in different environments can provide valuable information for testing evolutionary hypotheses about human adaptation. The comparative method can help us determine whether variation results from selection due to environmental factors, or is possibly selected for by cultural forces (which means that gene-culture co-evolution is occurring). However, a simple, statistical correlation between traits across cultures is complicated by the non-independence of cultures, as was first recognised in the 19th century by Francis Galton. The same problem applies in cross-species comparisons. Evolutionary biologists have developed phylogenetic comparative methods that can take account of the hierarchical interrelatedness of species and test for the co-evolution of traits on phylogenetic trees. Mace and Pagel (1994) argued that similar approaches can be used to test *cross-cultural* hypotheses. In this chapter, we will outline an example of the use of one of these approaches to test adaptive hypotheses explaining global variation in population sex ratio at birth.

Hierarchically related units, be they species or populations, cannot be considered as statistically independent in comparative tests. Below, we report that sex ratio at birth is more male-biased in European than in African countries. This could be related to higher levels of malnutrition in Africa. A simple statistical correlation across African and European populations with some correlate of nutrition might yield a highly significant result. However, there are a large number of variables that differ between Africa and Europe. A genetic trait co-evolving with sunshine, or malaria, or polygyny, to name some arbitrary examples, could equally underlie the observed trend. Each population in Africa differing from one in Europe does not represent an independent test of the hypothesis that nutrition is influencing sex ratio, because the populations in Africa are likely to be closely related to each other, as are those in Europe. Evolutionary biologists have developed a number of statistical approaches in which evidence for a change along the branches of a phylogenetic tree are linked to independent instances of change in the relevant trait (Felsenstein 1985b; Harvey and Pagel 1991; Pagel 1999a). Mace and Pagel (1994) argued that similar approaches can be used to test cross-cultural comparative hypotheses in biological and cultural anthropology.

Any statistical comparison does require some explicit model of evolutionary history; not using a tree is equivalent to assuming that all cultures are equally related, which we know is wrong. Networks would be very hard to estimate, and current statistical procedures cannot test for correlated evolution using networks. In the tests reported here, we use phylogenetic trees of human cultures based on genetic similarity (Cavalli-Sforza *et al* 1994). The weight of anthropological, genetic and archaeological knowledge indicates that, almost whatever the degree of cultural isolation, some populations are much more closely related to some cultures than they are to others. So whatever the shortcomings of a phylogenetic model of history, it is likely to be the best we have for our purposes here. Thus, whether the traits of interest are predominantly genetically, environmentally or culturally determined, phylogenetically controlled correlations are appropriate.

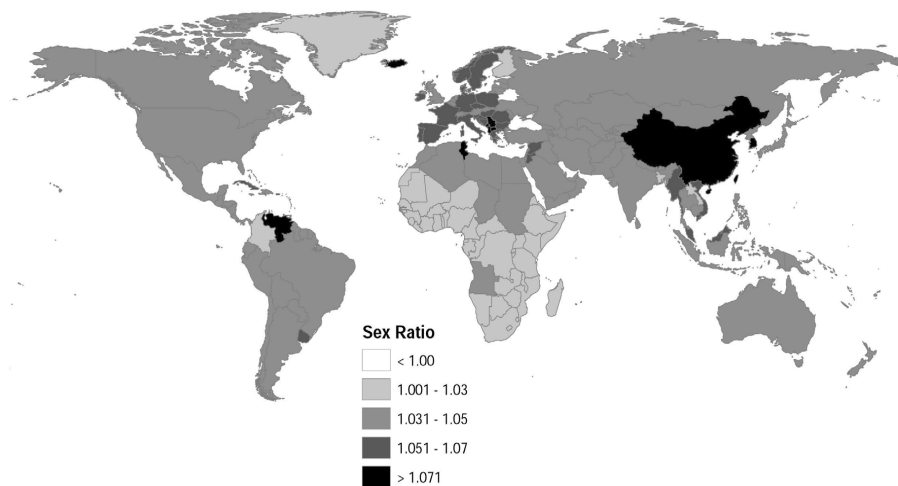
Variation in sex ratio at birth is a continuous trait, so we use Pagel's CONTINUOUS method to test for correlations between pairs of traits (Pagel 1997, 1999a, www.ams.rdg.ac.uk/zoology/pagel). This method applies a generalised least squares model to analyse continuously varying trait data on phylogenetic trees. Correlations between pairs of traits are found by the method of maximum likelihood, and tested via the likelihood ratio statistic. CONTINUOUS controls for the effects of phylogenetic relatedness, and simplifies to the conventional correlation across populations when the phylogeny has no influence on the data.

GLOBAL VARIATION IN SEX RATIO AT BIRTH

Figure 11.1 shows the global variation in sex ratio at birth. The data are taken from the US government CIA factbook archive (www.cia.gov/cia/publications/factbook), which is based on data compiled by numerous sources. Whilst few populations deviate greatly from 50:50, there is clear geographical variation in the small deviations observed. It is notable that sex ratios at birth in African countries are lower (less male-biased) than those in most of the rest of the world, and sex ratios at birth in Europe and much of Asia are high (more male-biased). In some extreme cases, specifically China and South Korea, it is likely that sex-specific abortion is so widespread that quite large deviations in sex ratio are being generated artificially (eg, Tuljapurkar *et al* 1995) and we have not included these two countries in our analyses. This artificial bias is due to unusually widespread and accessible advanced medical facilities combined with a strong cultural preference for males. But in most of the world's population where preferences are strong, such technology is not available, so the observed variation is likely to largely reflect natural variation in sex ratio at birth.

There is a large literature on the evolution of sex ratio. Darwinian theory predicts that the sex ratio of reproductive adults in a population will be close to 50:50 if the costs of producing and raising males and females are similar. Because every member of any sexually reproducing population has one mother and one father, the average reproductive success of males and females is always equal. If one sex becomes more numerous than the other, then a parent producing offspring of the rarer sex will leave more grandchildren. Hence strong selection pulls the sex ratio back towards 50:50, as is usually observed in sexually reproducing species. Crucially, however, Fisher (1930) noted that it is net parental

The Evolution of Human Sex Ratio at Birth: A Bio-cultural Analysis 209



¹ "Information is provided by Antarctic

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<http://www.cia.gov/cia/publications/factbook/index.html>.

Figure 11.1 Global variation in sex ratio at birth by country (source CIA World Factbook). Reproduced from Mace *et al* 2003 with permission of the publisher.

investment in boys and girls that should not differ; so if one sex is more costly to produce than the other, then the more costly sex will be under-represented in proportion to that additional cost. In humans, male babies are subject to slightly higher neonatal and infant mortality than are female babies (Wells 2000). Hence the average cost of raising a boy is lower than that of a girl, because the average number of years of parental investment given to boys is lower (as more of them receive almost no investment postpartum due to their early death). This is thought to underlie the slight male-bias in sex ratio at birth almost universally observed in human populations (Figure 11.1).

However, it is not only the costs of production that are relevant, but also the benefits, which in evolutionary terms are measured as reproductive potential. Trivers and Willard (1973) showed that, if resources invested in offspring have a greater impact on the future reproductive success of males than that of females,

then the optimal sex ratio of offspring could be dependent on the resources available to the mother. In most polygynous species, whilst average reproductive success of males and females is equal, variation in male reproductive success is generally much larger, and large body size often provides males with an advantage in the competition for mates. A female in poor condition is likely to produce small babies that may grow into small adults. Hence she will further her long-term reproductive success by producing a female baby. Females in good condition who can produce larger babies that will grow into tall adults, will do better by having a male. Evidence for condition-dependent sex ratio biases in line with these predictions has been shown in various populations of mammals, insects and birds (see West and Sheldon 2002 for a review of the evidence). There is less evidence from human populations, however. Gibson and Mace (2003) have shown that in an Ethiopian population undergoing a period of food shortage, thinner women were significantly more likely to have girls than less thin women. This study is one of the few that has focused on a homogeneous group of women experiencing food shortage, which may be the conditions under which such facultative sex ratio adjustment may be most evident. Mace and Eardley (2004) show that the female-biased sex ratio at birth among malnourished mothers was apparent across rural Ethiopia.

It is notable from Figure 11.1 that the lowest sex ratios at birth are observed in Africa, where food stress is likely to be highest. However, this cannot be readily explained by Trivers and Willard's hypothesis, as this hypothesis relates to condition dependence relative to others within the same population. Because males in Africa are not competing with males in Asia or Europe for mates, their size relative to each other is not relevant.

We believe that this bias must relate to differences in the costs and benefits to the parents of male and female children in different countries. Important costs could be biological, cultural or economic. First we will seek evidence that biological costs are important. There is some evidence that male children are more prone to starvation than female children (Widdowson 1976; Wells 2000). One possibility is that regions of higher sex ratio at birth are those where male mortality in infancy and childhood is high. We will test this by examining how the sex ratio at birth is related to the sex ratio in later childhood.

Alternatively, lower sex ratios may be the result of male births imposing higher costs in terms of the mother's health and future reproductive success than female births. Data from the USA show that mothers carrying male fetuses have about 10% higher energy intake than those carrying girls (Tamimi *et al* 2003). Male fetuses grow faster in the womb (Marsal *et al* 1996), and male babies are heavier at birth (Loos *et al* 2001) and are associated with a longer time elapsing for mothers to produce their next child (Mace and Sear 1997). It is therefore possible that the costs to the mother's health and future reproductive success of male births is larger than for female births, and that this cost will be most significant in populations where fertility is high and mortality rates (both for children and adults) are high. Below we will test for correlation between sex ratio at birth and other demographic parameters that might indicate the reproductive stress that women are under. All the country-level demographic data used are taken from the

The Evolution of Human Sex Ratio at Birth: A Bio-cultural Analysis 211

same demographic data sources as the sex ratio data, except for maternal mortality ratio, which is taken from WHO (1995).

Secondly, we examine economic cost differences between male and female children. In some countries, especially where there is polygynous marriage (see Pagel and Meade, Chapter 13 this book), men have to pay brideprice to the family of their bride in order to marry. Males compete for access to females using their resources to help them, and wealthy families tend to have greater reproductive success as a result. Competition between women is far less as all women tend to marry, and those that marry wealthy men have to share his resources with many wives, so the advantages of polygyny to females are slight or non-existent. In other countries, where monogamy is prevalent, females end up competing for several reasons. First, men are marriageable over a larger age-range, and some women end up unmarried. Secondly, wealthy men cannot have multiple wives, so the benefits of his wealth are exclusively those of whichever female is lucky enough to marry him. Parents frequently help their daughters compete in this marriage market by offering dowry (a payment made by the bride's family to the groom or his family). In societies where dowry is high, daughters can become very costly to raise into marriage, and this lies behind the female infanticide observed in some monogamous, Asian societies. Daughters with older sisters are at particular risk. In societies where brideprice is high, some men may find it hard to find mates, and in families with many older brothers, fathers sometimes cannot afford brideprice for their younger sons (Mace 1996). Thus marriage costs can make one sex more costly than the other. Sex ratio theory predicts that in these circumstances, the sex ratio may be more biased against the more costly sex. We test this hypothesis. It is possible that sex ratio itself could also influence payments, as the sex for which there was a shortage should be more in demand. Thus if sex ratio is related to marriage costs, it could be due either to marriage costs influencing the cost of raising a child, or to the sex ratio influencing the marriage costs. Either way, this would be evidence of some form of bio-cultural evolution occurring.

A PHYLOGENETIC COMPARATIVE ANALYSIS OF SEX RATIO, FERTILITY AND MORTALITY ACROSS HUMAN POPULATIONS

Here we present a cross-country comparative analysis of sex ratio at birth, where we seek to test the hypothesis that it correlates with other demographic variables, including sex ratio at higher ages, fertility and mortality levels in the general population. The distribution of the relevant traits across continents is clearly non-random, confirming the need for a method controlling for the non-independence of cultures. We use a phylogenetic comparative method based on a gene-based tree of human populations.

In this analysis we have restricted our analysis to the Old World. The populations of New World countries (the Americas, Australia, New Zealand) are now of mixed origin, and cannot therefore be informatively placed on phylogenetic trees. It is also notable that these countries appear to have more uniform sex ratios at birth near the world average of around 1.05 males/female,

which is what we would expect of mixed populations, if this trait is under genetic control. In the case of sex ratio at birth, we do not know to what extent sex ratio at birth is genetically determined; however, it is notable that black Americans, living in the USA, have a sex ratio at birth of 1.03, similar to that of most African populations, compared to 1.05 for white Americans (Martin *et al* 2002).

After selecting Old World countries for which the relevant data were available from our source, we identified the major ethnic groups of these countries and included only those where the major ethnic group could be identified on the genetic trees constructed by Cavalli-Sforza *et al* (1994). Cavalli-Sforza *et al* (1994) contains a worldwide genetic tree based on allele frequencies as well as separate, more detailed phylogenies for major world regions (Europe, Africa, West Asia, etc). We matched each country's largest ethnic group to Cavalli-Sforza *et al*'s populations in each of these smaller regional trees, and then constructed the overall phylogeny according to the backbone provided by the worldwide tree. The resulting tree had all branch lengths set equal to one. Countries with populations of less than one million were then excluded, as demographic data, especially on sex ratio at birth, might have been subject to estimation error. This left 74 countries, which are related according the tree shown in Figure 11.2.

We used Pagel's (1999a) phylogenetic method CONTINUOUS for detecting correlated evolution in continuous traits, to see whether sex ratio at birth is correlated with sex ratio in childhood or adulthood, or with fertility or mortality rates.

Table 11.1 summarises our results. The magnitude of the likelihood ratio (LR) is a measure of how strongly correlated the two measures are, controlling for shared phylogenetic history. λ (lamda) is a scaling parameter that assumes a

Table 11.1 Demographic correlates of sex ratio at birth, using CONTINUOUS.

Variables correlated	LR	p	λ	r(given λ)	
SRB \times SRC	24.21	0.000	0.69	0.70	***
SRB \times SRA	0.45	0.341	0.59	0.11	
SRB \times lnTFR	3.33	0.010	0.73	-0.30	**
SRB \times lnIMR	1.99	0.045	0.79	-0.23	*
LnTFR \times lnIMR	20.42	0.000	0.70	0.66	***
SRB \times lnMMR	2.60	0.023	0.70	-0.26	*

Key: SRB = sex ratio at birth, SRC = sex ratio in children between 0–14, SRA = sex ratio in adults between 15–65, lnTFR = natural log of the Total Fertility Rate, lnIMR = natural log of the mortality rate of those under one year of age, lnMMR = natural log of the maternal mortality ratio (mothers death at or around childbirth per 100,000 births). LR = likelihood ratio, λ is a scaling parameter, r(given λ) is the correlation coefficient when the scaling parameter is applied (see CONTINUOUS manual: www.ams.rdg.ac.uk/zoology/pagel).

The Evolution of Human Sex Ratio at Birth: A Bio-cultural Analysis 213

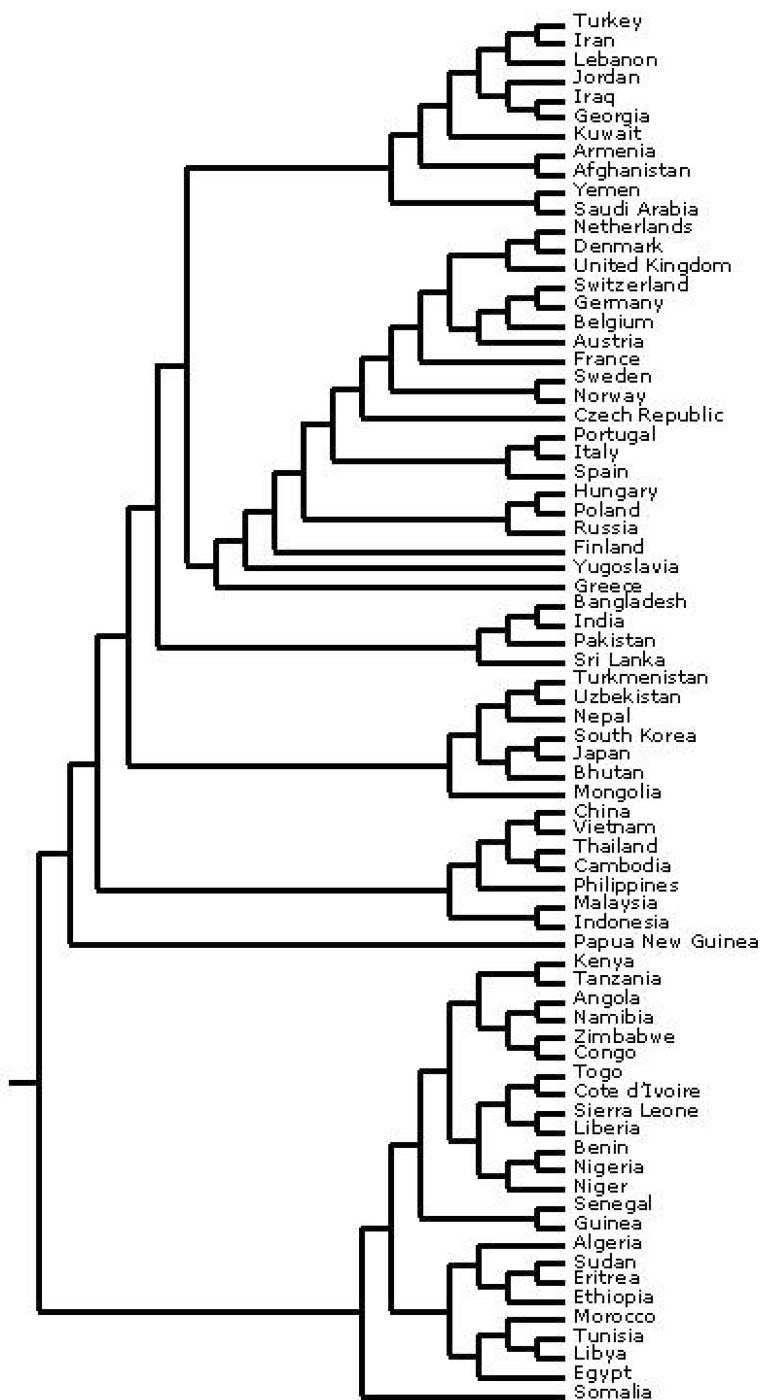


Figure 11.2 Phylogenetic tree of the dominant cultures in 74 countries, adapted from Cavalli-Sforza *et al* 1994.

Brownian motion model of evolution and corrects tree branch length accordingly (which tends to improve the fit of the model) (Pagel 1999a, CONTINUOUS manual: www.ams.rdg.ac.uk/zoology/pagel). r indicates the correlation coefficient.

Population sex ratio at birth and its correlation with sex ratio in children and adults

There is a very strong positive correlation between sex ratio at birth and the sex ratio of children between the ages of 0–14. Sex biases at birth continue into childhood. If high sex ratios at birth were compensating for high male mortality in childhood, then we would expect either no correlation or a negative correlation, which we do not see. Thus variance in sex ratios at birth across countries does not appear to be associated with variance in male infant or childhood mortality.

There is no correlation between sex ratio at birth and that in adulthood. This suggests that the birth sex ratios are not responses to biases in adult sex ratio. Sex ratios at birth are not predicted to be influenced by a systematic sex differences in mortality rates after the period of parental investment (ie, in adulthood). For example, even in populations where many adult males might die in warfare, those who survive are predicted to have very high reproductive success, so such effects are not predicted to bias sex ratio systematically. However, if the operational sex ratio (ratio of breeding males to breeding females) were to deviate due to some chance environmental fluctuation, then the rarer sex would be at an advantage, so sex ratio could be selected to adjust accordingly in some facultative manner. The measure used here is the sex ratio of 15–65 year olds. Although a proportion of the females included in this measure would be post-reproductive, this is close to the operational sex ratio of reproductive individuals; so a deviation from 50:50 in this measure probably indicates that the rarer sex should have higher reproductive success. If sex ratio at birth is influenced by that bias, then one might predict a negative correlation between sex ratio at birth and that in adulthood; however, this is not seen. There is little evidence, therefore, that sex ratios at birth are adaptive responses to sex-biased mortality either in infancy and childhood or in adulthood.

Sex ratio at birth and reproductive rate

There is a significant negative correlation between sex ratio at birth and both fertility rates and infant mortality rates. The total fertility rate and the infant mortality rate of a country are very strongly correlated with each other, so it is hard to assess the independent effects of fertility or mortality. However, the correlation with fertility rate is stronger. Hence it appears that in countries where mothers give birth to many children, they are more likely to have girls. There is also a significant negative correlation with the risk per birth of death in childbirth. This indicates that sex ratios at birth are lowest in those countries where women's health is most endangered by their high fertility. We know that the physiological burden of producing males and females differs, and it may be in high fertility

The Evolution of Human Sex Ratio at Birth: A Bio-cultural Analysis 215

populations that these cost differentials are greatest. High fertility may increase the health risk of pregnancy disproportionately for mothers of boys, due to their faster growth and larger size and hence higher energetic burden. Also, the net costs of raising girls may be lower in high fertility societies due to girls defraying their costs by helping their mothers with domestic and child-rearing duties (in ways that boys rarely do). Helle *et al* (2002) found in a high fertility, historical population that mothers with a large number of daughters had longer lifespans compared to those with a large number of sons, suggesting that daughters were defraying the costs of child-rearing which had long-lasting health benefits for the mother. Our results suggest that such an asymmetry in the costs of producing and raising each sex could be selecting for lower sex ratios in high fertility populations.

A PHYLOGENETIC COMPARATIVE ANALYSIS OF SEX RATIO AND MARRIAGE COSTS OF MALES ACROSS HUMAN POPULATIONS

We tested the hypothesis that if the net cost of one sex was higher than the other, due to marriage costs, then sex ratio at birth might evolve to produce less of the costly sex. In order to test this we used Murdock's Ethnographic Atlas to identify whether the main culture of a country gave dowry (which makes daughters costly) or brideprice (which makes sons more costly) at marriage. Unfortunately this data is available at the level of the culture, whereas the sex ratio data is available at the level of the nation state. Clearly in some cases the nation state consists of a number of different cultures, who could differ in the relevant variables; so although we used the marriage costs associated with the most common culture (as listed in the CIA World Factbook) this will inevitably have introduced some inaccuracy in multicultural states. The sample size was reduced, by the requirement that the relevant cultural data was available, to 56. The same phylogenetic tree was used, but for the remaining cultures missing values were entered, so they were not included in the analysis.

Table 11.2 shows the results of correlations between sex ratio and the presence or absence of brideprice (the groom giving money to the family of the bride at marriage) in that culture. The same correlations were repeated with the variable dowry, which was almost orthogonal to brideprice but in many cases with no brideprice there is no transfer of wealth in any direction. The number of cultures with dowry was rather smaller, and although correlations were all in the opposite direction to that of brideprice, none was significant and these results are not shown.

There is no evidence that sex ratio at birth is evolving with marriage payments. Thus gene culture co-evolution does not seem to have occurred in this case. There is also no evidence that sex ratio in childhood is correlated with brideprice. However, sex ratio in adulthood (15–64 year olds) does significantly correlate with the presence of brideprice. In populations with a higher sex ratio in adulthood, women must be dying at earlier ages than in those populations with lower sex ratios in adulthood. Thus one possible explanation is that where women are in

Table 11.2 Correlations between sex ratio and brideprice across cultures, using CONTINUOUS.

Variables correlated	LR	p	λ	$r(\text{given } \lambda)$
SRB \times Brideprice	0.19	0.534	0.60	0.083
SRC \times Brideprice	0.05	0.758	0.52	-0.04
SRA \times Brideprice	0.42	0.048	0.31	0.26 *

Key: SRB = sex ratio at birth, SRC = sex ratio in children between 0–14, SRA = sex ratio in adults between 15–65. LR = likelihood ratio, λ is a scaling parameter, $r(\text{given } \lambda)$ is the correlation coefficient when the scaling parameter is applied (see CONTINUOUS manual: www.ams.rdg.ac.uk/zoology/pagel).

shorter supply, men are more likely to be competing for brides and thus need to pay for them. Alternatively, the causation may be in the opposite direction. If the workloads of women are higher, or their status lower, to an extent that reduced the life expectancy, and this is related to brideprice in some way, this would cause such a correlation. However, it should be noted that female status can be very low in societies with dowry. Variation in sex ratio in adulthood in human populations is unlikely to be a genetic trait (as it is not correlated with sex ratio at birth, as shown in Table 11.1), so this is not an example of gene-culture co-evolution. But it does give an example of how the demography of a population and its cultural practices are interrelated.

DISCUSSION

Global data on biological and cultural variation in human populations is potentially informative for testing adaptive hypotheses about the evolution of such diversity, but statistical analyses must take into account population history. It has long been appreciated that population history and migration influence the biological and cultural make-up of a population. Human migration is both recent and ancient. The method used here helps us to untangle the effects of population history from those of natural selection or even cultural selection that generates this bio-cultural diversity *in situ*.

In the case of variation in sex ratio at birth, we highlight variation in a trait that shows large continental variation. Phylogenetic effects were very strong in every correlation. The high values of λ confirm this. Thus, in this case, a phylogenetic approach is especially important if Type I errors are to be avoided. We identify the physiological costs associated with high fertility as important correlates of low sex ratios at birth. We found no effect of marriage costs on sex ratio at birth. Perhaps marriage costs are not stable enough over time to allow such a bias to evolve, possibly because the cultural system evolves as sex ratio shifts, thus reversing the effect and stabilising the sex ratio at birth. There was a significant relationship between sex ratio in adulthood and brideprice, which is consistent with predictions from evolutionary theory. There is still the possibility with phylogenetic correlations, as with any correlation, that some third variable may be influencing these effects. The area remains wide open for further investigation.