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Offspring are lighter at birth and smaller in adulthood when born after a brother versus a sister in humans☆

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Abstract

In mammals, including humans, it is more costly to produce sons than it is to produce daughters, with maternal survival and subsequent reproductive success diminished more by producing male over female offspring. It is therefore predicted that offspring who are produced by mothers who have previously produced sons versus daughters will be compromised by the relatively high cost their mother incurred in the previous reproductive episode. Such effects are potentially important because characters that determine offspring survival and fecundity ultimately contribute to maternal fitness. Using questionnaire-based data from a contemporary human population, I show that birthweight (irrespective of their sex) is lower in individuals born after an elder brother than in those born after an elder sister. In addition, I show that both men and women who were born after a male versus a female sibling have reduced adulthood height, a known correlate of reproductive success in both sexes. The results suggest that producing sons may have a negative effect on the fitness of subsequent offspring, which has implications for calculations of maternal fitness and for optimal sex allocation.

Keywords: Evolutionary ecology; Early development; Cost of reproduction; Sex allocation; Birthweight; Anthropomorphics; Trivers–Willard hypothesis

1. Introduction

Reproduction carries physiological costs that can compromise an individual's ability to survive and invest in other progeny (Stearns, 1992). These costs, demonstrated in a wide range of taxa, are often manifested in the reproducing individual as compromised subsequent survival (Tavecchia et al., 2005) or subsequent reproductive success (Clutton-Brock, Guinness, & Albon, 1983). Alternatively, costs may impact the offspring of the breeding individual; for example, birds reared in artificially enlarged broods may gain less weight before fledging or suffer extra mortality risks (VanderWerf, 1992).

Reproductive costs increase not only as a function of the number of offspring produced in a given attempt but also as a function of offspring sex or sex ratio. Specifically, in mammals, there is a body of evidence showing that producing a son versus producing a daughter can reduce the survival probability of mothers (Gomendio, Clutton-Brock, Albon, Guinness, & Simpson, 1990), as well as their ability to invest in a following reproductive attempt (Bérubé, Bianchet, & Jorgenson, 1996; Clutton-Brock, Albon, & Guinness, 1981; Hogg, Hass, & Jenni, 1992). In addition, mothers may provide more nutritionally valuable milk for their sons (Landete-Castillejos, García, López-Serrano, & Gallego, 2004) and experience higher parasitic load (Festa-Bianchet, 1989) and lower postpartum weight accumulation (Birgersson, 1998) after weaning sons.

Evidence that producing sons is more costly than producing daughters for mothers extends to humans. Male infants have a faster rate of prenatal growth (Maršál et al., 1996) and are heavier at birth (Anderson & Brown, 1943); in addition, pregnant women carrying a male fetus have been shown to have a higher energy intake rate than those carrying a female fetus (Tamimi et al., 2003). Producing sons may also have more long-term consequences: In preindustrial Finland, the number of sons born was associated negatively

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with maternal life span (Helle, Lummaa, & Jokela, 2002); in poor women, it was associated positively with the risk of dying from infectious disease (Helle et al., unpublished data). However, the consequences of producing sons for mothers' ability to invest in future offspring and thus for the quality of the future offspring have been little considered, despite the fact that this would have implications for total maternal fitness (for recent exception, see Rickard, Russell, Lummaa, 2007). Nonetheless, there is some suggestion of an intergenerational cost of producing sons in studies of bighorn sheep *Ovis canadensis* (Bérubé et al., 1996) and humans (Blanchard & Ellis, 2001; Côté, Blanchard, & Lalumière, 2003; Magnus, Berg, & Bjerkedal, 1985; Nielsen et al., 2008; Trotnow, Bregulla, & Flügel, 1976): The offspring of mothers who had produced a son in the previous reproductive event may be lighter at birth than those of mothers who had produced a daughter in the previous reproductive event.

The association between previous investment in a son and lower birthweight of the subsequent offspring suggests that there may be long-term fitness consequences of producing a son, not only for the mother but also for her subsequent offspring. For instance, in addition to being a strong predictor of infant mortality risk (Karn & Penrose, 1952), low birthweight is associated with impaired cognitive development (Matte, Bresnahan, Begg, & Susser, 2001), risk of developing several diseases in adulthood (Barker, 1998), and adulthood stature (Eide et al., 2005; Gigante, Horta, Lima, Barros, & Victora, 2006; Li, Stein, Barnhart, Ramakrishnan, & Martorell, 2003; Sørensen et al., 1999), Such long-term associations between birthweight and adult phenotype raise the possibility that the early environment influences reproductive success in humans. For example, taller men tend to father more offspring (Mueller & Mazur, 2001; Pawlowski, Dunbar, & Lipowicz, 2000), and taller women may achieve greater reproductive success through lower infant mortality of offspring (Sear, Allal, & Mace, 2004). Indeed, birthweight itself has been shown to predict probability of marriage in men in two populations (Phillips et al., 2001; Vågerö & Modin, 2002).

The aim of this study was twofold. First, I investigated in a sample of cross-sectional data collected from university staff and students whether individuals born to mothers who previously produced sons are lighter at birth than those born to mothers who previously produced daughters. Second, I tested the prediction that lower birthweight in those with elder brothers versus those with elder sisters is reflected in the long term (i.e., adulthood) by reduced height and weight.

2. Methods

To investigate whether the sex of previous offspring was associated with the birthweight and adult morphometrics of subsequent offspring, I distributed a questionnaire to staff and students of the University of Glasgow who were not the firstborn in their family. Seventy-nine completed questionnaires were returned anonymously and included in the following analyses. The questionnaire requested data on both the respondents and their immediately older full sibling. Data requested included the following: individual's sex; sex of the elder sibling; birth order (i.e., the birth position of the respondent); birth interval (i.e., the number of months between the birth of the individual and that of his or her immediately older sibling); individual's birthweight and birthweight of the elder sibling (both through maternal recall, shown to be reliable elsewhere; Walton et al., 2004); and current (i.e., adult) age and morphometrics, including height and weight. All individuals were older than 17 years and were deemed fully adult (mean±S.E. age=23.64±0.76 years).

The predictors of birthweight, final height, and final weight were analyzed in three general linear models using the SAS (1990) statistical package. Whether or not individuals were born after a brother or after a sister was added as the primary fixed effect of interest in each of the three analyses. Birth order (range=2–8; mode=2) and birth interval (range=1–13 years; mean=3.5±2.2 years) were included as covariates in each of the three analyses, whereas each individual's sex was included as a cofactor. Current age was included as a covariate in the adult weight and height models (range=18–55 years; mean=24±0.8 years). Models were built with confounding terms entered first (and retained if significant) and the term of interest added last. All two-way interactions between the sex of the previous sibling and the above covariates/factors were considered, but none was significant. Residuals of all models were normally

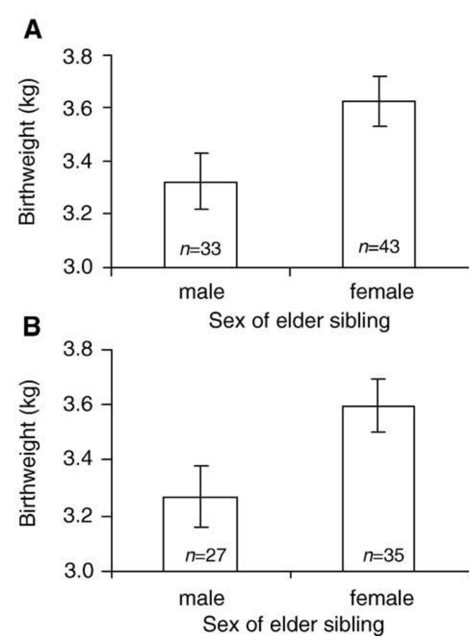

Fig. 1. Offspring birthweight (in kilograms) was lower if the elder sibling was male (A), and this remained the case even after controlling for the birthweight of the elder sibling (B). Graphs show predicted mean±1S.E. values.

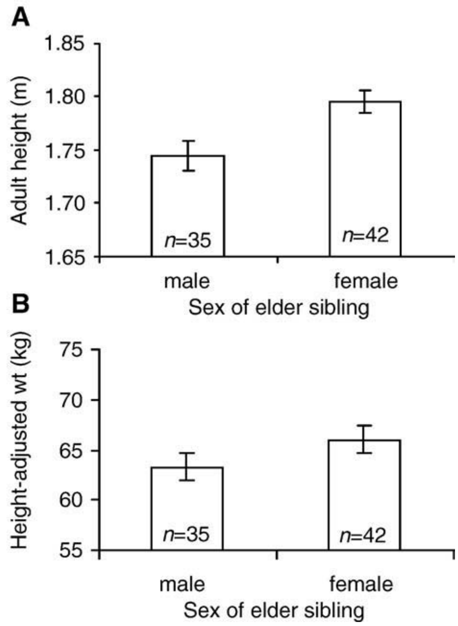

Fig. 2. Offspring born after an elder brother were (A) shorter in adulthood, even after controlling for own sex and number of elder siblings (birth order), but not (B) lighter after further controlling for these differences in height. Graphs show predicted means±1S.E. values.

distributed, and variances were homogenous (Levene's test, all $p>.05$). The sample size in each model varied slightly from 79 owing to incomplete questionnaires.

3. Results

3.1. Birthweight

Birthweight varied from 2.13 to 4.80 kg (mean±S.E.= 3.54±0.65 kg). It was not significantly associated with each respondent's birth order ($F_{1,75}$=1.02, p=.32), birth interval ($F_{1,73}$=0.55, p=.46), and sex ($F_{1,75}$=0.39, p=.53). However, it was significantly associated with the sex of a respondent's elder sibling ($F_{1,74}$=4.44, p=.039) (Fig. 1A), with those born after a brother being 9% lighter at birth than those born after a sister.

3.2. Long-term effects

Adult height varied from 1.52 to 1.93 m (mean±S.E.= 1.70±0.011 m). Men were significantly taller than women ($F_{1,76}$=51.92, p<.0001). Adult height was unaffected by birth order ($F_{1,74}$=3.66, p=.06), birth interval ($F_{1,72}$=0.11, p=.74), and current age ($F_{1,73}$=0.89, p=.35). After controlling for the above effects of own sex, I found that the height of respondents was significantly associated with the sex of their older sibling ($F_{1,74}$=4.48, p=.038) (Fig. 2A), with those born after a brother being 2.4% shorter than those born after a sister.

Adult weight varied from 41 to 100 kg (mean±S.E.=63.27± 1.26 kg). Men were significantly heavier than women ($F_{1,76}$=42.95, p<.0001), but adult weight was not associated with birth order ($F_{1,75}$=1.25, p=.27), birth interval ($F_{1,72}$=0.03, p=.86), and current age ($F_{1,73}$=0.52, p=.47). After controlling for the significant difference between men and women, I found that the weight of respondents in adulthood was significantly associated with the sex of their older sibling ($F_{1,74}$=5.35, p=.024), with those born after a brother being 7% lighter than those born after a sister. However, this effect disappeared after controlling for their adult height (Fig. 2B), suggesting that elder sibling sex-mediated differences in weight were simply caused by elder sibling sex-mediated differences in height (see above).

4. Discussion

In many mammal species, producing a son carries greater reproductive costs to the mother than producing a daughter, and these costs may also be incurred by the next offspring she produces. In the present study on contemporary humans, elder sibling sex was associated with a significant difference in the birthweight and final height of the focal individual: Those born after an elder brother were lighter at birth and shorter in adulthood than those born after an elder sister. These results corroborate findings of earlier studies on humans suggesting that producing a son reduces the birthweight of subsequent offspring (Blanchard & Ellis, 2001; Côté et al., 2003; Magnus et al., 1985; Nielsen et al., 2008; Trotnow et al., 1976), but this study is the first to show evidence that elder sibling sex may also have direct consequences for adult stature. There are at least four potential explanations for this result.

First, it is possible that elder sibling sex is not independent with respect to younger sibling birthweight and adult size. If this were the case, then elder sibling sex would not be the cause of any change in younger sibling birthweight, because they both would be consequences of a third factor. Specifically, it has been hypothesized that maternal condition may influence the likelihood of producing male versus female offspring, with mothers in relatively good physiological condition being more likely to produce sons (Trivers & Willard, 1973). Such an association might be expected to result in those with elder male siblings being heavier at birth (and possibly smaller or lighter as adults), a result opposite to that obtained here. More generally, if offspring sex ratio were not independent with respect to the outcomes and acting as a confounder in the present study, then individuals from brother–brother dyads would be the largest/heaviest and those from sister–sister dyads would be the smallest/lightest. However, this was not the case (see Results), and it is therefore reasonable to conclude that non-independence of elder sibling sex is unlikely to be behind the relationships I observed.

Second, if in our evolutionary past the contribution of sons to maternal fitness has varied in accordance with birth order (as might be the case under the primogeniture inheritance system), then mothers might have been selected to bias investment specifically toward their firstborn sons away from subsequent offspring. This idea generates at least two predictions: (1) mothers should have longer birth intervals after firstborn sons than after second-born sons, assuming birth intervals reflect mothers' propensity to bias care toward offspring, and (2) offspring born after the firstborn son should be lighter than those born after later-born sons. I found no evidence for either prediction. Birth intervals did not tend to be longer after firstborn sons than other offspring (general linear model; $F_{1,73}$=0.39, p=.53); neither were offspring from the same family lighter if they had one versus two elder brothers (Wilcoxon matched-pairs test=2, n=6, p=.69), although the sample used to test this was small.

Third, a greater investment made in producing and/or rearing any son (irrespective of whether firstborn or not, see above) might lead to a reduction in maternal resources available for subsequent offspring (Fessler, Navarrete, Hopkins, & Izard, 2005). This idea leads to at least two predictions: (1) subsequent offspring should be lighter after the birth of a heavy elder sibling irrespective of that sibling's sex and (2) increased birth intervals between consecutive offspring should ameliorate the negative effect of having an older brother on the birthweight of the second child. In contrast, the negative effect of an elder brother on a younger sibling's birthweight remains significant, even after controlling for the birthweight of the elder child ($F_{1,59}$=4.97, p=.03) (Fig. 1B), showing that the apparent additional cost to the mothers of producing sons was unlikely to be simply accounted for by the extra prenatal investment in resources for their growth. In addition, I found that the effect of elder sibling sex was not modified by the length of the birth interval preceding the birth of the focal individual (see Results), indicating that mothers were not able to "recover" from any additional demand of previously producing a son versus previously producing a daughter. These results suggest that the observed effects may not simply be consequences of increased macronutrients supplied to male versus female offspring, although this may be because the sample used was small and comprised a limited part of the maternal age/condition continuum (see Methods).

Finally, it is possible that producing a male versus a female offspring may interact with the mother via unexplored physiological mechanisms. For example, hormone profiles that are known to differ in fetuses according to sex (Clark, Crews, & Galef, 1991) may be reflected in the pattern of hormone diffusion across fetal membranes and amniotic fluid. In particular, testosterone produced by a male fetus can enter the maternal bloodstream, leading to elevated levels in the mother (Meulenberg & Hofman, 1991). This may interfere directly with the mother's ability to provide for future offspring by compromising her immunocompetence and increasing her susceptibility to costly disease (Klein, 2000), which in turn could reduce her ability to invest in subsequent offspring.

Further work is required to elucidate the exact route through which these effects might arise. Irrespective of the mechanism, clearly, over evolutionary time, sons must, at least on average, compensate for any cost they may have on their mother's inclusive fitness. However, whether they are also able to compensate for any reduction in the total fitness of their younger sibling is unclear. An individual's early rearing environment is known to have profound effects on future success and survival (Lummaa & Clutton-Brock, 2002). That I found sex of the elder sibling to influence the birthweight and adult size of the subsequent sibling suggests that offspring born after an elder brother might pay a fitness cost (Rickard, Russell, & Lummaa, et al., 2007). For example, birthweight is a strong predictor of viability (Karn & Penrose, 1952) and the long-term risk for illness (Barker, 1998), and both birthweight and final height have been shown to have positive effects on reproductive success (Mueller & Mazur, 2001; Pawlowski et al., 2000; Phillips et al., 2001; Sear et al., 2004).

As a consequence, the results of this study also have potential implications for epidemiologists. Human morphometrics (anthropomorphics) and growth rates are often invoked as risk factors for the development of disease in adulthood (Barker, 1998). The potential of the sex of an elder sibling to capture variation in this parameter is therefore of relevance to long-term studies that use measures of neonatal size and adult stature in this way. In addition, because of this broad association of variation in anthropomorphics with that in disease risk, there exists the potential that an individual's mother's reproductive history may have a direct influence on one's own physiological development. For this reason particularly, the mechanisms responsible for the intergenerational cost of sons observed here and elsewhere (Blanchard & Ellis, 2001; Côté et al., 2003; Magnus et al., 1985; Nielsen et al., 2008; Rickard, Russell, & Lummaa, 2007; Trotnow et al., 1976) warrant further attention.

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