Effect of Producing Sons on Maternal Longevity in Premodern Populations

Helle *et al.* (*1*) showed that producing and raising sons reduced the longevity of preindustrial Sami women, whereas daughters tended to have the opposite effect. They suggested that the life-shortening effect of sons could be attributed to higher endocrinological or physiological costs of producing sons compared with those of producing daughters, and that the life-elongating effect of raising daughters might be the outcome of daughters helping in the household of their mothers. To examine the validity of those ideas, we explored the costs of producing sons rather than daughters in the two premodern populations of Krummhörn (Ostfriesland, Germany, 1720 to 1874) and St. Lawrence valley (Quebéc, Canada, 1608 to 1760), applying the same data selection criteria and linear regression model as Helle *et al.* (*2*).

For the Krummhörn population, we found the same negative relationship between the number of sons born and the age of the mother at death, although this result was not statistically significant. There was also a very slight and likewise not significant positive correlation concerning the number of daughters born (sons: $\beta = -0.180 \pm 0.200$, $t = -0.900$, $P = 0.368$; daughters: $\beta = 0.049 \pm 0.209$, $t = 0.234$, $P = 0.815$) (Fig. 1, A and B). In the Quebéc population, we found a positive relationship between the number of sons or daughters born and maternal age, but only the latter relationship is significant (sons: $\beta = 0.081 \pm 0.092$, $t = 0.881$, $P = 0.378$; daughters: $\beta = 0.197 \pm 0.095$, $t = 2.062$, $P = 0.039$) (Fig. 1, C and D).

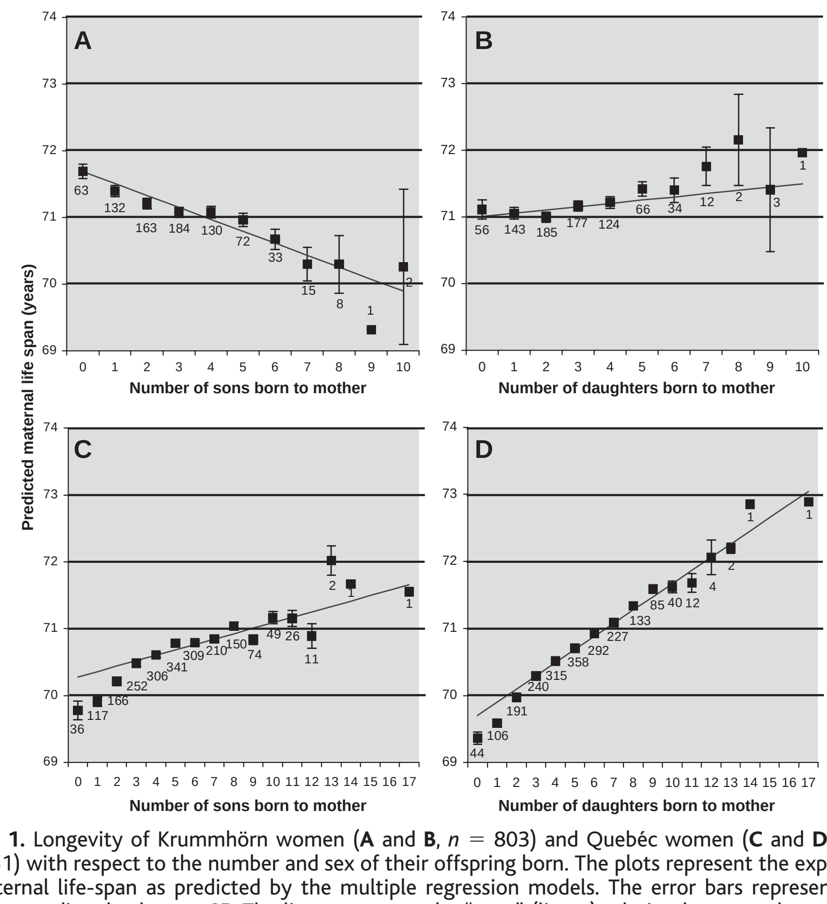

Fig. 1. Longevity of Krummhörn women (**A** and **B**, $n = 803$) and Quebéc women (**C** and **D**, $n = 2051$) with respect to the number and sex of their offspring born. The plots represent the expected maternal life-span as predicted by the multiple regression models. The error bars represent the mean predicted values ± SE. The line represents the "pure" (linear) relation between the number of sons (A and C) and daughters (B and D), respectively, based on the estimated coefficients and the median values of the remaining, non-depicted, covariates of the respective sample (Krummhörn: number of sons = 3, number of daughters = 3, paternal age at death = 70; Quebéc: number of sons = 5, number of daughters = 5, paternal age at death = 72). Numbers below the symbols represent the number of observations.

The Krummhörn case looks quite similar to what was found for the Sami, but the results are difficult to interpret. Broken down by economic status, we find a strong—although not significant—negative relationship between the number of sons and maternal age for the wealthy farmers ($\beta = -0.889 \pm 0.348$, $t = 1.326$, $P = 0.186$, $n = 66$) but an opposite effect for the poor workers ($\beta = 0.462 \pm 0.728$, $t = -1.217$, $P = 0.228$, $n = 303$) who were analyzed. With the Quebéc population, the effect of the number of sons was reversed relative to what was seen in the Sami population. Even less evidence for a relationship between number of sons or daughters and maternal longevity could be found when the analyses were restricted to the children raised to adulthood (*2*). It thus seems that the higher physiological costs of producing sons are unlikely to have a strong impact on maternal longevity in general. Instead, these effects—if they exist at all—are modulated decisively by yet unknown factors, probably of a sociocultural nature.

Life-history studies of historical populations, although fruitful in many aspects (*3*), sometimes suffer from a lack of information concerning influential covariates. In addition, specific sociocultural or population genetic conditions may make it difficult to generalize effects observed in such a population.

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References and Notes

1. S. Helle, V. Lummaa, J. Jokela, *Science* **296**, 1085 (2002).
2. Supplemental information, including data selection criteria and the description of different models and their estimated coefficients, is available at www.demogr.mpg.de/publications/files/beisesupp.pdf
3. E. Voland, *Evol. Anthropol.* **9**, 134 (2000).
4. We thank Bertrand Desjardins of the Programme de Recherche en Démographie Historique of the University of Montréal for providing the data of the St. Lawrence valley. We also thank J. W. Vaupel for some crucial suggestions and the two anonymous reviewers for clarifying comments.

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Response: Explaining human life-history evolution with hypotheses of evolutionary ecology is difficult, due to the multitude of confounding factors that may obscure true effects, or even reverse the expected patterns. The comment by Beise and Voland is a good example of the frustration and confusion such confounding factors may generate.

Life-history theory suggests that increases in reproductive investment are associated with reduced longevity (*1*). Increases in reproductive investment can also arise, among sexually dimorphic mammals such as humans, due to increases in the number of sons produced. Since females often invest considerably more in reproduction than males, physiologically, we further expect reproduction to inflict higher physiological costs on mothers than on fathers.

We found support for this biological cost hypothesis, with a tweak that negative effects on mother's longevity depended on the number of sons born, not on the total fecundity, and that the number of daughters actually had a positive effect on mother's longevity (*2*). We suggested that the negative effects of sons on maternal longevity may have arisen through sons' need for increased physiological demand during gestation and early postnatal development, because no such longevity effects were found in males (*2*). Giving birth to daughters does not come without cost, either—but overall, daughters may have had a positive effect on mother's longevity because they helped in the household tasks, reducing the total workload inflicted on the mother (*2*). Thus, we also invoked a sociocultural explanation of maternal longevity based on what is known of the social and cultural lives of the historical Sami people (*3*). This explanation counters the strict predictions of the biological cost hypothesis.

Beise and Voland questioned the validity of our statement based on similar analyses on premodern (but not natural state) agricultural populations of Krummhörn and Quebéc (*4, 5*). However, it is difficult to assess validity without subjecting our original results to an experimental or comparative test in a natural-state human population with gender-specific parental task-sharing. Instead of contrasting the biological and sociocultural hypotheses by comparing the effects of reproductive investment in mothers and fathers as in our study (*2*), Beise and Voland make a disputable attempt to refute our conclusions. Therefore, they are unable to comment on the relevance of the biological cost hypothesis in their populations, and hence, their findings do not challenge our conclusion that both cultural and biological processes interactively determined longevity of females in Sami.

Beise and Voland also resort to "unknown factors, probably of a sociocultural nature" as an explanation of longevity patterns that they (and we) observed. Unknown ecological, demographic, or cultural factors are always available as explanations, but it is the task of the researcher to find and separate the relevant from the irrelevant. For example, the Krummhörn and Quebéc populations certainly differed from the Sami population used in our study. Both of their populations relied on agriculture and trade of technology. The Krummhörn was a classical Central European rural community that at the time already had a strict class structure and advanced task-sharing in the society. The Quebéc population was initiated by a small number of migrants from France and then rapidly and successfully expanded over the next centuries. By stark contrast, the reindeer herders of northern Scandinavia were far removed, ecologically, demographically, and socioculturally, from both the Krummhörn and Quebéc populations studied by Beise and Voland.

For the above mentioned reasons, it is difficult to see how the analysis of Beise and Voland reflects on the validity of our conclusions or presents an advancement in our understanding of the factors that determine human longevity.

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