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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