

Research



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Evolutionary biology

Limited support for the X-linked grandmother hypothesis in pre-industrial Finland

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The level of kin help often depends on the degree of relatedness between a helper and the helped. In humans, grandmother help is known to increase the survival of grandchildren, though this benefit can differ between maternal grandmothers (MGMs) and paternal grandmothers (PGMs) and between grandsons and granddaughters. The X-linked grandmother hypothesis posits that differential X-chromosome relatedness between grandmothers and their grandchildren is a leading driver of differential grandchild survival between grandmother lineages and grandchild sexes. We tested this hypothesis using time-event models on a large, multigenerational dataset from pre-industrial Finland. We found that the presence of an MGM increases grandson survival more than PGM presence, and that granddaughter survival is higher than that of grandsons in the presence of a PGM. However, there was no support for the key prediction that the presence of PGMs improves granddaughter survival more than that of MGMs, diminishing the overall support for the hypothesis. Our results call for alternative explanations for differences in the effects of maternal and paternal kin to grandchild survival in humans.

1. Background

Kin help in humans can affect both reproductive traits [1] and survival [2] of related individuals, but not all relatives help equally: investment can differ between kin depending on the degree of genetic relatedness [3]. Aside from parents, grandmothers are one of the most important kin for child survival in natural fertility/mortality human populations [2,4–7]. Grandmothers contribute a quarter of their genes on average to their grandchildren, so helping raise their grandchildren can provide fitness benefits, and has been predicted to lead to the evolution of long post-reproductive life [4,8].

Grandmother influence on grandchild survival can, however, differ between the maternal and paternal lineages [5,6,9–11], often (but not always) with maternal grandmothers (MGMs) more beneficial than paternal grandmothers (PGMs) [2]. One potential explanation for this difference is provided by the X-linked grandmother hypothesis [12], which revolves around the differential inheritance of the X-chromosome between lineages: PGMs will always, assuming no extra-pair paternity, have 50% X-chromosome relatedness to their granddaughters, but 0% to their grandsons, while MGMs are 25% related to both grandsons and granddaughters through the X-chromosome. Given the relative number of genes on the X-chromosome and autosomes, PGMs are thus on average 23% related to grandsons and 27% to granddaughters [12]. Grandmother effects on grandchild survival should then follow a continuum by the order of relatedness of the grandmother to grandchild: PGM granddaughters > MGM granddaughters/grandsons > PGM grandsons. Three predictions arise from such relatedness differences [12]: (i) PGMs favour granddaughter (27% relatedness) survival over that of

their grandsons (23%), (ii) MGMs increase the survival of grandsons more than PGMs do (25% versus 23%), and (iii) granddaughters survive better with PGMs than with MGMs (27% versus 25%). Support for these predictions is, however, currently restricted to one meta-analysis of seven populations known to have grandmother effects [12], with limited statistical support for key predictions (see Discussion). Other work has been done in humans on differences in grandparental help by X-chromosome relatedness, but these relate more to grandparental investment than grandchild outcomes [13–15].

Here, we use longitudinal records on pre-industrial Finnish families with known grandmother effects on survival [4] to investigate whether there are sex differences in grandchild survival by grandmother lineage, and whether they adhere to the three predictions of the X-linked grandmother hypothesis.

2. Methods

We investigated sex and lineage differences in grandchild survival with a large and multigenerational dataset of pre-industrial Finnish families from 1731 to 1885. This population was a predominantly patrilocal agricultural society [16,17] that underwent the transition to industrialization only from the late nineteenth century onwards [18]. We used registers on births, deaths and marriages, maintained, by law, by Lutheran clergymen for the entire country from 1749 [19]. We included all grandchildren born between 1731 and 1880 in eight geographically separate parishes in Finland (Hiittinen, Jaakkima, Pulkki, Rautu, Tyrvää, Rymättylä, Kustavi and Ikaalinen) with the living status (dead/alive) of both grandmothers known. We focused on the first 5 years of a child's life (18 935 observations of 4494 grandchildren; 854 MGMs, 826 PGMs), when the grandmother's presence has the most influence on grandchild survival in the study population [4]. Grandmothers were coded as alive and present if they were alive and lived in the same or a neighbouring parish. If an individual had one or both grandmothers alive but living in a different, non-neighbouring parish, they were excluded from the analysis: only grandmothers living close by would have had the possibility of directly affecting grandchild survival. We then removed observation years if a mother and child were both recorded for the last time in that year (indicating a family-level event, e.g. dispersal) or if the child died within a week of their mother (indicating possible shared cause of death), neither of which would be within the control of a grandmother.

(a) Statistical analysis

We implemented time-event models with constant and time-varying variables at each grandchild age, using binomial generalized linear mixed-effects models (GLMMs) with logit-link function, implemented with *glmer* from the *lme4* package [20], to test predictions 1–3. Grandchild survival was coded as 1 (alive) versus 0 (dead) in a given year. Individuals were censored at age 5, or, if either they or a grandmother had no date of death, the age last known to be alive. In the full model, we included a sex by grandmother type (time-varying four-level factor: only MGM alive, only PGM alive, both alive, neither alive) interaction term as our variable of interest, grandmother type and sex as main terms, and also grandchild age (continuous; time-varying), number of living siblings (continuous; time-varying), mother age at birth (continuous), mother survival status (time-varying factor: alive, dead, unknown), whether the child was a twin or not, and childhood social class (landed, landless) as confounding variables. Mother ID was included as a random factor, nested within MGM ID, to account for shared variation between groups of siblings and cousins. PGM ID and father ID did not affect the

results, so they were excluded. We also included parish (8-level factor) and birth cohort (16-level factor, 10-year bins) as random factors, to account for spatial and temporal differences in living conditions and uneven spread of data. Model selection was then done by sequential removal of terms from the full model and comparison of Akaike information criterion (AIC) between the full model and these reduced models, leading to removal of childhood social class, mother age at birth, and number of living siblings. To test the significance of the interaction term in the final model, we used a likelihood ratio test, using the *mixed* function from the package *afex* [21].

To test the first prediction that PGMs favour granddaughters over grandsons, we then ran the above model without the interaction or grandmother type term on a subset of 'only PGM alive' ($n = 1102$ grandchildren, 3894 observations) to get the parameter estimate for any potential sex difference in survival. For the second and third predictions, that MGMs increase survival of grandsons more than PGMs and that granddaughters survive better with PGMs than with MGMs, we removed sex and the sex \times grandmother type interaction from the full model. The above model selection procedure was used, and the same terms were removed. This reduced model was then run separately on two subsets (grandmother type as main interest variable): grandsons only ($n = 2307$ grandchildren, 9596 observations) and granddaughters only ($n = 2187$ grandchildren, 9339 observations). All analyses were conducted with R v. 3.3.1 [22].

3. Results

Overall, over a quarter of grandchildren died before age 5 (27%; 28% of grandsons, 26.2% of granddaughters), 35.8% of grandchildren had both grandmothers alive at birth, and the effects of MGMs and PGMs on grandchild survival did not differ by grandchild sex ($\chi^2_3 = 2.29$, $p = 0.510$; electronic supplementary material, table S1). In line with the first prediction of the X-linked grandmother hypothesis (that the presence of PGMs is better for the survival of granddaughters than grandsons), survival was significantly higher for granddaughters compared to grandsons when only a PGM was alive and present ($\beta = 0.262$, s.e. = 0.132, $p = 0.047$; odds ratio (OR) 1.300[1.000, 1.680]; figure 1; electronic supplementary material, table S2a). We also found support for the second prediction: grandson survival was significantly lower with PGMs only than MGMs only ($\beta = -0.266$, s.e. = 0.134, $p = 0.046$; OR 0.766[0.590, 0.995]; figure 1; electronic supplementary material, table S2b). However, for the final prediction, that survival of granddaughters is higher with PGMs than MGMs, we found no support: there was no significant difference between granddaughter survival with PGMs only or MGMs only ($\beta = -0.083$, s.e. = 0.149, $p = 0.579$; OR 0.921[0.688, 1.232]; figure 1; electronic supplementary material, table S2c).

4. Discussion

We found insufficient evidence to support the X-linked grandmother hypothesis for differential grandmother effects on grandchild survival in pre-industrial Finland. There was no difference in survival for granddaughters with only a paternal or only a maternal grandmother. That grandsons survive better with MGMs over PGMs and that granddaughters survive better than grandsons in the presence of a PGM does not provide enough evidence for support of the X-linked grandmother hypothesis, as the hypothesized order of grandmother effects by grandchild sex [12] (see Introduction) does not hold true

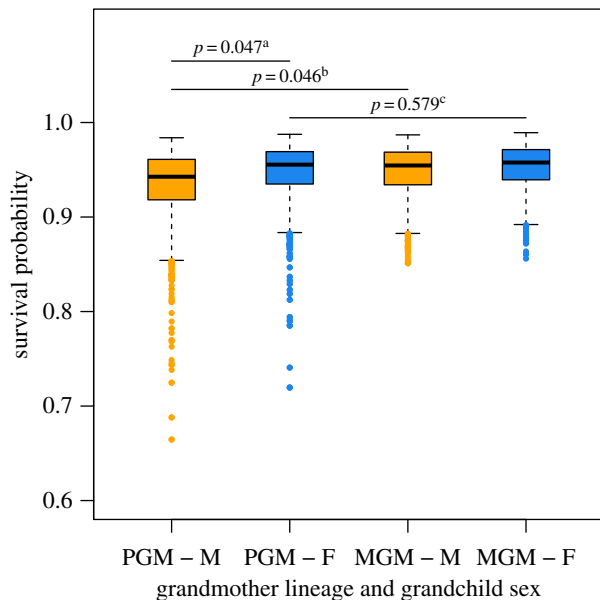


Figure 1. Boxplots of survival probability of grandchildren under 5 years of age by sex and grandmother lineage. MGM, maternal grandmother; PGM, paternal grandmother; M, male grandchild; F, female grandchild. Survival probabilities predicted from interaction model. p -Values are shown for (a) prediction 1, (b) prediction 2 and (c) prediction 3. (Online version in colour.)

without a difference in granddaughter survival between MGMs and PGMs. Instead, our results suggest the continuum of survival effects by grandmother lineage and grandchild sex was PGM granddaughters/MGM granddaughters/MGM grandsons > PGM grandsons in pre-industrial Finland (figure 1); X-chromosome relatedness cannot alone drive such differences.

The X-linked grandmother hypothesis has been proposed as a likely explanation for the observed differences in grandchild survival by grandmother lineage in humans, but our results, together with the lack of statistically robust support in the only previous test of the hypothesis, question the applicability of the hypothesis as the sole explanation for differences. First, odds ratios for each population in Fox *et al.* [12] were not calculated for direct comparisons, and instead of e.g. survival of grandsons with MGM versus survival of grandsons with PGM (prediction 2), [12] compared grandson with MGM versus no grandmother (of either type) and separately grandsons with PGM versus no grandmother, and then judged the direction of effects by comparing the values of the odds ratios. Such a lack of confidence intervals and statistical significances for the differences prevents assessment of the key predictions. To illustrate the problem, a similar approach

(and interpretation) with our data would suggest MGMs are more beneficial to granddaughters than grandsons on the basis that $OR\ 1.122 > 1.094$, even though there is no significant difference between survival of grandsons and granddaughters from direct comparison ($\beta = 0.080$, $s.e. = 0.126$, $p = 0.522$; $OR\ 1.084[0.847, 1.386]$). Second, their meta-analyses were based on this interpretation of the odds ratios, which were largely non-significant (23 of 28 across the seven populations [12]); the results of these analyses should be viewed with caution. Finally, the prediction of PGMs being more beneficial to granddaughters than MGMs was not actually tested with a meta-analysis, but was assumed to hold true on the basis that four of seven populations had a larger OR of survival for granddaughters in the presence of PGMs than in the presence of MGMs. Therefore, while the X-linked grandmother hypothesis could plausibly still be supported by these populations, direct statistical support is currently lacking. In any case, our study shows that the X-linked grandmother hypothesis may not offer a general explanation for differential effects by grandmother lineage (though it is possible that different mechanisms operate in different populations).

In summary, though we have shown two of the three main predictions of the X-linked grandmother hypothesis apply to this population of pre-industrial Finns, they are insufficient for supporting the hypothesis without the third prediction and lineage-specific survival continuum also holding true. Further work is required to identify which alternative explanations for differential lineage effects have a role in driving these differences, whether these potential underlying mechanisms work independently or interact with each other, and to formulate a robust unified theory for the prevalence of lineage-specific grandmother help in humans. Such alternative explanations include already widely cited possibilities, such as paternity uncertainty differences between maternal and paternal lineages [23], as well as thus-far untested factors in the context of grandmother help that are known to contribute to differences in helper effects in other cooperative-breeders, such as differences in helper age.

Data accessibility. Data and code supporting the article can be found in the electronic supplementary material.

Authors' contributions. S.N.C. analysed the data and drafted the manuscript. All authors were involved with study design and interpretation of results, amended the manuscript, gave final approval for publication and agree to be held accountable for the content herein.

Competing interests. We have no competing interests.

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