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Reproductive investment in pre-industrial humans: the consequences of offspring number, gender and survival

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The number and gender of offspring produced in a current reproductive event can affect a mother's future reproductive investment and success. I studied the subsequent reproductive outcome of pre-industrial (1752–1850) Finnish mothers producing twins versus singletons of differing gender. I predicted that giving birth to and raising twins instead of singletons, and males instead of females, would incur a greater reproductive effort and, hence, lead to larger future reproductive costs for mothers. I compared the mothers' likelihood of reproducing again in the future, their time to next reproduction and the gender and survival of their next offspring. I found that mothers who produced twins were more likely to stop breeding or breed unsuccessfully in the future as compared with women of a similar age and reproductive history who produced a same-gender singleton child. As predicted, the survival and gender of the offspring produced modified the costs of reproduction for the mothers. Giving birth to and raising males generally appeared to be the most expensive strategy, but this effect was only detected in mothers who produced twins and, thus, suffering from higher overall costs of reproduction.

Keywords: birth interval; cost of reproduction; litter size; sex allocation; twinning; trade-off

1. INTRODUCTION

An iteroparous mother must trade current with future reproductive investment in order to maximize her lifetime reproductive success (Stearns 1992; Kaplan 1996; Hill & Kaplan 1999). Current investment varies with the number of offspring born and, if the costs of producing males and females differ, with the sex ratio of those offspring (reviewed in Charnov 1982; Clutton-Brock 1991). In sexually size-dimorphic species, the number and gender of offspring in a current litter are therefore predicted to modify the future investment, reproductive success and survival of the mother.

Studies of sexually dimorphic mammals provide support for the idea that litters of different sizes and sex ratios can entail differential costs to the mother. Females commonly show longer birth intervals (Lee & Moss 1986; Boesch 1997; Cameron & Linklater 2000) and reduced subsequent litter sizes (Clark *et al.* 1990) after producing offspring of the more expensive gender. For example, red deer (*Cervus elaphus*) mothers that had previously reared a male calf were more likely to die during the following winter and, if they survived, less likely to produce a calf during the following season compared with mothers that reared females (Clutton-Brock *et al.* 1983). The survivorship of the offspring produced can further modify the costs of current reproduction. In red deer, those females that successfully raised a calf during the previous season had the lowest survival, fecundity and body condition in the next year compared with those that either did not reproduce or lost their offspring soon after birth (Clutton-Brock *et al.* 1989). Here, I investigate the consequences of litter size and sex ratio for future reproductive outcome in humans (*Homo sapiens*) living under pre-industrial conditions.

Humans are a modestly sexually size-dimorphic species in which 0.6–4.5% of all births (depending on the population) produce twins, who are usually born smaller than singletons (Bulmer 1970; Vogel & Motulsky 1986). Both twin and singleton females have slower intrauterine growth rates (Parker *et al.* 1984; Marsál *et al.* 1996) and smaller birth weights than twin and singleton males (Hoffman *et al.* 1974). Mortality and morbidity following birth are usually male-biased and the foetal growth of males is more retarded than that of females under stressful conditions (reviewed in Stinson 1985; Wells 2000). Hence, the costs of producing offspring appear to be gender-specific in humans and males tend to be the more expensive gender to produce.

The aim of this study is to examine the consequences of producing broods of different size and gender combinations in a current reproductive attempt for the future reproductive outcome of pre-industrial Finnish mothers (1752–1850). I investigate these costs in terms of a mother's time to next reproduction, the probability of her rebreeding and the gender and survival of her future offspring, whilst controlling for maternal age and previous reproductive history. I predict that producing and raising twins instead of singletons and males instead of females will require higher reproductive efforts at greater subsequent cost to the future reproduction of the mothers.

2. MATERIAL AND METHODS

(a) *Data and study populations*

The costs of raising broods of different size and gender combinations in pre-industrial humans were studied using unique Finnish population registers. The Lutheran Church has kept census, birth/baptism, marriage and death/burial registers

of each parish in the country since the seventeenth century (Luther 1993), which cover the whole population of Finland from 1749 onwards. By using these registers it is possible to follow the reproductive and marital details of each individual from birth to death, as the whole population practised the Lutheran religion and everybody who died (in most cases even including stillborn babies and infants who died before baptism) was buried in a cemetery and recorded in the book of deaths (Gille 1949).

The data were collected using church records from five rural parishes: three archipelagie (Hiittinen 60° N, 22°30′ E, Kustavi 60°30′ N, 21°30′ E and Rymättyla 60°15′ N, 22° E) and two mainland (Ikaalinen 61°45′ N, 23° E and Pulkkila 64°15′ N, 26° E) over the period 1752–1850 (see Lummaa *et al.* (1998*a*, 2001) for details). The study era ended before industrialism, more liberal economics and improvements in health care were likely to have had significant effects on survivorship and the standard of living in Finland, and before any of the modern birth-control methods were available for limiting fertility. The study populations often lived under food-restricted conditions, as famines were common throughout the study period and, even during normal harvest years, 5–10% of people consumed emergency foods (Jutikkala *et al.* 1980). Mortality was seasonal (see Lummaa *et al.* 1998*b*), with 29% of female singletons and 34% of male singletons dying before adulthood in the study populations (the corresponding figures for twins are 59 and 72%, respectively).

Details of all mothers who had delivered twins in the study parishes during the period 1752–1850 were obtained from the parish church registers. If the same mother had produced more than one set of twins then one of her twin deliveries was randomly chosen for further analysis. The analysis was further restricted to those women who were in permanent marriages when they delivered their twins and their subsequent offspring. I followed 242 mothers who produced twins from the birth of their twins through to the birth of their subsequent child (174 mothers) or until they were 50 years old and known to have ceased reproducing (68 mothers). Of the 242 mothers of twins, 61 gave birth to male–male twins, 108 to male–female twins and 73 to female–female twins. I recorded the survival of the mothers' twin offspring, the birth interval to their next delivery and the gender and survival of their next child. The survival of male–male twins during the study period was lower on average than the survival of female–female twins (Lummaa *et al.* 2001). Based on estimates of monozygotic and dizygotic twinning rates calculated from the ratio between same- and opposite-gender twins being born (Weinberg's rule) (see e.g. Bulmer 1970), the vast majority of the twins in the sample were likely to be dizygotic (the estimated dizygotic and monozygotic twinning rates in the Finnish archipelago during 1653–1949 were 16.4‰ and 2.8‰, respectively) (Eriksson 1973).

Each twin mother was paired with one or two mothers of singletons (depending on whether a gender-matching control singleton baby was found for both of the twins). Each singleton mother ($n = 354$) gave birth to a baby of the same gender and at the same time (± 3 weeks) as the twin mother, was of the same parity and age (± 3 years) and only delivered singletons during her lifetime. The reproduction of these singleton mothers and the survival of their offspring were then similarly followed as for twin mothers. Both mother types subsequently produced singletons in their next delivery (if rebreeding) and did not differ in their age or previous investment. Twin mothers were 33.7 ± 0.37 years old and had given birth to 3.0 ± 0.14 previous children, whilst singleton mothers were 33.7 ± 0.29 years old and had

3.2 ± 0.29 previous children. Mothers producing offspring of opposite genders did not differ in their age (twins, $F_{2,239} = 1.15$ and $p = 0.32$ and singletons, $F_{1,352} = 0.83$ and $p = 0.36$) or number of previous children (twins, $F_{2,238} = 0.18$ and $p = 0.84$ and singletons, $F_{1,349} = 0.04$ and $p = 0.85$).

(b) *Statistical analysis*

(i) *Time to next reproduction*

Since the possible numbers of survivors as well as the possible gender combination of a delivery differed between twin and singleton births, the factors affecting the time to next birth after producing twins or singletons (in mothers who subsequently rebred) were analysed separately. Differences in the time to next delivery between mothers with different twin gender combinations (male–male/male–female/female–female) and between mothers raising zero, one or two of these offspring to adulthood (15 years) were contrasted using two-way parametric ANOVAs (the general linear model procedure of the SAS Institute Inc. (1990)). The gender combination and survival of the twins and their interaction were entered into the analyses as fixed terms. After logarithmic transformation of the time to next delivery, the residuals of the ANOVA models were normally distributed and the variances were homogeneous (Levene's test, $p > 0.05$). Similarly, the interbirth interval for singleton mothers was examined by entering the gender and survival (survived/died) of the child and their interaction in the model as fixed terms. Maternal age, previous number of offspring, year and month of delivery, gender of the next delivery and resident parish were fitted in each model and included in the final model if significant in order to control for potentially confounding variables. An ANOVA approach was preferred here to hazard analysis because the birth data were complete (all mothers followed until menopause) and for some mothers the event (next reproductive attempt) never happened. Therefore, the probability that mothers did not reproduce again was analysed in a separate model from the time to next reproduction.

(ii) *Probability of rebreeding and gender and survival of the next offspring*

The factors affecting a mother's likelihood of ever rebreeding and the gender (male/female) and survival (survived/died) of her next offspring were modelled by logistic regression analysis with a binomial error structure and logit link function (MINITAB 12.1, Minitab Inc., State College, PA, USA). In order to simplify the models in these analyses, mixed-gender twin births were excluded and the number of survivors from each twin delivery was categorized in order to contrast those births that did not produce any survivors with those producing at least one survivor. This was feasible because there appeared to be no contrasting differences between these categories (data not shown). The response variables (the probability of rebreeding and the gender and survival of the next offspring) were modelled in terms of the number of offspring previously produced (twins/singleton), their gender (male(s)/female(s)) and survival (0/1+ survived) and, if significant, their interactions. Maternal age, total number of previous offspring, year and month of delivery, birth interval, gender of the next delivery and resident parish were included in the final models if applicable and significant in order to control for potentially confounding effects.

All tests are two-tailed with means ± 1 standard error recorded.

Table 1. The role of the number, gender and survival of previously produced offspring in explaining a mother's time to next reproduction and probability of rebreeding, and the gender and survival of her next offspring.

(The sample sizes in parentheses refer to the numbers of mothers in each analysis. Only significant or marginally significant ($p < 0.1$) covariates that were controlled for are presented here. See § 2 for the other (non-significant) variables and interactions between the three main effects tested that were removed from the final models. The F-value refers to the time to next reproduction and the z-value refers to the probability of rebreeding and the gender and survival of the next offspring.)

maternal reproductive trait	F/z	d.f.	p
time to next reproduction after twins ($n = 174$)			
gender of previous offspring	1.64	2	0.20
survival of previous offspring	6.97	2	0.0012
gender × survival	3.62	4	0.0075
age of mother	9.04	1	0.0031
time to next reproduction after singletons ($n = 286$)			
gender of previous offspring	0.33	1	0.56
survival of previous offspring	12.47	1	0.0005
age of mother	6.82	1	0.0095
birth year of previous offspring	4.53	1	0.034
probability of rebreeding ($n = 484$)			
number of offspring in previous delivery	2.35	1	0.019
gender of previous offspring	0.91	1	0.36
survival of previous offspring	0.97	1	0.33
number × survival	−2.28	2	0.023
survival × gender	−1.02	2	0.31
number × gender	−1.76	2	0.078
number × survival × gender	2.06	4	0.040
age of mother	6.47	1	0.000
total number of previous offspring (corrected for maternal age)	−2.80	1	0.005
gender of next offspring ($n = 381$)			
number of offspring in previous delivery	−0.34	1	0.74
gender of previous offspring	1.69	1	0.092
survival of previous offspring	0.93	1	0.35
number × gender	−2.57	2	0.010
number × survival	1.84	2	0.065
survival of next offspring ($n = 380$)			
number of offspring in previous delivery	−2.91	1	0.004
gender of previous offspring	−0.77	1	0.44
survival of previous offspring	1.54	1	0.12
number × gender	1.67	2	0.095

3. RESULTS

(a) *Time to next reproduction*

The interbirth interval of mothers reproducing after singleton versus twin deliveries did not differ after controlling for the higher mortality rate among twins ($F_{1,456} = 0.87$ and $p = 0.35$). Instead, the interbirth interval of both twin and singleton mothers was affected by whether their offspring survived or died (table 1), with the interbirth interval being greater for mothers whose offspring survived (singleton mothers, 30 ± 1.4 months versus 36 ± 1.0 months and twin mothers, 26 ± 1.5 months versus 36 ± 1.9 months (one survived) versus 32 ± 2.6 months (two survived)) (see figure 1a for singleton mothers and figure 1b for twin mothers).

The interbirth interval of singleton mothers was not affected by the gender of their previous offspring, irrespective of whether their offspring survived or died (table 1 and figure 1a). In contrast, if a mother produced two offspring at a time, their offspring's gender modified the time to next reproduction. There was a significant inter-action in twin mothers between gender combination and the survival of their previous offspring on the interbirth interval (table 1 and figure 1b). The interbirth interval was greatest following the production of male–male twins and smallest following female–female twins when both of the twins died (33 ± 3.6 months versus 24 ± 2.4 months) ($t_{41} = 2.01$ and $p = 0.05$) or both survived (41 ± 4.2 months versus 29 ± 3.5 months) ($t_{22} = 2.08$ and $p < 0.05$). However, when only one of the twins from a male–male or a female–female delivery survived, the interbirth interval was less if the survivor was a male than if the survivor was a female (30 ± 3.7 months versus 41 ± 3.6 months) ($t_{34} = -2.00$ and $p = 0.05$). In the case of a mixed-gender twin delivery from which only one offspring survived, the gender of the survivor had no effect on the subsequent interbirth interval ($t_{31} = 0.45$ and $p = 0.51$).

Only maternal age of the potentially confounding factors (see § 2) was significant for twin mothers, with the time to next birth increasing with increasing maternal age (table 1). In addition to maternal age, year of delivery had a significant effect on the interbirth interval for
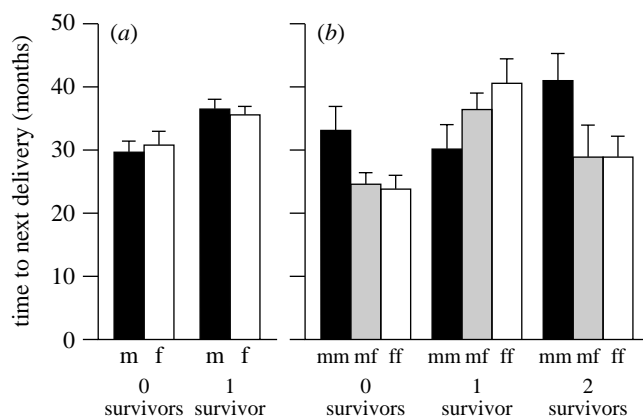
Figure 1. Time to next reproduction (in months) (+s.e.) after (*a*) a singleton delivery and (*b*) a twin delivery according to the number of survivors from these deliveries. Male singleton births (m) are depicted in black and female singleton births (f) are depicted in white. Male–male (mm) twin births are depicted in black, male–female (mf) twin births are depicted in grey and female–female (ff) twin births are depicted in white.

Figure 2. Percentage of mothers not rebreeding after (*a*) a singleton delivery and (*b*) a twin delivery according to the number of survivors from these deliveries. Male singleton births (m) are depicted in black and female singleton births (f) are depicted in white. Male–male (mm) twin births are depicted in black and female–female (ff) twin births are depicted in white.

singleton mothers, with birth intervals tending to increase over the 100-year study period (table 1).

(b) *Probability of rebreeding*

Mothers producing twins were more likely to terminate reproduction than mothers producing a singleton at a similar age and with a similar birth history (figure 2). The gender and survival of the offspring produced further affected these differences.

The three-way interaction between the number, gender and survival of previous offspring in the model examining a mother's likelihood of having future offspring after a given delivery was significant (table 1). This followed from the differential effects of offspring gender and survival on the probability of future reproduction in mothers who previously produced twins versus singletons. Nineteen per cent of the mothers giving birth to a singleton offspring ceased reproducing. Neither the survival nor gender of the singleton child affected the likelihood of a mother rebreeding (figure 2*a*). Twenty-eight per cent of the mothers who produced twins terminated reproduction. Here, the mothers were more likely to cease reproducing after producing two males than two females (figure 2*b*). The survival of the offspring produced only significantly affected a mother's future reproduction in the case of male twins. If a mother lost both of her male twins, she was more likely to continue reproducing than if she raised at least one of the twins (figure 2*b*).

Older mothers were more likely to terminate reproduction than young mothers (table 1). In addition, the total number of previously produced offspring affected a mother's likelihood of reproducing again: mothers with few earlier children were more likely to continue reproducing, even if they were of an older age (table 1). None of the other possible additional factors were statistically significant.

(c) *Gender of the next offspring*

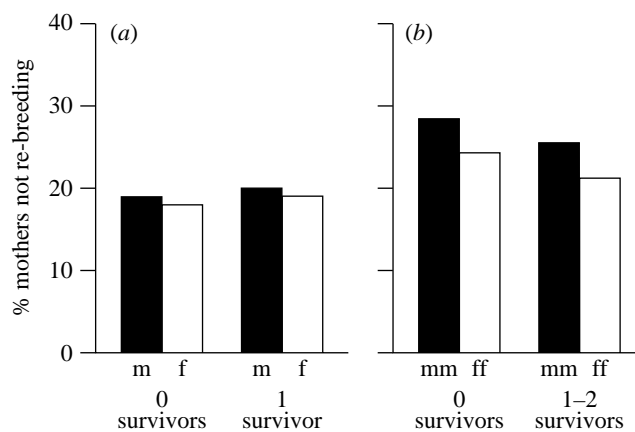The gender of a mother's next offspring depended on the interaction between the number and survival of previously produced offspring (table 1). This (marginally significant) interaction reflected the differential effect of whether a mother raised her previous offspring in mothers who produced twins versus a singleton only. Survival of the previous child in singleton mothers did not affect the gender of their next offspring (figure 3*a*). However, when the number of offspring produced at a time increased from one to two, the gender of a mother's next child was influenced by whether any of the previous twins had survived. If at least one of the twins survived, the mother was more likely to produce a female next time than would have been the case if she had not raised either of the twins (figure 3*b*).

Similarly, the gender of previously produced offspring only influenced the gender of the next child if the mother produced two offspring at a time (table 1). Twin mothers who produced males were more likely to produce a female singleton in the following delivery than those who produced females, whereas there was no such effect for those who previously produced a male or female singleton (figure 3). Moreover, mothers who gave birth to male–female twins, only one of which survived, were more likely to produce a female next time if the survivor was a male and a male next time if the survivor was a female ($\chi_1^2 = 4.87$ and $p = 0.027$) (figure 4).

None of the potentially confounding variables reached statistical significance and they were therefore excluded from the final model.

(d) *Survival of the next offspring*

A mother's next child was significantly more likely to survive if the mother had previously produced a singleton as compared with producing twins (table 1 and figure 5). The number of offspring raised to adulthood from the previous delivery did not significantly affect the survival of the next offspring in either the case of singleton or twin births (table 1). However, similar to the findings about the other future reproductive parameters, there was a tendency for the gender of previous offspring to affect the survival of the next child only when mothers produced
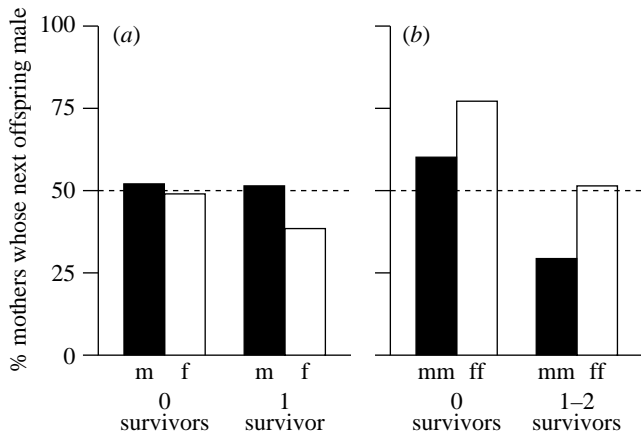
Figure 3. Percentage of mothers next producing a male offspring after (*a*) a singleton delivery and (*b*) a twin delivery according to the number of survivors from these deliveries. Male singleton births (m) are depicted in black and female singleton births (f) are depicted in white. Male–male (mm) twin births are depicted in black and female–female (ff) twin births are depicted in white. The broken horizontal line indicates an equal probability of next producing a male or a female.
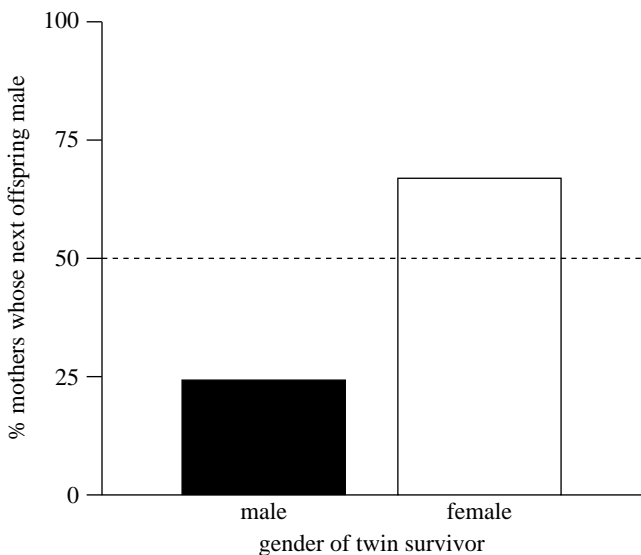

Figure 4. Percentage of mothers next giving birth to a male offspring after a male–female twin delivery producing one survivor of male gender (black bar) or of female gender (white bar). The broken horizontal line indicates an equal probability of next producing a male or a female.

twins (table 1). Twin mothers who produced males tended to be more likely to lose their next offspring than twin mothers who produced females, whereas no such gender difference was observable in mothers giving birth to singletons of either gender (figure 5). None of the potential confounding sources of variation were significant and they were therefore excluded.

4. DISCUSSION

I studied how the number, gender and survival of offspring produced per reproductive attempt by pre-industrial Finnish women affected their subsequent reproductive output, namely the probability of rebreeding, the
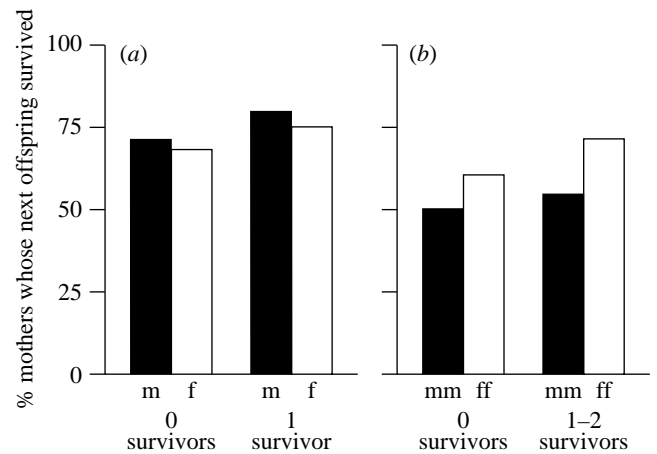

Figure 5. Percentage of mothers whose next offspring survived after (*a*) a singleton delivery and (*b*) a twin delivery according to the number of survivors from these deliveries. Male singleton births (m) are depicted in black and female singleton births (f) are depicted in white. Male–male (mm) twin births are depicted in black and female–female (ff) twin births are depicted in white.

time to next reproduction and the gender and survival of their next offspring. The results of this study provide support for the hypothesis that producing enlarged broods in humans entails a larger cost for mothers' future reproduction, as predicted by life-history theory (Williams 1966). As predicted, these costs were further modified by the gender and survival of the offspring produced. Giving birth to and raising males generally appeared to be the most expensive strategy in terms of the future reproductive success of a mother, but it is noteworthy that producing sons was more costly than producing daughters only if the mother produced twins, thus suffering from higher overall costs of current reproduction.

First, I examined how producing twins instead of a singleton child affected a mother's subsequent reproduction. Twinning in pre-industrial conditions was only rarely advantageous for a mother's lifetime reproductive success (Lummaa *et al.* 1998a). Twin children had reduced survival (Haukioja *et al.* 1989; Gabler & Voland 1994) and maternal mortality rates were higher when delivering twins relative to singletons (Lummaa *et al.* 1998a). This study shows that producing twins not only affected a mother's current reproductive success, but also had long-lasting consequences for her future reproduction as well. Mothers producing twins were more likely to fail to raise their next offspring or to terminate reproduction completely as compared with mothers producing a same-gender singleton child at the same age and with the same birth history. Brood size *per se* did not affect either the time needed for the woman to conceive again or the gender of her next offspring. Rather, these effects depended on the survival and gender of the twins and singletons produced.

Second, I studied the gender-specific costs of reproduction and how these varied with the survival of the offspring produced. It has been argued that, if maternal condition affects the reproductive success of male offspring more than that of female offspring, mothers in good condition should produce more males (Trivers & Willard 1973). Although the exact mechanism (e.g. unequal fertilization rate versus selective abortion versus differential foetal

mortality of the sexes) for differential sex allocation of this kind still remains poorly understood in most studies (Krackow 1995), there is considerable evidence from mammals that mothers in superior condition tend to produce more offspring of the gender with a higher reproductive variance (Hardy 1997). For instance, dominant females in red deer produced more sons than their subordinates (Clutton-Brock *et al.* 1984). Moreover, there is some evidence of potentially adaptive differential investment in offspring of different gender in humans, e.g. nineteenth century Mormons (Mealey & Mackey 1990), Mukogodo hunter–gatherers (Cronk 1991), Hungarian gypsies (Bereczkei & Dunbar 1997) and Gabbra pastoralists (Mace & Sear 1997). I found that pre-industrial Finnish women were more likely to produce a female child after a successful twin delivery (i.e. where they raised at least one offspring) or after producing two males as compared with an unsuccessful twin delivery or after producing two girls. This effect was less strong after a singleton birth. Producing twins over singletons or two offspring of the more expensive gender instead of just one could be predicted to entail a larger energetic expenditure on current reproduction and a subsequent decrease in maternal condition. It is therefore not surprising that the sex-ratio bias was more obvious after such a reproductive event.

An offspring sex-ratio variation of the kind detected here could be adaptive if it increased the reproductive value of offspring of the overproduced gender. I found a trend in that a mother's next offspring could have the lowest survival expectation if the mother had previously produced two offspring of the more expensive gender, but this needs to be confirmed in further studies. In this light it might have paid for a male–male twin mother next to produce a female offspring with a better overall survival probability. It still remains to be examined whether the gender and survival of the previous offspring affected some measure of the next child's reproductive success. That such long-term consequences of maternal condition on offspring reproductive success are feasible in humans (reviewed in Lummaa & Clutton-Brock 2001) was shown in a study on pregnant women experiencing the Dutch Hunger Winter at the end of the Second World War (1944–1945). Female babies that were exposed to famine *in utero* had offspring of lower birth weight themselves, and their children suffered from higher mortality before and after birth as compared with mothers not exposed to famine as a foetus (Lumey & Stein 1997). In order to show that the relationship between twin survival or gender and bias in the gender of the next offspring were not a product of overall differences in female quality and lifetime offspring sex ratio, the 'quality' of the mothers with a differing gender composition of their twins was compared. There were no differences between these mothers in their length of reproductive lifespan, lifetime fertility or sex ratio or the number of offspring raised to adulthood (Lummaa *et al.* 2001).

The birth interval length in pre-industrial humans with no access to an advanced contraceptive method has often been thought to reflect the amount of maternal investment in the first-born offspring (e.g. Mace & Sear 1997). This is in line with the finding of this study showing that the birth intervals following the birth of twins or singletons depended on how many of the

children produced survived. Birth intervals could also reflect the differential costs of producing males versus females. The time to next reproduction in the rural Finnish women studied here differed after producing male and female offspring, but only significantly so after giving birth to two children of a given gender. If a mother managed to raise both twins, those raising two males had a considerably longer interval before giving birth to their next offspring than mothers raising two females. That it took longer to recover and give birth again for mothers producing two males even in the case when both of them died (usually within weeks after birth) indicates that the difference in the costs of raising males and females is already set *in utero*, as is predicted from the faster growth rate of male foetuses and their larger weight at birth (Hoffman *et al.* 1974; Parker *et al.* 1984; Marsál *et al.* 1996). It was therefore surprising that, when only one of the same-gender twins survived, the longest birth interval appeared to be after raising a female. There is no satisfying explanation for this, given that the time to the next delivery was similar between male–female twin deliveries in which only the male or the female survived and between singleton deliveries of opposing gender. Preferential care of offspring of one gender has been reported to be one of the most common reasons for gender-specific mortality (Blaffer Hrdy 1987), but there is no evidence for preferential treatment of male or female children in the populations studied here, although this possibility could not be excluded. Active infanticide is known to have been very exceptional, partly because it was highly criminalized and, if practised, severely punished.

In conclusion, the analysis of the effects produced by the number and gender of offspring on future maternal fitness revealed that producing children of the more expensive gender only had negative effects on a mother's future reproduction in the case of enlarged broods. This is not surprising, given that humans are less sexually size-dimorphic than many other mammals for which such effects have been reported earlier. The number, survival and gender of the offspring produced in the pre-industrial Finnish women studied here together appeared to determine their optimal reproductive strategy. Studies focusing on the future reproductive consequences of broods of differing size and sex ratio in different socioeconomic and/or ecological settings are needed in order to reveal how resource availability shapes a mother's energy allocation to the competing demands of reproduction and the strength of their trade-off between current and future investment.

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