Gender difference in benefits of twinning in pre-industrial humans: boys did not pay

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Summary

1. We studied how differences in the cost of producing male and female offspring in humans affected the productivity of twin vs. singleton deliveries in two ecologically different areas of pre-industrial (1752–1850) Finland. Given the higher energy requirements of male infants, we predicted sons to suffer more from increased litter size and food scarcity than daughters.

2. We found that the number of offspring surviving to adulthood from a twin delivery differed between the archipelago and mainland areas of rural Finland. On the mainland areas, where crop failures and subsequent famines were common throughout the centuries, twin deliveries were much less successful than in the south-west archipelago, where food conditions were traditionally more stable and survival was ensured by fishing.

3. Productivity of twin deliveries was modified by the gender composition of the twins; female–female twin births were generally most successful and male–male births least successful.

4. On the mainland, giving birth to twins of any gender composition never increased the mothers’ reproductive success beyond giving birth to either a male or female singleton, whereas in the archipelago mothers could increase their reproductive output by producing twins. This was because in the archipelago female–female twin deliveries contributed on average more than one adult offspring to the breeding population, whereas a singleton delivery of either gender produced only about 0·7 adults.

5. Our results show that increases in litter size and variability of food conditions increased male mortality. High female twin survival in the archipelago led to higher fitness of twinning mothers in relation to mothers with only singletons. Twinning has traditionally been significantly more common in the archipelago as compared to the mainland, but contrary to the prediction, there were no apparent differences in the frequency of male–male and female–female twins being born.

Key-words: food conditions, litter size, mortality, reproductive success, sex ratio.

Introduction

In sexually size-dimorphic mammals, males are normally larger than females. This size dimorphism is usually present at birth and becomes more marked while offspring are dependent on parental care. In such species, male offspring require more resources than females to sustain the faster growth rates needed to attain the larger body size (reviewed in Clutton-Brock 1991). Therefore, costs of rearing a male are often higher than costs of rearing a female. In addition, male offspring are more sensitive to adverse maternal and/or environmental conditions than females, particularly during the early stages of development (reviewed in Clutton-Brock, Albon & Guinness 1985; Stinson 1985).

Life-history theory predicts a trade-off between quality and quantity of offspring (Roff 1992; Stearns 1992). Given the differential survival of male and female offspring in sexually dimorphic species, resource availability may alter the fitness benefits of producing litters of different size and sex ratio. In this type of
system, the number and the gender of offspring in a litter may be traded off. In line with this, Williams (1979) suggested that in species with small litters and differences in the costs of producing sons and daughters, mothers in very poor condition should produce a single offspring of the cheaper sex; those in slightly better condition a singleton of the more expensive sex; those in good condition twins of the cheaper sex; and those in very good condition twins of the more expensive sex. Consequently, adverse environmental conditions could be predicted to have unequal gender-specific effects on the survival of singleton and twin offspring. Some empirical studies support the prediction that environmental conditions affect the size and sex ratio of litters in mammals. For instance, experimental food restriction led to male-biased litter reduction in wood rats (Neotoma floridana Ord) (McCleure 1981), while exposure to social and nutritional stress during pregnancy led to reduced litter sizes with female-biased final sex ratios in golden hamsters (Mesocricetus auratus Waterhouse) (Labov et al. 1986; Pratt, Huck & Lisk 1989).

In humans (Homo sapiens L.), 6–45% of all births, depending on the population, produce more than a singleton offspring (Vogel & Metulsky 1986). Because twin children suffered higher mortality than singletons under pre-industrial conditions (Haukioja, Lemmetinen & Pikkola 1989; Gao & Grummer-Straun 1993; Gabler & Voland 1994), twinning is presumed to have been selected against in the past (Haukioja et al. 1989), except under the most favourable conditions (Lummaa et al. 1998a). In humans, females have slower intrauterine growth rates than males (Parker et al. 1984; Marsal et al. 1996), and both singleton and twin boys are slightly heavier at birth than singleton or twin girls (Brenner, Edelman & Hendricks 1976; Hoffman et al. 1974). As in many other mammals, male offspring appear to be more sensitive to environmental stress than females. During growth and development, mortality and morbidity following birth are usually male-biased, and fetal growth of males is more retarded than that of females under stressful conditions (reviewed in Stinson 1985; Wells 2000). This suggests that the costs of producing offspring are gender-specific in humans, and that males are the more expensive gender to produce.

In this study, we examine the costs and benefits of producing male and female singletons and twins in pre-industrial (1752–1850) humans living in two ecologically different areas of Finland. We investigate how the difference in the cost of producing boys and girls affects the productivity of twinning, and how the fitness benefits of male and female singleton and twin offspring respond to stable and variable food conditions. A mammalian mother faces a compromise between the number of young per litter and the amount of investment per individual young, and given the higher energy requirements of male infants, we predict that sons suffer more from increased litter size and food scarcity in pre-industrial humans.

Materials and methods

DATA AND STUDY POPULATIONS

The productivity of male and female singleton and twin deliveries in variable and stable food conditions was studied using unique Finnish population registers. The Lutheran Church has kept census registers, birth/baptism registers, marriage registers and death/burial registers of each parish in the country since the 17th century (Haukioja et al. 1995). From 1749 onwards, the records cover the entire population of Finland. Using these registers, it is possible to follow the reproductive and marital details of each individual from birth to death. Practically all who died (in most cases including even stillborn and infants who died before baptism) were buried in a cemetery and recorded in the book of deaths (Gille 1974). As in many other mammals, male offspring are slightly heavier at birth than singleton or twin girls (Brenner, Edelman & Hendricks 1976; Hoffman et al. 1974). As in many other mammals, male offspring are slightly heavier at birth than singleton or twin girls (Brenner, Edelman & Hendricks 1976; Hoffman et al. 1974). As in many other mammals, male offspring are slightly heavier at birth than singleton or twin girls (Brenner, Edelman & Hendricks 1976; Hoffman et al. 1974).

Two study areas were chosen for the comparison of sex-specific singleton and twin survival rates: poor rural mainland areas (parishes Ikaalinen 61°45' N, 23° E and Pulkkilä 64°15' N 26° E) where crop failures and subsequent local famines had been common throughout the centuries; and the adjacent archipelago of Åland and Åboland in south-west Finland (parishes Håttinen 60° N 22°30' E, Kustavi 60°30' N 21°30' E,
and Rymättyla (60°15' N 22° E), where food availability has traditionally been relatively constant (Sonnenm 1974). Lummaa et al. (1998a) showed that the fitness consequences of twinning differed between these areas during the pre-industrial era. Mothers with a tendency for twin deliveries were selected against on the mainland, but not in the archipelago. In the archipelago, the lifetime reproductive success (number of all offspring surviving to adulthood) of mothers with twins equalled or exceeded that of mothers having singletons.

In contrast to the archipelago, mothers of twins on the mainland experienced a reproductive disadvantage in comparison to mothers of singletons due to both increased maternal and child mortality. Interestingly, the tendency towards heritable dizygotic twinning (Parisi et al. 1983) was considerably higher in the archipelago than on the mainland, but not in the archipelago. In the archipelago, the lifetime reproductive success (number of all offspring surviving to adulthood) of mothers with twins equalled or exceeded that of mothers having singletons.

<table>
<thead>
<tr>
<th>Maternal trait</th>
<th>Area</th>
<th>Delivery type</th>
<th>Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age at twin birth</td>
<td>251</td>
<td>0.98, NS</td>
<td>0.87, NS</td>
</tr>
<tr>
<td>Children before twins</td>
<td>250</td>
<td>5.47, NS (0.02)</td>
<td>0.29, NS</td>
</tr>
<tr>
<td>Children after twins</td>
<td>245</td>
<td>2.21, NS</td>
<td>0.37, NS</td>
</tr>
<tr>
<td>Birth interval after twins</td>
<td>174</td>
<td>1.37, NS</td>
<td>0.29, NS</td>
</tr>
<tr>
<td>Reproductive lifespan</td>
<td>242</td>
<td>3.26, NS</td>
<td>0.27, NS</td>
</tr>
<tr>
<td>Lifetime sex ratio</td>
<td>243</td>
<td>2.33, NS</td>
<td>54.51, &lt; 0.05 (&lt; 0.0001)</td>
</tr>
<tr>
<td>Total no. of children</td>
<td>244</td>
<td>7.98, &lt; 0.05 (0.005)</td>
<td>0.08, NS</td>
</tr>
<tr>
<td>No. of adult offspring</td>
<td>213</td>
<td>0.52, NS</td>
<td>0.08, NS</td>
</tr>
</tbody>
</table>

Table 1. Differences in maternal reproductive traits between archipelago and mainland areas and between females with different twin delivery types (male–male, male–female, female–female). Significance values are adjusted to be table-wide [sequential Bonferroni correction, k = 8; beside the final significance (in parentheses) is the P-value before Bonferroni correction if P < 0.05].

Statistical analysis

The differences in reproductive traits between mothers with different twin delivery types and between the areas were contrasted using two-way parametric ANOVAs (GLM procedure of SAS, SAS Institute Inc. 1990) Area, delivery type and their interaction were entered in the analyses as fixed terms. Residuals of all the models were normally distributed and variances were homogeneous (Levene’s test, P > 0.05). Because several related reproductive parameters were calculated for the same set of mothers, the significance values were adjusted using a table-wide sequential Bonferroni correction (Rice 1989). Sample sizes in these analyses varied due to failure to follow some mothers throughout their reproductive lifespan. Using multivariate analysis of variance (MANOVA), which would allow correction of the significance levels for multiple tests when two or more response variables are tested from the same set of individuals (Scheiner 1994) did not change our conclusions. Therefore, we present here the results from only the univariate ANOVAs because they permit the maximum possible number of individuals to be included in each model, whereas the MANOVA technique only included those mothers for whom all of the tested variables were recorded.

The differences in survival between twin and singleton girls and boys were analysed using Kaplan–Meier survival plots (± SE). Exact age at death was calculated assuming 365 days in each year. Cumulative survival estimates are given from birth to the age of 10 years.
Due to the small number of deaths occurring after infancy, survival estimates could not be obtained for all the compared categories up to the age of 15, which was the age used in the other analyses. Kaplan–Meier survival estimates were calculated using Genstat™ (Genstat Committee 1993).

The productivity of twin deliveries consisting of different gender combinations (mm, mf, ff) was analysed in terms of the number of individuals that survived to adulthood (15 years of age) on the mainland and the archipelago. The number of survivors from a twin delivery (0/1/2) was used as a response variable in multinomial logit models where the independent variables were area (mainland vs. archipelago), gender combination (mm, mf, ff) and their interaction. Logit models were constructed with the CATMOD procedure of SAS (SAS Institute Inc. 1990). The survival of singletons to adulthood (survived/died) was also modelled entering gender, area and their interaction as independent variables in the models. The best model was chosen to be the most parsimonious one with best explanatory power, using maximum likelihood analysis of variance.

Results

FITNESS PAYOFF OF TWIN AND SINGLETON DELIVERIES

Survival of singleton males and females were very similar throughout childhood (Fig. 1) and the productivity of singleton deliveries did not differ between the areas ($\chi^2 = 0.75$, d.f. = 1, $P = 0.39$), or between males and females ($\chi^2 = 0.01$, d.f. = 1, $P = 0.94$). The survival probability of an individual singleton child was always higher than that of an individual twin child (Fig. 1). However, under certain conditions, a twin delivery gave rise on average to more offspring reaching adulthood than a singleton delivery (Fig. 2).

The most parsimonious model of the productivity of twin deliveries contained the main effects of area and delivery type. Productivity of twin deliveries in terms of number of offspring surviving to adulthood was higher in the archipelago compared to the mainland areas (Fig. 3, $\chi^2 = 5.82$, d.f. = 2, $P = 0.05$). The number of offspring surviving to adulthood from mm, ff and mf twin deliveries
Gender difference in benefits of human twinning
differed significantly ($\chi^2 = 10.98$, d.f. = 4, $P = 0.03$), all-female births being the most productive and all-
male births being the least productive (Figs 2 and 3).

The model that fitted the data best did not contain
the interaction term between area and delivery type. However, when all twin deliveries including male off-
spring (mf and mm) were combined in the analysis and
the productivity of male and female twin deliveries was
compared within each area, it was found that on the
mainland, on average 0.58 (± 0.06 SE) offspring per
twin birth reached adulthood, and that there was no
effect of delivery type ($\chi^2 = 2.86$, d.f. = 2, $P = 0.24$).
The situation was different in the archipelago, where
the average number of children surviving from each
twin birth was 0.81 (± 0.07), and this was affected by
the type of delivery ($\chi^2 = 6.85$, d.f. = 2, $P = 0.03$). The
high productivity of twin deliveries in the archipelago
appeared to be due to very high survival of girls from
the ff deliveries in this area (Figs 1 and 2). This was
the only type of twin delivery that on average produced
more adult offspring than a singleton delivery (Fig. 2).

Girls from mixed sex deliveries also seemed to have an
advantage in the archipelago. In 74% (17/23) of the
cases where only one of the mf twins survived, the sur-
vivor was female ($\chi^2 = 4.35$, d.f. = 1, $P = 0.04$). No
such difference was observed on the mainland, where
in 54% (13/24) of the cases the sole survivor was the girl
($\chi^2 = 0.04$, d.f. = 1, $P = 0.83$).

**Gender of Twins and Maternal Reproductive Parameters**
To measure the ‘quality’ of the mothers with different
types of twin deliveries in each area, several reproductive
parameters were compared between them. No differences
were found between mothers with mm, mf and ff twins,
or between the areas in most of the parameters we assessed
(Table 1). However, there was a significant difference in
the total number of offspring delivered between mothers
between the archipelago and mainland areas (Table 1).
Total fertility was higher on the mainland compared to
the archipelago, probably resulting from increased child
mortality and the cultural tradition for shorter duration
of breast-feeding on the mainland study sites, which
modified the time to the resumption of ovulations after
a pregnancy (see Lummaa 1999). Furthermore, the sex
ratio of offspring (proportion of males) delivered over
the whole lifespan differed between mothers of mm, mf
and ff twins, being most male-biased in the mothers of
mm twins (0.62 ± 0.02), and most female-biased in the
mothers of ff twins (0.32 ± 0.02, Table 1). This differ-
ence disappeared when twin offspring were excluded from
the calculation of a mother’s lifetime offspring sex
ratio ($F = 2.12$, d.f. = 2, $P = 0.12$).

**Discussion**
We found support for our prediction that the fitness
payoff of twin deliveries in pre-industrial Finnish
populations depended on the gender of the produced
offspring. As predicted, an increase in litter size from
one to two only paid off in the more productive and
predictable environment of the archipelago, but not on
the mainland with a history of repeated famines and
shortage of resources. It is noteworthy that even in the
archipelago only the fitness benefit of ff, but not mm or
mf twins, exceeded that of singletons, suggesting that
the optimal strategy when twinning would have been to
produce girls.

A closer look at our results reveals that in the main-
land areas, production of a singleton baby of either
gender was always more beneficial for the mothers’
reproductive success than giving birth to twins of any
gender composition. The negative effect of twin deliv-
eries on the mothers’ lifetime reproductive success was
increased by the fact that mothers with twins experi-
enced higher postpartum mortality rates than mothers
who produced only singletons (Lummaa et al. 1998a).
On the mainland, mothers with a tendency towards
twin deliveries were therefore selected against. In the
south-west archipelago of Finland where food condi-
tions were more stable and survival was ensured by fish-
ing, mothers could increase their reproductive output
by producing twins. It appears that this was because ff
and mixed gender twin deliveries produced about the same
number of adult offspring as the singleton deliveries in
the archipelago. Consequently, in the archipelago, the
total lifetime reproductive success (number of adult
offspring) of mothers with twins equalled or exceeded
that of mothers with only singleton offspring (Lummaa
et al. 1998a). Twinning frequencies have traditionally
been much higher in the archipelago than in main-
land areas of Finland (Eriksson 1973). One possible
explanation for this may be the positive selection on
mothers with a tendency towards twinning revealed in
this study.

In the archipelago, ff deliveries produced on average
more than just one offspring to adulthood, and were
clearly the most productive gender combination. This
suggests that mothers should have favoured girls when
producing twins. Primary sex ratio manipulation in
twins has been a controversial topic (e.g. Williams
1979; Clutton-Brock & Iason 1986), but there is some
evidence of potentially adaptive differential investment
in offspring of different gender in humans (e.g. nine-
teenth century Mormons, Mealey & Mackey 1990;
contemporary Mukogodo hunter-gatherers, Cronk
Hungarian Gypsy populations invested more heavily
in daughters than in sons compared to coresident
Hungarians. This strategy appeared to pay in terms of
maximizing fitness since the Gypsies gained more
grandchildren through their daughters than through their
sons. Among the pre-industrial Finns, the difference in
total number of offspring raised to adulthood did not differ significantly between mothers of different types of twins, but our sample sizes may have been too small to detect such a difference. Furthermore, during our study era (1752–1850), there were no significant differences in frequencies of mm or ff twins being born in the archipelago (Eriksson 1973). However, there is some evidence from other populations that the probability of a twin being a girl is larger than that of a singleton child being a girl (Bulmer 1970; Eriksson 1973).

An increase in litter size may represent increased reproductive effort, which may influence survival and future reproduction of both the parent and its offspring (Williams 1966). Given the life-history theory prediction for a trade-off between quality and quantity of offspring (Roff 1992; Stearns 1992), we may ask whether the surviving twin offspring are equal to singletons in terms of future fitness benefits for the parent? In 18th and 19th century Germany, twins tended to have lower maternal prospects than singleton children (Gabler & Voland 1994). Women who were born as twins had a lower probability of marrying within their natal parish and higher risk of dying single. Twin females also had a higher emigration rate than singleton women. The difference was not significant for twin males. No data are available about the actual numbers of grandchildren born for mothers with female or male twins, but because daughters (twin and singleton) from families with twin offspring were on average more fertile than daughters from families without twins in the German sample, Gabler & Voland (1994) estimated the number of grandchildren to be higher for mothers with female twins compared to mothers with singleton only, and lower for mothers with male twins.

Differences in the productivity of twin deliveries of differing gender composition may be a consequence of differences in maternal condition or the amount of parental investment. 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). There is considerable evidence from other mammals that mothers in superior condition tend to produce more offspring of the gender with higher reproductive variance. For instance, in red deer (Cervus elaphus L.), dominant females produce more sons than the subordinates (Clutton-Brock, Albon & Guinness 1984, 1986). As maternal dominance affects the breeding success of male offspring more than that of females, variation in offspring sex ratio is likely to increase the female's expected number of grandchildren. In the Saharan arratu (Ammotragus lervia sahariensis Pallas), an ungulate giving birth to singletons or twins, only the most dominant individuals give birth to mm twins who require the largest amount of maternal investment (Cassinello & Genovese 1996). To compare the 'quality' of the Finnish mothers in our study with differing gender composition of their twins, we recorded the length of their reproductive lifespan, fecundity (total number of children delivered) and number of offspring raised to adulthood. None of these parameters differed between mothers with twins of different gender compositions. However, in both areas the sex ratio of all the offspring delivered was male biased in mothers with mm twins and female biased in mothers with ff twins, but this difference was caused mainly by the gender of the twins rather than a by a consistent bias in offspring sex ratio throughout the lifespan.

Low birth weight is regarded as an important determinant of infant mortality in humans (McCormick 1985). Both singleton (Hoffman et al. 1974; Brenner et al. 1976) and twin (Corney et al. 1979) males are, on average, born heavier than girls, but they die more often than females during the period following birth (Stinson 1985; Rydhström 1990; Wells 2000). This may be because, for a given gestational age, birth weight tends to be greater for males than for females (Lubchenko et al. 1963), indicating that a female infant of the same birth weight as a male is in fact born older, more mature, and therefore is perhaps better able to survive. The increased risk of mortality in twin pregnancies even in conditions with modern health care is partly a result of the lower birth weight and gestational age at delivery of multiple pregnancies (McCarthy et al. 1981; Power & Kiely 1994). Chen, Voeh & Oh (1993) showed that in a sample of modern American twins, if twin pairs had significantly longer gestation period than either mm or mf twins. This may explain why if twins had superior survival prospects in our study compared to other twin types, at least when the food conditions were stable. Aaby et al. (1995) reported similar survival data for rural Senegal, where infants from ff twin deliveries had lower mortality in childhood compared to other types of twins. It was not studied, however, how productive the twin deliveries were in relation to singleton births of either gender in this population.

In our study, not only girls from ff but also from mf deliveries had survival advantage over the boys. 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). Tendency to favour one gender over the other should be most obvious in mf twins where resources have to be shared between them. Girls from mixed twin deliveries were reported to suffer higher mortality than the male co-twins in rural Bangladesh (Chowdhury et al. 1990). However, because the survival disadvantage was only present in the mf twins, and not between the mm and ff twins, and because the difference was only established after a few months of life, it was suggested to be due to preferential care for male children when resources were divided between a male and female child (Chowdhury et al. 1990). We are not aware of any evidence for preferential treatment of male or female children in our study populations, although this could not be excluded. Active infanticide is known to have been very exceptional, partly because it was highly criminalized.
and, if practised, severely punished. The fact that singletone males and females in our study had very similar survival rates in both areas suggests that the gender differences in twin mortality were not due to differential treatment by parents, but rather due to gender-specific susceptibility to increased nutritional stress resulting from an increase in litter size. Singleton boys in our study populations experienced a decreased survival in comparison to the girls only immediately after birth (Lummaa et al. 1999b), which is in line with those studies on other species showing highest sensitivity of males compared to females particularly during the early stages of development (Clutton-Brock, Albon & Guinness 1985).

In conclusion, our analysis of the fitness payoffs of twin and singleton deliveries in pre-industrial Finnish people suggests that environmental and gender-specific factors together determined the optimal reproductive strategy in these humans. As the evolutionary response to these processes is complicated, it is not surprising that more dramatic local variation in twinning response to these processes is complicated, it is not surprising that more dramatic local variation in twinning rate and offspring sex ratio was not found. However, our results suggest that the mechanism that led to higher twinning frequency of the populations inhabit-

References

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