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Will granny save me?

Birth status, survival, and the role of grandmothers in historical Finland

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Abstract

Grandmothers play a crucial role in families enhancing grandchild wellbeing and survival but their effects can be context-dependent, and the children born in poor conditions are most likely to benefit from the investments made by helping grandmothers. In this study, we examined, for the first time, whether grandmothers' presence modified associations between adverse birth status and survival up to 5 years of age. In detail, we verified, whether *(i)* firstborns, *(ii)* twins, *(iii)* children born within 24 months after their sibling, and *(iv)* children followed by short interval (i.e. their younger sibling was born within 24 months) survived better when either their maternal, paternal, or both grandmothers were present. Moreover, we evaluated whether illegitimate children survived better when the maternal grandmother was present. We used an extensive and largely pre-industrial demographic dataset collected from parish population registers kept by the Lutheran Church of Finland from years 1730−1895. We show that although grandmother presence cannot mitigate adverse effects of many poorer birth conditions, grandchildren whose next sibling was born after a short interval survived better when the maternal grandmother was present. Taken together, these findings highlight an important role of grandmothers in compensating the mother's investment in the new baby, thus enabling overall faster successful reproductive rate of mothers. Whilst the opportunity for grandmothers to mitigate the risks of adverse birth statuses is limited, this study does show – through the beneficial effect on survival for those with a short subsequent birth interval – that grandmothers can increase their daughters' and their own reproductive success.

Keywords: altruism; cooperative breeding; intergenerational effects; mortality;

1. Introduction

The presence of helping kin is known to partially or wholly mitigate costs of breeding across a range of cooperative species (Hatchwell, 1999; Koenig, Walters, & Haydock, 2011; Komdeur, 2006; Lynch, Lummaa, Htut, & Lahdenperä, 2019), including humans (Sear & Coall, 2011; Sear & Mace, 2008). Grandmothers in particular are often found to be highly important for grandchild outcomes in humans, both in terms of biological fitness (Hawkes, O'Connell, Blurton Jones, Alvarez, & Charnov, 1998; Lahdenperä, Lummaa, Helle, Tremblay, & Russell, 2004; Rebecca Sear & Mace, 2008) and for general health and wellbeing (Tanskanen & Danielsbacka, 2018). The fitness benefits accrued from helping kin are hypothesised to have played a role in the evolution of extended post-reproductive life (Hawkes et al., 1998; Lahdenperä et al., 2004), a rare life history trait (Ellis et al., 2018) and one of those separating humans from other great apes. However, we cannot assess the evolutionary importance of grandmothering on extended post-reproductive life and menopause without first knowing under what conditions are grandmothers most useful. In populations with high rates of childhood mortality, grandchildren survive better when grandmothers are alive and present, and it is frequently found that maternal grandmothers have a more beneficial effect than paternal grandmothers (Chapman, Pettay, Lummaa, & Lahdenperä, 2019; Sear & Mace, 2008). Outside of this, relatively little is known about whether grandmothers are constantly beneficial, or only under certain conditions or to specific children.

The life course of individuals can be highly influenced by the living conditions in their families, determined by their own birth status (e.g. birth order, singleton/twin/triplet, birth intervals), and the availability of helping kin (Sear & Coall, 2011). Independently of helper presence, birth order is a particularly important predictor of health: firstborns have lower Apgar scores (a test given to newborns right after birth in which heart rate, respiratory effort, reflex irritability, muscle tone and color is assessed; it is a predictor of neonatal mortality(Finster & Wood, 2005)), a higher risk of being born prematurely (<37 weeks) (Brenoe & Molitor, 2018), and a lower birth weight than laterborns (Juntunen, Laara, & Kauppila, 1997; Wells et al., 2011; Wilcox, Chang, & Johnson, 1996), with lower birth weight associated with a lower chance of survival (Wilcox, 2001). Furthermore, firstborn children are less healthy, and it remains so up to age seven, although they have a health advantage in adolescence (Brenoe & Molitor, 2018). Whilst results from studies on the association between birth order and survival are inconsistent in the direction of effects, they typically show that firstborn survival is different from that of their laterborn siblings. As is often the case in human studies, there are exceptions to birth order having a role in survival (Campbell & Lee, 2009; Dong, Manfredini, Kurosu, Yang, & Lee, 2017; Knodel & Hermalin, 1984), but there is a larger tendency towards some kind of effect on early-life survival, whether it is lower for firstborns (DaVanzo, Hale, Razzaque, & Rahman, 2008; Faurie, Russell, & Lummaa, 2009), later-borns (Modin, 2002; Park, Han, & Kye, 2018; Penn & Smith, 2007), or as a U-shape association, indicating middle born children have the highest survival (Mishra, Ram, Singh, & Yadav, 2018).

Time between births may also affect health. The World Health Organisation recommends an interval of at least 24 months before attempting the next pregnancy, to reduce the risk of adverse maternal, perinatal, and infant outcomes (WHO, 2007). Systematic reviews of studies performed in both economically developing countries and economically developed countries confirm that short inter-pregnancy intervals are related to higher risk of preterm birth, low birth weight and small-for-gestational age (Ahrens, Nelson, Stidd, Moskosky, & Hutcheon, 2018; A. Conde-Agudelo, Rosas-Bermudez, Castano, & Norton, 2012; Agustin Conde-Agudelo, Rosas-Bermúdez, & Kafury-Goeta, 2006; Kozuki et al., 2013), and increased infant (Ahrens et al., 2018) and toddler mortality (Fotso, Cleland, Mberu, Mutua, & Elungata, 2013; Molitoris, 2017;

Rutstein, 2005). In addition, children born after short birth intervals are more likely to be underweight (Rutstein, 2005). A short inter-birth interval also poses higher risks for a mother - inter-birth intervals shorter than 15 months are associated with increased risks of maternal death and many complications during pregnancy including elevated risk of bleeding in third trimester, anemia, premature rupture of membranes, puerperal endometritis (Agustin Conde-Agudelo & Belizán, 2000), pre-eclampsia, and increased blood pressure (Razzaque et al., 2005).

Whilst outcomes relating to length of the preceding interval are extensively studied, outcomes of having a short subsequent birth interval have been studied only in a few populations. Children followed by short birth interval (their younger sibling was born within 20 months after them) had more than a two-fold higher risk of mortality in early childhood compared with lastborn children (Fotso et al., 2013). Similarly, a child's risk of mortality between 1-4 years can more than double when their mother gets pregnant by their first birthday (DaVanzo et al., 2008).

Thirdly, being born as a twin poses a higher risk of a low Apgar score, of preterm delivery, and of having a birthweight of less than 2,500g (Olusanya, 2011). Twins are at higher risk of being stunted and underweight when younger than 5 years (Ntenda & Chuang, 2018), and have a higher risk of mortality than singletons (Gabler & Voland, 1994; Sear, Shanley, Mcgregor, & Mace, 2001; Sparks, Wood, & Johnson, 2013). Lastly, being born as a child of a single mother is followed by many consequences. Those children had a higher risk of being born small-for-gestational age, having low birth weight, being born prematurely, or having a low Apgar score (Grjibovski, Bygren, & Svartbo, 2002; Raatikainen, Heiskanen, & Heinonen, 2005; Shah, Zao, & Ali, 2011). Single motherhood is associated with elevated risk of preterm birth in countries where over 80% of births occur to married women (Zeitlin, Saurel-Cubizolles, & Ancel, 2002). In a historical Swedish population, infants born to single mothers had higher mortality compared to infants born to married women (Sovio, Dibden, & Koupil, 2012). Despite a wealth of literature on the role of grandmothers and on poor birth statuses for the survival of children, few have consolidated the two to investigate whether grandmother presence could mitigate these detrimental effects of a worse birth condition. This is important, as grandmaternal effects can be context-dependent (Chapman et al., 2019), and the children born in poor conditions are most likely to benefit most from the investments made by the helping grandmother.

In this study, we examine, for the first time, whether grandmother presence modified associations between adverse birth status and survival in a pre-industrial Finnish population, in which beneficial grandmother effects have been detected (Lahdenperä et al., 2004). In detail, we will verify whether (i) firstborns, (ii) twins, (iii) children born within 24 months after their sibling, and (iv) children followed by short interval (i.e. their younger sibling was born within 24 months) survive better when either their maternal, paternal, or both grandmothers were present. In addition, we will investigate whether (v) illegitimate children survived better when the maternal grandmother was present. As it is typically found that maternal grandmothers are more beneficial for grandchild survival, and as we have previously found no effect of paternal grandmothers in this population (Chapman et al., 2019), we predict that maternal grandmother presence will increase childhood survival in all cases. Grandfathers were not examined here, because it was shown previously in our population that their presence was not associated with grandchildren survival (Lahdenperä, Russell, & Lummaa, 2007). This is, to our knowledge, among the first examinations of associations between grandmothers' presence and grandchildren survival with relatively worse birth status at the beginning of life.

2. Material and Methods

2.1. Study population and data collection

We tested grandmother effects on grandchild survival using an extensive pre-industrial demographic dataset collected from parish population registers kept by the Lutheran Church of Finland. From 1749, these records covered nearly the entire population of Finland (Gille, 1949). These registers detail information on e.g. births, deaths, and marriages, allowing us to reconstruct full life-histories of individuals and their descendants. Finland in the pre-industrial period was largely agrarian, and we have split individuals into two social classes: landed (farm owners, merchants) and landless (tenant farmers, fishermen, craftsmen, servants, labourers, crofters). Mortality before 5 year of age was high (Chapman, Pettay, Lummaa, & Lahdenperä, 2018; Chapman et al., 2019; Pettay, Lahdenperä, Rotkirch, & Lummaa, 2016), adult lifespan was over 60 years (Griffin, Hayward, Bolund, Maklakov, & Lummaa, 2018). Industrialization and the demographic transition began from around the 1870s in Finland (Hjerppe, 1989; Scranton, Lummaa, & Stearns, 2016). Our study period of 1730-1895 therefore largely pre-dates industrialisation and much of the demographic transition, which brought about medical and social advances that led to decreases in birth rates and in child mortality (Liu & Lummaa, 2014; Scranton et al., 2016). Due to data availability (e.g. birth of twins) study periods slightly differ for each of the five analysed groups of grandchildren.

2.2. Statistical analysis

All analyses were performed with R v. 3.4.2 (Team, 2019). Significance was determined at the level of $\alpha = 0.05$.

2.3. Survival effect of maternal and paternal grandmothers up to 5 years of age

We analysed the survival of grandchildren up to age 5 years in the presence of grandmothers, as 27% of deaths in this population occurred before 5 (Chapman et al., 2018) and decreased thereafter. We used discrete time-event analyses, a method that combines a few important strengths. Firstly, it allowed us to include both time-independent (e.g. maternal age at birth) and time dependent variables (e.g. maternal survival status). Secondly, the method allows for inclusion of censored individuals. Thirdly, it allowed us to include random effects in order to account for shared family and environmental conditions. We implemented the discrete time-event analyses (Allison, 1982) with generalised linear mixed models (GLMMs) and the logit link function using *glmer* from R package *lme4* (Bates, Maechler, Bolker, & Walker, 2015), with grandchild survival status each year as the response variable (binomial: 1 – alive vs 0 – dead). Grandmother survival was coded as a time-varying 4-level factor: both alive, both dead, only maternal grandmother alive, only paternal grandmother alive. We only included individuals if their living grandmothers were residing in the same parish – those living too far away are unlikely to be able to help and therefore may mask any effects of grandmother presence, but they cannot be treated as dead either. We have included region of Finland in the models since there were regional differences in household system in the 18th and 19th centuries (Moring, 1998). In the archipelago the availability of food was rather high and constant with the possibility to benefit from what the sea offers. Mainland areas were poorer, and their survival depended solely on agriculture, with crop failures and famines commonly taking place.

2.3.1 Firstborns

We analysed 4997 observational years (where each row in the data is one observation year, so a child who survived up to 5 year of age had 5 rows in the dataset) for 1175 first-born individuals born between 1733 and 1894, all of whom had the status of both grandmothers known (Table 1). In the initial full model we included grandmother type (four levels: maternal grandmother alive n=274, paternal grandmother alive n=214, both grandmothers alive n=551, and neither grandmother alive n=136), sex of grandchild, mother age at birth (both linear and quadratic), number of later born siblings, social class (two levels: landed vs landless), index child age, maternal survival status (two levels: alive vs dead), region of Finland (two levels: mainland vs archipelago), maternal and paternal grandmother age at grandchild's birth. Of these, grandmother type, index child age, maternal survival status, and number of living siblings were time-varying.

2.3.2. Twins

We analyzed 757 observational years for the 216 children in our dataset born as a twin between 1745 and 1893 (Table 1). Again, all these individuals had the survival status of their grandmothers known. In the initial full model we included grandmother type (four levels: maternal grandmother alive n=50, paternal grandmother alive n=48, both grandmothers alive n=66, and neither grandmother alive n=52), sex of grandchild, mother age at birth (both linear and quadratic), number of living siblings, social class (two levels: landed vs landless), index child age, maternal survival status (two levels: alive vs dead), region of Finland (two levels: mainland vs archipelago), maternal and paternal grandmother age at grandchild's birth, birth order (continuous) and inter-birth interval (two levels: <24 months vs =>24 months or firstborns). Of these, grandmother type, index child age, maternal survival status, and number of living siblings were time-varying.

2.3.3. Preceding birth interval < 24 months

We analyzed 5957 observational years out of 1432 individuals who were born within two years after their sibling (Table 1). Children were born between 1757 and 1894; out of this group 266 with neither grandmother, 377 with maternal grandmothers, 293 with paternal grandmothers, and 496 with both grandmothers. In the initial full model we included grandmother type (four levels: maternal grandmother alive, paternal grandmother alive, both grandmothers alive, and neither grandmother alive), sex of grandchild, mother age at birth (both linear and quadratic), number of living siblings, social class (two levels: landed vs landless), index child age, maternal survival status (two levels: alive vs dead), region of Finland (two levels: mainland vs archipelago), maternal and paternal grandmother age at grandchild's birth, birth order (continuous), whether child was born as a twin and elder sibling status (two levels: dead vs alive). Of these, grandmother type, index child age, maternal survival status, and number of living siblings were time-varying.

2.3.4. Subsequent birth interval < 24 months

We included 5196 observational years out of 1450 children followed by short interval i.e. their younger sibling was born within 24 months (Table 1). Our sample was limited to closed intervals i.e. no lastborns were included in the sample. Children were born between 1756 and 1894. In the initial full model we included grandmother type (four levels: maternal grandmother alive n=355, paternal grandmother alive n=285, both grandmothers alive n=574, and neither grandmother alive n=236), sex of grandchild, mother age at birth (both linear and quadratic), number of living siblings, social class (two levels: landed vs landless), index child age, maternal survival status (two levels: alive vs dead), region of Finland (two levels: mainland vs archipelago), maternal and paternal grandmother age at grandchild's birth, birth order (continuous) and inter-birth interval (two levels: <24 months vs =>2 months or firstborns). Of these, grandmother type, index child age, maternal survival status, and number of living siblings were time-varying.

2.3.5. Illegitimate children

We included 4992 observational years out of 1201 children born out of wedlock between 1786 and 1894 (Table 1). In the initial full model we included maternal grandmother type (two levels: alive n=656 vs dead n=545), sex of grandchild, maternal age at birth (both linear and quadratic), number of living siblings, social class (two levels: landed vs landless), index child age, maternal survival status (two levels: alive vs dead), whether child was born as a twin, region of Finland (two levels: mainland vs archipelago), maternal grandmother age at grandchild's birth, birth order (continuous) and inter-birth interval (two levels: <24 months vs =>24 months or firstborns). Of these, maternal grandmother type, index child age, maternal survival status, and number of living siblings were time-varying.

In all tested models, random terms included mother identity (ID) nested in maternal grandmother ID (except from models on firstborns and twins when only maternal grandmother ID was used), to account for variation between groups of siblings (from mother ID) and cousins (from grandmother ID), and birth cohort (with ten-year bins e.g. 1730-1739 etc.; number of cohorts varied from 12 to 17 depending on the model), to account for shared social and environmental conditions. In the model on twins, exclusion of either random effect did not affect model estimates. Each fixed term (with the exceptions of grandmother type, maternal survival status, grandchild age in each model) was removed with the function *drop1*, with their values for the Akaike information criterion (AIC) then compared to the AIC of the full model. Terms were only retained if AIC increased by >2 upon removal (i.e. the model AIC was lower with the term included than excluded), to avoid overfitting of the model (Burnham & Anderson, 2002).

Following this procedure, we removed: *(i)* mother age at birth (both linear and quadratic), social class, region of Finland, and both terms for grandmother age at grandchild birth from the model on firstborns; *(ii)* sex, both terms for grandmother age at grandchild birth, and inter-birth interval from the model on twins; *(iii)* sex, mother age at birth (both linear and quadratic), social class, region of Finland, both terms for grandmother age at grandchild birth, and elder sibling status from the model on preceding birth interval; *(iv)* sex, mother age at birth (both linear and quadratic), social class, region of Finland, both terms for grandmother age at grandchild birth from the model on following birth interval; and *(v)* birth order, sex, mother age at birth (both linear and quadratic), number of living siblings, social class, maternal grandmother age at birth of the grandchild, and inter-birth interval from the model on illegitimate children. The reduced, more parsimonious models were then run, with the grandmother type 'none' always set as the reference level.

3. Results

3.1. Firstborns

In historical Finland firstborns had overall worse survival probability than middle and laterborns (Faurie et al., 2009). We did not find evidence that the presence of grandmothers improved the firstborns' poorer survival up to 5 years of life (Table S1). Firstborns' chance of survival did not significantly differ between those with no living grandmothers and those with a living maternal grandmother (OR = 0.92, 95% CI: 0.57–1.48), paternal grandmother (OR = 0.95, 95% CI: 0.57–1.56), or both grandmothers (OR = 1.14, 95% CI: 0.72–1.78) (Figure 1a). This model is accounting for the significantly increased survival chance with child age (OR = 1.34, 95% CI: 1.16–1.55) and decreased survival chance if the mother had died (OR = 0.11, 95% CI: 0.05–0.25) – those who lost their mother had an 89% reduction in their probability of survival to age 5. Furthermore, firstborn girls had a higher chance of survival compared to boys (OR = 1.48, 95% CI: 1.10–1.97), similarly to the general pattern of sex-specific early-life survival in this population (Chapman et al., 2018).

3.2. Twins

Twins in historical Finland had lower survival than singletons (Lummaa, Jokela, & Haukioja, 2001). However, we did not find evidence that the presence of grandmothers improved this low survival of twins up to 5 years of life (Table S2). Twins' chance of survival did not significantly differ between those with no living grandmothers and a living maternal grandmother (OR = 0.97, 95% CI: 0.47–2.03), paternal grandmother (OR = 1.10, 95% CI: 0.55–2.20), or both grandmothers (OR = 0.83, 95% CI: 0.40–1.74) (Figure 1b). Instead, twins' chance of survival increased with: child age (OR = 1.89, 95% CI: 1.52–2.36), mother's age at birth (linear OR = 1.80, 95%CI: 1.24–2.53 and quadratic OR = 0.99, 95% CI: 0.99–1.00, number of living siblings (OR = 1.65, 95% CI: 1.32–2.07) and decreased with an increasing birth order (OR = 0.67, 95% CI: 0.53–0.84). Maternal survival status did not impact chance of twin survival (OR = 0.53, 95% CI: 0.21–1.30). In addition, those twins who were born in landless class had a higher chance of survival compared to those born in landed class (OR = 2.78, 95% CI: 1.33–5.82) and those born on the mainland had lower chance of survival compared to those born in the archipelago area (OR = 0.52, 95% CI: 0.30–0.90).

3.3. Preceding interval < 24 months

The shorter the preceding interval, the higher the mortality of children aged between 0-15 years (Lahdenperä, Russell, Tremblay, & Lummaa, 2011). However, we did not find an effect of grandmother presence on survival up to 5 years for children born after such short birth intervals (Table S3). Probability of survival did not significantly differ between those children with no living grandmothers and those with a living maternal grandmother (OR = 0.98, 95% CI 0.71–1.36), paternal grandmother (OR = 0.99, 95% CI: 0.71–1.38), or both grandmothers (OR = 1.00, 95% CI: 0.73–1.37) (Figure 1c). Chances of survival increased with child age (OR = 1.55, 95% CI: 1.42–1.69) and number of living siblings (OR = 1.22, 95% CI: 1.09–1.37), and decreased with an increasing birth order (OR = 0.86, 95% CI: 0.79–0.93), being born as a twin (OR = 0.39, 95% CI: 0.21–0.72), and after losing a mother (OR = 0.23, 95% CI: 0.12–0.44).

3.4. Subsequent interval < 24 months

Survival of children followed by short birth interval is significantly lower compared to children followed by birth intervals longer than 24 months (Blurton Jones, 2016). Having both grandmothers alive improved the chance survival of children when their birth was followed by a short birth interval by 40% (OR = 1.40, 95% CI: 1.05–1.87); Figure 1d and Table S4). This was likely driven by maternal grandmother presence (OR = 1.41, 95% CI: 1.04–1.91), as there was no effect on odds of survival when only a paternal grandmother was alive (OR = 1.16, 95% CI: 0.85–1.58). In addition, the chance of survival was improved with increasing child age (OR = 1.77, 95% CI: 1.62–1.93), number of living siblings (OR = 1.19, 95% CI: 1.06–1.34) and being a girl (OR = 1.26, 95% CI: 1.05–1.52), but worsened with increasing birth order (OR = 0.82, 95% CI: 0.75–0.88). Maternal absence was not significant for the odds of survival (OR = 1.33, 95% CI: 0.19–9.46), though this is perhaps unsurprising in this case – mother survival is most important in the first few years of life (Lahdenperä et al., 2011), and the children in this analysis all had a living mother at least up until the subsequent birth.

3.5. Illegitimate children

Illegitimate children suffered higher mortality compared to legitimate children (Turpeinen, 1979). We did not find an effect of maternal grandmother presence on the survival of illegitimate children to the age of 5 (OR = 1.12, 95% CI: 0.89–1.40; Figure 1e and Table S5). Their chance of survival increased with age (OR = 1.48, 95% CI: 1.35–1.61), but was negatively affected by being born as twin (OR = 0.28, 95% CI: 0.16–0.49), or after losing a mother (OR = 0.13, 95% CI: 0.06–0.28). Probability of survival was also affected by the region of Finland in which illegitimate children were born - those born in the mainland area had a worse chance of survival compared to those born in archipelago area (OR = 0.63, 95% CI: 0.46–0.87).

4. Discussion

In this study, we set out to test grandmother effects on survival of grandchildren born with into potentially challenging birth situations. Using an extensive largely pre-industrial data set for a Finnish population, we have shown that grandmother presence mostly does not mitigate poorer birth conditions. However, if the subsequent birth was after a short interval (under 24 months), grandchildren had a 41% higher chance to survive till 5 years of age when the maternal grandmother was present. Taken together, these findings highlight a limited, albeit important, role of grandmothers who compensate the mother's investment in the new baby, and thereby allow faster birth rates without sacrificing child survival.

We did not find an effect of grandmother presence on survival of firstborns. We hypothesised that such an effect of grandmother presence on firstborn survival would be likely since being a mother for the first time could be challenging and grandmothers could be a great source of informational, emotional, and instrumental support (Scelza & Hinde, 2019). Though there is a chance that grandmothers were still reproducing themselves when their first grandchild was born − and therefore were less interested in helping their daughters/daughters-in-law − only 6.6% of mothers delivered a child within 2 years of their first grandchild (Lahdenperä, Gillespie, Lummaa, & Russell, 2012), and this is therefore unlikely to have driven our result. Grandmother may play a significant role for women who become mothers at a very young age. In Nordic countries and in Finland, in particular, mean age at first marriage was relatively high (Moring, 2003). As stated by Moring (2003) mean age at first marriage was 24 years between 1750-1790 and 25 years between 1878-1895 and driven by the necessity to have income (a profession, a farm, or a croft). There were also observed differences between regions and groups with different socio-economic status. For example, landless women born in Western Finland between 1790-1810 were on average 29.3 years at first marriage as compared to landed women who were 24.8 years. For women born in Eastern Finland between 1790-1825, the corresponding ages were 24.5

vs. 23.6 years for landless and landed women. Even though young age seems not to be risk factor in this population, it was shown previously in another non-industrial population that maternal grandmothers are more important for mothers under 25 years of age (Blurton Jones, 2016), though this study did not test whether they were mothers for the first time or not. In our sample, despite 55% of mothers giving birth for the first time before the age of 25, we did not observe a beneficial role of grandmothers on the survival of the firstborn grandchild. However, though this does not support our hypothesis, it is not altogether surprising: grandmothers may not be crucial for firstborns since the grandchild does not have to compete for resources with their sibling (resource dilution hypothesis), and, as indicated by Knodel and Hermalin (1984), sibship size could be more important for mortality than birth order. Further, we did not find an effect of grandmother presence on twin survival. We have shown that those born on the mainland had lower chance of survival compared to those born in the archipelago area which is consistent with previous study from our population (Lummaa, Haukioja, Lemmetyinen, & Pikkola, 1998). Twins have higher risk of mortality within the first week of life compared to single-born children (Bellizzi, Sobel, Betran, & Temmerman, 2018), and have a higher overall risk of death (Lummaa et al., 2001). It has been shown that twins are more often born to older mothers (Hazel, Black, Smock, Sear, & Tomkins, 2020; Helle, 2008), who may already be more experienced. This may explain why grandmothers were of no importance for twin survival. Moreover, we did not find an effect of grandmother presence on survival of illegitimate children, despite evidence of grandmothers improving survival for illegitimate children of sex workers in 19th century (Vainio-Korhonen, 2018). These suggest that grandmothers are not particularly important for infant survival in historical Finland and grandmother's effects can be context-dependent, and that the presence of the mothers is most crucial in these early years. Indeed, previous work in this population has found beneficial effects of grandmother presence to be limited to post-weaning years (Chapman et al., 2019).

Despite grandmother presence not being associated with improved infant survival for most of the poor birth statuses we investigated, we did find significant effect of grandmother presence on child survival for those who were followed by a sibling within 24 months. In this scenario, the mother is more focused on the new baby, but the focal child still requires a lot of attention; the opportunity and need for a grandmother to improve the older sibling's chances of survival are there. As pointed by Hawkes and colleagues (Hawkes, O'Connell, & Blurton Jones, 1997), with help from others, a mother should be able to wean sooner and allocate more effort to the next child. By supporting the older child through a potentially hazardous period, the grandmother is thus able to increase her daughter's reproductive rate and success and thereby her own indirect fitness. As mentioned above, grandmother survival effects in this population are expressed in the years following weaning (Chapman et al., 2019). Similar effects of post-weaning being an important period are shown on studies of the Hadza in Tanzania: nursing mothers reduced foraging time when they had a new baby, and since foraging time is important for children's nutritional status, the grandmothers play an important role in supporting children's well-being by offsetting this reduction in foraging time by mothers (Hawkes et al., 1997). This effect is especially strong for children weaned young. In the Hadza, for example, grandmothers help improve grandchildren nutritional status which can be important for their survival status. The effect of maternal grandmothers on nutritional status of grandchildren was observed also in Aka population: grandmothers improved growth, measured by weight-for-age and weight-for-height standards, of children in the post-weaning phase (36 to <72 months of age in this population) (Meehan, Helfrecht, & Quinlan, 2014). Moreover, it was recently shown in a Hadza population that (weaned) children aged 1 to 5 years of age without a living grandmother had lower weight and upper arm circumference compared to those with no living grandmother. Further those children had a doubled risk of dying compared to those with living grandmother (Blurton Jones, 2016).

We did not find an effect of grandmothers on survival of grandchildren who were preceded by a short interval. One of the reasons for this could be that the mother's attention was mostly on the index child (i.e. the newborn), who would not require independent supplementation from a grandmother. Maternal survival was especially important for these dependent youngest children, as has been shown previously (Lahdenperä et al., 2011); if the mother died, these children had a significant reduction in their probability of survival.

The effect of short succeeding birth intervals on survival of the child of interest (the index child) has received less attention in the literature (Fotso et al., 2013). There is a problem of reverse causality – the death of the index child may be the cause, not the consequence, of a short interval. It arises from the fact that when the index child dies, the succeeding interval may be short because of absence or very short period of breastfeeding, and, as a consequence, lactational amenorrhoea is shorter and the mother is able to conceive sooner (Valeggia & Ellison, 2001). However, in this study we overcame the problem of reverse causality because we analyzed only children who survived at least until the time when the younger sibling was born. We can then explain the effect for subsequent birth interval as follows: the mother is more focused on the new baby, but the focal child still needs lots of attention. This brings us also to the explanation why the short preceding birth interval has no effect – the mother is looking after the focal child as the newborn.

Overall, grandmothers in this population had little effect on the survival of grandchildren born with an adverse birth status. However, this does not diminish the role of grandmothering:

mortality of these children was highest in the first couple of years, when the mother would breastfeed, and hence the opportunity for grandmothers to help (other than through advice or dietary supplementation for the mother) was negligible. Overall 27% of deaths in this population occurred before 5 (Chapman et al., 2018), and often from infectious diseases. Moreover, short inter-birth intervals may lead to higher rates of infant and child mortality because closely spaced siblings are susceptible to disease that can be easily transmitted from an older to a younger sibling with a limited immune system (horizontal transmission) (Molitoris, 2017). Whilst the opportunity for grandmothers to mitigate the risks of adverse birth statuses is limited, this study does show – through the beneficial effect on survival for those with a short subsequent birth interval – that grandmothers can increase the possibility for mothers to have several dependent young children with short birth-intervals in line with the Grandmother hypothesis (Hawkes et al., 1998).

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Appendix A. Supplementary data

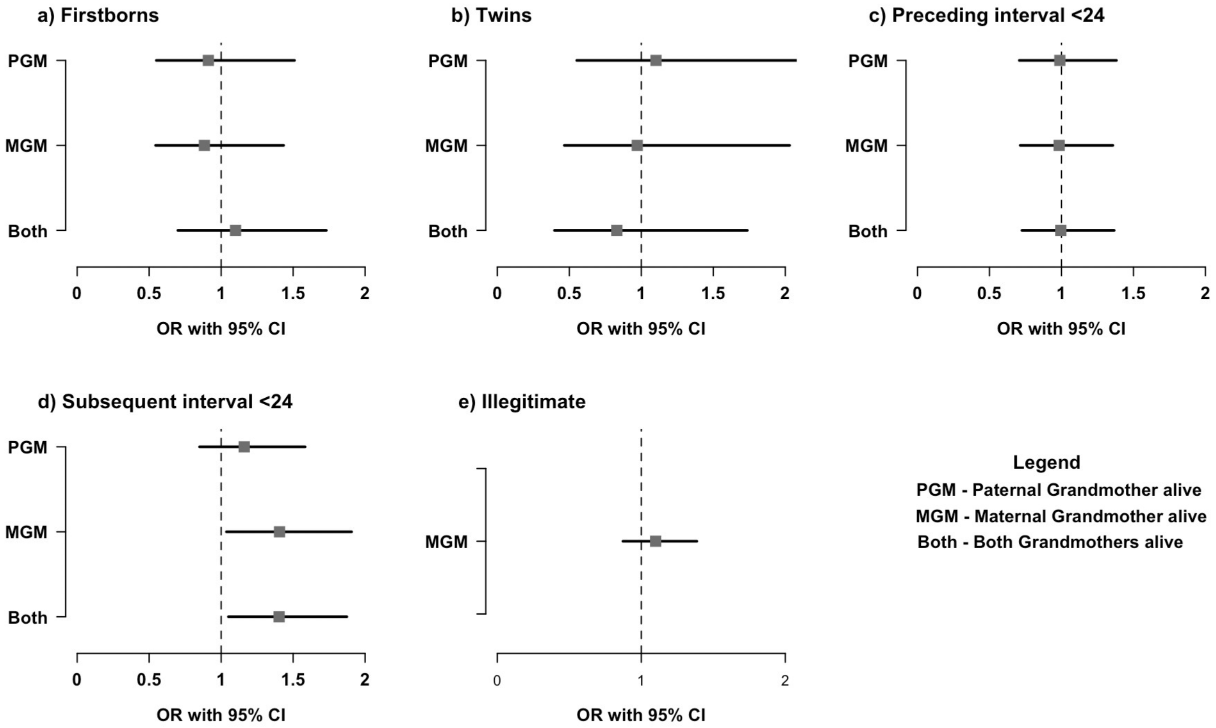

Figure 1. Generalized linear mixed model results of grandmothers' presence on grandchildren survival: a) firstborns, b) twins, c) grandchildren preceded by birth interval <24 months, d) grandchildren succeeding by birth interval <24 months, e) illegitimate children. Higher odds ratio (OR) indicates increased survival compared to the reference group (neither grandmother alive).

Table 1. Descriptive statistics of studied groups of grandchildren all of whom had the status of both grandmothers known.

Variable	Firstborns N = 1175		Twins N = 216		Individuals with short preceding interval N = 1432		Individuals followed by short interval N = 1450		Illegitimate children N = 1201	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Maternal age at 1st birth	24.66	4.53	31.13	5.57	30.05	5.55	28.27	5.51	27.57	6.05
Number of living siblings/Later born siblings*	0.46	0.62	2.91	1.71	2.53	1.72	2.16	1.73	0.68	1.01
Maternal grandmother's age at grandchild's birth	55.49	7.92	62.45	8.14	60.93	8.99	59.02	8.90	58.82	8.71
Paternal grandmother's age at grandchild's birth	58.68	8.85	64.94	9.35	63.87	8.95	62.17	8.85	-	-

*in model on firstborns

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