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Are human natal sex ratio differences across the world adaptive? A test of Fisher's principle

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Running head: Adaptive sex ratio variation in humans?

12 **Abstract**

13 Fisher's principle states that natural selection favours an equal number of male and female births
14 at the population level, unless there are sex differences in rearing costs or sex differences in
15 mortality before the end of the period of parental investment. Sex differences in rearing costs
16 should be more pronounced in low- than in high-resource settings. We, therefore, examined
17 whether human development index and sex differences in child mortality contribute to the natural
18 variation in human sex ratio at birth across the globe. As predicted by Fisher's principle, the
19 proportion of male births increased with both increasing male-biased childhood mortality and
20 level of development of each country. However, these relationships were absent after accounting
21 for spatial autocorrelation in the residuals, which our inference is conditioned on. This work
22 shows how the failure to account for residual spatial autocorrelation can lead to incorrect
23 conclusions regarding support for predictions from sex allocation theory.

24

25 Keywords: adaptation; *Homo sapiens*; sex allocation; sex ratio; spatial autocorrelation.

26

Introduction

After many years of research on the human sex ratio at birth (SRB), this topic continues to fascinate. Confined for a long time to more developed regions, reliable estimates on SRB now exist for most countries [1]. There are more male than female births in all countries, but the degree of male bias varies considerably across the globe even when excluding countries known for practicing sex-specific abortion [1]. Countries in tropical latitudes produce fewer sons compared to countries in temperate and subarctic regions [2]. Yet, the adaptive significance of natural variation in SRB between countries is currently unknown.

Fisher's principle of equal investment is the bedrock of sex allocation theory [3]. Extending the argument of Düsing ([4], translated in [5]), Fisher [6] claimed that parents should, on average, divide their 'expenditure' equally between the sexes. The logic behind the Fisher's argument has been nicely expounded by Hamilton [7], and Trivers [8] more precisely defined this expenditure as 'parental investment', i.e. any behaviour provided to the offspring by the parents that improves offspring fitness, but that decreases parent's future survival or reproductive success. Fisher's principle states that natural selection favours an equal number of male and female births at the population level, unless there are differences in the relative costs of rearing male and female offspring or sex differences in mortality of offspring before the end of the period of parental investment [3,6,9–12]. If sex-biased mortality occurs after the period of parental investment, then it has no influence on sex allocation [9,10].

Specifically, if juvenile males show higher mortality than females during the period of parental investment, then average sex ratios at the beginning of parental investment (conception or birth) should be biased towards males and biases should be reversed by the end of the period of parental investment to maintain equal total investment in the two sexes (fig. 1a). Fisher himself pointed out, the human SRB follows this pattern [6]. Mortality is higher in boys than girls in most

parts of the world [13], but the male disadvantage varies both in space and time [14,15]. It remains to be determined whether variation in SRB across countries can be attributed to sex differences in childhood mortality. The relative costs of raising boys and girls may also vary across countries. For a given age, boys are likely to be energetically more expensive than girls in part because of the sexual size dimorphism [16]. For example, the energy intake of pregnant women in Boston (USA) is about 10% higher when they are carrying a boy rather than a girl [17] and American mothers produce richer milk for sons than daughters [18]. However, evidence that these energetic costs translate into fitness costs for the mother is controversial, at least in terms of lifespan [19,20]. Results from animal studies suggest that fitness costs of reproduction and sex differences in rearing costs can only be evident under unfavourable ecological conditions [12]. Thus, raising a boy may have larger costs to the mother's subsequent survival or reproductive success than raising a girl in developing countries, but not in developed countries. These fitness costs should reduce any tendency to produce an excess of boys (fig. 1b).

Here, we use most recent estimates of natural SRB in various countries to test these hypotheses. We expect that the proportion of male births increases with both the male-biased mortality between birth and age of 5 years (U5MR sex ratio) and human development index (HDI) recorded for each country.

Material and methods

(a) Data

Chao and colleagues [1] compiled an extensive database from vital registration systems, censuses and surveys and developed Bayesian methods to estimate the number of male live-births divided by number of female live-births for 212 countries from 1950 to 2017. These ratios are provided without details about the number of males and females. Here, we calculated SRB as the

proportion of males (i.e. $SRB = N_{\text{males}} / (N_{\text{males}} + N_{\text{females}})$) combining the ratio ($N_{\text{males}} / N_{\text{females}}$) obtained from [1] and the annual total number of live births for each country (N_{total}) from the UN World Population Prospects (WPP) 2019 [21]:

$$- N_{\text{females}} = N_{\text{total}} / ((N_{\text{males}} / N_{\text{females}}) + 1)$$

$$- N_{\text{males}} = N_{\text{total}} - N_{\text{females}}$$

Note that estimates of N_{total} from UN WPP were also used by Chao and colleagues [1]. For each country, we calculated the average of ten values of SRB taken during the period 2008-2017. This 10-year timespan represents a good compromise of the relative benefits of long and short periods (see [2] for more details), and estimates of U5MR sex ratios and HDI are available in most countries during 2008-2017. As the focus of this work is natural variation in SRB, 12 countries with strong evidence of sex-selective abortions during 1970-2017 [1] were excluded from the analysis. U5MR sex ratios, expressed as the ratios of male to female rates of under-five mortality, were obtained from UN Inter-agency group for Child Mortality Estimation [22]. U5MR sex ratios were also estimated with Bayesian methodology [14]. The HDI is a summary measure of average achievement in key dimensions of human development: a long and healthy life, being knowledgeable and have a decent standard of living. The HDI is the geometric mean of normalized indices for each of the three dimensions, and the higher a country scores the higher its human development is considered be. HDI values are taken from the UN Development Programme [23]. We calculated an average U5MR sex ratio and HDI for each country over the same 10-year period (2008-2017).

(b) Statistical analyses

All analyses were performed using R version 4.0.2 [24] and code is available in supplementary material. We first tested for the additive effects of U5MR sex ratio and HDI on SRB using a

binomial generalized linear model (GLM, $n = 172$). We checked the model fit diagnostics and as observed SRB values display a strong spatial structure (fig. 2a), we paid particular attention to residual spatial autocorrelation (lack of independence between geographically close countries) which can affect tests and parameters estimates in statistical modelling [25]. Latitude and longitude for the centroid of each country were obtained from the rgeos package, and spdep and field packages were used to compute spatial weights as inverse geodesic distances. Patterns of spatial autocorrelation were detected by drawing maps using ggplot, and we computed Moran's index I using the spatial weights and tested it by a randomization procedure. When spatial correlation in the residuals was detected, this was taken into account with a spatial model (GS-GLM) using the package spaMM [26]. This model was designed to fit spatial autocorrelation in the residuals variance-covariance matrix using a Matérn structure defined at the global scale with the function fitme [26]. We used parameter estimates and their 95% confidence intervals (CI) to assess effects of U5MR sex ratio and HDI.

Results

Spatial autocorrelation was high in observed SRB values ($I=0.271$, $p=0.001$, fig. 2a). The simple GLM showed that SRB became more male-biased with U5MR sex ratio, as well as with HDI (table 1a). However, there was a clear spatial pattern in the residuals, which highlights significant positive spatial autocorrelation ($I=0.096$, $p=0.001$, fig. 2b) indicating that explanatory variables did not catch all the spatial structure of SRB values. So adding a spatial correlation structure in the model is important to obtain unbiased tests and parameter estimates. The spatial model (GS-GLM) showed that neither U5MR sex ratio nor HDI exerted statistically significant influences on SRB (table 1b). This latter model has adequately captured positive spatial autocorrelation ($I=-0.028$, $p=0.968$, fig. 2c).

Discussion

Comparative approaches have been relatively underexploited in the field of sex allocation [10]. While it is often impossible to predict whether the average SRB of a single population should be biased, and if so, in what direction, it is possible to make relative predictions for how the average SRB should vary across populations [10,27]. Such a comparative analysis was carried out here to test some predictions from Fisher's principle. This principle predicts that parents compensate for higher mortality in males during the period of parental investment by producing male-biased SRB [6,9]. Human SRB for the entire world population follows this pattern, but this is not the case for between-country variation since we detected no significant relationship between U5MR sex ratio and SRB from 172 countries. In addition, we found no evidence for a significant effect of HDI on SRB.

Determining the period of parental investment in humans is a major challenge given the extremely long period of offspring dependence [28]. Because infancy and early childhood is the period during which offspring require the most direct care [29], we investigated the influence of sex differences in mortality between birth and age of 5 years on SRB. Nevertheless, it would be informative to repeat this analysis using sex differences in mortality between birth and the conclusion of adolescence once such estimates will be available for most countries. Furthermore, recent studies could call into question the general consensus that sex-biased mortality after parental investment does not influence SRB [30,31]. It could be argued that parental investment starts around conception. However, costs of gestation are small in comparison with those of lactation in mammals [32] and the sex ratio at conception in US women is not male-biased [33].

At the heart of Fisher's principle lies frequency-dependant selection, so this principle can only operate if offspring sex ratio is heritable [34]. The question of heritability of SRB in humans

has been addressed by some studies. Using a population genetic model with 1224 parent-offspring pairs, Gellatly [35] found a significant heritability of SRB by male, but not female offspring. With a larger sample size (14 015 421 pairs), a near zero heritability of SRB was observed in 20th century Sweden [36]. According to the authors, this lack of heritability renders “Fisher’s principle untenable as a framework for understanding human offspring sex ratio” [36]. However, the principle makes no inference that sex ratio is heritable when the population is at equilibrium.

We are aware of some limitations of our study. First, U5MR sex ratio during 2008-2017 does not necessarily represent past conditions in which SRBs have evolved. Several laboratory studies that have altered the sex ratio of animal population and monitored the direction of subsequent changes show that Fisherian evolution is a slow mechanism [10]. For example, in *Drosophila mediopunctata* the sex ratio changes from 16% of males to 32% of males in 49 generations, with an estimated 330 generations to reach 50% of males [37]. Because data on U5MR sex ratios are available for most countries in the world from 1990, a test of the influence of past U5MR sex ratios on SRB of all countries is clearly a challenge for the future. Another consideration is that the definition of population is easy to understand in conceptual terms but difficult to operationalize. Considering one country as one population is bound to be a simplification of reality. It would be interesting to examine whether the correlations tested here are significant at a more local scale (e.g., village level in some countries).

It is crucial to distinguish between spatial autocorrelation in the response variable and in the residuals [38]. There is clear evidence of spatial autocorrelation in SRB of countries and further studies need to be done to understand which factors explain this structure. The presence of autocorrelation in the residuals of a model can be inherent to the response variable, due to the omission of relevant explanatory variables or misspecification of the relationship among

variables (e.g., a quadratic function can fit the data better than a linear one). If residual autocorrelation is present, even after model improvements (e.g., use of non-linear model, integration of new explanatory variables), it represents a nuisance that needs to be taken into account by appropriate methods [38]. Spatial autocorrelation in the residuals violates the assumption of independence and leads to the underestimation of standard errors, and elevated type I errors, if not accounted for [25]. In other words, failure to account for residual spatial autocorrelation can result in falsely rejecting much more often than expected, the null hypothesis, while it is true. This phenomenon is well known in the literature of macroecological and biogeographical modelling [38,39]. The present study underlines the importance of controlling residual spatial autocorrelation in sex allocation studies, and therefore cautions against studies that ignore it. An approach that uses a simple linear model and ignores residual spatial autocorrelation would have led to the incorrect conclusion that it had demonstrated that the impeccable logic of Fisher's principle explains natural variation in human SRB across the globe.

Data accessibility. Data are available in the Dryad Digital Repository:

<https://datadryad.org/stash/dataset/doi:10.5061/dryad.kkwh70s3g> [40]

Authors' contribution. M.D designed the study, collected the data, and wrote the manuscript; S.D analysed the data and wrote the manuscript. All authors gave final approval for publication and agree to held accountable for the work performed therein.

Competing interests. We have no competing interests.

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195

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- 295 41. Trivers R. 1985 *Social evolution*. Menlo Park, USA: The Benjamin/Cummings publishing.
- 296
- 297

298 Table 1. Parameter estimates and 95% confidence intervals (CI) from two type of models
 299 including sex ratio at birth (SRB) as dependent variable, and sex differences in child mortality
 300 (U5MR sex ratio) and human development index (HDI) as independent variables (n=172).

301

302

type of model	parameter	estimate	95% CI
a) GLM	Intercept	-0.007	
	U5MR sex ratio	0.028	[0.019; 0.036]
	HDI	0.032	[0.029; 0.035]
b) GS-GLM	Intercept	0.034	
	U5MR sex ratio	0.006	[-0.027; 0.038]
	HDI	0.010	[-0.005; 0.026]

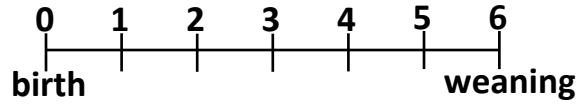
303 **Figure legends**

304 Figure 1. The Fisher's principle predicts that both sex differences in mortality during the period
305 of parental investment and sex differences in rearing costs per unit of time should affect the
306 evolution of SRB (redrawn from [41]). In this hypothetical species, parental investment
307 (rectangle) is assumed to last 6 years and to be equal each year. At the population level, total
308 investment in each sex (cumulative surface area of the rectangles) is equal. a) Mortality is high in
309 males, but not in females. SRB is strongly male-biased and bias is reversed by the end of the
310 period of parental investment. b) An increased parental investment in males (larger rectangles)
311 reduces the tendency to produce an excess of this less viable sex.

312 Figure 2. Maps of observed data and model residuals. a) Average sex ratio at birth (SRB) during
313 2008-2017 by country. b) Deviance residuals for the simple generalized linear model (GLM). c)
314 Deviance residuals for the spatial GLM that considers a Matérn correlation structure (GS-GLM).
315 Symbols for countries are colored by values and the size is proportional to the average number of
316 births. Values for Moran's I index of autorrelation and p-value of the associated test are
317 indicated.

a)

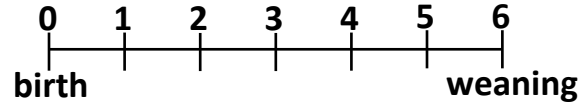
*Period of parental
investment (years)*



b)

Submitted to Biology Letters

*Period of parental
investment (years)*



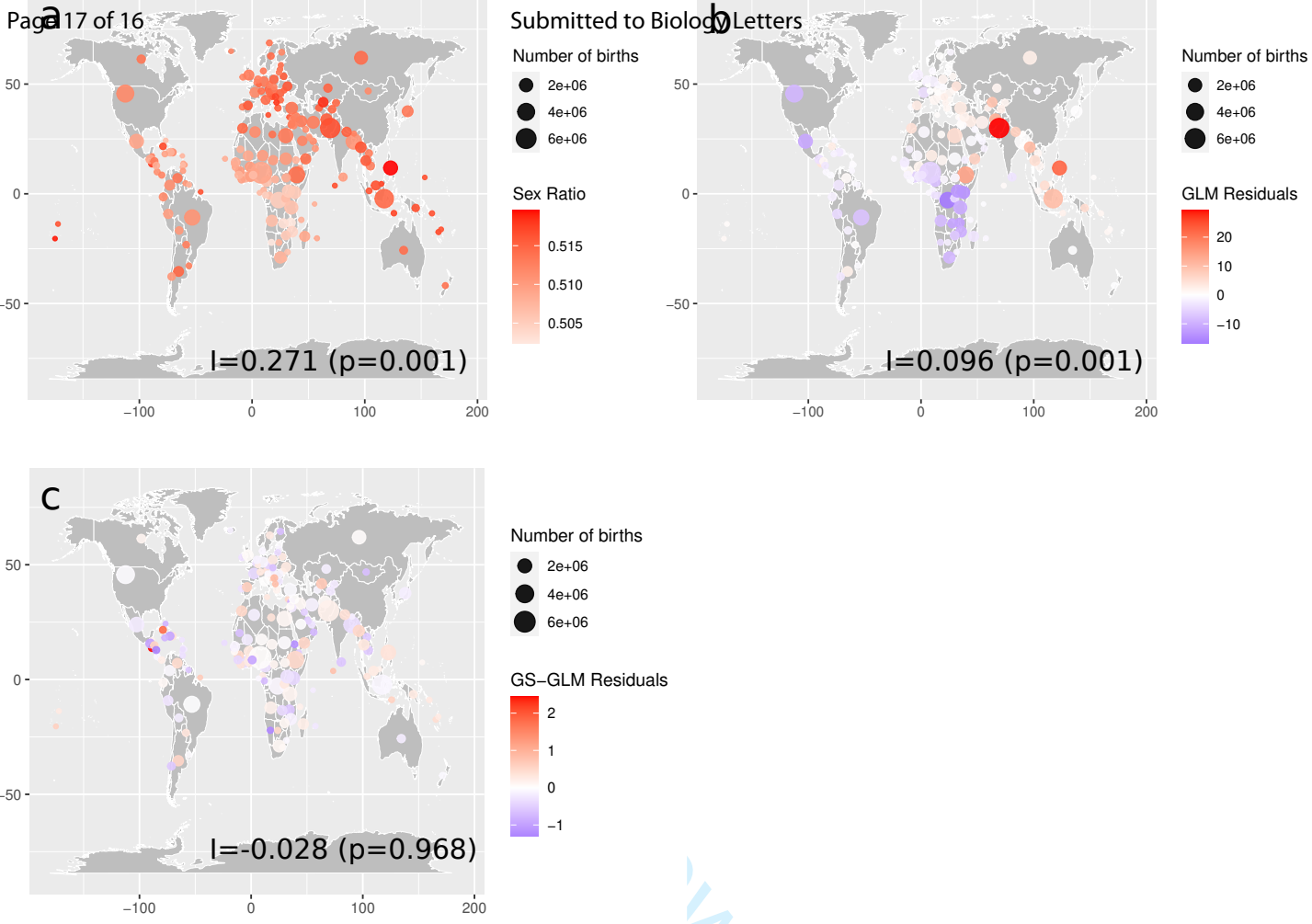


Figure 2