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SELECTION FOR INCREASED BROOD SIZE IN HISTORICAL HUMAN POPULATIONS

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Abstract.—Human twinning rates are considered to either reflect the direct fitness effects of twinning in variable environments, or to be a maladaptive by-product of selection for other maternal reproductive traits (e.g., polyovulation). We used historical data (1710–1890) of Sami populations from Northern Scandinavia to contrast these alternative hypotheses. We found that women who produced twins started their reproduction younger, ceased it later, had higher lifetime fecundity, raised more offspring to adulthood, and had higher fitness (individual λ) than mothers of singletons in all populations studied. For example, an average of 1.2 offspring survived to adulthood from a twin delivery, irrespective of its sex ratio, whereas only 0.8 offspring survived to adulthood from a singleton delivery. Only if mothers started reproduction at very late age ($>$37 yr), or had a very long reproductive life span ($>$20 yr), was it more beneficial to produce only singletons. These findings suggest that twin deliveries among Sami could not be explained as a maladaptive by-product of selection for other maternal reproductive traits. In contrast, our results suggest that twinning was under natural selection, although the strength of selection was likely to have been context dependent.

Key words.—Correlational selection, fitness, insurance ova, lambda, life history, twins, *Homo sapiens*.

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In humans, population twinning rates vary by more than a factor of 15, ranging from 0.33 % (Millis 1959) to an extreme of 5.57 % (Little and Thompson 1988). However, the evolutionary factors shaping human brood size are still poorly understood. Twinning is commonly associated with increased maternal mortality at childbirth (Haukioja et al. 1989; Gabler and Voland 1994; McDermott et al. 1995), an elevated risk of stillbirths (Gabler and Voland 1994; Sear et al. 2001), and higher child mortality (Haukioja et al. 1989; Pison 1992; Guo and Grummer-Starun 1993; Gabler and Voland 1994; McDermott et al. 1995; Beiguelman and Franchi-Pinto 2000; Sear et al. 2001). These well-defined costs imply that, in general, natural selection should not favor twinning, and thus brood size of one is expected to be the norm and twinning rates to remain low (this concerns only dizygotic twinning, non-heritable monozygotic twinning rates are assumed to be fairly constant; Vogel and Motulsky 1986).

The adaptive argument above attempts to explain the observed variation in human twinning rates by variable selection on twinning (i.e., variation in the fitness effects of twinning), and therefore suggest that twinning is directly under natural selection. The key for testing this hypothesis is to recognize the environmental and demographic factors that favor, or select against, twinning. For example, in 19th century southwestern Finland, resource stability in the archipelago areas favored twinning (greater lifetime reproductive success of mothers delivering twins), whereas in poorer nearby mainland areas it was more profitable to produce only singletons (Lummaa et al. 1998, 2001). Twinning frequencies were also higher in the archipelago, supporting the idea that twinning may have been favored by natural selection in this area, and selected against in mainland areas (Lummaa et al. 1998). Therefore, this view holds that (1) the propensity for twinning may either be selected for or against, and that (2) variation in twinning rates among populations reflects variation in the historical selection gradients for twinning (Vogel and Motulsky 1986). We refer to this hypothesis as the ‘‘natural selection’’ hypothesis for variation in twinning rates.

However, the profitability of twinning for maternal fitness often remains lower than the profitability of a singleton delivery (Haukioja et al. 1989; Sear et al. 2001). In addition, when the reproductive success of twin mothers has been observed to exceed that of singleton mothers, it has not been known whether twin deliveries as such have been directly responsible for the higher fitness of twin mothers (Gabler and Voland 1994; Sear et al. 2001). Therefore, the observed variation in twinning rates has been proposed to result from covariance with some other maternal reproductive traits (e.g., polyovulation and subsequent fertility) that are directly under natural selection. Twinning may thus be considered as a maladaptive by-product that has a higher incidence in populations where selection has favored high rates of polyovulation and fertility (‘‘insurance ova’’ hypothesis, cf. Anderson 1990). The most compelling evidence for this hypothesis comes from shorter interbirth intervals observed among twin mothers, suggesting that mothers with a tendency to deliver twins enjoy improved conceivability (e.g., Bulmer 1959; Allen and Schachter 1971; Hogberg and Wall 1992: Sear et al. 2001; but see Lummaa et al. 1999). To summarize, the ‘‘insurance ova’’ hypothesis suggests that (1) twinning is maladaptive, and (2) variation in twinning rates is a by-product of selection on other reproductive traits.

The demarcation point between these two hypotheses is the direct fitness benefits of twinning. The ‘‘insurance ova’’ hypothesis views twinning as maladaptive due to its high costs, whereas the ‘‘natural selection’’ hypothesis views twinning as either adaptive, or maladaptive, depending on the environment. Therefore, findings that twin mothers appear to have higher overall fertility, fecundity, or lifetime reproductive success than mothers who only produce one offspring at a time (Bulmer 1959; Eriksson and Fellman 1967; Allen and Schachter 1971; Hogberg and Wall 1992; Gabler and Voland 1994; Madrigal 1995; Lummaa et al. 1998; Sear et al. 2001) can be taken to argue for both hypotheses. Since the direct contribution of twin deliveries to maternal fitness has been unknown even in those studies reporting higher reproductive success of twin mothers, these alternative hypotheses have not, hitherto, been contrasted with the empirical evidence. Our goal here is to contrast these two hypotheses with demographic data and, in particular, to evaluate the direct fitness consequences of twinning in pre-modern human populations.

We investigated the fitness consequences of twinning in three historical Sami populations. First, we used a rate-sensitive measure of fitness (individual λ, McGraw and Caswell 1996) to compare fitness between twin and singleton mothers. Second, we compared several components of fitness, that is, lifetime fecundity and reproductive success (number of offspring raised to adulthood), as well as key maternal reproductive life-history traits (age at first and last reproduction, reproductive life span, and interbirth intervals) between twin and singleton mothers. Third, we re-evaluated the reproductive performance of twin mothers in relation to singleton mothers after replacing the fitness contribution of each twin delivery with an expected fitness contribution of a singleton delivery, and assessed whether this conveyed a significant fitness loss to twin mothers. These analyses are relevant because they reveal whether twin mothers would have had higher fitness independently of twinning, and whether or not twinning offered greater fitness gains than producing singletons only among mothers with a propensity for twinning. Fourth, we studied potential differences in selection gradients of key life-history traits between twin and singleton mothers in order to examine if fitness of twinning depended on the expression of other life-history traits. Finally, we compared the survival probabilities of twin and singleton offspring to the age of 18 years to determine the productivity of twin versus singleton deliveries. This analysis reveals the direct contribution of twins compared to singletons to maternal fitness, which is required to contrast the ‘‘insurance ova’’ and ‘‘natural selection’’ hypotheses.

MATERIALS AND METHODS

Study Populations

We used demographic data of three different natural-fertility Sami populations (Utsjoki, Inari, and Enontekiö) from Northern Scandinavia collected from the Finnish parish registers (see Käär et al. 1996, 1998; Helle et al. 2002a, b). These data consist of information on continuous baptism, burial, and marital registers for individuals born in a population during the 17th to 19th centuries. We recorded the reproductive performance for all married women born in years 1710–1890. These Sami were traditional nomadic, or seminomadic, reindeer herders who also practiced hunting and fishing for their livelihood, and experienced natural mortality due to the lack of advanced medical care (Itkonen 1948). Each population occupied large, partially overlapping, geographic areas, where people lived in small family groups or villages (Itkonen 1948). Child mortality rates ranged form 79% to 83% across the three populations. Population-specific twinning rates are given in Table 1.

TABLE 1. Twinning rates in three historical Sami populations of northern Scandinavia during the years 1710–1890.

Population	Twin deliveries	Singleton deliveries	Twinning rate (%)
Utsjoki	10	1280	0.78
Inari	35	2298	1.50
Enontekiö	36	3462	1.03

Statistical Analyses

To compare reproductive performance between twin mothers (mothers who had a twin delivery, n at max = 60) and singleton mothers (mothers who had only singleton deliveries, n at max = 1186), we calculated age at first and last reproduction, length of reproductive life span, interbirth intervals, and the number of offspring delivered and subsequently raised to adulthood (age 18) for each woman. For a comparison of fitness, we calculated a rate-sensitive estimate of fitness (individual λ) measured as the dominant eigenvalue of the individual-based projection matrix including age-specific fecundities and survival probabilities (McGraw and Caswell 1996). This estimate incorporates both the scheduling and the quantity of reproduction into a single estimate (for examples where individual λ has been used in human life-history studies, see Käär and Jokela 1998; Korpelainen 2000). Age-specific fecundity (measured as the number of offspring surviving to age 18) and survival were calculated in two-year periods throughout a women’s reproductive life span. Age-specific fecundities were further divided by 0.5 to account for male offspring not contributing directly to the growth rate in a sexually reproducing species. Values of λ were calculated with MATLAB software (Mathworks, Inc., MA).

Statistical comparisons of fitness and its components between twin and singleton mothers were conducted with two-tailed nonparametric Mann-Whitney U-tests, because the residuals could not be adequately transformed to satisfy the requirements of normality and homogeneous variances. Sample sizes in these analyses varied slightly due to variation in the completeness of the data.

We also examined the effect of twinning on individual λ after controlling for the effects of key maternal life-history traits (age at first reproduction and reproductive life span) on fitness, using multiple regression analysis with twinning included as a categorical covariate (i.e., as in analysis of covariance). In other words, we estimated linear selection gradients (i.e., standardized partial regression coefficients), which describe the intensity of selection on a trait (Arnold and Wade 1984). Age at last reproduction was omitted from this analysis due to obvious collinearity problems; reproductive life span is a linear combination of age at first and last reproduction. Interbirth interval was also excluded from the analysis, because it cannot be computed for mothers who

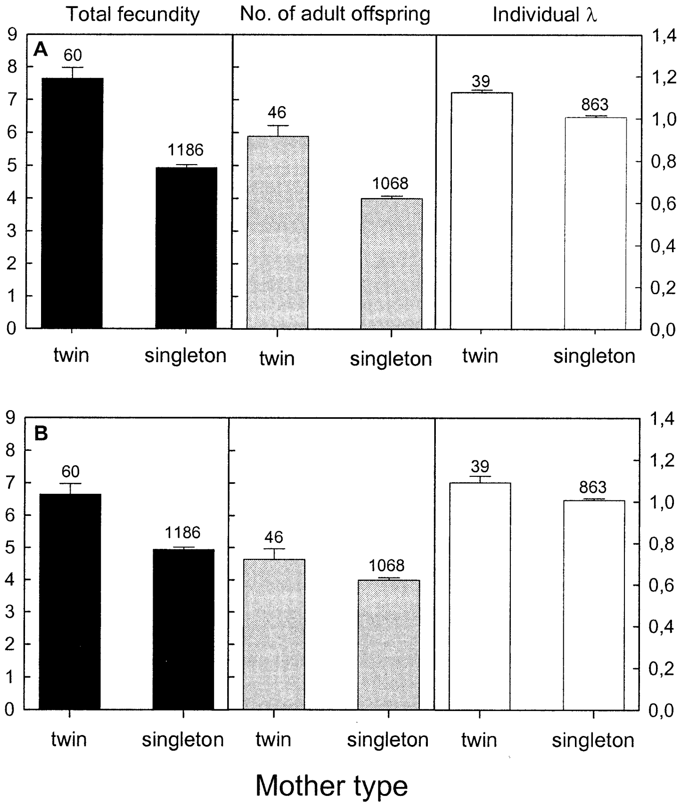

FIG. 1. Total fecundity (black columns), number of adult offspring (gray columns), and individual λ (white columns) of twin and singleton mothers in historical Sami. Error bars depict standard errors of means and numbers above the error bars depict number of observations. (A) represents original data and (B) represents data where twin births are replaced with the expected number/productivity of singleton births.

reproduced only once. Interactions between mother type (twin or singleton) and maternal life-history traits were first added into the model in order to reveal potential correlational selection between the studied life-history traits (Brodie 1992; Svensson et al. 2001), and, if statistically significant, included in the final model using the backward model fitting method.

Finally, we used generalized linear mixed models to compare survival probabilities of twin and singleton offspring to the age of 18 years. Other factors included in this model were gender and population. We fitted the model using the Generalized Estimating Equations (GEEs) with binomial errors and logit link function by procedure GENMOD of SAS (SAS Institute 1990; Zeger and Liang 1996; McCulloch and Searle 2001). Because the mothers were likely to vary in their likelihood of offspring survival (Madise and Diamond 1995; Curtis and Steele 1996), we included a family identity as a hierarchical factor into the model to account for the correlated measures of offspring survival within each mother. All interactions between explanatory variables were first added into the model and, if statistically significant ($\alpha < 0.05$), included in the final model using the backward model fitting method.

RESULTS

Comparison of Fitness and Key Life-History Traits

Twin mothers had higher lifetime fecundity ($Z = 7.07$, $P < 0.0001$), they raised more offspring to adulthood ($Z = 5.13$, $P < 0.0001$), and had higher fitness than singleton mothers ($Z = 4.64$, $P < 0.0001$) (Fig. 1A). These results were consistent across all three populations. Although twin mothers did not have shorter interbirth intervals, they did have longer reproductive life spans than singleton mothers; starting reproduction younger and terminating it later (Table 2).

To test the actual contribution of twin deliveries to this observed fitness advantage, we replaced the productivity of twin births with that of singleton births by calculating the probability of a singleton offspring reaching adult age for each twin mother, and used that probability as the replacement value. In the case of individual λ, we assigned offspring as survived or died based on a random number drawn from a binomial distribution with mother-specific probability of offspring survival to adulthood. The analysis showed that twin mothers had higher fecundity ($Z = 4.84$, $P < 0.0001$), tendency to raise more offspring to adulthood ($Z = 1.73$, $P = 0.084$), and greater fitness ($Z = 3.85$, $P < 0.0001$) than singleton mothers, even if they would have had a singleton offspring instead of a twins (Fig. 1B). This suggests that twin mothers were of higher phenotypic quality than singleton mothers.

However, the replacement of twin deliveries with the expected contribution of a singleton delivery resulted in significant reduction in lifetime reproductive success (paired t-test; 5.89 vs. 4.64, $t_{45} = 31.18$, $P < 0.0001$), but not in individual λ (1.12 vs. 1.09, $t_{38} = 1.28$, $P = 0.21$) of twin mothers. Thus, although twin mothers appeared to have been of higher phenotypic quality, these results partly suggest that twin mothers might have experienced fitness loss if they had produced a singleton delivery instead of a twin delivery, and therefore lend further support to the ''natural selection'' hypothesis. The result that the rate-sensitive measure of fitness, individual λ, failed to show a significant reduction in fitness is to be expected, because the production of twins is often related to high maternal age (Bulmer 1959; Gabler and Voland 1994; Sear et al. 2001), and calculation of λ weights the analysis in favors of early reproduction (i.e., λ is more insensitive to late reproduction).

TABLE 2. Comparison of key maternal life-history traits (mean ± SE) between mothers with twin deliveries and mothers producing singletons only; n = number of observations.

Life-history trait	n	Twin mothers	n	Singleton mothers	Z	P
Age at first reproduction	56	25.52 ± 0.59	1068	27.51 ± 0.17	−2.71	0.0068
Age at last reproduction	60	40.93 ± 0.62	1168	38.34 ± 0.20	2.60	0.0094
Reproductive life span	56	15.38 ± 0.92	1068	10.65 ± 0.22	4.71	<0.0001
Interbirth interval (months)	55	32.43 ± 1.59	891	35.54 ± 0.44	−0.61	0.54

TABLE 3. Selection gradient analysis of twinning and maternal life-history traits on individual λ. β denotes linear selection gradients (i.e., standardized partial regression coefficients) and γ to correlational selection gradients (Full model: $F_{5,853} = 384.37$, $R^2 = 0.693$, $P < 0.0001$).

Source	β	γ	df	MS	*F*	*P*
Mother type (twin/singleton)			1	0.016	5.49	0.0194
Age at first reproduction	−0.334		1	0.012	4.27	0.039
Reproductive life span	0.405		1	0.169	58.96	<0.0001
Mother type × age at first reproduction		0.333	1	0.011	3.65	0.057
Mother type × reproductive life span		0.435	1	0.020	6.93	0.0086
Residual			853	0.003		

Selection Gradient Analysis

Twin mothers had higher fitness (measured as individual λ) than singleton mothers (adjusted means: 1.09 vs. 1.06 for twin and singleton mothers, respectively), even after the effects of age at first reproduction and reproductive life span on fitness were accounted for (Table 3). Moreover, age at first reproduction was negatively, and reproductive life span positively, associated with fitness (Table 3). However, we also found a significant interaction (i.e., correlational selection) between mother type and age at first reproduction, and mother type and reproductive life span (Table 3). This suggests that selection for increased reproductive life span was stronger for singleton mothers, whereas the selection for earlier age at first reproduction was stronger for twin mothers (Fig. 2).

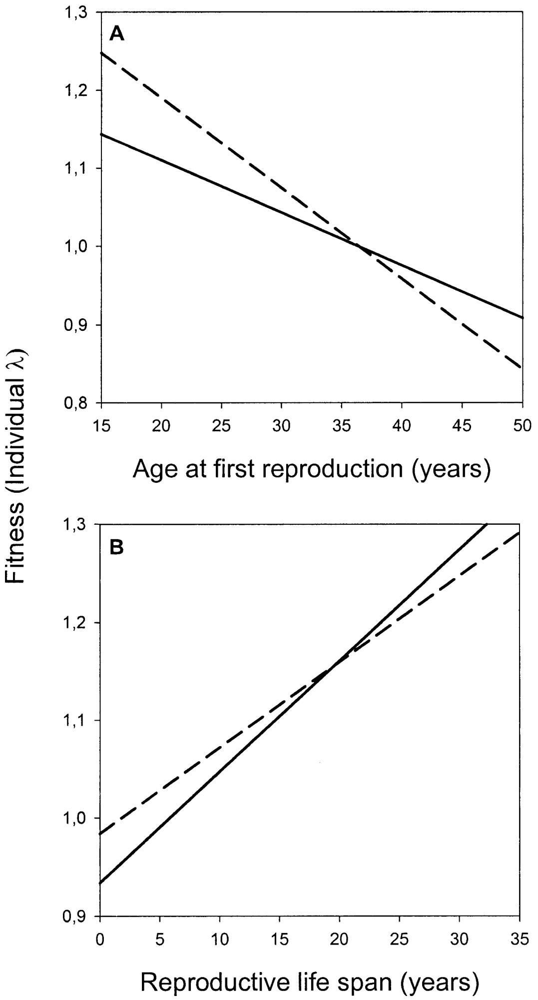

FIG. 2. Selection gradient analysis of age at first reproduction (A) and reproductive life span (B) on individual λ in twin (dashed line) and singleton mothers (solid line). Values of individual λ are predicted values from the model presented in Table 4.

Productivity of Singleton versus Twin Deliveries

Singleton survival to adulthood was similar in both twin (84%) and singleton mothers (82%) ($\chi^2_1 = 1.47$, $P = 0.23$), irrespective of their gender ($\chi^2_1 = 0.16$, $P = 0.69$). In contrast, the survivorship of twins (60%), again irrespective of their gender, was markedly lower than that of singletons (Table 4; Fig. 3). However, because twin births produce two offspring at a time, the twin deliveries of Sami mothers produced an average of 1.2 (2 × 0.6) adult offspring per delivery compared to approximately 0.8 offspring per singleton birth. Thus, twins were clearly more profitable to produce than singletons, again supporting the ''natural selection'' hypothesis. Although offspring survival differed between populations, this was independent of whether the offspring was a singleton or a twin (interaction between delivery type and population was not significant, Table 4). None of the other interactions met the acceptance criterion of $\alpha < 0.05$, and thus, for example, the productivity of a twin delivery was independent its sex ratio.

DISCUSSION

We have shown that mothers who produced twins during their lifetime generally had higher fitness than mothers who only produced one offspring at a time among historical Sami women. This fitness advantage of twin mothers was manifested through all components of fitness and reproductive life-history traits studied except for interbirth intervals, a latter being predicted by the ''insurance ova'' hypothesis. In addition, the productivity of twin deliveries of any gender combination markedly exceeded the productivity of singleton deliveries. However, the fitness benefits of twinning depended partly on the expressions of other life-history traits: when mothers started reproduction late, or had a particularly long reproductive life span, it was more advantageous to produce singletons only. These results indicate that the tendency for twinning in these historical human populations may not have been merely a maladaptive by-product of selection for other maternal reproductive traits, but likely favored by natural

TABLE 4. Factors explaining offspring survival probability to the age of 18 among premodern Sami. Number of offspring included in the analysis was 6722 and 141 for singletons and twins, respectively.

Source	df	χ^2	P
Delivery type (twin/singleton)	1	17.33	<0.0001
Sex	1	2.30	0.13
Population	2	13.34	0.0013

selection, although the strength of selection was likely to have been context dependent.

A fitness advantage of delivering twins over singletons has been suggested in recent studies by Gabler and Voland (1994), Lummaa et al. (1998, 2001), and Sear et al. (2001), although the way in which delivering twins conveys a fitness advantage is not known. When we replaced twin deliveries with the expected productivity of a singleton delivery, we found that twin mothers would have had higher fitness than singleton mothers independently of twinning. This together with the finding that reproductive performance of twin mothers exceeded that of singleton mothers in almost every measured variable indicates that twin mothers were generally of higher phenotypic quality, as proposed earlier by Sear et al. (2001). This may imply a ''silver spoon'' effect arising either from the higher genetic or environmental condition of twin mothers and result in a positive covariation between different fitness components (van Noordwijk and de Jong 1986; Houle 1991). However, this result, as such, is not sufficient to contrast the ''natural selection'' and ''insurance ova'' hypotheses, because the hypotheses differ in the expected direct benefits of twin deliveries on maternal fitness. Instead, it suggests that the propensity for twinning would have spread in favorable environmental conditions irrespective of whether twinning itself had been selectively beneficial, neutral, or detrimental.

In the Sami populations studied, the productivity of a twin delivery, irrespective of its sex ratio, was on average 1.2 adult offspring, whereas singleton deliveries produced only 0.8 adult offspring. Thus, these Sami remain the first premodern humans where twin deliveries, independently of the genders of twins, are found to be selected over singleton deliveries. Moreover, if twin mothers would have delivered a singleton instead of twins, they would have suffered fitness loss. These findings suggest that natural selection may have directly favored twinning in these populations, and thus strongly supports the ''natural selection'' hypothesis.

However, we also found that the intensity of selection for earlier age at first reproduction was stronger for twin mothers, whereas selection for increased reproductive life span was more intense for singleton mothers (see Fig. 2). In addition, Figure 3 shows that the regression lines for twin and singleton mothers cross, suggesting that production of singletons was more advantageous than producing twins, only when a woman had begun to reproduce at an old age (>37 years), or when she had a long reproductive life span (>20 years). In other words, fitness benefits of twinning were context dependent among the Sami women, as expected for traits under correlational selection (Brodie 1992; Svensson et al. 2001; Sinervo and Svensson 2002).

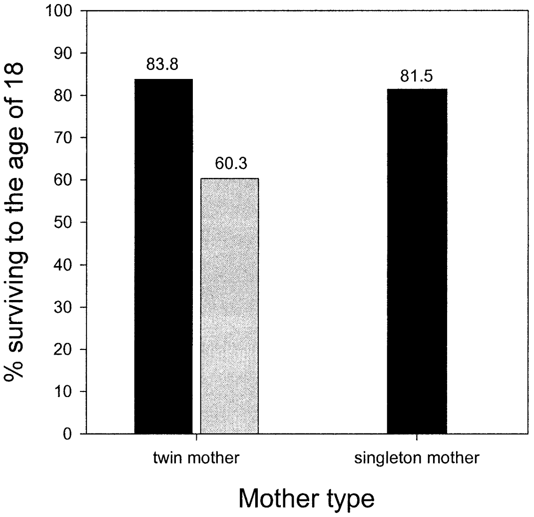

FIG. 3. Proportion of offspring surviving to adulthood (age 18) of twin and singleton mothers. Black columns represent offspring from a singleton delivery and gray column from a twin delivery.

The reason for the suggested maladaptive nature of twinning has often been the poor survival of twins: for example, in rural Gambia, only 17% of twins reached adulthood, compared with more than of 46% of singletons (Sear et al. 2001). Likewise, in rural Finland less than 34% of twins reached adulthood when the respective singleton survival was over 70% (Haukioja et al. 1989). Only in the archipelago of Southwestern Finland has the productivity of a twin delivery been shown to exceed that of a singleton delivery, but these only concerned girl-girl twins (Lummaa et al. 2001). High productivity of twinning in these Sami populations reflects relatively low overall offspring mortality of both twins and singletons in both genders compared to other populations studied (see Fig. 3).

These results do not support the view that twinning was merely a maladaptive by-product of selection for other maternal reproductive traits, such as polyovulation. This ''insurance ova'' mechanism (Anderson 1990) is suggested to have evolved to account for the high embryo and fetus loss in humans (estimated to range from 15% to 78% of all conceptions, reviewed in Forbes 1997). One prediction of this hypothesis is that twin mothers should be able to conceive more rapidly due to the higher rate of polyovulation. Evidence for shorter birth intervals among twin mothers suggests that this might be the case in some populations (Bulmer 1959; Allen and Schachter 1971; Hogberg and Wall 1992: Sear et al. 2001; but see Lummaa et al. 1999). In this study, twin mothers did not have shorter interbirth intervals than singleton mothers. More likely, the fertility advantage of twin mothers was manifested by their earlier onset, and later termination, of reproduction.

Despite the observed selection for twinning, population twinning rates indicate that twinning was a rather rare event among the Sami studied (Table 1). One possible explanation for this may be that the genetic propensity for twinning, although carried by many females, may only be expressed under favorable conditions, or among high quality individuals. Assuming that the genetic propensity for twinning is more likely to be expressed under favorable conditions, the twinning rate of the population should be an underestimate of the frequency of females carrying the genes that promote twinning (''vanishing twin phenomenon,'' cf. Boklage 1990). Unfortunately, we were unable to test this idea due to the lack of records of the appropriate variables reflecting environmental conditions or family wealth. We may also expect that the frequency of genes promoting twinning was affected by the costs and benefits of twinning. The benefits of twinning may often be overcome by the costs of increased risk of both maternal and offspring mortality and production of defective offspring (Ball and Hill 1999), particularly when the environment turns unfavorable. Moreover, because twin births are often related to high maternal age (e.g., Bulmer 1959; Gabler and Voland 1994; Sear et al. 2001), high mortality may simply have reduced the number of old females in a population, and thus lowered population twinning rates. Therefore, explanations for low twinning rates in humans may be both the condition-dependent expression of genes promoting twinning and strong selection against twinning in temporally variable environments.

We have shown here that twin mothers generally had higher reproductive success than singleton mothers, and that twin deliveries themselves had a positive effect on fitness over singleton deliveries in these historical Sami populations. However, the strength of selection on twinning appears to have been context dependent: if mothers begun to reproduce at very late age, or if they had a long reproductive life span, it was more beneficial to produce singletons only. Despite the higher fitness of twin mothers, twinning rates of these populations may have remained low because the propensity for twinning may be expressed only in favorable conditions, and temporally variable environment may impose strong selection on twinning during unfavorable periods.

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