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Elder brothers affect the life history of younger siblings in preindustrial humans: social consequence or biological cost?

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Abstract

Sex-specific sibling interactions are potentially important in human ecology. It is well established that in patrilineal societies that sons suffer from the presence of brothers because of competition for inheritance. However, offspring (of both sexes) might also suffer from being born after an elder brother because of the greater costs sons may entail for their mother. Evidence that the cost of producing sons is higher has been gained from studies of ungulates and humans, with some of this cost being manifested as lower birthweight or reproductive performance of offspring born following a male. Using church record data from preindustrial Finland, we shed light on this process by investigating the demographic 'mechanisms' by which offspring born following an elder brother are compromised. First, we show that, for both men and women in this population, being born after an elder male sibling is associated with reduced probability of reproducing, a later age at first reproduction, and longer interbirth intervals. Second, we show that the primary effect of interest is a reduced probability of reproducing in those born after an elder brother (even among only those who married). Finally, we show that the total number of elder brothers who survived to adulthood has a negative effect on male offspring only, and this effect is independent of the elder brother effect above. We highlight that differences in the success of human offspring are not always social in origin as is often perceived but can also be biological, resulting from differential costs for mothers of producing male versus female offspring.

Keywords: Adaptive sex ratio variation; Reproductive costs; Inclusive fitness; Trivers-Willard hypothesis

1. Introduction

Sex-specific sibling interactions have been shown to influence variation in offspring fitness throughout vertebrates (Uller, 2006). In humans, several anthropological studies have described how the number and sex of (particularly elder) siblings can influence an individual's survival and reproductive success. A recurring pattern is that the presence of elder brothers decreases the marriage prospects, resources and reproductive success of younger male siblings. Findings along these lines have been reported among 19th century Swedes (Low, 1991), as well as the Kenyan Gabbra pastoralists (Mace, 1996) and Kipsigis (Borgerhoff Mulder, 1998). The most likely explanation for such patterns is that they are due to competition driven by patrilineal inheritance and the corresponding bias of parental investment in elder sons (Borgerhoff Mulder, 1998; Low, 1991; Mace, 1996). In contrast, strong parental preferences against daughters on the Indian subcontinent has been shown to substantially increase the mortality risk of girls with elder sisters (Muhuri & Preston, 1991).

In contrast to the consequences of sex-specific sibling competition, evidence from industrialised societies suggests that being born to a mother who has previously produced a son can have negative consequence in both males and females. Of six studies documenting the association between elder sibling sex and birthweight, four found that both male and female newborns were lighter at birth when born following an elder brother versus an elder sister (Trotnow, Bregulla & Flügel, 1976; Magnus, Berg and Bjerkedal, 1985; Nielsen et al., 2008; Rickard, 2008), while two found that only the birthweight of boys was affected by the sex of their elder sibling (Blanchard and Ellis, 2001; Côté,

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Blanchard, & Lalumière, 2003). Furthermore, a study also able to record adult size for the same individuals found that both males and females with elder brothers achieved a shorter final height on average than those with elder sisters, suggesting that the apparent birthweight difference may have important long-term consequences for phenotype in adulthood (Rickard, 2008).

That being born after a male sibling can have long-term phenotypic consequences for the subsequent offspring of both sexes led us to hypothesise that differences between the success of children can be biological in origin. In particular, if mothers incur a higher cost as a result of producing a male versus female offspring, then the fitness of offspring born after an elder brother might be reduced irrespective of the sex of the current offspring. In a previous study, we utilized a large sample of church record data from preindustrial Finland to show that individuals born to a mother who had previously produced a son had reduced lifetime fecundity and eventual lifetime reproductive success compared with those born following a daughter (Rickard, Russell, & Lummaa, 2007).

In the present study, we first explore which of the four fecundity-increasing life-history traits are influenced by the sex of the elder sibling: probability of reproducing (i.e., being recruited into the breeding population), age at first reproduction, mean length of interbirth intervals between offspring and reproductive lifespan. Second, we determine the life-history trait through which elder sibling sex most compromises the lifetime fecundity of the subsequent offspring. Finally, we investigate whether or not the cost of sons is acquired cumulatively by examining whether each elder brother preceding the focal individual has an additional effect on reproductive success or whether only the sex of the immediately elder sibling matters.

In all analyses, we pay particular attention to the task of differentiating between ‘biological’ and ‘social’ explanations. There are a number of modifiers which can be used in analysis to give an accurate indication of whether the elder sibling sex effect is driven by biological or social factors. First, if there is a tendency to bias investment in sons, we would expect it to only affect younger female siblings. Second, if the investment bias is subject to family resources, we would expect the effect to be strongest in the very richest families (the landowners). Third, if there is bias in investment towards sons who would be more likely to receive the majority of their parents’ inheritance, then the effect might be stronger in those born after an elder male sibling from a high birth order. Finally, if the effect is driven by high preferential investment, then we would not expect to see the pattern in those whose elder sibling died in infancy. Accordingly, we pay particular attention to testing these predictions in all analyses in the paper, by examining the effect of interactions between elder sibling sex and (a) the sex of the focal (younger) sibling, (b) family social class, (c) an individual’s birth order, and (d) elder sibling death before 6 months of age.

2. Methods

To investigate which younger sibling life-history traits were associated with elder sibling sex, we analysed data from preindustrial Finnish farming and fishing communities (Rickard, Russell, & Lummaa, 2007). These data were collected from population registers maintained by the Lutheran church in the 18th and 19th centuries. The church systematically recorded all births, deaths, and marriages within parishes, as well as migrations between them (Luther, 1993). This allows for most individuals to be tracked across their entire reproductive lifespan and, hence, for reliable estimates of reproductive life-history traits to be determined. Furthermore, data on men’s occupation allows for some variation in access to resources to be accounted (Karskela, 2001). We categorize each family as poor (e.g., farmless families and servants), middle-class (e.g., tenant farmers, smiths and sailors), or wealthy (e.g., priests, officers, farm-owners and shipmasters) (for details see Pettay, Helle, Jokela, & Lummaa, 2007).

The key defining characteristics of the population of Finland at this time may be described as: (1) low life expectancy at birth; (2) natural fertility; (3) relatively late age at first reproduction; and (4) strict social monogamy. A large proportion of deaths occurred due to infectious disease (Helle, Lummaa, & Jokela, 2004). Life expectancy at birth of the sample we used was 23 years±28 S.D. and, at adulthood (15 years), was 53 years±19 S.D. Comprehensive data on infanticide are unavailable, but there are only a few recorded incidences in the study parishes at this time (Lummaa, Pettay, & Russell, 2007), and there is no indication in our sample of an unusual bias in the sex ratio of reported births (50.7% male), so unreported infanticide is unlikely to be a confounder in this study. Among those individuals tracked for their entire potential reproductive life (up to 45 years of age in women, 50 years in men), the mean number of offspring delivered/sired was 4.1±3.5 S.D. (including only reproductive individuals 5.4±3.0 S.D.). However, because of the low child survival rate, the mean number of offspring raised to adulthood (15 years of age) was only 2.2±2.2 S.D. (including only reproductive individuals 2.9±2.2 S.D.). Median age at first reproduction was relatively late (Walker et al., 2006)—at 26.7 years in the case of men and 25.4 in the case of women. Mean reproductive lifespans for men and women were 12.9 years±6.9 S.D. and 12.5±6.1 S.D., respectively. Overall, 97% of reproductive individuals were married, and since divorce was forbidden, marriage to more than one partner was only possible in the event of spousal death. Although 100% genetic monogamy is improbable, levels of extrapair paternity (EPPs) are probably towards the lower end of the range of estimates for human populations (i.e., <3%), due to strict social sanctions governing extra-marital relations (Pettay, Kruuk, Jokela, & Lummaa, 2005). Moreover, EPPs are an unlikely source of confounding bias in the context of this study, since their occurrence would only introduce an extra source of variance into our estimates.

We initially followed the survival and reproductive events of 653 reproductive women (the P generation) from five farming/fishing parishes (Lummaa, Pettay & Russell, 2007; Pettay et al., 2007) born during the years 1709–1815. We also recorded the full life history data for their 4515 offspring born to them (F_1 generation) as well as the birth and subadult mortality of their 7846 grand-offspring (the F_2 generation). The focal generation of the present study, from which the above descriptive data are derived, is the F_1 generation. The statistical analyses used to address the three questions of this study are described below. All statistical analyses were conducted using SAS (SAS Institute, release 9.1, 2002-2003), using the GENMOD and MIXED functions in SAS (SAS, 1990). Mother's identity was fitted as a random term to account for the use of repeated offspring within families. Significance of two-tailed p values was taken at <.05, and Type III sums of squares were used.

2.1. Effect of elder sibling sex on life-history traits

Four underlying life-history traits are known to influence lifetime fecundity in our population: probability of reproducing, age at first reproduction, interbirth intervals, and reproductive lifespan. Consequently, we investigated whether individuals whose mother had previously produced a son versus a daughter experienced (1) reduced probability of reproducing, (2) increased age at first reproduction, (3) increased offspring interbirth intervals, and (4) reduced reproductive lifespan. Prior to analysis, we removed individuals from the full sample that did not meet the requirements needed to address the questions of this study. These were those who were firstborn to their mothers or who were twins or born directly after twins (n=1746), those for whom we lacked corresponding data on covariates and cofactors (see below for details, n=141), and those remaining individuals who did not survive to adulthood (n=975). Some of the analyses below required the use of one of two subsets of these remaining 1653 individuals. Analysis of the probability of reproduction used all 1653 individuals. Analysis for age at first reproduction was carried out on subset (a) which included all individuals who reproduced at least once (n=1067), while analyses of mean interbirth interval and reproductive lifespan were carried out on subset b (all those who reproduced at least twice, n=934).

In each analysis, prior to investigating the effect of the term of interest (i.e., elder sibling sex), we determined the importance of covariates and cofactors that were potentially associated with the response term and used these to produce a minimal model. These were social class (3-level factor), study parish (5-level factor), birth order when all born siblings considered (born birth order) and when only those siblings who survived to 15 years of age were considered (survived birth order), family size when all born siblings considered (born family size) and when only those siblings who survived to 15 years of age were considered (survived family size), birth cohort, the interval separating the birth of the focal individual and their elder sibling and the focal individual's own sex. Some additional terms, specific to individual models, were also fitted where necessary (see below). Statistics and significances are reported for each term when it was entered into a model with all other significant terms. Only terms that were significant at the p=.05 level under these conditions were retained in the minimal model. In the case of correlated terms (i.e., born birth order and survived birth order; born family size and survived family size), only the term with the lowest p value was included in the minimal model. Once our minimal model was obtained, we fitted our term of interest and checked all two-way interactions between our term of interest and all terms introduced to the model (irrespective of whether they were retained in the minimal model or not), but none was significant in any of the four analyses. Results are given in Table 2 for significance levels of four interactions between elder sibling sex and other fixed terms that are of particular interest (focal individual sex, social class, born birth order, survived birth order, and the death of an elder sibling prior before 6 months of age).

(1) The probability of reproducing at least once (0/1) was considered as a binary response term in a generalised linear mixed model with a logit link function and binomial denominator fixed at 1. We tested the influence of elder sibling sex on the probability of reproducing after controlling for additional terms (see above) for all available F_1 individuals (n=1653, delivered by 525 mothers, 1-9 offspring/mother). (2) Age at first reproduction was defined as the individual's age at the time of the birth of his or her first recorded offspring. This term was investigated as a continuous response term in a linear mixed effects model with normal error structure, after a logarithm transformation. We tested the influence of elder sibling sex on an individual's age at first reproduction in all F_1 individuals who reproduced at least once in their lives (subset a, n=1067, delivered by 452 mothers, 1-8 offspring/mother). (3) Mean interbirth interval was calculated for individuals by dividing reproductive lifespan (years between age at first and last reproduction) by the number of births attributed to them. Individuals included were those in subset b (i.e., those individuals who reproduced on at least two separate occasions, n=934, delivered by 438 P mothers, 1-8 offspring/mother). Again, a linear mixed effects model was conducted with normal error structures after logarithm transformation. In addition to fitting the potential confounders introduced above, we also fitted reproductive lifespan, since interbirth intervals tend to be longer in those individuals with long reproductive lifespan. (4) Reproductive lifespan is the number of years between first and last reproduction. A linear mixed effects model with normal error structures was conducted using data from subset (b). In addition to those terms introduced above, we fitted two further terms. These were whether or not an individual survived and was tracked to the end of their reproductive life

(45 years of age for women, 50 years for men) and their age at first reproduction, since individuals who begin reproducing late are more likely to have a short reproductive lifespan on average.

2.2. Elder sibling sex, life-history traits, and lifetime fecundity

While the results of the above analyses (see Section 2.1) will indicate the impact of elder sibling sex on the life history of a given offspring, they will not elucidate the relative importance of impacts on each trait for lifetime fecundity. For example, if elder sibling sex has the most significant effect on the least important life-history trait for lifetime fecundity, then effect sizes and statistical significances generated from analyses in Section 2.1 will alone, tell us little about the biological importance of a result. Yet, understanding the magnitude and relative importance of each elder sibling sex-effect for fecundity is essential to understanding the biological significance of the results generated from Section 2.1. Consequently, our aim here is to determine the biological importance (measured as life-time fecundity) of elder sibling sex effects on the four underlying life-history components above.

To this end, we (a) used the effect sizes (i.e., slopes) and standard errors of the effects of elder sibling sex on each life-history trait, generated from the four analyses above (Section 2.1, see Table 1), in conjunction with (b) effect sizes and standard errors of each life-history trait on lifetime fecundity. In the case of (b), we constructed a linear mixed effects model with normal error structures in which lifetime fecundity was fitted as the response term, three of the four (see below) life-history traits were fitted as fixed explanatory terms of interest and maternal identity was fitted as a random term. Effect sizes were generated, with parish and social class fitted as cofactors, for age at first reproduction, mean interbirth interval and reproductive lifespan; in the case of mean interbirth interval, age at first reproduction and reproductive lifespan were also fitted as covariates and in the case of reproductive lifespan, age at first reproduction, and mean interbirth interval were also fitted as covariates. We then calculated the magnitude of the elder-sibling sex effect on the three life history traits for lifetime fecundity. For example, in the case of age at first reproduction, being born after a male is associated with an increase in age of 0.55±0.24 (S.E.) years, and for every yearly increase in age at first reproduction, 0.16±0.016 (S.E.) fewer offspring will be produced. Hence, the elder sibling sex effect on lifetime fecundity arising through its effect on age at first reproduction equates to 0.55×0.16.

The one exception was for the probability of reproducing. In this case, meaningful effect sizes could not be generated on lifetime fecundity since those that do not breed have zero fecundity and those that do breed have nonzero fecundity, by definition. As a consequence, effect sizes would be essentially one and the error would be zero. Instead, we used the fact that those that did not breed would have had zero children while those that bred at least once were, on average, likely to produce the mean number for the populations (i.e., 5.1 offspring±0.089 S.E. in this subsample.). We then calculated lost fecundity due to being born after an elder brother versus elder sister multiplying 5.1 by the probability of reproducing after being born after an elder brother (0.62) and sister (0.67), respectively, and subtracting the two products.

2.3. Preceding vs. all elder sib effects on lifetime reproductive success

While Rickard, Russell and Lummaa (2007) concentrated solely on the influence of the sex of the preceding offspring on the reproductive success of the subsequent offspring, it is of course possible that previous siblings have a cumulative effect on the success of the younger offspring. Consequently, we investigated here whether the total number of elder male siblings was a greater predictor of Lifetime Reproductive Success (LRS) (number of offspring raised to 15 years of age) than the effect of the immediately preceding sibling being male. First, we restricted our data to those suitable for addressing this question. We removed individuals that were twins or of unknown sex as well as those who were born to a mother who had at some point previously produced either of these (*n*=1226 removed). We also removed first-borns and those that did either not survive to adulthood (15 years of age) or who were not tracked for their entire reproductive lives (*n*=2444 excluded). This resulted in a total sample of 845 F_1 offspring born to 365 mothers. For each individual we then counted both the number of preceding male siblings that were born (irrespective whether they died or survived) and that survived to adulthood (both born and survived to adulthood).

Table 1

Effect sizes±1 S.E. generated from (a) analyses conducted to determine elder sibling sex effects on underlying life-history traits (see Section 2.1, Table 2) and (b) analyses conducted to determine the effects of each life-history trait on lifetime fecundity (see Section 2.2)

	Elder sibling sex effect on life-history trait (reference elder sister)		Life-history trait effect on fecundity	
Trait	Effect	S.E.	Effect	S.E.
Probability of reproducing	−0.06	0.02		
Age at first reproduction	0.036	0.0038	0.16	0.016
Interbirth interval	0.12	0.016	0.31	0.0082
Reproductive lifespan	-0.052	0.0034	1.62	0.038

Note that effect sizes of probability of reproduction could not be generated in (b) because those that did not breed have zero fecundity and those that did have non-zero, by definition. Hence, the effect size of the probability of reproducing on lifetime fecundity is essentially one with no error.

LRS was then entered as the response term in a generalized linear model with a Poisson error structure and a log link function. Parish and social class were fitted as cofactors, and maternal identity was fitted as a random term to control for the use of multiple individual from the same family. Birth order (born or survived) in this sample was not itself associated with LRS and, so, was not entered into any final model. Our two explanatory terms were number of elder siblings of each sex and the sex of the previous sibling. If the elder sibling sex effect were cumulative, then after including both terms in a model predicting lifetime fecundity, we would expect number of elder male siblings to be significant and (immediately) elder sibling sex to become nonsignificant. Finally, two-way interactions between the explanatory terms and both focal individual sex and social class were checked for significance (see Introduction). We weighted the analysis by the proportion of offspring whose survivorship to 15 years of age was unknown to control for failure to follow some offspring to adulthood.

3. Results

3.1. *Effect of elder sibling sex on life-history traits*

First, approximately 65% of individuals who survived to adulthood produced at least one child. The probability of reproducing varied with parish and relatively fewer poor individuals reproduced than rich and middle-class individuals. The probability of reproducing also declined with increasing birth order (survived birth order effect stronger). After controlling for these associations, we found that individuals whose mother had previously produced a male versus a female >offspring experienced a significant five percentage-point reduction (67–62%) in the probability of reproducing (Table 2). We found no evidence to suggest that this result was modified by the sex of the focal individual, social class, or birth order. We did find a marginally significant interaction between elder sibling sex and death of the elder sibling during infancy, but the direction was not consistent with the confounding ‘social’ explanation (see Table 2 and Discussion).

Second, the median age at first reproduction was 26.8 years (range, 16.2–60.9) for men and 25.4 years (range, 16.0–50.2) for women. Age at first reproduction differed between parishes and varied among cohorts. In addition, women reproduced earlier than men, the rich reproduced earlier than the poor and middle-classes, those from smaller families reproduced earlier than those from larger families, and those of low birth order reproduced earlier than those of high birth orders. Finally, offspring born after a short birth interval reproduced later than those born after a longer birth interval. After controlling for these associations, we found that individuals whose mother had previously produced a male first reproduced 7 months later than individuals whose mother had previously produced a female offspring. This

Table 2
Statistical significance of predictor terms used to explain variance in life-history traits (Section 2.1)

	Response			
Predictor	Probability of reproducing	Age at first reproduction	Mean inter birth intervals	Reproductive lifespan
Social class	$\underline{\chi^2_2=21.74}$***	$\underline{F_{2,1051}=5.47}$**	$\underline{F_{2,919}=8.72}$***	$\underline{F_{2,914}=4.11}$*
Parish	$\underline{\chi^2_4=9.93}$*	$\underline{F_{4,422}=6.36}$***	$\underline{F_{4,391}=9.40}$**	$\underline{F_{4,359}=5.84}$**
Born birth order	$\chi^2_1=5.76$*	$F_{1,1055}=2.85$	$F_{1,923}=1.10$	$F_{1,922}=1.72$
Survived birth order	$\underline{\chi^2_1=10.70}$**	$\underline{F_{1,1051}=13.89}$**	$F_{1,923}=0.51$	$F_{1,921}=0.67$ cohort
Born family size	$\chi^2_1=0.14$	$F_{1,461}=0.29$	$F_{1,420}=2.02$	$F_{1,379}=1.57$
Survived family size	$\chi^2_1=0.28$	$F_{1,392}=10.63$**	$F_{1,368}=0.01$	$\underline{F_{1,325}=3.94}$*
Cohort	$\chi^2_1=0.02$	$\underline{F_{1,407}=6.35}$*	$F_{1,390}=1.01$	$F_{1,352}=0.01$
Mother’s preceding birth interval	$\chi^2_1=0.05$	$\underline{F_{1,1047}=10.54}$**	$F_{1,917}=0.11$	$F_{1,914}=3.50$
Own sex	$\chi^2_1=1.58$	$\underline{F_{1,1035}=29.64}$***	$\underline{F_{1,916}=4.25}$*	$\underline{F_{1,919}=19.30}$**
Elder sibling sex	**$\chi^2_1=5.10$, p=.024**	**$F_{1,1039}=3.76$, p=.053**	**$F_{1,917}=5.12$, p=.024**	**$F_{1,918}=0.21$, p=.65**
Elder sibling sex–social class	**$\chi^2_2=0.17$, p=.92**	**$F_{2,1033}=0.99$, p=.071**	**$F_{1,914}=1.03$, p=.36**	**$F_{1,915}=0.65$, p=.52**
Elder sibling sex–born birth order	**$\chi^2_1=0.22$, p=.64**	**$F_{1,1036}=0.13$, p=.72**	**$F_{1,911}=0.38$, p=.54**	**$F_{1,913}=0.95$, p=.33**
Elder sibling sex–survived birth order	**$\chi^2_1=0.50$, p=.48**	**$F_{1,1023}=0.06$, p=.81**	**$F_{1,898}=0.05$, p=.82**	**$F_{1,892}=0.43$, p=.51**
Elder sibling sex–own sex	**$\chi^2_1=0.25$, p=.62**	**$F_{1,1016}=2.65$, p=.10**	**$F_{1,898}=0.61$, p=.43**	**$F_{1,900}=1.09$, p=.30**
Elder sibling sex–elder sibling died before/after 6 months of age	**$\chi^2_1=2.98$, p=.084**	**$F_{1,1036}=0.00$, p=.95**	**$F_{1,909}=0.25$, p=.62**	**$F_{2,910}=0.68$, p=.41**

The table comprises of two sets of terms. The first set (normal font) is all those terms investigated as being potentially associated with variance in the response term but not actually of direct interest to the study. The statistics for these were obtained when each term was included in a model containing only other such terms that famsize were significant. Underlined terms are those that were included in the final models to which the terms of interest (see below) were added. Due to collinearity, not all significant terms were included in the final model (e.g., in the model predicting age at first reproduction, survived birth order was included in the final model, but born birth order was not). The second set of terms (bold font) is those that were under investigation in Section 2.1 of the present study. We produced separate models for each of these, containing statistically significant covariates and cofactors, the term of interest, lower-order terms from which two-way interactions were comprised (e.g., elder sibling sex and own sex in the case of the elder sibling sex–own sex interaction), and reported the exact significances observed. Models are Type III sums of square. F indicates F test (lower case refers to degrees of freedom).

* $p<.05$.

** $p<.01$.

*** $p<.0001$.

result was not modified by the sex of the subsequent offspring, birth order, or death of the elder sibling in infancy (Table 2). A nonsignificant trend suggest that it could be modified by social class (see Table 2 and Discussion).

Third, mean interbirth interval averaged 2.2 years (range, 0.52–9.8). Mean interbirth interval was found to vary according to parish and social class and was shorter in men than in women, presumably because they were able to remarry more rapidly after losing their spouse (3 months vs. 12 months). After controlling for these associations and for reproductive lifespan [$F_{(1,925)}$=480.28, p<.0001], we found that those whose mother had previously produced a son had an average birth interval between offspring that was 5 weeks longer than those whose mother had previously produced a daughter. This result was not modified by the sex of the subsequent offspring, social class, birth order, or elder sibling death in infancy (Table 2).

Fourth, reproductive lifespan averaged 12.8 years (range, 1.0–40.2 years). Reproductive lifespan differed between study parishes, was shorter in the poor than in the rich and middle class, was longer in those from larger families and was shorter for women than for men, presumably because men were more likely than women to remarry following the death of their spouse (unpublished results). After controlling for these effects and the additional significant confounder of age at first reproduction [$F_{(1,923)}$=166.72, p<.0001], we found that reproductive lifespan did not differ significantly between those born following a male versus a female sibling, nor did we find this result to be modified by the sex of the subsequent offspring, social class, birth order, or elder sibling death in infancy (Table 2).

3.2. Elder sibling sex, life-history traits, and lifetime fecundity

The sex of an individual's elder sibling had a significant effect on the probability that they would reproduce in adulthood, the age at which they first did so, and their mean interbirth intervals if they reproduced more than once (Table 2). Whether or not an individual reproduces in their lifetime will obviously have a fundamental effect on lifetime fecundity, but the actual effect size cannot be determined (see Methods). The standardised effects (i.e., effects derived from models after dividing all values of a trait by the mean value of that trait) of the other three traits on lifetime fecundity were 1.66±0.022 for reproductive lifespan (controlling for age at first reproduction and inter-birth interval), −1.13±0.03 for birth intervals (controlling for reproductive lifespan and age at first reproduction), and −1.35±0.13 for age at first reproduction. By using the formula [effect term A−effect term B/square root (S.E. term A+S.E. term B)] and comparing the resulting value against a t distribution with degrees of freedom generated from the mixed model using Satherthwaite's correction, we can estimate whether the effect sizes generated differ significantly from one another. Of the three traits, fecundity is significantly more influenced by reproductive lifespan than mean birth intervals (t_{487}=2.33, p=.02), but there was no difference in the effect sizes in the other comparisons (reproductive lifespan vs. age at first reproduction: t_{487}=0.79, p>.4; age at first reproduction vs. birth intervals: t_{487}=0.55, p>.5).

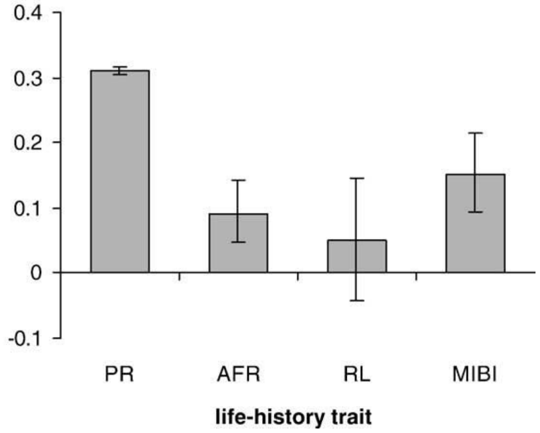

Fig. 1. Estimated reductions (means±S.E.) in fecundity associated with the effects of being born following an elder brother on key underlying life-history traits. PR, probability of reproducing; AFR, age at first reproduction; MIBI, mean interbirth interval; RL, reproductive lifespan.

Calculations revealed that fecundity was most compromised by the effects of elder sibling sex on the probability that the subsequent sibling would reproduce in their lifetimes (Fig. 1). We estimated that offspring born after an elder brother would produce on average 0.3 fewer offspring in their lifetimes as a consequence of reduced probability of reproducing. By contrast, elder sibling sex effects on age at first reproduction and birth intervals were half as important for fecundity: offspring born after a male sibling had 0.15 and 0.09 fewer offspring through increases to age at first reproduction and birth intervals, respectively. Finally, elder sibling sex effects on reproductive lifespan were insufficient to be associated with predictable changes to fecundity, mainly because of high variation in the elder sibling sex effect.

3.3. Preceding vs. all elder sib effects on lifetime reproductive success

As with our previous study (Rickard, Russell, & Lummaa, 2007), we found LRS (number of children raised to adulthood) to be higher in the rich and middle class than in the poor classes (χ^2_2=55.06, p<.0001) and to vary significantly between study parishes (χ^2_4=10.76, p=.029). After controlling for these effects, we found that the total number of elder brothers surviving was negatively associated with LRS in males only (interaction effect size −0.13±0.026, χ^2_1=5.09, p=.024). Despite this interaction, the effect of (the preceding) elder sibling sex on both males and females remained significant (χ^2_1=7.29, p=.0070). Importantly, the effect sizes of elder sibling sex on the success of (both male and female) younger offspring remained unchanged when the number of elder brothers was considered in the analysis (elder brother *own sex interaction included: 0.18±0.067; excluded: 0.17±0.063). This indicates that although the number of survived elder brothers has a negative impact on male lifetime reproductive success (as might be expected in a patrilineal society), this effect is separate from the effect of immediately elder sibling sex on the LRS of individuals of both sexes. Number of born elder brothers was not associated with LRS either overall (0.0016±0.95, χ^2_1=0.00, *p*=.95) or in males only (0.018±0.54, χ^2_1=1.34, *p*=.51), supporting the conclusion that the effect of the number of surviving elder brothers was caused by postbirth sibling competition for resources. Other interactions between number of born or survived elder brothers and sex or social class were all nonsignificant (all *p*>.05).

4. Discussion

In humans, variation in individual development is associated with the sex and age of siblings. Such patterns can often be explained by inheritance practices or bias in the economic value of the two sexes causing parental investment to vary with sex and birth order of children. However, evidence from studies of wild animals as well as studies of human birthweight suggest there may also be a higher physiological cost of producing sons versus daughters (Rickard, Russell, & Lummaa, 2007). In previous articles, we showed that individuals born to mothers who had previously produced a son had reduced size both at birth and in adulthood (Rickard 2008) and lower lifetime fecundity and reproductive success (Rickard, Russell, & Lummaa, 2007) than those born to mothers who had previously produced a daughter. In the present study, we showed that three out of four fecundity-associated life-history traits investigated were associated with elder sibling sex (probability of reproducing, age at first reproduction, mean interbirth intervals, but not reproductive lifespan) and that of these three potential mediators of reduced lifetime fecundity, it was the reduction in the probability of reproducing that most accounted for the lower lifetime fecundity in those born after an elder male sibling. Finally, we showed that the influence of elder brothers born on reproductive success was not itself cumulative, although the number of surviving elder brothers was negatively associated with reproductive success in males only, an effect which occurred independently of our main effect of interest.

The present study supports our hypothesis that there is a biological effect of the sex of a mother's previous offspring on her subsequent child, not contingent on any social factors that vary within this population. Our tests of confounding interactions showed our results to be consistent (Table 2). The effect of being born after an elder brother per se was not generally worse for males, those in the higher social classes, those of low birth order, or those whose elder sibling survived beyond infancy. There was a nonsignificant tendency for those in the rich social class to suffer the greatest delay in age at first reproduction as a result of elder sibling sex [*F*(2,1033)=0.99, *p*=.070], an effect which could be attributed to higher investment in elder sons in landowners, but this was not the primary route through which elder sibling sex influenced fecundity (Fig. 1). Another nonsignificant interaction showed that the effect of being born following a male versus a female on reducing probability of reproducing actually tended to be greater when that elder sibling died in infancy (χ^2_1=2.98, *p*=.084). This may be due to phenotypic differences in the offspring of mothers whose offspring died versus those whose offspring lived (although we controlled for between-family variation by including a random term in each model for mother's identity); in any event the direction of the relationship does not support the 'social' explanation, since the elder sibling sex effect is clearly present in those whose sibling died at a young age. Finally, although elder brothers do, if they survive, appear to have a detrimental effect on the reproductive success of younger male siblings, the elder sibling sex effect of principle interest to this study occurs in addition to this social effect and is not confounded by it.

Due to sample size restrictions, we cannot completely eliminate the possibility that elder sons received preferential investment in the first few months of postnatal life. However, we consider it unlikely that variation in preferential parental investment in such a short period of parental care could be responsible for the patterns observed; 47% of deaths categorised as being before 6 months of age actually took place before one month of age, and 75% before 3 months. If we extend the period of potential variation in preferential parental investment back to the period of in utero development, then there is a greater potential for variation in parental (maternal) strategy to influence development of elder siblings. However, we consider such an explanation unlikely. In the absence of any significant modifier of the main relationship, the most parsimonious explanation for it is a relatively fixed higher cost of producing sons.

A possible reason for the higher cost of a mother producing a son versus a daughter is the long-term consequences incurred by direct physiological interaction between a mother and her unborn male offspring. One possibility is hormonal interaction. It is well established that hormones can be transmitted across amniotic fluid and foetal membranes (Ryan & Vandenbergh, 2002; Uller, 2006). We have previously shown that female twins who share the womb with a male cotwin have lower probability of marrying, reduced fecundity and reduced lifetime reproductive success than those whose cotwin was female (Lummaa, Pettay, & Russell, 2007), one plausible explanation for which is a masculinising effect of male foetal testosterone on the developing female cotwin. It is also possible that male foetal testosterone may enter the maternal bloodstream (Meulenberg & Hofman, 1991) and, through compromised immunity (Klein, 2000), initiate a chain of events that impact the mother's ability to provision her next offspring. One possible explanation for the negative effects of elder brothers on birthweight is maternal immune responses to male-specific minor histocompatibility antigens. However, the evidence supporting this hypothesis involves a cumulative effect of elder brothers on subsequent offspring (Blanchard & Ellis, 2001; Côté, Blanchard & Lalumière, 2003; Nielsen et al., 2008), whereas our 'biological' effect was not shown to be cumulative. Distinguishing between the possible explanations would ideally require prospective studies so that maternal physiological states can be measured before and after producing an offspring of either sex.

Regardless of how the cost of being born following an elder brother is manifested, we found that, by far, the most important route through which elder sibling sex affected lifetime fecundity was through reducing the probability of reproducing (i.e., being recruited into the breeding population). Considering the different determinants of reproductive success of men and women, it is interesting that both should be affected in the same way. Taking figures from the raw data, 68% of men born after an elder female sibling reproduced, whereas 64% of those born following an elder male sibling did. In women, the figures from the raw data are 66% versus 60%, respectively (note that the numbers appear low because the sample includes all individuals who survived to adulthood, regardless of whether they died before reaching, or were not successfully followed to, the end of their potential reproductive life). The percentage point reduction in the probability of reproducing for men and women are thus 6% and 4% respectively, but in the final model, the interaction between elder sibling sex and the sex of the focal individual was not significant (χ^2_1=0.34, p=.55). We investigated the nature of the relationship between elder sibling sex and the probability of reproducing further by (i) adding to the final model the age to which it was known the individual in question survived and (ii) considering only those individuals in the data who married and thus had the opportunity to legitimately reproduce (n=1170). Interestingly, (i) the relationship remained unchanged when we added known lifespan to the model, indicating that elder sibling sex did not influence probability of reproducing through influencing adult survival or follow-up attrition and (ii) elder sibling sex was marginally significantly associated with probability of reproducing even when considering only those who married (χ^2_1=3.45, p=.063, other significant terms in model: parish, own sex), suggesting that both men and women born after a male elder sibling on average experienced some subfecundity. Probability of marriage itself was not influenced by elder sibling sex (χ^2_1=1.00, p=.32 after controlling for survived birth order), so difference in the opportunity of reproducing is unlikely to be part of the mechanism responsible for the elder brother effect. The fact that men and women have a similarly reduced probability of reproducing when their elder sibling was male suggests that the cost of being born after an elder brother may have consequences spread across a variety of physiological systems, affecting overall adult quality of both men and women.

It would be interesting if other studies were carried out on populations of humans and wild animals to determine the repeatability/variability of our findings. This could be carried out on demographic and epidemiological datasets containing data on (a) sibling order and sex as well as (b) some measure of reproductive ability. The potential existence in mammals of a cost of producing sons manifest in the adulthood of subsequent offspring may be of widespread significance to different areas of ecology. It has possible implications for our understandings of population sex ratios, reproductive costs, sibling conflict, and the long-term consequences of early conditions in both humans and other species.

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