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The fitness of twin mothers: evidence from rural Gambia

by

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Abstract

We used a longitudinal database from a natural fertility population in rural Gambia to compare the overall fertility of mothers who had given birth to twins at some point in their reproductive history and mothers who had only ever given birth to singletons. We found that twin mothers had shorter birth intervals, higher age-specific fertility and more surviving children than singleton mothers. This suggests that, despite the considerably higher mortality of twins found in this population, twin mothers have a fitness advantage over singleton mothers, even in the absence of modern medical care. We ran a simple simulation model to estimate the relative fitness of twin and singleton mothers, and found that the model also estimated higher fitness for twin mothers. Further, girls who went on to become twin mothers were of higher anthropometric status than those who became singleton mothers during their teenage years.

Key words: twins, fertility, polyovulation, anthropometric status

Introduction

Twin births are a relatively rare event in humans, though twinning rates vary considerably across populations (Bulmer, 1970; Pison, 1992). The twinning rate in sub-Saharan Africa overall is about 20 per 1000 (‰) births (Pison, 1992): estimates range from a low of 11 ‰ (in Kenya: van Ginneken and Muller, 1984) to 45 ‰ (in Nigeria: Nylander, 1969). These differences are thought to be due to variation in the rate of dizygotic twinning, as monozygotic twinning rates are usually found to be relatively constant at 3.5-4 ‰ in most populations studied (Bulmer, 1970).

The rarity of twinning suggests that women are adapted to bear a single offspring per gestation. If this is the case then why does twinning exist at all? The high mortality rates associated with multiple births for both mother (e.g. Haukioja et al., 1989; Gabler and Voland, 1994; McDermott et al., 1995) and child (e.g. Cantrelle and Leridon, 1971; Pison, 1992; Guo and Grummer-Straun, 1993; Gabler and Voland, 1994; McDermott et al., 1995; Beiguelman and Franchi-Pinto, 2000) imply that twinning is maladaptive. Dizygotic twinning, which results from the fertilisation of two separate ova, is known to have a genetic basis (e.g. Wyshak, 1965; Schmidt et al., 1983) so is potentially subject to natural selection against deleterious traits. That a tendency to produce twins is still maintained in human populations, albeit at a low level, suggests that women with the twinning tendency may have a fitness advantage over other women despite the lower productivity of twin compared to singleton births. A profitable approach to investigate this may be to compare the overall fertility of twin and singleton mothers, rather than concentrating on twin births themselves. Fertility is defined as the total number of births to a woman. Completed fertility is therefore the total number of births to a woman at the end of her reproductive lifespan. Fecundity is the physiological capacity to bear children. Any fitness advantage should only apply to mothers of dizygotic twins, and not mothers of monozygotic twins. Monozygotic twinning, the division of a single fertilised egg into two embryos, is not thought to be an inherited trait.

Evidence that twins are conceived more rapidly than singletons has been found in a number of Western populations, which suggests higher fecundity of twin mothers (Allen and Schachter, 1971; Bulmer, 1959a; Eriksson and Fellman, 1967; Hogberg and Wall, 1992). One study which distinguished between mothers of monozygotic twins and mothers of dizygotic twins found that only dizygotic twin mothers had a fecundity advantage over singleton mothers (Philippe and Roy, 1989), as predicted by the hypothesis that dizygotic twinning is maintained in human populations because of a fitness advantage. In contrast, a study of a historical Finnish population found no significant difference in the length of birth intervals between twin and singleton mothers (Lummaa et al., 1999). Higher completed fertility of twin mothers has also been observed in a number of populations (Gabler and Voland, 1994; Lummaa et al., 1998; Madrigal, 1995). In all three cases, this higher fertility was more than enough to compensate for the higher mortality of twins so that twin mothers also had higher fitness (i.e. more children surviving to adulthood) than mothers of singletons. Again, at least some historical Finnish populations appear to contradict this trend (Lummaa et al., 1998). However, most studies of contemporary populations have investigated populations where medical care and/or contraception are available. The Finnish studies that failed to find higher fitness among twin mothers used historical datasets from populations where medical care was limited. Based on these Finnish results, Haukioja et al. (1989) has suggested that twin births did not confer any fitness advantage in the past, when the high mortality rate of twins negated the potential gains of a twin birth. If twin mothers have a fitness advantage over singleton mothers then a tendency towards twinning may be selected for, even if a twin birth is no more productive than a singleton birth, provided that mothers of twins have higher overall fertility than mothers without the twinning tendency. We tested the hypothesis that twin mothers have higher fertility than singleton mothers using data from a population where no contraception and little medical care was available, and as a consequence mortality and fertility were both high. In addition, we compared the sex ratio of the children of twin and singleton mothers and the anthropometric status of twin and singleton mothers to determine whether twin mothers have other phenotypic characteristics which distinguish them from women who have never given birth to twins.

Data

The data we use come from four villages in rural Gambia. This area has been the site of a long-term study by the Medical Research Council (MRC) since 1950. Between

1950 and 1980 Sir Ian McGregor collected data from these villages in order to investigate the effects of disease in a tropical environment (McGregor, 1991). In 1950 he set up a system whereby all births and deaths that occurred in these four villages were recorded by literate village recorders. He also returned at least once a year to the study site to conduct surveys in which he collected data on the anthropometric and health status of individuals. During these surveys additional information on marriage, migration and residence patterns was collected to supplement the demographic information obtained by the village recorders. In 1974 the MRC Dunn Nutrition Unit also began research in the area. Their focus was on the nutritional status of this population, and they set up a permanent research station in one of the villages, Keneba. As part of this research station a medical clinic was established, which has given free medical care to all villagers since 1974. This has affected the demography of the study site by dramatically reducing mortality and making contraception available (Lamb et al., 1984; Weaver and Beckerleg, 1993). We have therefore confined the analysis that follows to the period between 1950 and 1974, when the area was typical of a traditional high fertility, high mortality Gambian community.

The residents of these Mandinka villages are patrilineal, patrilocal and Muslim. The villages largely depend on subsistence agriculture. Women are responsible for much of the subsistence work, while men supplement their subsistence farming with a little cash cropping of groundnuts. In this polygynous society, marriage for women occurs early and is universal. Divorce is not uncommon, but remarriage follows rapidly so women spend very little time outside a marital union during their reproductive years. Between 1950 and 1974 both fertility and child mortality were high: women averaged a total of about 7 livebirths but more than 40% of their children died before the age of 5 years.

Results

Of 3136 births between 1950 and 1974, 50 were twin births (there were no higher order births): a twinning rate of 15.9 ‰. Twinning rates increase with both maternal age and parity (Fig. 1). This pattern is broadly similar to that observed in other studies, though most find an increase with maternal age up until the late 30s after which it declines (e.g. Bulmer, 1959; Gabler and Voland, 1994 but see Hogberg and

Wall, 1992). When both maternal age and parity are entered into a logistic regression on the probability of twin birth, maternal age is significantly related to twinning but parity is not (maternal age: $\chi^2 = 6.18$, df = 1, p = 0.013; parity: $\chi^2 = 0.11$, df = 1, p = 0.735).

Mortality

Table 1 gives mortality rates for twins, singletons and singleton siblings of twins born between 1950 and 1974. Stillbirth rates and particularly neonatal mortality rates are considerably higher for twins than for their singleton siblings or other singletons. Mortality rates during the post-neonatal period are only slightly elevated for twins, however, and mortality rates between 1 and 14 years of age are slightly lower. This pattern of very high mortality in early life followed by mortality rates similar to singletons in later childhood (as shown in Fig. 2) conforms with other studies on twin mortality (Guo and Grummer-Straun, 1993; Pison, 1992). This results in less than 20% of liveborn twins reaching adulthood, compared to more than 40% of singletons.

Multilevel models were used to analyse the effects of being a twin or a singleton sibling of twins on the probability of stillbirth or child death. In recent years, a number of studies have found evidence of familial association in mortality risks which may be due to genetic, behavioural or socio-economic factors that are shared by children of the same mother (Das Gupta, 1990; Madise and Diamond, 1995; Curtis and Steele, 1996). If there is a correlation between the survival probabilities of children with the same mother, then observations are not independent. The multilevel approach allows for correlation in mortality risks between siblings by inclusion in the model of a family-specific random effect. To analyse the effects of multiple birth status on stillbirths a binary response model was fitted to the probability of stillbirth using MLwiN (Goldstein et al., 1998). This model takes the form:

$$\log\left(\frac{p_{ij}}{1 - p_{ij}}\right) = \alpha + \boldsymbol{\beta}'\mathbf{x}_{ij} + u_j$$

where p_{ij} = is the probability that child *i* in family *j* is stillborn; α is a constant; $\mathbf{x}_{ij}$ is a vector of covariates with associated parameters $\boldsymbol{\beta}$; and u_j is the family-level random effect which is assumed to follow a normal distribution with zero mean and variance σ_u^2. This model reveals that, controlling for maternal age at birth, birth order and sex of child, being a twin is a highly significant predictor of being stillborn ($\chi^2 = 11.91$, df = 1, $p < 0.001$), whereas singleton siblings of twins do not have elevated risks in comparison to other singleton births ($\chi^2 = 0.30$, df = 1, $p = 0.581$).

Multilevel discrete-time event history models were used to analyse the effects of being a twin or a sibling of twins on the mortality of livebirths. In this case the probability of death is modelled as a function of time, again using MLwiN. Define y_{tij} as the child survival indicator, where $y_{tij} = 1$ if child i in family j dies at time t and $y_{tij} = 0$ if the child survives beyond time t. We use a random effects discrete-time logit model which takes the form:

$$\log\left(\frac{h_{tij}}{1 - h_{tij}}\right) = \alpha_t + \boldsymbol{\beta}'\mathbf{x}_{tij} + u_j$$

where $h_{tij} = \Pr(Y_{tij} = 1 \mid Y_{t-1,ij} = 0)$ is the hazard that child i in family j dies at time t; α_t is a function of time; $\mathbf{x}_{tij}$ is a vector of covariates (which may be constant over time or time-varying) with associated parameters $\boldsymbol{\beta}$; and u_j is the family-level random effect which is assumed to follow a normal distribution with zero mean and variance σ_u^2. These models have the advantage of being able to include censored data (data where the event of interest has not yet occurred). Children were censored at the age at which they were last seen alive if they disappeared from the dataset through migration, or on the 1st January 1975 if they were still alive at this date. Separate models run on neonatal, post-neonatal, 1-4 year and 5-14 year mortality, again controlling for maternal age at birth, birth order and sex of child, indicate that being a twin significantly elevates the risk of mortality for neonates ($\chi^2 = 74.27$, df = 1, $p < 0.001$) and post-neonates ($\chi^2 = 55.10$, df = 1, $p < 0.001$). Odds ratios obtained from the models suggest that the risk of death for twins is approximately 12.5 times greater than that of singletons during the neonatal period but only 1.28 times greater during the post-neonatal period. Mortality rates between 1 and 4 years ($\chi^2 = 1.33$, df = 1, $p = 0.248$) and between 5 and 14 years ($\chi^2 = 2.58$, df = 1, $p = 0.108$) are not significantly greater for twins. The probability of death for singleton siblings of twins does not differ from that of other singletons at any age (neonatal model; $\chi^2 = 1.01$, df = 1, p = 0.314; post-neonatal model: $\chi^2 = 0.45$, df = 1, p = 0.500; 1-4 years model; $\chi^2 = 1.70$, df =1 , p = 0.192; 5-14 years model: $\chi^2 = 0.25$, df = 1, p = 0.613).

Maternal mortality rates are also usually observed to be higher for twin than for singleton births. We only have data on maternal deaths for two of the four villages, so our dataset is too small to permit a meaningful analysis, but of the 16 maternal deaths that occurred between 1950 and 1974, one of them was the result of a twin birth. This gives rates of maternal mortality of 3.3% per twin birth and 0.8% per singleton birth.

Fertility

We performed a number of tests comparing the fertility of twin and singleton mothers between 1950 and 1974. Twin mothers are defined as those women who gave birth to twins at some point during their reproductive careers; singleton mothers are women who only ever gave birth to singletons. Though we only analysed fertility up until the end of 1974 to exclude any possible effects of the medical centre on fertility, we do have demographic records up until the present. We therefore used these records to identify as twin mothers women who gave birth to twins after 1974. As the majority of women who were reproducing in our 1950-74 sample would have completed their fertility by 1999, we have complete fertility histories for all women who remained resident in these four villages. This should exclude the possibility of biasing the sample of twin mothers towards younger women by only including women who gave birth to twins early in their reproductive careers. Unless otherwise stated, for all the following analyses we only included women born in 1935 or later, as these women would have been 15 years or more in 1950. Very few women gave birth before the age of 15 years, so by only including women who were at least 15 years old in 1950 we can be reasonably confident that none of our fertility histories are left-censored. If women disappeared from the dataset, because of death or migration, they were censored at the age at which they were last recorded in the dataset and no further assumptions were made about their fertility. Those women who were known to still be alive and resident in one of the four villages after 1974 were censored at the age they had reached on 1st January 1975.

Firstly, we compared the fertility of twin and singleton mothers, controlling for age. We then looked at components of fertility: inter-birth intervals and age at first and last birth.

Age-specific fertility

We analysed the correlation between fertility and being a twin mother, controlling for age, between 1950 and 1974 using ANCOVA models (Fig. 3). Each women was entered into the model as one observation point: her fertility at her age of censoring was the response variable of interest. We ran 4 models using 4 different dependent variables: total number of births (including stillbirths) before 1975, number of livebirths before 1975, number of deliveries before 1975 (i.e. twins were counted as a single delivery) and number of surviving children on 31st December 1974. In each model the woman's age at censoring was included as a covariate. In each case there was a highly significant relationship between the measure of fertility and being a twin mother. Twin mothers had significantly more births ($F_{1,631} = 21.53$, $p < 0.001$), more livebirths ($F_{1,631} = 16.34$, $p < 0.001$), more deliveries ($F_{1,631} = 7.19$, $p = 0.008$) and more surviving children ($F_{1,631} = 6.56$, $p < 0.011$) than singleton mothers. This suggests that the higher fertility of twin mothers is not solely due to the twin birth, and that the higher mortality of twins does not cancel out the twin mothers' fertility advantage.

Birth intervals

All birth intervals between 1950 and 1974 were included in this analysis. Table 2 shows the mean length of birth intervals after the birth of twins, singleton siblings of twins and singletons. Three types of interval are shown: all intervals, intervals after livebirths and intervals between livebirths where the index child survived to at least 1 year (to control for confounding effects of the death of the child). In all cases, the mean inter-birth interval after singleton siblings of twins is approximately 3.5 months shorter than after singletons. This data has been subjected to a fully controlled multi-level discrete-time hazards analysis. The model is identical to that described for the analysis of child mortality, but in this case we are modelling the probability of birth, rather then death, over time. Again, the multi-level approach is necessary to control for the correlation between the length of the birth intervals of any one mother. This model also controlled for a number of other variables known to influence the length of birth intervals: age of death of index child, maternal age, birth order, and sex of child. This model confirmed that twin mothers have significantly shorter birth intervals than mothers of singletons (χ^2 = 12.82, df = 1, p < 0.001).

Age at first birth

All women born in 1935 or later who reached the age of 25 years before 1975 and who were 25 or less when they gave birth to their first child were included in this analysis. In this population girls are usually married before puberty and start to have intercourse with their husbands at menarche (Thompson, 1965), so most of the variation in age at first birth is likely to be due to variation in physiological capacity to conceive, rather than variation in age at marriage. It is probable that women who were older than 25 at their first birth either have missing information on earlier births, or have some physiological difficulties in conceiving so were excluded from the analysis. This population then seems an ideal test of whether mothers of twins conceive earlier than mothers of singletons. Mean age at first birth for mothers of twins is 18.77 ± 1.80 (n=26) and 18.84 ± 2.55 (n=249) for mothers of singletons (t = 1.710, df = 267, p = 0.859). There is thus little evidence that mothers of twins begin their reproductive careers earlier than mothers of singletons.

Age at last reproduction

For this analysis we included all women who were born in 1920 or later, who were at least 45 years old in 1975 (so would have had their last birth before 1975) and who survived to at least age 45 years before they died or were censored. Mean age at last birth for twin mothers in this sample was 39.8 ± 3.8 (n=9) and 36.8 ± 7.5 (n=100) for singleton mothers, which approached significance (t = -2.03, df = 14, p = 0.06).

Sex ratio of children

We analysed the sex ratio of children born to twin and singleton mothers. The sex ratio of children born to singleton mothers was close to 50:50 (1270/49.5% males and 1294/50.5% females). The children of twin mothers, particularly the singleton children of twin mothers, had a slightly male biased sex ratio (twins: 52/53.6% males and 45/46.4% females; singletons: 144/55.2% males and 117/44.8% females). Chisquared tests on these data indicate that the sex ratio of all three categories of children is not significantly different from 50:50 (singletons: $\chi^2 = 0.22$, df = 1, p = 0.636; twins: $\chi^2 = 0.50$, df = 1, p = 0.477; singleton siblings of twins: $\chi^2 = 2.79$, df = 1, p = 0.095).

Anthropometric status

We also compared the anthropometric status of twin and singleton mothers using measurements taken between 1950 and 1974 (Table 3). Firstly, to avoid the confounding effects that childbirth has on female nutritional status, we compared the nutritional status of girls who had not yet given birth but who went on to become mothers of twins or mothers of singletons. ANCOVA models were used for this analysis, and in all models village of residence was included as a fixed factor as there are known to be differences in nutritional status between the villages of this study (Billewicz and McGregor, 1982). At age 14 girls who became twin mothers were slightly, but not significantly taller, than girls who became mothers of singletons ($F_{1, 225} = 3.15$, p = 0.08). Girls who became twin mothers did have significantly higher weight-for-height than singleton mothers both when body mass index (BMI) was entered as the dependent variable ($F_{1, 225} = 11.76$, p = 0.001), and when weight was the dependent variable and height entered as a covariate ($F_{1, 224} = 11.10$, p = 0.001). We also compared the adult (i.e. 15 years and older) heights and weights of twin and singleton mothers. The mean heights of twin and singleton mothers were compared using an ANCOVA model, again controlling for village of residence. Twin mothers were slightly, but not significantly taller than singleton mothers ($F_{1, 330} = 1.32$, p = 0.251). Finally, the weights and BMIs of twin and singleton mothers were compared using multilevel regression models fitted in MLwiN. These models can be used on repeated measures data to control for the correlated measurements within a single woman by the inclusion of a random variable which is allowed to vary between women (Goldstein 1995). It is necessary to use these models on weight and BMI data because, unlike height, these measures of anthropometric status fluctuate during adulthood, due to variation in food availability, workload and the influence of disease. Though twin mothers were slightly heavier and had slightly higher BMIs, these were not significant differences (weight: $\chi^2 = 0.27$, df = 1, p = 0.604; BMI: $\chi^2 = 0.43$, df = 1, p = 0.510).

Fitness of twinning

We are unable to test empirically whether twin mothers would have had higher fitness (i.e. more children surviving to adulthood) than singleton mothers under conditions of natural fertility and natural mortality because none of the women for whom we have accurate fertility data reached menopause before the medical clinic began providing medical care to our study villages. Instead we have modelled mathematically the relative fitness of twin and singleton mothers using a simple simulation model. Table 4 lists the parameters used in the model (all calculated from data collected between 1950-74). In this case we calculated fitness for women at the start of their reproductive careers as the total expected number of daughters surviving to 15 years.

$$\text{Fitness} = \sum (b/2)\, l_{\text{child}}\ e^{\mu\text{birth}}\ l_{\text{mother}}(x),$$

where b = number of children per delivery (i.e. singleton birth $b = 1$, twin birth $b = 2$), l_{child} = probability of the child surviving to age 15 years, μbirth = probability of maternal death, and $l_{\text{mother}}(x)$ = probability of the mother surviving to age x (which is calculated from the product of the annual mortality rate and the length and number of interbirth intervals and the probability of dying following each birth). We assume that twin mothers have only one twin birth during their reproductive career and that they have a probability of 0.11 of having a twin birth per delivery. Women with no twin births or more than one are omitted from the analysis. The simulation is run a sufficient number of times for the variance in fitness to drop below the reported level of accuracy.

Using this model we estimate that singleton mothers have a fitness of 1.56 (daughters surviving to adulthood) and twin mothers a fitness of 1.63. We have used maternal mortality values obtained from our Gambian dataset for this model, but these were calculated from small sample sizes. Other estimates of maternal mortality in the Gambia are somewhat higher than our own: maternal mortality was estimated retrospectively to be about 1% per birth in the mid 1970s (Graham et al., 1989) and a prospective study in the early 1980s obtained an even higher figure of 2.4% per birth (Greenwood et al., 1987). Other estimates of maternal mortality associated with twinning in populations without modern medical care are also higher than our own estimates: 4.8% and 4.4% per twin birth in historical Germany (Gabler and Voland, 1994) and Finland (Haukioja et al., 1989) respectively. Though there is undoubtedly variation in the level of maternal mortality between populations it is possible we have underestimated maternal mortality from our small dataset. We therefore ran the model a number of times using different levels of maternal mortality to estimate how high maternal mortality would have to be to counteract the fertility advantage of twin mothers. The model shows that maternal mortality associated with a twin birth would have to be about 14% before the fitness of twin mothers is reduced to that of singleton mothers (Fig. 4).

Discussion

We have demonstrated that during a period of natural fertility and mortality twin mothers have higher age-specific fertility, shorter birth intervals and later age at last reproduction than singleton mothers. The faster birth intervals indicate that twin mothers are able to conceive more quickly than singleton mothers. That twin mothers also had significantly more surviving children than singleton mothers suggests that the higher fertility of twin mothers compensates for the higher mortality of twins. We find clear differences in the fertility of twin and singleton mothers despite the heterogeneous nature of the twin mother sample, which presumably includes both mothers of dizygotic twins and mothers of monozygotic twins (who are not predicted to have a fertility advantage over singleton mothers). These results indicate a fitness advantage for twin mothers. One factor which may affect the relative fitness of twin and singleton mothers is the higher maternal mortality associated with a twin birth. However, given that maternal mortality is a relatively rare event (even after the birth of twins) and that twin mothers are only at higher risk after their twin births and not their singleton births, it seems unlikely that the higher maternal mortality associated with twin births would be enough to reduce the fitness of twin mothers to the level of singleton mothers. Our simple simulation model suggests that twin mothers do have a fitness advantage over singleton mothers, and that the level of maternal mortality associated with twinning would have to be unrealistically high to eliminate the fitness advantage of twin mothers.

One hypothesis which has been proposed to explain the maintenance of twinning within human populations is the insurance ova hypothesis (Anderson, 1990). This suggests that twinning is an 'error' that arises as a side effect of polyovulation, a mechanism which increases fertility by compensating for embryo mortality. Calculating the exact proportion of conceptions that fail to come to term is difficult but estimates vary from a low of 15% (of clinically recognisable pregnancies) to a high of 78% (estimated from a mathematical model of the likelihood of pregnancy: reviewed in Forbes, 1997). If a substantial proportion of pregnancies is aborted, releasing more than one ovum each cycle should increase the probability that any one cycle will result in a live birth. This theory only applies to dizygotic twinning and not monozygotic twinning, as the former is dependent on polyovulation whereas the latter is not. Our analysis supports the prediction of the insurance ova hypothesis that twin mothers will have faster birth intervals and higher fertility than singleton mothers.

If this fitness advantage is genetic in origin then it is perhaps surprising that twinning rates are so low in human populations. It is possible that mothers of twins are the extreme end of a continuum of fertility which ranges from mothers without the tendency to polyovulate, through polyovulating mothers who do not give birth to twins to polyovulating mothers who do give birth to twins. Twin mothers may be those women who polyovulate most frequently, and therefore have the highest probability of conceiving twins, but there may also be variation among women in the probability that a twin conception will be brought to term. It is known that many more twins are conceived than born (the 'vanishing twin' phenomenon: Landy, 1982; Boklage, 1990; Kelly et al., 1991; Blumenfeld et al., 1992), and there may be some phenotypic qualities of twin mothers that allow them to bear the elevated costs of a twin pregnancy. Studies of Western populations have observed that twin mothers tend to be taller and heavier than singleton mothers (Campbell et al., 1974; Corney et al., 1981; Wyshak, 1981), and that twinning rates decline during periods of privation (Bulmer, 1959b). This suggests a link between high nutritional status and the ability to bear twins, just as relationships have been found between nutritional status and fecundity (Popkin et al., 1993; Tracer, 1996; Bentley, 1999; Sear, R., Mace, R. and McGregor, I.A., unpublished manuscript). The results of this study provide the first evidence that this relationship between twinning and nutritional status, although less marked than in modern Western populations, also holds in a natural fertility, natural mortality environment.

Further support for the hypothesis that twin mothers are ‘supermums’ may be obtained from the sex ratio of their children. The sex ratio of twins themselves tends to be lower than that of singleton children (Bulmer, 1970), although this was not found in our study. However, Gabler and Voland (1994) found that the singleton children of twin mothers were significantly male biased in 18th and 19th century Germany. Male foetuses are larger than female foetuses and male babies have a significantly higher energy intake than female infants (Hoffmans et al., 1988). Male children are therefore a greater energetic drain on their mothers during pregnancy and lactation, and women may need to be in relatively good condition to give birth to many sons. Our results, though in the expected direction of male bias among the singleton children of twin mothers, do not show that the sex ratio of twin mother’s children is significantly different from 50:50.

The phenotypic quality of the mother may influence twinning rates by affecting the rates of polyovulation, and/or by affecting the probability that a twin conception is brought to term. Twinning rates increase with maternal age: in this study twinning occurs at a frequency of 5.8 ‰ among 15-19 year old mothers, but 31.7 ‰ among mothers over the age of 40 years. Anderson suggested that this increase in twinning rates might be due to an adaptive increase in polyovulation with age, to compensate for the increasing number of defective ova that are produced. It has also been suggested that the screening mechanism which rejects defective embryos relaxes with increasing maternal age (Stein et al., 1986). This may occur as a part of the senescence of the reproductive system, although Kloss and Nesse, (1992) propose that it is an adaptive response to the mother’s declining reproductive capacity, as the costs of rejecting a viable embryo begin to outweigh the costs of producing a defective child. If the embryo screening mechanism is also responsible for reducing ‘defective’ multiple conceptions to the optimum brood size of one, then both mechanisms may be responsible for the increasing incidence of twinning with maternal age (Ball and Hill, 1999). It is unlikely that twin births themselves are ever adaptive (at least in the high mortality environments characteristic of the vast majority of human history), but there is evidence that the survival probabilities of twins may increase with increasing maternal age (Voland and Gabler, 1994). The costs of the ‘error’ of a twin birth may therefore be lower in older women. Similarly, the sensitivity of the embryo screening mechanism may be conditional on the phenotypic fitness of the mother, being more rigorous when the mother is in poor condition and the costs of a multiple pregnancy or defective child would be high. Nevertheless, it should be noted that this embryo screening mechanism is controversial (Krackow, 1998; Warburton and Warburton, 1998).

In summary, in a natural fertility and high mortality environment twin mothers have higher fertility than singleton mothers that cannot merely be accounted for by their twin births. There is some evidence that this may lead to higher fitness among twin mothers. We have also found indications that twin mothers may be of higher phenotypic quality than women who only give birth to singletons. This suggests that variation in body condition of women may contribute to variation in the probability of twinning within populations. This does not necessarily imply that twinning itself is adaptive, it may be a conditional strategy in women of high phenotypic quality, or it may be that women of high phenotypic quality merely suffer fewer costs from the error of a twin birth.

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Table 1: mortality rates for twins, singleton siblings of twins and singletons born between 1950 and 1974

	Twins	Singleton siblings of twins	Singletons
N (all births)	99*	263	2583
Stillbirth rate (per 1000 births)	111.11	45.63	37.94
N (livebirths where age at censoring† known in months)	75	217	2058
Neonatal mortality rate‡ (per 1000 livebirths)	429.53	83.53	67.50
Post-neonatal mortality rate§ (per 1000 livebirths)	160.00	133.64	138.89
1-4 years mortality rate (per 1000 livebirths)	160.00	208.82	205.14
5-14 years mortality rate (per 1000 livebirths)	13.70	29.27	27.00
Proportion of liveborn children that:			
survived to 15 yrs	0.17	0.41	0.465
died before 15 yrs	0.76	0.45	0.435
censored† before 15 yrs	0.07	0.14	0.10

* 99 twins are included in the analysis because one mother gave birth to one twin but died before the second could be delivered

† censored cases are those where the event of interest (i.e. death) has not yet occurred

‡ deaths in first month of life

§ deaths between 1-11 months of life

Table 2: mean length of inter-birth intervals ± SD (in months) after twins, singleton siblings of twins and singletons born between 1950 and 1974

	Twins	Singleton siblings of twins	Singletons
All intervals			
N	37	232	1952
IBI	27.95 ± 15.65	30.29 ± 11.60	33.81 ± 16.15
After livebirths			
N	35	222	1887
IBI	28.26 ± 16.03	30.77 ± 11.45	34.15 ± 15.75
Between livebirths where index child (or at least one twin) survived to 1 year			
N	19	157	1347
IBI	35.16 ± 16.23	32.82 ± 9.56	36.45 ± 14.43

Table 3: comparison of anthropometric status of twin and singleton mothers. All measurements are dry season measurements taken from non-pregnant women between 1950 and 1974 (± SD)

	Age 14 years		Adult (15+ years)	
	Twin mothers	Singleton mothers	Twin mothers	Singleton mothers
N	14	215	25	304
Height (cm)	147.72 ± 8.23	146.52 ± 6.88	157.51 ± 5.77	156.32 ± 5.64
Weight (kg)	38.65 ± 7.89	35.88 ± 5.88	50.08 ± 6.69	47.62 ± 5.88
Body mass index (kg/m^2)	17.51 ± 1.90	16.61 ± 1.46	20.10 ± 1.82	19.48 ± 1.79

Table 4: parameters used to model fitness of twin and singleton mothers

	Twin mothers	Singleton mothers
Adult mortality (per year)	0.007	0.007
Maternal mortality (per delivery)	0.008 (singleton birth) 0.033 (twin birth)	0.008
Age at first birth (years)	18.8	18.8
Age at last birth (years)	39.8	36.8
Length of reproductive lifespan (years)	21.6	18.9
Mean interbirth interval (years)	2.58 (after singletons) 2.42 (after twins)	2.83
Probability of twin birth (per delivery)	0.11	0
Probability of child surviving to 15 years	0.41 (singletons) 0.17 (twins)	0.465

Figure 1: twin births per 1000 deliveries by maternal age at birth

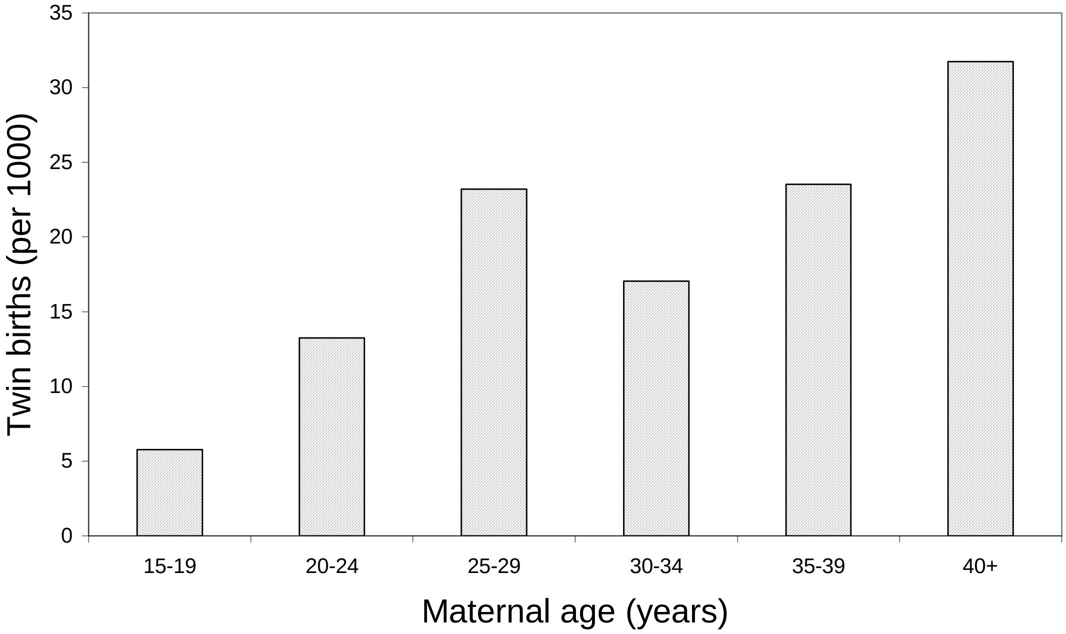

Figure 2: Kaplan-Meier survival plot comparing survival rates of liveborn twins (dashed line), singleton siblings of twins (solid line) and other singletons (dotted line) between 1950-74

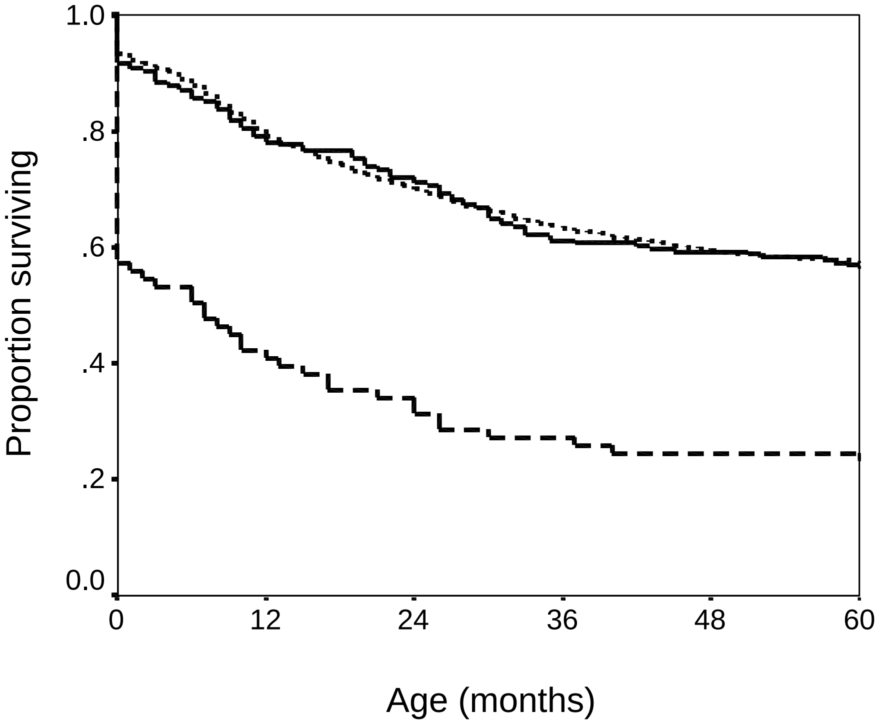

Figure 3: age-specific fertility ± SE of twin mothers (open bars) and singleton mothers (hatched bars) between 1950-74

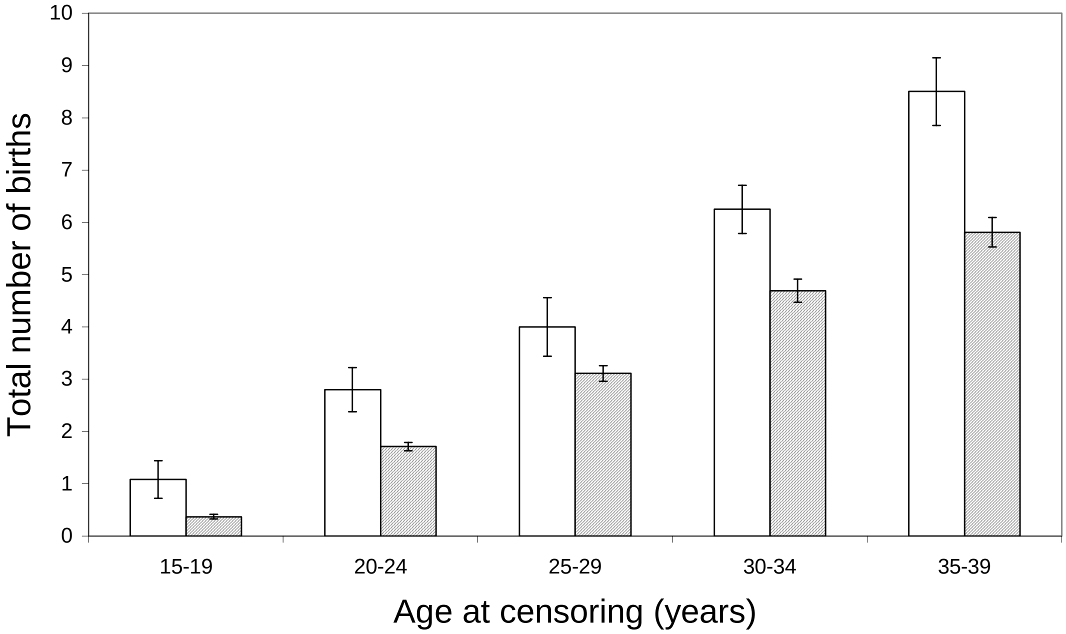

Figure 4: fitness (measured by number of daughters surviving to age 15 years) estimated from simulation model for twin (dashed line) mothers by level of maternal mortality associated with twin births. Solid line shows estimated fertility of singleton mothers with constant level of maternal mortality associated with singleton births (0.008%)