

Does polyovulation counterbalance a high abortion rate in humans?

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Abstract

We tested the fertilization insurance hypothesis of human twinning, which suggests that twin births should be seen as an unadaptive consequence of polyovulation compensating for high spontaneous abortion rates in humans. Females with high incidence of polyovulation were predicted to benefit by becoming pregnant more rapidly and by having a higher likelihood of successful pregnancy than other females. As a disadvantage, polyovulating mothers should be more prone to presumably maladaptive twin deliveries. We studied birth intervals of twin and singleton mothers living in pre-industrial Finland by using demographic records of local churches. The analysis revealed that, contrary to the prediction of the fertilization insurance hypothesis, polyovulating females did not display shorter intervals between deliveries. Therefore, if the tendency towards polyovulation and therefore occasional twin births in humans is adaptive and maintained by natural selection, other benefits should be evident.

Introduction

Twinning rates in human (*Homo sapiens* L.) populations vary from 0.6 to 4.5% (Vogel & Motulsky, 1986). As twin births have probably not constituted any direct fitness advantage for females in the past due to the high child and maternal mortality risk following twinning (Haukioja *et al.*, 1989; but see Lummaa *et al.*, 1998a), twin frequencies in different populations remain enigmatic. Anderson (1990) suggested that the purpose of polyovulations might be to produce 'insurance ova'. Spontaneous abortions have been estimated to occur in 15–78% of all human conceptions (for review, see Forbes, 1997). Mothers with a higher incidence of polyovulation are therefore predicted to benefit by becoming pregnant more rapidly and by having a higher likelihood of successful pregnancy (still with only one zygote normally surviving as viable newborn) than mothers who lack an effective fertilization insurance system. A disadvantage, however, is that polyovulating mothers should be more prone to presumably maladaptive twin deliveries.

Here we provide what is, to our knowledge, the first direct test of the insurance ova hypothesis. We compared

the birth interval length of mothers giving birth to at least one pair of twins during their lifetime with that of mothers delivering only singleton offspring. Mothers who gave birth to twins were expected to have a higher rate of polyovulations (Martin *et al.*, 1991; Boomsma *et al.*, 1992; Gilfillan *et al.*, 1996) and, if the insurance ova hypothesis applied, a more efficient fertilization insurance system than females never giving birth to more than one offspring at a time. In the light of Anderson's (1990) hypothesis, we predicted that the birth intervals of twin mothers would be shorter than those of singleton mothers, following from their expected greater ability to compensate for embryo (or fetus) loss during pregnancy by the release of extra ova.

Materials and methods

Our data were collected from the unique Finnish population registers which local churches have maintained since the early seventeenth century. Our study era covers the years from 1752 to 1850, therefore ending before industrialisation and improvement in health care were likely to have had significant effects on survivorship and standard of living. The five study parishes (Hiittinen 60°N 22°30'E, Ikaalinen 61°45'N 23°E, Kustavi 60°30'N 21°30'E, Pulkila 64°15'N 26°E and Rymättylä 60°15'N

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22°E) are situated in the south-west archipelago and southern inland areas of the country. During the study period, economic life of these populations was based almost exclusively on agriculture (also fishing in archipelago), thus reducing socioeconomic differences among individuals.

We analysed the birth intervals of a total of 165 twin mothers. Each twin mother was paired with a control mother of equal age (± 3 years) who had delivered only singleton children during her lifetime. The control mother for a given twin mother had delivered a singleton offspring at the same time (± 3 weeks) as the twin mother delivered her twins, with the constraint that both had the same number of earlier children (for details, see Haukioja *et al.*, 1989). To ensure that the delivery frequency of a given mother was not biased for instance by a time lag in remarriage after the death of a spouse, we included in our analysis only women who had delivered all of their offspring while in a permanent marriage, and whose spouse did not die before the woman had reached the age of 40 years. The mean (\pm SE) lifetime offspring number for twin mothers was 7.49 ± 0.19 and that for singleton mothers 6.69 ± 0.18 ($n = 160$, $t = 3.36$, $P = 0.001$), but the reproductive success of twin mothers (number of offspring raised to adulthood) was either lower or equal to that of singleton mothers, depending on the environmental conditions (Lummaa *et al.*, 1998a).

Potential confounding elements able to affect the relationship between twinning and birth interval include various psychological and physiological factors that could independently affect birth intervals. In particular, the process of having twins may itself influence birth intervals for socioeconomic reasons. In our study, this was controlled by excluding from the analyses those birth intervals which followed a twin delivery. Another problem could arise if the fertility differences among women caused twinning to covary with birth interval by default, without polyovulation having evolved as an insurance policy. Our data show that although twin mothers gave birth to altogether larger numbers of babies, fertility in terms of number of lifetime deliveries did not differ between twin and singleton mothers (6.38 ± 0.19 vs. 6.69 ± 0.18 , respectively; $n = 160$, $t = 1.30$, $P = 0.19$).

Results and discussion

We found that the mean birth interval did not differ between mothers with a tendency towards twinning and mothers with only singleton offspring. The twin mothers' mean delivery interval, calculated over all births, was 34.1 ± 0.81 months and that of singleton mothers 35.0 ± 0.92 months ($n = 165$, $t = 0.77$, $P = 0.44$; the smallest difference significant at the α -level of 0.05 and 90% confidence would have been 3.6 months). Twin mothers tended to conceive more rapidly after the twin birth than control mothers after their singleton delivery

($n = 112$, $t = 2.34$, $P = 0.02$), but this was most likely a consequence of the higher infant mortality among twin offspring (in 9.1% of the twin deliveries both infants died within 3 weeks after the birth, while 1.8% of the singletons born at the same time died; $\chi^2 = 8.46$, d.f. = 1, $P < 0.01$). Interrupted lactation probably led to the faster resumption of the menstrual cycle in twin mothers. Excluding birth intervals following twin deliveries, the difference in the birth interval length of twin (34.44 ± 0.85 months) and singleton mothers (35.0 ± 0.92) was about half of a menstrual cycle ($n = 165$, $t = 0.46$, $P = 0.65$; the smallest significant difference would have been 3.7 months). The gestation period in twin pregnancies is about 3 weeks shorter than in singleton pregnancies (Bulmer, 1970), so the true difference in birth interval length may be shorter still.

Anderson (1990) suggests that polyovulation may contribute insurance against genetic defects as well as nongenetic developmental failures while monozygotic fission insures only against the latter. Thus, since the existence of monozygotic twinning at any frequency greater than zero cannot be explained by the insurance ova hypothesis, only an analysis of dizygotic twinning is directly relevant in testing the insurance ova hypothesis. Furthermore, since probably only production of dizygotic twins has a genetic component (Parisi *et al.*, 1983), only their production could have been moulded by natural selection. Although monozygotic twins represent a smaller fraction of all the twins born (Bulmer, 1970), we tried to analyse separately birth intervals of mothers who surely produced dizygotic twins to verify the results of the pooled data, which most likely consisted of both types of twin mothers. This analysis was based on a smaller sample size and, consequently, its statistical power to detect differences in birth intervals was relatively weak. Given the demographic nature of our data, we could assume that the group of mothers who delivered twins of different sex had a higher genetic tendency towards twinning than the others: all twins of an opposite gender are dizygotic, while twins of same sex may be either mono- or dizygotic. Restricting the group of twin mothers to those mothers whose twins were of different sex, we confirmed that the mean birth interval did not differ between twin and singleton mothers (twins 34.1 ± 1.26 months, singletons 35.2 ± 1.52 months; $n = 77$, $m = 2$, $P = 0.73$; the smallest significant difference would have been 5.5 months).

Our data do not lend support to Anderson's idea that twinning remains an epiphenomenon of adaptive fertilization insurance. Twin mothers with a higher incidence of polyovulation did not appear to derive an advantage from the trait in terms of increased birth frequency. This suggests that if the tendency towards polyovulation and therefore occasional twin births is adaptive and maintained in populations by natural selection, other benefits should be evident. Humans have the highest receptivity among primates, i.e. females can be fertilized at any time

of the year, with no specific periods of sexual activity (Lummaa *et al.*, 1998b). This might effectively decrease the difference in profitability between the reproductive schedules of polyovulation and single ovulation females, questioning the validity of the insurance ova hypothesis in humans. Furthermore, there is evidence that twin births might not always be errors of reproduction even under premodern conditions, but may sometimes remain selectively neutral at least in some human populations (Lummaa *et al.*, 1998a).

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