

# 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.

*Journal of Animal Ecology* (2001) **70**, 739–746

## 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

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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) (McClure 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.), 0.6–4.5% of all births, depending on the population, produce more than a singleton offspring (Vogel & Motulsky 1986). Because twin children suffered higher mortality than singletons under pre-industrial conditions (Haukioja, Lemmetyinen & Pikkola 1989; Guo & Grummer-Straun 1993; Gabler & Volland 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; Marsál *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 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 (Luther 1993). 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 1949). Moreover, the whole population of the study area practiced the Lutheran religion and the local clergymen were obliged by law to submit accurate population records of their parishes to the state. For these reasons, the Finnish and other Scandinavian church registers provide some of the most reliable sources of demographic data on old human populations.

Our study covers the years from 1752 to 1850. The study era thus ends before industrialism, more liberal economics and improvement in health care are likely to have had significant effects on survivorship and standard of living in Finland. In most parts of the country, frost nights during early summer and rain coinciding with harvest time in the autumn often led to unpredictable crop failures and subsequent famines (Jutikkala, Kaukiainen & Åström 1980). However, even during normal harvest years, 5–10% of people consumed emergency foods (Jutikkala *et al.* 1980). Transportation networks in the country were poorly developed until the mid-19th century and the famine areas were therefore forced to cope on their own. During famines, the most common causes of death were infectious diseases such as cholera, scarlet fever and smallpox, which spread among the malnourished people (Turpeinen 1978). Adult mortality tended to be highest in spring, whereas infant mortality peaked during the summer months (Turpeinen 1979; Lummaa *et al.* 1998b; Moring 1998). During the study era seasonal variation in food conditions and mortality was smallest in south-west Finland (coast and archipelago of Åland and Åboland), probably as a consequence of milder winters in these areas and an opportunity for a multiple-pursuit economic system where farming was accompanied by fishing, hunting and animal husbandry (Soininen 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 Pulkkila 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 Hiittinen 60° N 22°30' E, Kustavi 60°30' N 21°30' E,

**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  $P < 0.05$ ]

Maternal trait	<i>n</i>	Area		Delivery type		Interaction	
		$F_{d.f.}$	<i>P</i>	$F_{d.f.}$	<i>P</i>	$F_{d.f.}$	<i>P</i>
Age at twin birth	251	0.98 <sub>1</sub>	NS	0.87 <sub>2</sub>	NS	0.84 <sub>2</sub>	NS
Children before twins	250	5.47 <sub>1</sub>	NS (0.02)	0.29 <sub>2</sub>	NS	0.55 <sub>2</sub>	NS
Children after twins	245	2.21 <sub>1</sub>	NS	0.37 <sub>2</sub>	NS	0.58 <sub>2</sub>	NS
Birth interval after twins	174	1.37 <sub>1</sub>	NS	0.29 <sub>2</sub>	NS	0.37 <sub>2</sub>	NS
Reproductive lifespan	242	3.26 <sub>1</sub>	NS	0.27 <sub>2</sub>	NS	0.76 <sub>2</sub>	NS
Lifetime sex ratio	243	2.33 <sub>1</sub>	NS	54.51 <sub>2</sub>	<b>&lt; 0.05</b> (< 0.0001)	1.67 <sub>2</sub>	NS
Total no. of children	244	7.98 <sub>1</sub>	<b>&lt; 0.05</b> (0.005)	0.08 <sub>2</sub>	NS	0.37 <sub>2</sub>	NS
No. of adult offspring	213	0.52 <sub>1</sub>	NS	0.08 <sub>2</sub>	NS	0.87 <sub>2</sub>	NS

and Rymättylä 60°15' N 22° E), where food availability has traditionally been relatively constant (Soininen 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 the 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 areas 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 until the breakdown of genetic isolates in the beginning of the 20th century (Eriksson 1973; Eriksson *et al.* 1988). Dizygotic (DZ) twinning can be distinguished from monozygotic (MZ) twinning because all opposite-gender twins are always DZ, and the proportion of DZ twins among the same-gender twins (a mixture of MZ and DZ twins) can be assessed based on the rate of opposite-gender twins (see Bulmer 1970). We confirmed the difference in twinning rate between archipelago and mainland in an earlier study (Lummaa *et al.* 1998a), and found that in a sample of randomly selected parishes from each area, twinning frequency equalled 21.3‰ in the archipelago and 14.9‰ on the mainland during the study era ( $F = 35.32$ , d.f. = 1, 25,  $P < 0.0001$ ). These results suggest that differences in the predictability of food conditions between these areas may have led to differential selection on twinning frequencies and to an increase in the twinning frequency in the archipelago (Lummaa *et al.* 1998a).

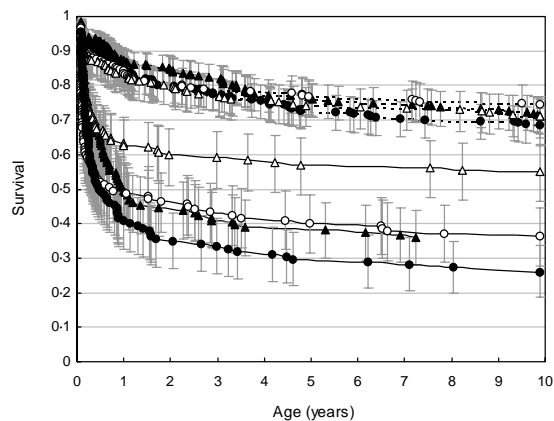
Offspring survival to adulthood (age 15 years) was used as a measure of the benefits of producing singletons vs. twins. We followed the survival of 123 pairs of twins in the archipelago and 129 pairs of twins on the mainland. In the archipelago, 31 of the twin pairs were male–male (mm), 51 were male–female (mf) and 41 were female–female (ff). For mainland areas, the sample size for corresponding groups was 33 (mm), 60 (mf)

and 36 (ff), respectively. All mothers had given birth to only one pair of twins during their lifetime. For comparison, survival to the age of 15 for the singleton children of the twin mothers (in the archipelago 229 girls and 227 boys; on the mainland 300 girls and 308 boys) was also recorded. In humans, the probability of a twin pregnancy changes with maternal age and parity (Bulmer 1970; Vogel & Motulsky 1986). In this study the mothers' ages or numbers of earlier children produced before delivering twins did not differ significantly between the areas or mothers with different twin delivery types (Table 1).

#### 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 ( $\pm$  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.



**Fig. 1.** Kaplan–Meier survival plot ( $\pm$  SE) from birth until age 10 for twin (solid lines) and singleton (broken lines) children living in archipelago (open symbols) and mainland areas (filled symbols) of pre-industrial Finland. Males for each area and delivery type are shown with circles and females with triangles. Note that singleton survival is always higher than twin survival, with no differences between areas or genders.

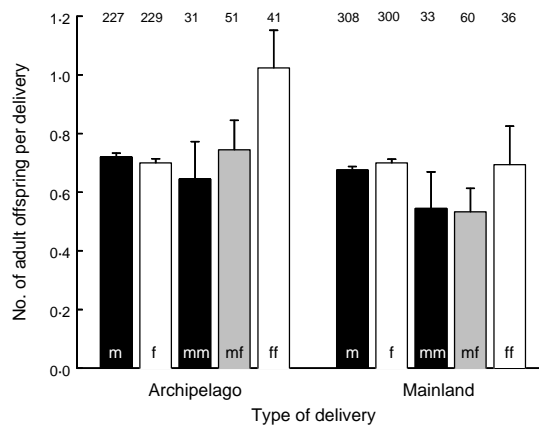
Due to the small number of deaths occurring after infancy, survival estimates could not be obtained for all the compared categories up to the age of 15, which was the age used in the other analyses. Kaplan–Meier survival estimates were calculated using GENSTAT<sup>TM</sup> (Genstat Committee 1993).

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 using CATMOD 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

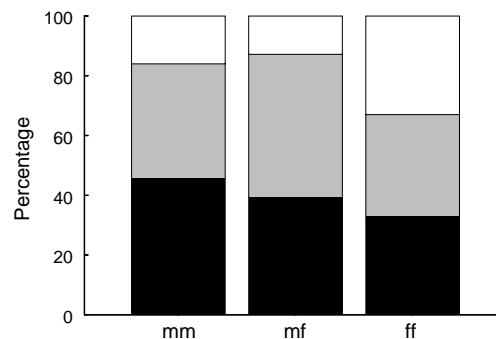
### FITNESS PAYOFF OF TWIN AND SINGLETON DELIVERIES

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

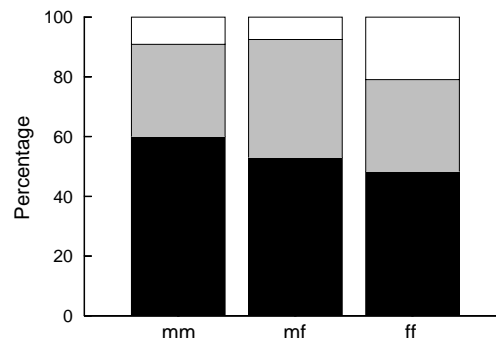


**Fig. 2.** Mean number of offspring ( $\pm$  SE) surviving to age 15 from singleton and twin deliveries consisting of males (m and mm; black columns), a male and a female (mf; grey columns) and females (f and ff; white columns) in archipelago and mainland areas of pre-industrial Finland. Sample sizes are given above each column.

### (a) Archipelago



### (b) Mainland



**Fig. 3.** Percentage of twin deliveries producing zero (black share), one (grey share) or two (white share) adult offspring in (a) archipelago and (b) mainland areas of Finland according to gender composition of the twin delivery (mm = male–male, mf = male–female, ff = female–female).

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

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 offspring (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  $0.58 (\pm 0.06 \text{ SE})$  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  $0.81 (\pm 0.07)$ , 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 survivor 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 living in 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 ( $0.62 \pm 0.02$ ), and most female-biased in the mothers of ff twins ( $0.32 \pm 0.02$ , Table 1). This difference 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 mainland 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 deliveries on the mothers' lifetime reproductive success was increased by the fact that mothers with twins experienced higher maternal 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 conditions were more stable and survival was ensured by fishing, mothers could increase their reproductive output by producing twins. It appears that this was because ff twin deliveries contributed, on average, more than one adult offspring to the breeding population, whereas a singleton delivery produced only about 0.7 adults on average (irrespective of the gender). All-male 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 mainland 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 mammals 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. nineteenth century Mormons, Mealey & Mackey 1990; contemporary Mukogodo hunter-gatherers, Cronk 1991). Bereczkei & Dunbar (1997) demonstrated that 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 parents? In 18th and 19th century Germany, twins tended to have lower marital prospects than singleton children (Gabler & Volland 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 & Volland (1994) estimated the number of grandchildren to be higher for mothers with female twins compared to mothers with singletons 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 arrui (*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 & Gomendio 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 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 (Lubchenco *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, Vohr & Oh (1993) showed that in a sample of modern American twins, ff twin pairs had significantly longer gestation period than either mm or mf twins. This may explain why ff 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 lowered 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 a 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 singleton 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.* 1998b), 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 rate and offspring sex ratio was not found. However, our results suggest that the mechanism that led to higher twinning frequency of the populations inhabiting the archipelago was the high fitness payoff of ff twins, while the production of boys did not pay.

### Acknowledgements

We would like to thank Risto Lemmetyinen and Mirja Pikkola for their invaluable efforts in collection of the church book material, Terho and Pilkkko Koira for continuous inspiration throughout the study, Jani Lindström, Andy F. Russell and Ben C. Sheldon for helpful comments on the manuscript and Jason Gilchrist for simple but yet so important statistical assistance. This study was funded by Academy of Finland (VL, JJ and EH), Emil Aaltonen Foundation (VL) and Swiss National Science Foundation (JJ, grant number 31-59242-99).

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Received 21 November 2000; revision received 8 March 2001