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# A trade-off between having many sons and shorter maternal post-reproductive survival in pre-industrial Finland

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A bias in reproduction towards sons, which are energetically more costly than daughters, has been suggested to shorten parental lifespan, but previous results have been mixed. Reproductive costs should be most evident in low rather than high resource settings, and are not expected to be severe in men, because women pay higher direct costs of reproduction. We, therefore, used demographic data from pre-industrial Finland to investigate whether the number of sons and daughters born affected their parents' post-reproductive survival and whether this was related to parent's resource availability. Irrespective of access to resources, mothers, but not fathers, with many sons suffered from reduced post-reproductive survival, and this association decreased as mothers aged. Our results provide evidence that Finnish mothers traded long post-reproductive lifespan for giving birth to many sons.

## 1. Introduction

Reproduction and somatic maintenance are energetically costly, and thus a trade-off is expected between the allocation of resources to reproduction versus somatic maintenance and repair [1]. Consequently, high investment in reproduction should result in shorter lifespan. The severity of such trade-offs may, however, depend on sex, with one sex (typically females) bearing a higher energetic cost of reproduction [2] and also on resource availability, with survival costs of investing heavily in reproduction being particularly evident among individuals experiencing scarcer resources [3]. In accordance with these ideas, in many taxa, reproductive costs are commonly found to be most pronounced among individuals with limited access to resources [4–6].

In humans, evidence for shorter parental lifespan in relation to increased reproductive investment is still controversial [7–10]. This trade-off is often investigated by relating the total number of children to the total lifespan. However, delivering sons compared with daughters is likely to be energetically more costly for the mothers, because sons are heavier and larger at birth [11,12] and they require more energy during gestation [13] and lactation [14]. In line with this, Helle *et al*. [15] were the first to suggest that shorter maternal lifespan may be related to the number of sons born rather than to the total number of children born. Since then, the potential association between offspring sex and parental lifespan has attracted lots of attention, but the results remain still mixed [16].

We investigated the associations of the number of sons and daughters born on post-reproductive survival in Finnish women and men. Given the expected resource-dependence of reproduction–survival trade-offs [3], we study how the numbers of sons and daughters born affected post-reproductive survival of women and men in relation to their resource availability, measured by socio-economic status. It is predicted that reproductive costs should be strongest in

**Table 1.** Cox regression model of the association between post-reproductive survival and the number of sons and daughters born in Finnish women and men. (In women, the influences of age at last reproduction, the number of sons (see §3), socio-economic status and birth area were time-dependent (Wald $\chi^2_1 > 5.86$, $p < 0.012$), whereas in men the influences of age at last reproduction and birth area were time-dependent (Wald $\chi^2_1 > 6.19$, $p < 0.013$). NS, number of sons; ND, number of daughters; and SES, socio-economic status.)

| | women | | | men | |
|---|---|---|---|---|---|
| | d.f. | Wald $\chi^2$ | *p*-value | Wald $\chi^2$ | *p*-value |
| NS | 1 | 9.56 | 0.002 | 0.08 | 0.78 |
| ND | 1 | 0.62 | 0.43 | 1.21 | 0.27 |
| age at last reproduction | 1 | 97.0 | <0.0001 | 5.55 | 0.019 |
| SES | 2 | 6.69 | 0.035 | 6.55 | 0.038 |
| birth cohort | 2 | 642.0 | <0.0001 | 273.2 | <0.0001 |
| birth area | 4 | 164.1 | <0.0001 | 118.6 | <0.0001 |
| twinning status | 1 | 0.05 | 0.83 | — | — |
| NS × SES | 2 | 0.75 | 0.69 | 0.57 | 0.75 |
| ND × SES | 2 | 0.98 | 0.61 | 1.63 | 0.44 |

women, owing to their higher direct energetic costs of reproduction, and among those belonging to the poorest socio-economic status [2,10]. To evaluate the potential alternative explanation that the post-natal survival of sons and daughters may further influence their association to parental lifespan owing to social influences [17], we repeated our analyses by including only those offspring who survived to adulthood.

## 2. Material and methods

### (a) Demographic data

We used demographic data collected from Finnish parish registers kept by the Lutheran Church, which allow individuals to be followed from birth, through their reproductive history and adult life, to death [18]. These data were collected from individuals born originally in eight Finnish parishes (south-western archipelago: Hiittinen, Kustavi and Rymättylä; western mainland: Ikaalinen, Pulkkila and Tyrvää; eastern mainland: Rautu and Jaakkima) but their descendants and spouses were born all over Finland. All individuals born abroad were excluded from the analyses. During the pre-industrial period, the mainland parishes were mainly dependent on agriculture, whereas archipelago populations supplemented agriculture with fishing. Since our study period covers the seventeenth to twentieth centuries, industrialism (here, mainly the wood processing industry) and a modern lifestyle had some influence on the study individuals; but because 95 per cent of the individuals studied were born before 1950, when Finland was essentially still an agricultural society, our data involve mainly individuals who lacked modern birth-control methods and modern medical care.

From these records, we collected information on post-reproductive lifespan and offspring characteristics, including number, sex and survival to age 15 for a total of 11 166 women who did not die at childbirth and 6360 men with complete information on reproductive performance (see the electronic supplementary material, text S1 and table S1 for descriptive statistics). Our analyses were not restricted to individuals living to some pre-defined age (e.g. 50 in women), as done in previous studies. This was because (i) in women, there is no obvious reason why the costs of reproduction should be restricted to post-menopausal mothers only; (ii) in both sexes it is likely that, even without deliberate birth-control, some individuals ceased reproduction before their physiological age-limit; and (iii) in men no strict age-limit for fertility can generally be defined. Based on the socio-economic status of a husband in the family, we classified each family as poor, middle or wealthy ([19], see also the electronic supplementary material, text S2 and table S2)).

### (b) Statistical analyses

The association between the number of sons and daughters born and those who survived to adulthood, and post-reproductive survival of their mothers and fathers was examined using separate Cox regression models [20]. Post-reproductive survival was defined as the number of years between an individual's last child being born and their death. Age at last reproduction was included in the models to control for between-individual differences in age at last reproduction and, thus, in entry to the risk set [20]. For those individuals with unknown age at death (for instance, owing to migration), the year of last recorded appearance (if available) was regarded as 'age at death' and these individuals were treated as right-censored observations [20]. The models included socio-economic status, birth area (archipelago, west-Finland, south- and east-Finland, central-Finland, and north-Finland) and birth cohort (before 1800, 1800–1900, after 1900), as well as interactions between the number of offspring of either sex born and socio-economic status. To aid the interpretation of the coefficients of the number of offspring of each sex in the presence of interactions, these variables were grand mean centred prior to analyses [21]. In women, we also controlled for whether they produced twins or not [22]. Assumptions of proportional hazards were examined by also fitting time-dependent coefficients of explanatory variables (i.e. cross-products of survival time and predictors in question). If statistically significant, these were retained in the model [20]. A robust sandwich covariance matrix was used to account for clustered survival times because our data contained a large number of siblings [20]. Analyses were conducted with SAS statistical package v. 9.3 (SAS Institute Inc, Cary, NC, USA, 2002–2010).

## 3. Results

Women's post-reproductive survival declined with the number of sons they gave birth to (table 1; hazard ratio (HR) (95% CI) = 1.070 (1.025, 1.117)). This association did

not depend on their socio-economic status (see table 1 and electronic supplementary material, text S3 and table S3), but was age-dependent ($\chi^2_1 = 7.84$, $p = 0.005$, HR (95% CI) = 0.998 (0.997, 1.000)). That is, the survival costs of the number of sons born decreased linearly as women aged. The number of daughters born was not associated with women's post-reproductive survival (table 1; HR (95% CI) = 1.016 (0.977, 1.057)). In men, neither the number of sons (HR (95% CI) = 1.007 (0.961, 1.055)) nor daughters born (HR (95% CI) = 0.973 (0.926, 1.022)) were related to post-reproductive survival, irrespective of their socio-economic status (table 1). The number of sons and daughters surviving to adulthood were not related to either parent's post-reproductive survival (see the electronic supplementary material, text S4 and table S4).

## 4. Discussion

Our results show that producing sons shortened the post-reproductive lifespan of Finnish women and that this association detoriated as mothers aged. This supports our hypothesis that production of sons is more energetically costly than the production of daughters. The reduction of reproductive costs with age may be owing to the potential beneficial social influences of surviving sons, as the number of adult sons was unrelated to post-reproductive lifespan in these women. No such associations were found in men, which is consistent with men investing less direct energetic resources in reproduction than women [2]. Because these associations were not mediated by socio-economic status in either sex, our results do not seem to support the model of resource-mediated life-history trade-offs [2,10]. This may be owing to the overwhelming reproductive costs of having many sons, which could not be avoided even among those women belonging to the highest socio-economic stratum.

The question of the importance of offspring sex composition on the survival costs of reproduction in humans remains open. In addition to studies aiming to contrast the biological and social components of this association, we would benefit from evaluating the potential, not necessarily directly resource-linked, physiological ways whereby such costs might be mediated on women's lifespan. As originally proposed [15], the negative influence of producing many sons might be related to female hormone profiles. In mammals, accumulating evidence now suggests that high concentrations of circulating maternal testosterone skews offspring sex ratio towards males [23,24]. High levels of testosterone are also known to impair maternal immune function [25] and may thus explain the potential negative association between the number of sons born and post-reproductive survival in women. Likewise, glucose metabolism may also mediate the survival costs of having many sons, as diabetic mothers are found to overproduce sons [26], but they may also suffer from reduced lifespan [27]. By contrast, a recent genetic study has suggested that women who are carriers of the *BRCA1/2* mutation may produce proportionally fewer sons [28] and have higher post-reproductive mortality [29]. Given the complexity of phenotypic associations reported in the literature [16], there is thus a need to understand the underlying biological and social mechanisms linking offspring sex composition to parental survival [17].

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