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

3

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5

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10

11 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

27 **Introduction**

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

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

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

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

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

68

69 **Material and methods**

70 **(a) Data**

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

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

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

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

80 Note that estimates of N_{total} from UN WPP were also used by Chao and colleagues [1]. For each
81 country, we calculated the average of ten values of SRB taken during the period 2008-2017. This
82 10-year timespan represents a good compromise of the relative benefits of long and short periods
83 (see [2] for more details), and estimates of U5MR sex ratios and HDI are available in most
84 countries during 2008-2017. As the focus of this work is natural variation in SRB, 12 countries
85 with strong evidence of sex-selective abortions during 1970-2017 [1] were excluded from the
86 analysis. U5MR sex ratios, expressed as the ratios of male to female rates of under-five mortality,
87 were obtained from UN Inter-agency group for Child Mortality Estimation [22]. U5MR sex ratios
88 were also estimated with Bayesian methodology [14]. The HDI is a summary measure of average
89 achievement in key dimensions of human development: a long and healthy life, being
90 knowledgeable and have a decent standard of living. The HDI is the geometric mean of
91 normalized indices for each of the three dimensions, and the higher a country scores the higher its
92 human development is considered be. HDI values are taken from the UN Development
93 Programme [23]. We calculated an average U5MR sex ratio and HDI for each country over the
94 same 10-year period (2008-2017).

95

96 **(b) Statistical analyses**

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

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

112

113 **Results**

114 Spatial autocorrelation was high in observed SRB values ($I=0.271$, $p=0.001$, fig. 2a). The simple
115 GLM showed that SRB became more male-biased with U5MR sex ratio, as well as with HDI
116 (table 1a). However, there was a clear spatial pattern in the residuals, which highlights significant
117 positive spatial autocorrelation ($I=0.096$, $p=0.001$, fig. 2b) indicating that explanatory variables
118 did not catch all the spatial structure of SRB values. So adding a spatial correlation structure in
119 the model is important to obtain unbiased tests and parameter estimates. The spatial model (GS-
120 GLM) showed that neither U5MR sex ratio nor HDI exerted statistically significant influences on
121 SRB (table 1b). This latter model has adequately captured positive spatial autocorrelation ($I=-$
122 0.028 , $p=0.968$, fig. 2c).

123

124 **Discussion**

125 Comparative approaches have been relatively underexploited in the field of sex allocation [10].

126 While it is often impossible to predict whether the average SRB of a single population should be

127 biased, and if so, in what direction, it is possible to make relative predictions for how the average

128 SRB should vary across populations [10,27]. Such a comparative analysis was carried out here to

129 test some predictions from Fisher's principle. This principle predicts that parents compensate for

130 higher mortality in males during the period of parental investment by producing male-biased SRB

131 [6,9]. Human SRB for the entire world population follows this pattern, but this is not the case for

132 between-country variation since we detected no significant relationship between U5MR sex ratio

133 and SRB from 172 countries. In addition, we found no evidence for a significant effect of HDI on

134 SRB.

135 Determining the period of parental investment in humans is a major challenge given the

136 extremely long period of offspring dependence [28]. Because infancy and early childhood is the

137 period during which offspring require the most direct care [29], we investigated the influence of

138 sex differences in mortality between birth and age of 5 years on SRB. Nevertheless, it would be

139 informative to repeat this analysis using sex differences in mortality between birth and the

140 conclusion of adolescence once such estimates will be available for most countries. Furthermore,

141 recent studies could call into question the general consensus that sex-biased mortality after

142 parental investment does not influence SRB [30,31]. It could be argued that parental investment

143 starts around conception. However, costs of gestation are small in comparison with those of

144 lactation in mammals [32] and the sex ratio at conception in US women is not male-biased [33].

145 At the heart of Fisher's principle lies frequency-dependant selection, so this principle can

146 only operate if offspring sex ratio is heritable [34]. The question of heritability of SRB in humans

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

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

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

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

184

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

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

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

190 **Competing interests.** We have no competing interests.

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195

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- 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]

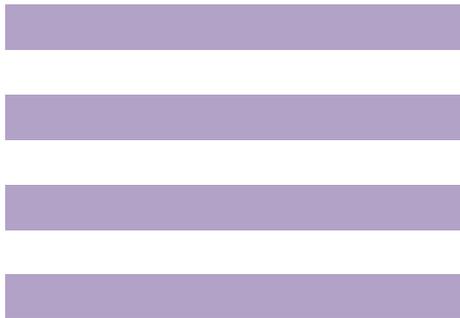
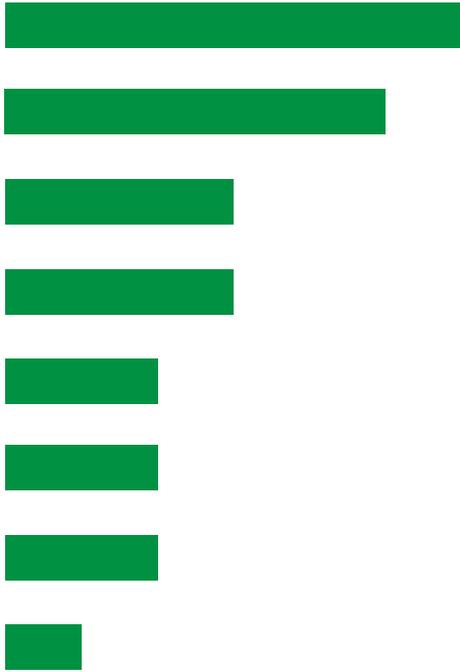
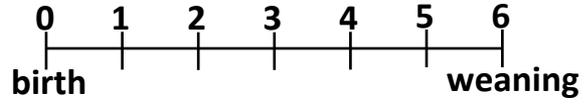
303 Figure legends

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.

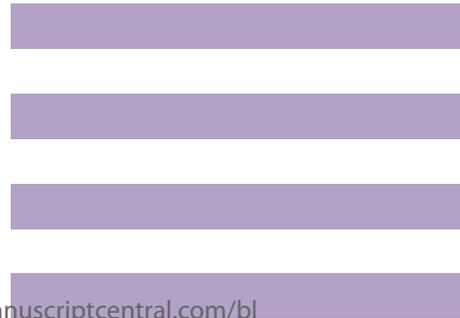
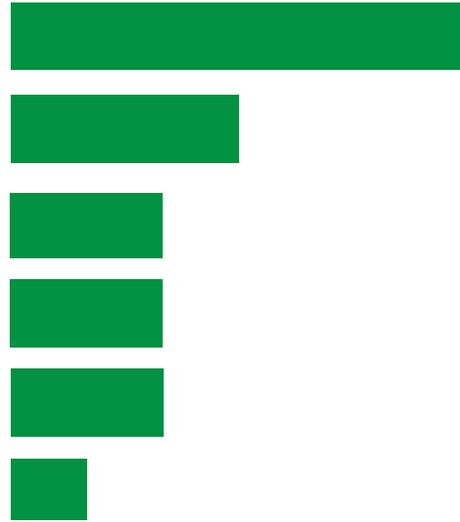
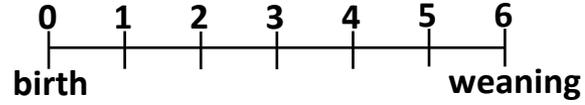
a)

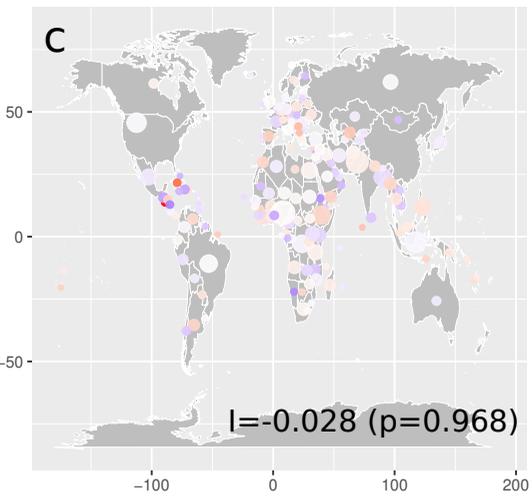
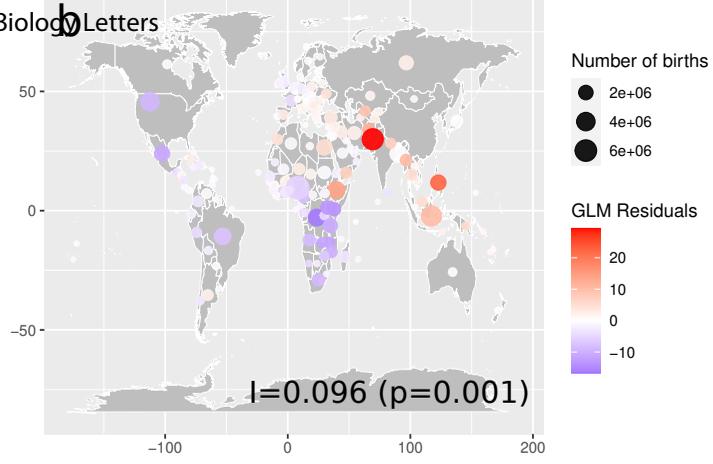
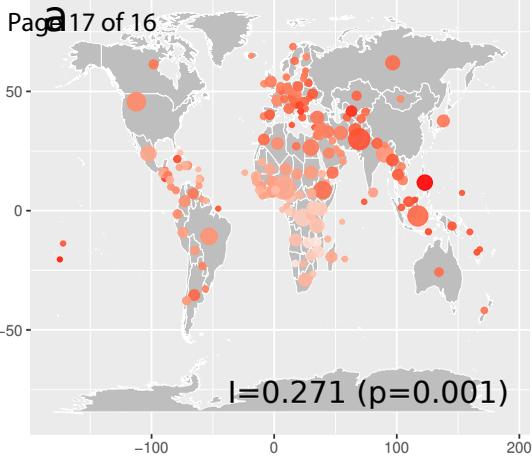
Period of parental investment (years)



b)

Period of parental investment (years)





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