EPIDEMIOLOGY

Sons Reduced Maternal Longevity in Preindustrial Humans

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In humans, sons are physiologically more demanding to produce than daughters, as indicated by their faster intrauterine growth rate (*1*) and heavier birth weight (*2*) and the longer time it takes mothers producing sons to reproduce again (*3*). Large, and particularly strongly male-biased, family size is thus predicted to reduce maternal longevity (*4*). However, the long-term effects of gender-biased reproductive investment remain unknown. Here we show that in preindustrial humans, the number of sons delivered reduced expected maternal longevity, whereas the number of daughters raised improved it.

We used demographic data collected from Finnish church records to study how total family size and the numbers of sons and daughters produced affected the longevity of preindustrial Sami women in northern Scandinavia. During the study period, 1640–1870, these Sami depended mainly on reindeer herding, fishing, and hunting for their livelihood and experienced natural mortality because of a lack of advanced medical care (*5*).

The data were analyzed with multiple regression models, which allowed us to separate the relative effects of offspring gender and number on maternal longevity. We controlled for spouse's age at death, because living conditions were likely to deteriorate for single-parent families. To focus on the long-term effects, we included only postmenopausal women, i.e., women who lived to over 50 years of age, in our analyses.

We found that maternal longevity was not related to the total number of children born or raised to adulthood (children born: $\beta = -0.11 \pm 0.19$ years, $t = -0.58$, $P = 0.559$; adult children: $\beta = 0.11 \pm 0.22$ years, $t = 0.48$, $P = 0.634$), suggesting that large families were raised by wealthy individuals (*6*). Instead, we found evidence for a significant gender bias in costs of reproduction on maternal longevity. Relative to daughters, giving birth to sons significantly shortened the expected life-span of the mother (Fig. 1A). The magnitude of this effect corresponded to a 34-week (ranging from 4 to 64 weeks with 95% confidence) reduction in life-span per son born. Giving birth to daughters, instead of sons, had a positive, but statistically nonsignificant, effect on maternal longevity (Fig. 1B). When we repeated the same analysis using the numbers of sons and daughters raised to adulthood (i.e., 18 years old), the daughters' positive effect on maternal longevity became stronger than the sons' negative effect (Fig. 1, C and D). These results remained qualitatively unchanged when only mothers living over 45 years were included (*7*). Moreover, the numbers of sons or daughters born or raised to adulthood had no effect on paternal longevity (*7*).

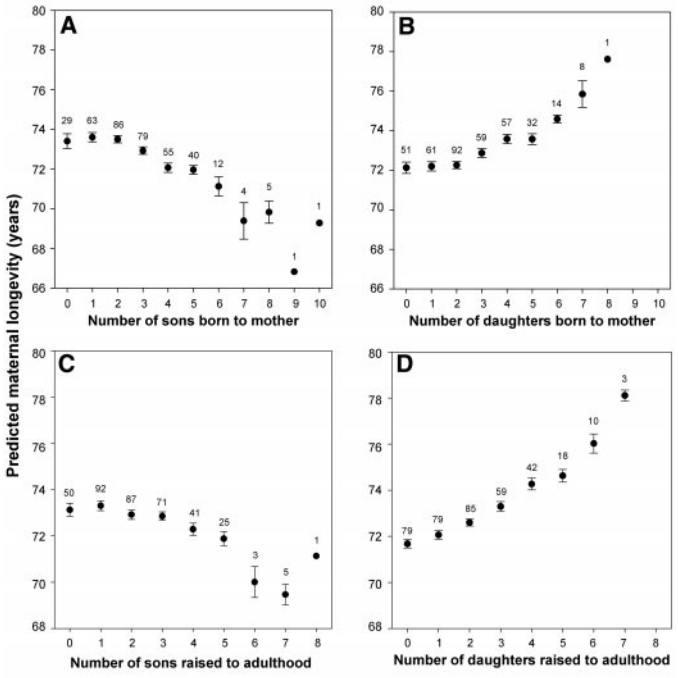

Fig. 1. Longevity of Sami women ($n = 375$) with respect to the gender of their offspring born (**A** and **B**) or raised to adulthood (**C** and **D**). Panels represent expected maternal longevity as predicted by the multiple regression models (mean predicted values ± SE). Numbers above the symbols represent the number of observations. Maternal longevity was significantly negatively related to the number of sons born ($\beta = -0.65 \pm 0.29$, $t = -2.24$, $P = 0.026$) (A) and positively, but nonsignificantly, related to the number of daughters born ($\beta = 0.44 \pm 0.29$, $t = 1.50$, $P = 0.133$) (B). The negative effect of the number of sons raised to adulthood was not statistically significant ($\beta = -0.52 \pm 0.32$, $t = -1.61$, $P = 0.110$) (C) , whereas the number of daughters raised to adulthood had a statistically significant positive effect on maternal longevity ($\beta = 0.66 \pm 0.31$, $t = 2.12$, $P = 0.035$) (D).

Our results suggest that giving birth to sons had a higher relative long-term survival cost for mothers than giving birth to and raising daughters. This gender bias may be due to the lower direct physiological costs of daughters and to the human family system in which daughters help their mothers in their everyday tasks. Moreover, pregnancies with male fetuses are associated with elevated maternal testosterone levels (*8*). Testosterone is an immunosuppressor and may thus play a role in accelerating immunosenescence and consequently decreasing the survival into old age of mothers who have born several sons (*9*). Our results reveal that both the direct effects of reproductive investment and the social effects of gender-biased family structure seem to be important determinants of female life-span.

References

1. K. Marsál *et al.*, *Acta Paediatr.* **85**, 843 (1996).
2. R. J. F. Loos, C. Derom, R. Eeckels, R. Derom, R. Vlietinck, *Lancet* **358**, 560 (2001).
3. R. Mace, R. Sear, *J. Biosoc. Sci.* **29**, 499 (1997).
4. T. B. L. Kirkwood, M. R. Rose, *Philos. Trans. R. Soc. London Ser. B Biol. Sci.* **332**, 15 (1991).
5. T. Itkonen, *The Lapps of Finland*, vol. 2 (WSOY, Porvoo, Finland, 1948).
6. A. J. van Noordwijk, G. de Jong, *Am. Nat.* **128**, 137 (1986).
7. S. Helle, V. Lummaa, J. Jokela, data not shown.
8. W. H. James, *J. Theor. Biol.* **180**, 271 (1996).
9. F. Fagnoni *et al.*, *Blood* **95**, 2860 (2000).

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