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**Sons shorten mother's lifespan in pre-industrial families with high level of infant
mortality**

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Abstract

In dimorphic vertebrates where males are larger than females, the energetic costs of producing and rearing sons can exceed those of daughters. In humans, differences in maternal energy intake suggest that sons require 10% and 7% more energy than daughters during pregnancy and lactation, respectively. Due to a trade-off between reproduction and somatic maintenance, having sons is expected to have a more pronounced detrimental impact on mother's lifespan than having daughters. A limitation of previous studies investigating this hypothesis is that the increased mortality cost of having sons were assumed to affect all mothers equally. Using a dataset from a preindustrial Quebec population monitored over two centuries, we found that the number of sons decreased post-menopausal lifespan only in mothers experiencing high infant mortality. Our study highlights the importance of inter-individual variation in environmental conditions and maternal health when studying effects of offspring sex on reproductive costs.

Keywords: cost of reproduction, preindustrial humans, maternal lifespan, offspring sex ratio

Translated title

Les fils réduisent la longévité maternelle dans des familles préindustrielles où la mortalité infantile est élevée

Translated abstract

Chez les vertébrés dimorphiques où les mâles sont plus grands que les femelles, les coûts énergétiques pour produire et élever un fils peuvent dépasser ceux des filles. Chez les humains, les différences d'apport énergétique maternel suggèrent que les fils ont besoin de 10% et 7% d'énergie en plus pendant la grossesse et l'allaitement, respectivement. En raison d'un compromis entre la reproduction et la maintenance somatique, avoir des fils devrait avoir un impact négatif plus prononcé sur la longévité de la mère qu'avoir des filles. L'une des limites des études antérieures portant sur cette hypothèse est que la mortalité accrue liée au fait d'avoir

des fils était supposé affecter toutes les mères de la même manière. En utilisant un jeu de données provenant d'une population québécoise préindustrielle suivie sur deux siècles, nous avons constaté que le nombre de fils réduisait la longévité post-ménopausique seulement chez les mères ayant une forte mortalité infantile. Cette étude souligne l'importance de la variation interindividuelle des conditions environnementales et de la santé maternelle lors de l'étude des effets du sexe de la progéniture sur les coûts de reproduction.

Introduction

The limited amount of resources that an organism can acquire and allocate to different biological functions imposes trade-offs between life-history traits (Stearns 1992). Thus, a high energy allocation toward reproductive effort should limit the energy available for somatic maintenance and repair, leading to a decrease in future reproduction or survival (Kirkwood 1977, 2017; Lemaître et al. 2015; Douhard et al. 2021). The occurrence and the magnitude of such reproductive costs can, however, depend on both the sex of the parents and their offspring. In the vast majority of mammalian species, only mothers provide care (Stockley and Hobson 2016), and offspring of the larger sex, typically males, require more maternal resources (Clutton-Brock 1991). Some studies on wild long-lived mammalian populations (Gomendio et al. 1990; Berube et al. 1996; Douhard et al. 2020) have shown that the production of sons is costlier than that of daughters for mothers reducing both their probabilities of future reproduction and survival. However, the higher costs of producing sons in humans are equivocal.

There are substantial differences in the physiological development of boys and girls (Jasienska 2020). Boys are heavier and larger at birth (Loos et al. 2001), and pregnant women carrying boys have a 10% higher energy intake than those carrying girls (Tamimi 2003), emphasizing that boys require more energy during pregnancy. In line with these sex differences in energy requirements, post-menopausal lifespan in pre-industrial Sami women decreased by 0.65 years for each son born, but increased by 0.44 years for each daughter born (Helle et al. 2002). However, subsequent studies did not detect any higher mortality costs of having sons than daughters and have thus cast doubts on the occurrence of a reproductive cost modulated by offspring sex in humans (e.g. Beise and Volland 2002; Jasienska et al. 2006; Cesarini et al. 2007; Kim 2022).

Several factors, largely neglected so far, could potentially shed new light on these observed discrepancies between studies (Helle 2018, 2019). First, the costs of having sons (or offspring more generally) may be expressed at the individual level, but cannot be detected between individuals because it is masked by individual differences in resource acquisition (Van Noordwijk and de Jong 1986) or health (Gagnon 2015). For instance, higher costs of sons may manifest only in individuals experiencing scarcer resources (Gomendio et al. 1990; Van De Putte et al. 2004). Second, while studies typically considered the number of sons born, pregnancy accounts only partially to the differential energetic costs of sons and daughters because sons consume more milk than daughters (da Costa et al. 2010) and lactation is much more energy-demanding than pregnancy (Butte and King 2005; Jasienska 2009, 2020). Consequently, a consideration of the maternal care stage until the end of the lactation period, rather than just pregnancy, may allow a more accurate assessment of the differential costs of sons and daughters on post-menopausal lifespan.

A previous study proposed that the negative effect of the number sons on post-menopausal lifespan is not initiated during pregnancy and lactation, but later in the mother's life (Van De Putte et al. 2004). The authors proposed that resource competition between mothers and adolescent sons was higher than that between mothers and adolescent daughters ("*Male-dominated intra-household resource competition*" hypothesis). Specifically, they suggested that in patriarchal societies adolescent sons use their role in physical labour to obtain a larger share of resources within the household, primarily food, and thus have a negative effect on maternal longevity in poor families.

In this study, we examine differential costs of sons and daughters on maternal post-menopausal lifespan, measured here as the lifespan of women having already survived at least until 45, using an exceptionally detailed dataset from a preindustrial population living in the St. Lawrence Valley (Quebec, Canada) during the 17th and 18th centuries (Dillon et al. 2018). We addressed

the following questions with their corresponding predictions. First, are there higher costs of producing sons on maternal post-menopausal lifespan when neglecting inter-individual variation in such a cost? Based on a previous study in this population (Beise and Voland 2002), we predicted a weak influence of the number of sons on maternal lifespan (Prediction 1). Second, do the costs of sons on maternal lifespan vary across women? The pre-industrial Quebec population faces a rather strong spatial environmental variability, inhabitants living south of the St-Lawrence River benefited from much better agricultural yields than their northern counterparts (Gagnon 2012). Moreover, the offspring mortality during the first year of life is very high (and can even reach 20 or 30%, see (Bergeron et al. 2014)) and it has been previously suggested that women who lost a large fraction of their infants are in poor health, likely due to insufficient resources (Spielmann 1989; Gagnon et al. 2009). Infant mortality incorporates a wide range of socio-ecological factors such as nutrition, nursing practices, health, sanitation and infectious disease epidemics that were common at the time of our study (Amorevieta-Gentil 2010; Gagnon-Sénat 2022; Shanahan et al. 2022). Finally, it has been suggested that women who give birth to their last child at an old age are likely to be in better health than others (Gagnon et al. 2009; Jasienska 2020). We thus expected that post-menopausal lifespan should decline as number of sons increases particularly for women living in the North of the St-Lawrence River, for women facing a high infant mortality and for women with a young age of last birth (Prediction 2). Third, do the costs of sons on maternal lifespan depend at which stage of development sons are counted? Because breastfeeding is more energetically costly than pregnancy, we expected that the strength of relationships between the number of sons and the post-menopausal lifespan to be stronger when considering the number of sons surviving to 14 months (average end of lactation in this population (Henripin 1954a)) rather than at birth (Prediction 3a). Alternatively, if an intrahousehold competition between adolescent sons and mothers is high, we should observe a stronger relationship between the number of sons and the

post-menopausal lifespan when considering sons surviving to 18 years rather than at 14 months (Prediction 3b).

Material & Methods

Study area and population

Data were extracted from the Registre de la Population du Québec Ancien (RPQA) database, consisting of family reconstitutions of the Québec's population from 1621 to 1799 based on parish registers (Dillon et al. 2018). The Québec population was founded in 1608 with the colonisation by French (Boleda 2008). Settlers began to spread 500 km along the St Lawrence valley and had an average of 10 children per family (Charbonneau et al. 1993; Gagnon 2012). This colony is considered as a 'semi-closed population' in spite of some emigration during short periods and under special circumstances (Dillon et al. 2018). It is also considered as pre-industrial since the industrial revolution did not begin until the 19th (Clark and Northrup 2003). During the period 1608-1799, most inhabitants were farmers and their family was dependent from the resources produced (Greer 1985). Food resources were more abundant on the south than on the north shore of the St Lawrence River due to better environmental conditions. Specifically, the southern inhabitants had larger lands and they benefited from higher crop yields (mostly in wheat) with 5.8 bushels of grain per acres sown versus 4.9 bushels in the north for a same surface corresponding to 389.8 kg per hectare versus 328.5 kg per hectare (Harris and Matthews 1987; Gagnon 2012). During this period there was two urban parishes, Quebec City and Montreal while the other parishes were rural.

Living conditions changed considerably over the study period. There was a greater proportion of people living in urban areas in the 18th century than in the 17th (Gadoury et al. 1985). In parallel, there was an increase of infant mortality (defined as proportion of infants who died before one year old) (Henripin 1954b; Charbonneau and Henripin 1975). Increase in population

density, especially in cities, favoured the spread of diseases (Mazan and Gagnon 2007), in addition to an increase of insalubrity. Epidemics of various diseases occurred during the study period, including typhus (1687 & 1748-1750), smallpox (1640, 1669-1670 & 1702-1703) and measles (1714-1715) (Amorevieta-Gentil 2010). In addition to these epidemics, several wars led to periods of famine, notably between 1689 and 1694 (inter-colonial wars) and between 1756 and 1763 (War of Conquest) (Amorevieta-Gentil 2010). However, in our dataset the variability in infant mortality was 5 times larger between mothers within a given year than between years (Table S1), suggesting that infant mortality captures well the conditions at a household scale. Similar to most historical well-documented populations (Nenko et al. 2014), information regarding the socio-economic status of women were missing for women included in our analyses.

Data-filtering criteria

We applied various filters on the database to extract the data required for our analyses (Fig. S1). First, we removed data for women with missing information, such as unknown lifespan, husband lifespan, age at childbirth, sex of children, and children lifespan. We then further refined the sample by only including individuals born in Québec, as immigrants tend to have better survival rates (Gagnon et al. 2009) and probably different environmental conditions at birth. We also limited the dataset to women with only one marriage (Van De Putte et al. 2004) and those who survived at least to 45 years old. Lifespan cut off was set at age 45 because it represents the age at which 99% of the women stopped reproduction in the population (Engelhart et al. 2019). We removed 37 women having children after this age. We only included women who lived their entire reproductive lives in one type of parish (rural or urban) and at one geographic location (south or north shore of the St- Lawrence River), as indicated by the birth parish of their children. Our dataset contains cohorts from 1621 to 1799. Individuals were

monitored until 1835, year of the last recorded death. Consequently, to ensure that we only had women with a complete reproductive history, we had to include women whose reproductive history ended no later than 1799, which means that we only included women born before 1754. We also performed analyses on a more restrictive dataset, including only women born no later than 1713, the latest cohort in which at least 95% of women died in 1799. Consequently, we distinguished two datasets, one comprising cohorts from 1621 to 1754 and the second including cohorts from 1621 to 1713.

Statistical analyses

In previous studies, the potential association between the number of sons and the post-menopausal lifespan was assessed using two methods. The first method consisted of including both the number of sons and the number of daughters as explanatory variables in the same model (Helle et al. 2002), while the second one considered both the number of sons and the total number of children as explanatory variables in the same model (Cesarini et al. 2007). Currently, there is no consensus as to which method to use for assessing the differential costs of sons and daughter on maternal lifespan. However, the number of sons and the number of children were highly correlated in our dataset, regardless of the age at which sons and children were considered (Spearman coefficient of correlation, $r_s > 0.85$, Fig. S2A, S2C & S2E), leading to collinearity issues when both variables were simultaneously included in the same model (Dormann et al. 2013). We thus chose to use the number of sons and the number of daughters in our analyses, to assess the costs of producing sons while accounting for family size. We fitted linear mixed-effects models (LMM) performed in R version 4.3.1 (R Core Team 2023). We included two random effects: the family ID corresponding to a unique identifier to account for family effects between sisters and the mother birth year to account for temporal variation such as epidemics or stochastic events (Bruckner et al. 2018). In the 1621-1754 cohorts, representing 1886 women, 1359 had a unique family ID and 248 had sisters that also reached all selection

criteria. We grouped mothers' birth year by decade, as there were 31 years out of 107 in which fewer than 10 women were born in the 1621-1754 cohorts. We also applied grouping in the 1621-1713 cohorts, where of the 66 years in which mothers' births were distributed, 24 included less than 10 women born.

To test our first prediction, we fitted a LMM with post-menopausal lifespan as a response variable and the number of sons born as an explanatory variable. The other explanatory variables are: number of daughters born, maternal age of last birth, wave front, infant mortality, geographic location, urbanity, husband lifespan (see Table 1 for a detailed description). This model was rerun replacing the number of sons and daughters born by those surviving to 14 months and then 18 years. Then, to examine whether the costs of sons on post-menopausal lifespan were higher (or only detectable) under harsh conditions of resource availability or in women in a poor health (Prediction 2), we fitted the same LMMs as above (Prediction 1) but we separately added three groups of two interactions. These interactions were between (1) infant mortality and number of sons/daughters, (2) geographic location and number of sons/daughters and (3) age at last birth and number of sons/daughters. For predictions 1 and 2, we reported the slopes (\pm SE) between the independent variables and the post-menopausal lifespan and associated P-values in tables. We assessed significance by using an alpha of 5% and we considered a tendency when the p-value was less than 10%. To visually represent interactions between two continuous variables, we used the Johnson-Neyman technique (Long 2022) which shows how the slope of the relationship between the number of sons and the post-menopausal lifespan in Y axis varies depending on a given variable of interest (i.e. infant mortality, geographic location or age at last birth) in X axis. For this, we used the 'interactions' package in R (Long 2022). To test whether the relationship between the number of sons and maternal lifespan depended on the age at which the number of sons is counted, more specifically at birth, 14 months and 18 years (Prediction 3), we investigated whether the confidence intervals

95% for these relationships overlapped or not. The distribution of the post-menopausal lifespan is represented in Fig. S3, and those of model residuals in Fig. S4 to S7.

Table 1

Results

Are there higher costs of sons on maternal post-menopausal lifespan?

We found no or little evidence of costs of sons on post-menopausal lifespan, regardless of the age at which sons were considered in the 1621-1754 cohorts as well in the 1621-1713 cohorts (Table S2 & S3, Fig. 1 & S8). The number of sons born only tended to be negatively correlated with post-menopausal lifespan in the 1621-1754 cohorts (Fig. 1). In addition, we consistently found a negative relationship between the infant mortality and the post-menopausal lifespan (Table S2 & S3). Otherwise, we found a negative effect of urbanity on the post-menopausal lifespan in the 1621-1754 cohorts only (Table S2). There was a positive effect of husband lifespan on post-menopausal lifespan in the 1621-1713 cohorts, and the 1621-1754 cohorts showed a trend in the same direction (Table S2 & S3). Finally, we found no effect of number of daughters, age at last birth, geographic location and wave front on the post-menopausal lifespan, regardless of cohorts or developmental stage of the children (Table S2 & S3).

Fig.1

Do the costs of sons on maternal post-menopausal lifespan vary across mothers?

In the 1621-1754 cohorts, the interaction between the number of sons surviving to 14 months or 18 years and infant mortality on post-menopausal lifespan was statistically significant (Table 2). When sons and daughters were considered at 14 months, we found costs of sons on post-menopausal lifespan only for women with an infant mortality rate exceeding 0.20 and these costs increased with increasing infant mortality (Fig. 2B). For instance, the model predicts that

women with an infant mortality of 0.21 and 0.75 experienced a decrease by 123 and 585 days of post-menopausal lifespan for each son surviving to 14 months, respectively (Fig. 2B). Similarly, when the number of sons and daughters were considered at 18 years, we found costs of sons on post-menopausal lifespan only for women with an infant mortality rate above 0.26 and these costs also increased as infant mortality increased. The model predicts a decrease of post-menopausal lifespan by 149 days per son in women with an infant mortality rate of 0.27 and a decrease by 536 days per son in women with an infant mortality of 0.75 (Fig. 2C). Although not significant, the interaction between the number of sons born and infant mortality in the 1621-1754 cohorts revealed a trend for increasing costs of having sons on post-menopausal lifespan when the level of infant mortality is increasing (Table 2 & Fig. 2A). Results obtained in the 1621-1713 cohorts are similar, even though the interaction between the infant mortality and the number of sons surviving to 14 months and 18 years are only trends (Table S4 to S6, Fig. S9). We found no evidence for interactions between the number of sons and the geographic location or between the number of sons and age at last birth on post-menopausal lifespan both in both the 1621-1754 cohorts (Tables 3 & 4) and the 1621-1713 cohorts (Table S5 & S6). Regarding the main effects of urbanity and husband's lifespan, the results were similar to those described above for prediction 1, both in the 1621-1754 (Table 2 to 4) and in the 1621-1713 cohorts (Table S4 to S6).

Table 2

Fig. 2

Table 3

Table 4

Do the costs of sons on maternal lifespan depend at which stage development sons are counted?

The costs of sons found in women facing a high infant mortality remained equivalent regardless the age at which sons were considered, as shown by 95% confidence intervals overlapping in the 1621-1754 cohorts, as well in the 1621-1713 cohorts (Fig. S10).

Discussion

Returning to our original predictions, we found an overall weak effect of the number of sons on maternal lifespan (support for prediction 1), as the number of sons born only tended to be negatively correlated with post-menopausal lifespan in the 1621-1754 cohorts. Our second prediction, stating that the costs of sons on maternal lifespan varies across women was partially supported. We found higher costs of sons over daughters surviving to 14 months and 18 years on post-menopausal lifespan in women having a high infant mortality but not living in the North of the St-Lawrence River or having children in older age. Our third prediction was not supported because the costs of sons on maternal lifespan did not vary with the developmental stage at which sons were counted.

Our results suggest that ecological and biological factors act together to modulate the costs of producing and raising sons on post-menopausal lifespan. Indeed, we found survival costs of having sons on post-menopausal lifespan in women with higher rate of infant mortality, a common proxy of environmental conditions and maternal health in human and wild populations (Wilson et al. 2006; Gagnon et al. 2009; Griffin et al. 2018; Nenko et al. 2018). Infant mortality captures a wide range of socio-ecological factors such as nutrition, nursing practises, health, sanitary conditions and epidemic of infectious disease (Amorevieta-Gentil 2010; Gagnon-Sénat 2022; Shanahan et al. 2022). Although inhabitants living south of the St-Lawrence River benefited from better agricultural yield than their northern counterparts, thus potentially a better

nutrition (Gagnon 2012), we did not find higher costs of sons on post-menopausal lifespan in women living in the North of the St-Lawrence River. These results are not comparable with those using infant mortality because geographic location was measured at the population level while infant mortality was quantified at the family level. Unfortunately, we do not have data on food availability, the income for each family or the medical follow-up of each mother, which would allow us to determine whether high infant mortality predominantly reflects a poor nutrition or poor health.

Like infant mortality, the age at last birth has been suggested as an important indicator of maternal health. Although women giving birth at an older age have higher risks of complications such as anaemia, obstetric complications and a higher risk of mortality, an old age at last birth can also be a sign of good health (Jasienska 2020). Previous studies support this contention, reporting a positive relationship between the maternal post-reproductive lifespan and the age at last birth (Sun et al. 2015). Using this indicator, Gagnon and colleagues (2009) found that the trade-off between number of children and post-50 lifespan is stronger for women who gave birth to their last child at a young age. We also expected costs of sons on post-menopausal lifespan especially in women with a young age at last birth. However, our results did not confirm this prediction. Of the two health indicators we used, we only found costs of sons on post-menopausal lifespan when we integrated the infant mortality differences between women. A possible explanation is that infant mortality captures more factors such as nutrition, nursing practises, health, sanitary conditions and infectious diseases compared to the age at last birth.

Pregnancy involves an average energy expenditure of 89, 286 and 466 kcal day⁻¹ for each trimester in women with a gestational gain of about 12 kg, whereas lactation involves an energy expenditure 626 kcal day⁻¹ on average (Butte and King 2005). Because the differential energetic costs of sons and daughters are present during pregnancy and continue into lactation, as shown

by the 10% more energy required by the mother during the pregnancy of a boy and the 7% higher milk consumption of boys during lactation (Tamimi 2003; da Costa et al. 2010), it was expected that the higher energy cost of lactation for mother would reinforce the costs of sons on post-menopausal lifespan. However, the costs of sons were not amplified, as we did not find higher costs of sons when they were considered at 14 months rather than at birth. It is possible that differences in milk consumption between the sexes was not large enough to have a greater impact on maternal lifespan than the difference in energy costs between the sexes during pregnancy.

The costs of rearing sons detected in this study could have several origins such as physiological (i.e. linked to the increased metabolism during pregnancy and lactation), social (i.e. intra household competition emerging during adolescence) or a combination of the two. One potential social mechanism to explain the emergence of the costs of sons from adolescence is rooted in the sociocultural gendered division of responsibilities (Helle et al. 2002; Van De Putte et al. 2004). In preindustrial patriarchal societies, sons usually help their father at the farm (Lachance 2002), while daughters were more likely to help at home. For mothers this means that a son may simply add to her workload, while a daughter may assist in the house, lightening her domestic and caregiving responsibilities. In addition, mothers may be at a greater disadvantage in the competition for resources within households when they had more teenage sons (Van De Putte et al. 2004). Our analysis has tried to disentangle between the various possible origins of the costs of sons. Typically, the analysis at birth captures the costs of sons occurring during pregnancy, the analysis at 14 months captures the costs of sons occurring during pregnancy and lactation and lastly, the analysis at 18 years captures the cumulative costs of sons occurring during pregnancy, lactation and adolescence. Consequently, if the costs of sons on post-menopausal lifespan has a social origin only, then the costs of sons should be present only at age 18 while if the origin is physiological only (i.e. linked to the increased

metabolism during pregnancy and lactation), we should detect costs of sons at birth and/or 14 months without exacerbated costs at 18 years. On the contrary, if the origin is rather a mixture of physiological factors and social factors, then the costs of sons should be present at every age where they are considered, but with a stronger effect at 18. Our results showed costs of sons on post-menopausal lifespan only in women facing a high infant mortality at every age in which sons were considered (Fig. 1), but there was not any difference in the effect sizes obtained between ages considered, as shown by the overlapping between sons age categories (Fig. S10). Therefore, the costs of sons detected only in women facing a high infant mortality seems to have a physiological origin during pregnancy. Our results are similar to those of studies focusing on Finnish and Utah populations, which also showed that maternal lifespan was negatively affected by the production of sons, regardless of how long sons survived (Helle et al. 2002; Harrell et al. 2008; Helle and Lummaa 2013).

In line with the predictions that trade-offs between life history traits are more likely to be detected when the environment is unfavourable (Stearns 1992; Douhard et al. 2021), the costs of having and raising sons was more acute for women suffering from a high infant mortality and thus likely living in an inhospitable environment (Gagnon et al. 2009). However, the physiological mechanisms linking sons' production to post-menopausal lifespan are yet to be identified. Recently it has been suggested that inflammaging (i.e. the increase in inflammatory factors throughout life without any sign of severe infectious disease (Franceschi et al. 2006; Pawelec et al. 2020)) could be such a key mediator (Marttila et al. 2015). For example, a study performed in a rural Polish population revealed that each son increase the concentration in C-reactive protein by 11% and Interleukin 6 by 6% (two markers of inflammation) in mothers (Galbarczyk et al. 2021). Since the chronic inflammation underpinning inflammaging is considered as a key physiological mediator of the ageing process (López-Otín et al. 2023) and is suspected to be tightly associated with both mortality and morbidity (Ferrucci and Fabbri

2018), it constitutes a promising candidate to explain relationships between post-menopausal lifespan and the number of sons produced. Furthermore, several conditions during pregnancy may magnify the effect of the number of sons on inflammaging, such as infections and malnutrition (Zavatta et al. 2022). Alternative mechanisms related to the immunosuppressor effects of androgens have also been advanced (Helle et al. 2002; Næss et al. 2017) but their effects remain largely equivocal (Roberts et al. 2004; Merklings et al. 2018).

The trade-off between maternal post-reproductive lifespan and the proportion of sons has been studied many times in different populations and using different methodologies since the first study to examine this trade-off (Helle et al. 2002). Yet, only a small proportion of these studies have been able to detect costs of sons (Helle et al. 2002, 2010; Harrell et al. 2008; Helle and Lummaa 2013; Christiansen 2014; Næss et al. 2017). Although we might expect that such costs were more prevalent in preindustrial populations than in current populations (e.g. due to the lack of medical care), this does not seem to be the case as this trade-off has been demonstrated in both types of populations (e.g. *modern* - Christiansen 2014; Næss et al. 2017 and *preindustrial* - Helle et al. 2002, 2010). Similarly, while a study reported a negative effect of the number of sons on maternal longevity in the poorest social class only (Van de Putte and colleagues 2004), this was not the case in other populations (Hurt et al. 2006; Cesarini et al. 2007) suggesting that social class may be a limited indicator of heterogeneity between women. Here we used the infant mortality as an indicator of heterogeneity between women and given that the variability in infant mortality is much higher between mothers within a year than between years (Table S1), this indicator mainly captures differences in maternal health, that may be due to genetic factors, while the social class cannot. However, further studies are needed to determine whether infant mortality is a better measure than the social status and to determine the relative contribution of genetic and environmental factors (including during the early life period) to maternal infant mortality. Another possible reason for the detection of this trade-off

using the infant mortality could also be related to demographic factors, such as the high parity in historical Quebec, which could make the costs of reproduction more detectable (Gagnon et al. 2009).

The detection of costs of sons on post-menopausal lifespan only when we accounted for differences in environmental conditions and maternal health highlight the importance of considering inter-individual variability when quantifying the costs of producing sons. This decrease of lifespan concerns only post-menopausal women which could be seen, at least at first glance, as less important from an evolutionary point of view given that the strength of natural selection is weak at old age (Hamilton 1966). However, in the pre-industrial Quebec population, reproductive success was higher when grandmothers were alive, likely because they helped their daughters with childcare (Engelhardt et al. 2019). Thus, post-menopausal lifespan has important fitness consequences for subsequent generations, reinforcing the evolutionary implications of our findings.

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Statement of Authorship

M.D and L.I conceived the study. L.I. performed the statistical analysis, with input from M.D, P.B, J.-F L, and F.P. All authors wrote the manuscript.

Data and Code Accessibility

The datasets and code used in this study are available on Zenodo:

<https://doi.org/10.5281/zenodo.11185119>

The data used in this study were extracted from the Registre de la Population du Québec Ancien (RPQA) administered by le Programme de recherche en démographie historique of the Université de Montréal. More information is available on the official website:

<https://www.prdh-igd.com/fr/le-prdh>

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Tables section

Table 1: An overview of the variables used for analyses in the 1621-1754 cohorts.

Variable	Metrics		Rationale
	Mean	SD	
Continuous:			
Maternal post-menopausal lifespan (years)	69.30	11.43	Response variable.
Husband lifespan (years)	65.91	13.91	In agricultural and patriarchal populations, as is the case here, family resources depend on the husband's crops (Greer 1997), suggesting the presence of a positive husband-wife lifespan relationship.
Number of daughters born	3.128	2.41	Allows accessing the differential costs of sons and daughter during pregnancy on maternal lifespan.
Number of daughters surviving to 14 months	2.35	2.02	14 months correspond to the expected end of lactation. Consequently, this variable allows accessing the differential costs of sons and daughter during pregnancy and lactation on maternal lifespan.
Number of daughters surviving to 18 years	1.92	1.81	18 years correspond to the expected end of adolescence. Consequently, this variable allows accessing the differential costs of sons and daughter during pregnancy, lactation and adolescence on maternal lifespan.
Number of sons born	3.12	2.38	Allows accessing the differential costs of sons and daughter during pregnancy on maternal lifespan.
Number of sons surviving to 14 months	2.21	1.98	14 months correspond to the expected end of lactation. Consequently, this variable allows accessing the differential costs of sons and daughter during pregnancy and lactation on maternal lifespan.
Number of sons surviving to 18 years	1.81	1.81	18 years correspond to the expected end of adolescence. Consequently, this variable allows accessing the differential costs of sons and daughter during pregnancy, lactation and adolescence on maternal lifespan.
Maternal age of last birth (years)	36.87	6.61	Indicator of health, women having children at old age are expected to be in better health than others (Gagnon et al. 2009; Jasienska 2020).
Wave front (years)	62.02	34.24	Refers to the gradual settlement of the territory, represented by the number of years between the opening of a given parish and the first birth in that parish. Due to favourable living conditions, women living on the wave front had higher fertility (Moreau et al. 2011), and possibly a better survival.

Infant mortality (%)	29	31	Indicates the proportion of infants who died before reaching one year of age. It was included as an indicator of environmental conditions and health (Shanahan et al. 2022) (Gagnon et al. 2009).
Qualitative:	Number of women		
Geographic location (South)	973		The north shore of the St-Lawrence River represents a poorer environment while the south indicates a better one, reflecting the disparities in agricultural yields between the two regions (Harris and Matthews 1987; Gagnon 2012).
Urbanity (yes)	386		The type of parish, classified as urban or rural. Due to insalubrity and higher spread of diseases, a higher infant mortality rate was observed in urban parishes (Mazan and Gagnon 2007). The impact on adult lifespan was unknown.
Random effect:	Number of unique values		
Family ID	1358		Corresponds to a unique identifier to accounting for family effects between sisters.
Mother birth year	107		Account for temporal variation such as epidemics or stochastic events (Bruckner et al. 2018). We grouped them by decades to have at least 10 women born in each class.
Total sample size (number of women)	1886		

Table 2: Parameters estimates from linear mixed models of the association between post-menopausal lifespan and the number of sons born, surviving to 14 months and 18 years in pre-industrial Québec women born between 1621 and 1754 when integrating the infant mortality as an indicator of heterogeneity of women (N=1886 women).

	Born			Surviving to 14 months			Surviving to 18 years		
Fixed effect:	Estimates	SE	p-value	Estimates	SE	p-value	Estimates	SE	p-value
Intercept	68.110	2.058	<0.001	68.000	2.036	<0.001	68.032	2.030	<0.001
Infant mortality	-0.948	1.251	0.449	-1.161	1.085	0.285	-1.150	1.048	0.273
Number of sons	-0.115	0.191	0.545	0.159	0.217	0.464	0.192	0.231	0.406
Number of daughters	0.061	0.190	0.749	-0.036	0.214	0.866	-0.041	0.234	0.862
Husband lifespan	0.031	0.019	0.114	0.032	0.019	0.095	0.031	0.019	0.103
Age of last birth	0.005	0.050	0.924	0.002	0.049	0.970	0.003	0.048	0.957
Geographic location (South)	0.084	0.545	0.878	0.050	0.543	0.927	0.056	0.544	0.919
Urbanity (yes)	-1.766	0.864	0.041	-1.780	0.861	0.039	-1.787	0.859	0.038
Wave front	0.003	0.010	0.779	0.002	0.010	0.833	0.002	0.011	0.847
Infant mortality x Number of sons	-0.385	0.489	0.431	-2.351	0.827	0.005	-2.215	0.919	0.016
Infant mortality x Number of daughters	-0.142	0.487	0.770	0.665	0.779	0.393	0.155	0.885	0.861
Random effect:	Variance			Variance			Variance		
Family ID	14.900			14.400			17.700		
Mother birth year	0			0			0		
Model residual variance:	115.000			115.000			114.800		

Table 3: Parameters estimates from linear mixed models of the association between post-menopausal lifespan and the number of sons born, surviving to 14 months and 18 years in pre-industrial Québec women born between 1621 and 1754 when integrating the shore as an indicator of heterogeneity of women (N=1886 women).

	Born			Surviving to 14 months			Surviving to 18 years		
Fixed effect:	Estimates	SE	p-value	Estimates	SE	p-value	Estimates	SE	p-value
Intercept	68.816	2.096	<0.001	68.862	2.061	<0.001	69.041	2.052	<0.001
Geographic location (South)	-0.655	0.983	0.505	-0.142	0.898	0.874	-0.361	0.847	0.670
Number of sons	-0.345	0.185	0.063	-0.257	0.220	0.244	-0.233	0.242	0.336
Number of daughters	0.001	0.191	0.996	0.080	0.223	0.718	-0.016	0.245	0.946
Husband lifespan	0.031	0.019	0.105	0.031	0.019	0.103	0.031	0.019	0.103
Age of last birth	0.009	0.050	0.860	-0.012	0.049	0.800	-0.015	0.047	0.757
Infant mortality	-1.905	0.889	0.032	-2.149	0.982	0.029	-2.083	0.961	0.030
Urbanity (yes)	-1.744	0.865	0.044	-1.873	0.862	0.030	-1.847	0.860	0.032
Wave front	0.001	0.011	0.931	0.003	0.011	0.764	0.003	0.011	0.813
Geographic location x Number of sons	0.215	0.248	0.386	0.062	0.296	0.835	0.175	0.323	0.587
Geographic location x Number of daughters	<0.001	0.247	0.999	0.001	0.291	0.997	0.021	0.323	0.948
Random effect:	Variance			Variance			Variance		
Family ID	14.800			15.000			15.000		
Mother birth year	0			0			0		
Model residual variance:	115.000			115.000			115.000		

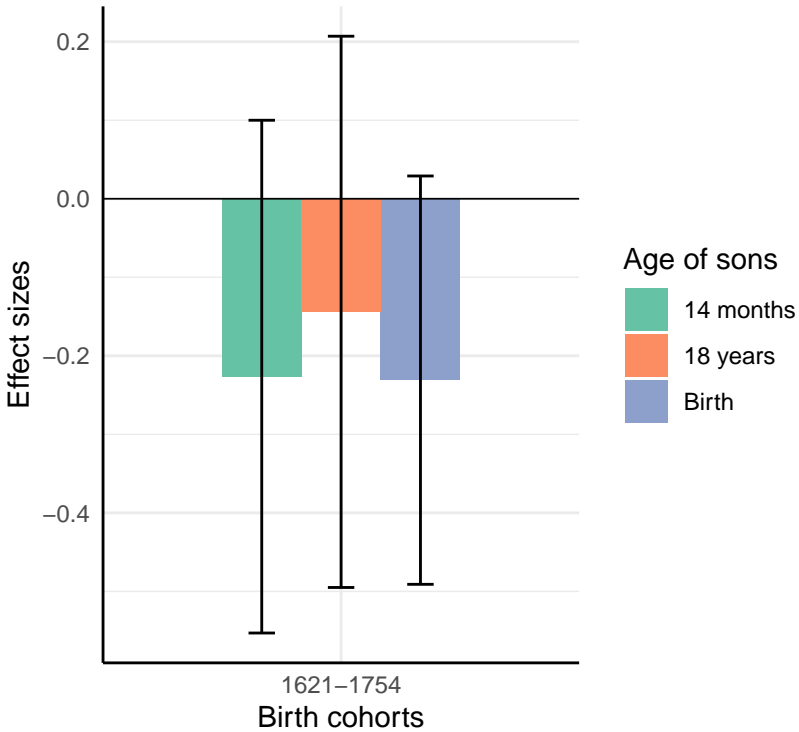
Table 4: Parameters estimates from linear mixed models of the association between post-menopausal lifespan and the number of sons born, surviving to 14 months and 18 years in pre-industrial Québec women born between 1621 and 1754 when integrating the age of last birth as an indicator of heterogeneity of women (N=1886 women).

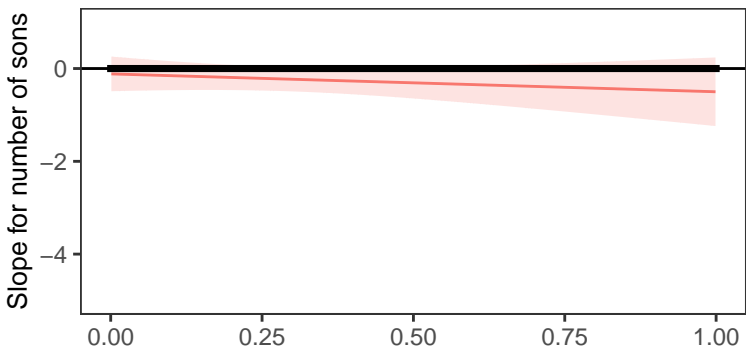
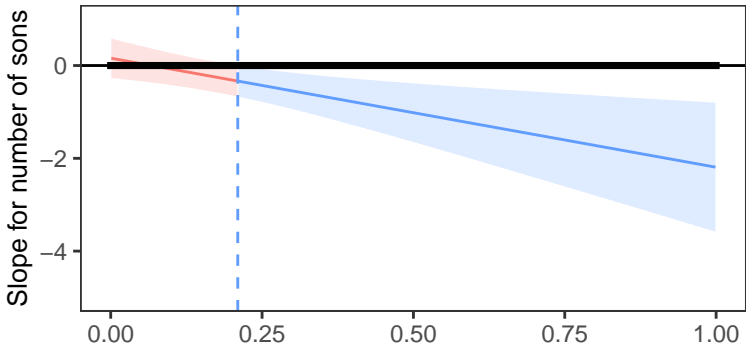
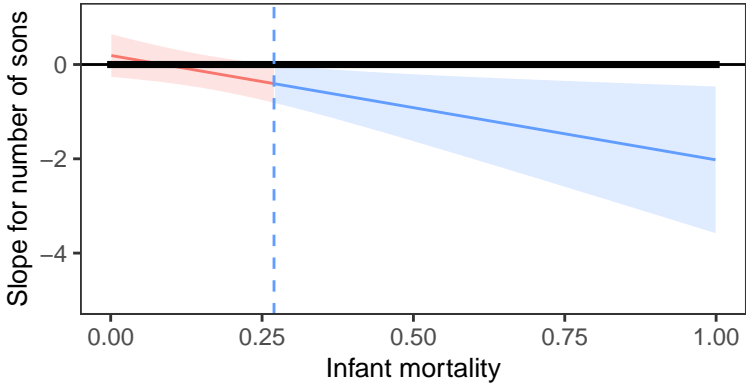
	Born			Surviving to 14 months			Surviving to 18 years		
Fixed effect:	Estimates	SE	p-value	Estimates	SE	p-value	Estimates	SE	p-value
Intercept	69.617	2.718	<0.001	69.456	2.549	<0.001	68.422	2.435	<0.001
Age of last birth	-0.020	0.065	0.760	-0.026	0.059	0.665	-0.005	0.056	0.923
Number of sons	-0.817	1.089	0.453	-1.390	1.376	0.313	-0.570	1.510	0.706
Number of daughters	-0.216	1.049	0.837	0.493	1.258	0.695	0.814	1.390	0.558
Husband lifespan	0.030	0.019	0.126	0.030	0.019	0.118	0.031	0.019	0.105
Geographic location (South)	0.017	0.542	0.975	0.010	0.543	0.985	0.017	0.544	0.975
Infant mortality	-1.913	0.890	0.032	-2.297	1.020	0.024	-2.044	0.988	0.039
Urbanity (yes)	-1.788	0.866	0.039	-1.915	0.863	0.027	-1.898	0.862	0.028
Wave front	0.002	0.011	0.848	0.004	0.011	0.743	0.003	0.011	0.752
Age of last birth x Number of sons	0.015	0.027	0.591	0.029	0.034	0.394	0.011	0.037	0.771
Age of last birth x Number of daughters	0.005	0.026	0.835	-0.011	0.031	0.731	-0.020	0.034	0.553
Random effect:	Variance			Variance			Variance		
Family ID	15.100			15.100			15.000		
Mother birth year	0			0			0		
Model residual variance:	114.800			114.900			115.000		

Figure legends

Fig. 1. The slopes between the number of sons and post-menopausal lifespan considering the three ages at which the number of sons were considered. Black bars represent 95% confident interval. These slopes were extracted from models shown in Table S2.

Fig. 2. Johnson-Neyman plot assessing how the relationship between the number of sons and the post-menopausal lifespan in Québec mothers (Y axis) varies depending on infant mortality (X axis) when sons were considered at birth (A), surviving to 14 months (B) or surviving to 18 years (C). Vertical blue dots lines represent the value of infant mortality at which the relationship between the number of sons and the post-menopausal lifespan changes from non-significant (red part) to significant (blue part) at significance level of 5%. Fill around lines corresponds to the 95% confident interval.



A Birth**B** 14 months**C** 18 years

**Supplementary information for Sons shorten mother's lifespan in pre-industrial families
with high level of infant mortality**

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Table S1: Mc Fadden's R-squared of models investigating the origin of the variation in infant mortality. We performed three generalized mixed effect models with a binomial family and we calculated the Mc Fadden's R-squared of each model to quantify the variance explained by each variable.

Model structure	1621-1754 cohorts	1621-1713 cohorts
Infant mortality ~ Mother ID	0.294	0.236
Infant mortality ~ Year of birth	0.062	0.031
Infant mortality ~ Year of birth + Mother ID	0.325	0.273

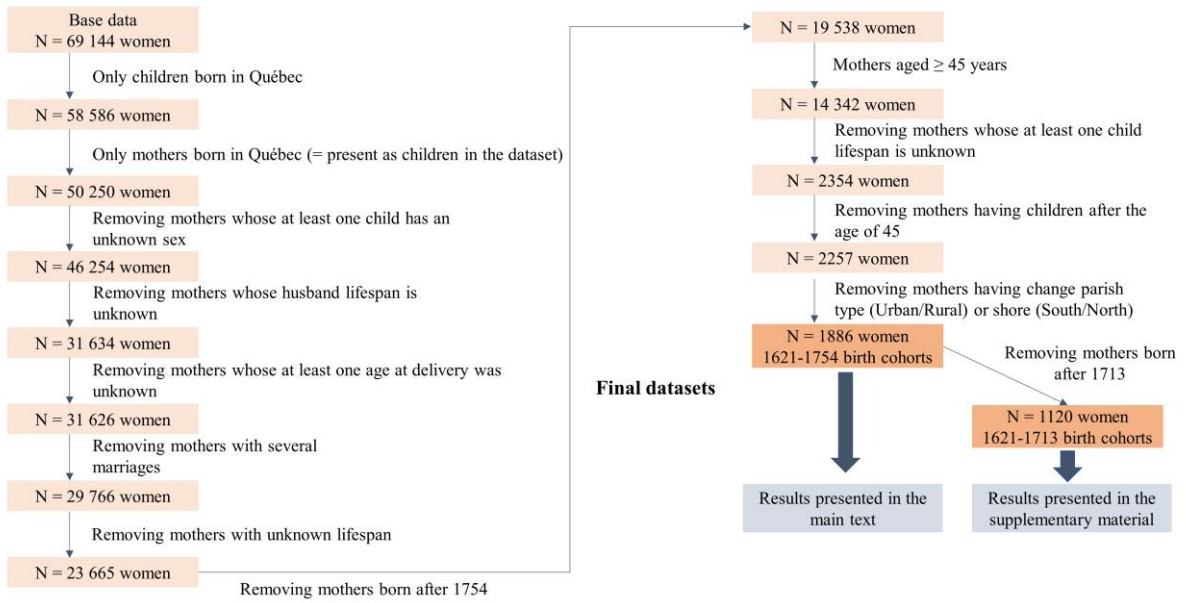


Fig. S1: Selection criteria applied to our dataset before analyse

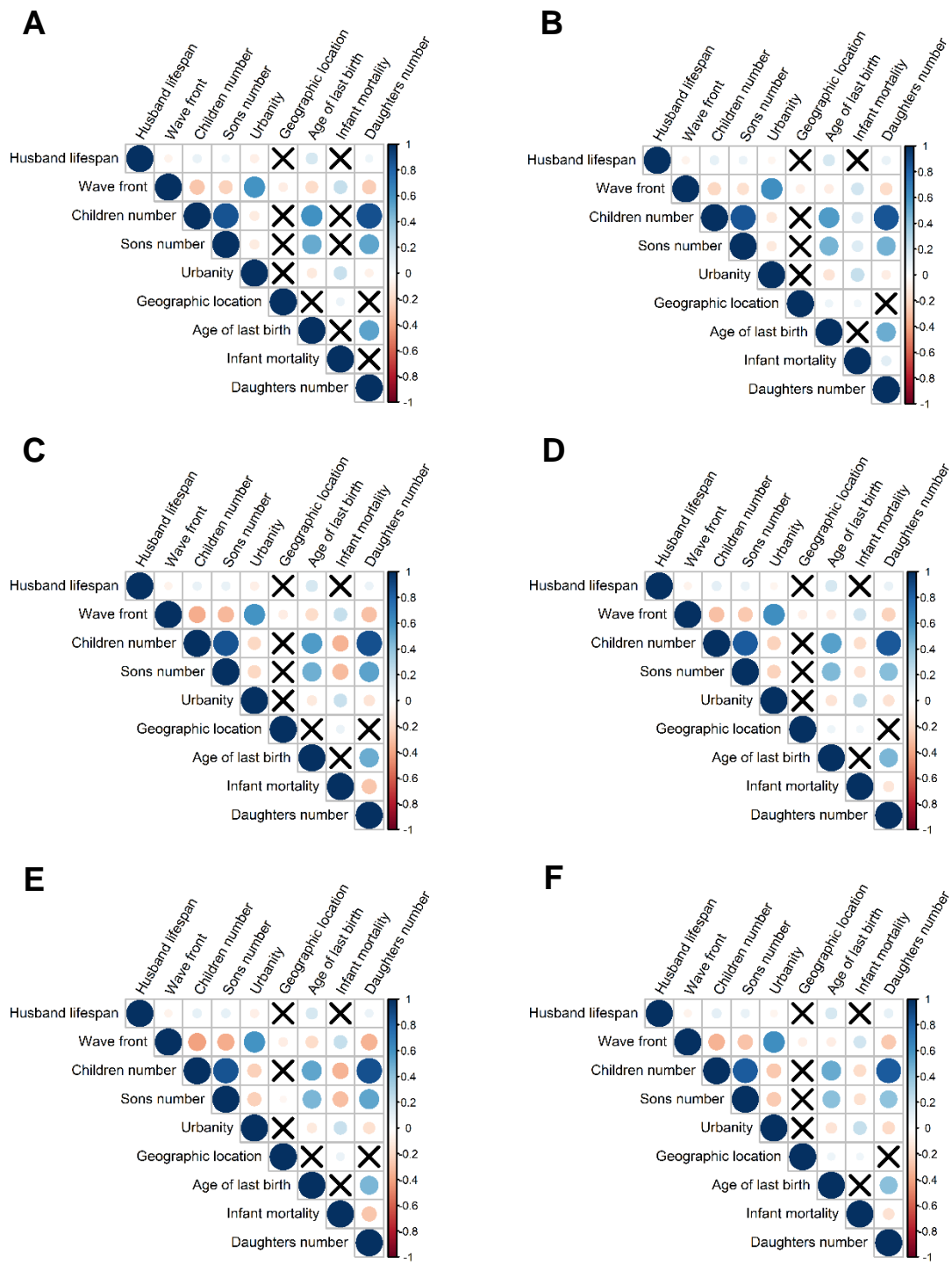


Fig. S2: Representation of correlations between variables in the 1621-1754 cohorts (A, C & E) and in the 1621-1713 cohorts (B, D & F). The panel (A and B) represents sons and daughters born, (C & D) surviving to 14 months and (E & F) surviving to 18 years. Crosses indicate that the correlation between the two variables is not significant ($p > 5\%$) while circles indicate significant correlations. The colour gradient indicates the strength of the correlation and its

direction. The colour scale is located to the right of each graph. For instance, the correlation between the number of sons surviving to 14 months and the infant mortality in the 1621-1754 cohorts is relatively weak with correlation coefficient of 0.3.

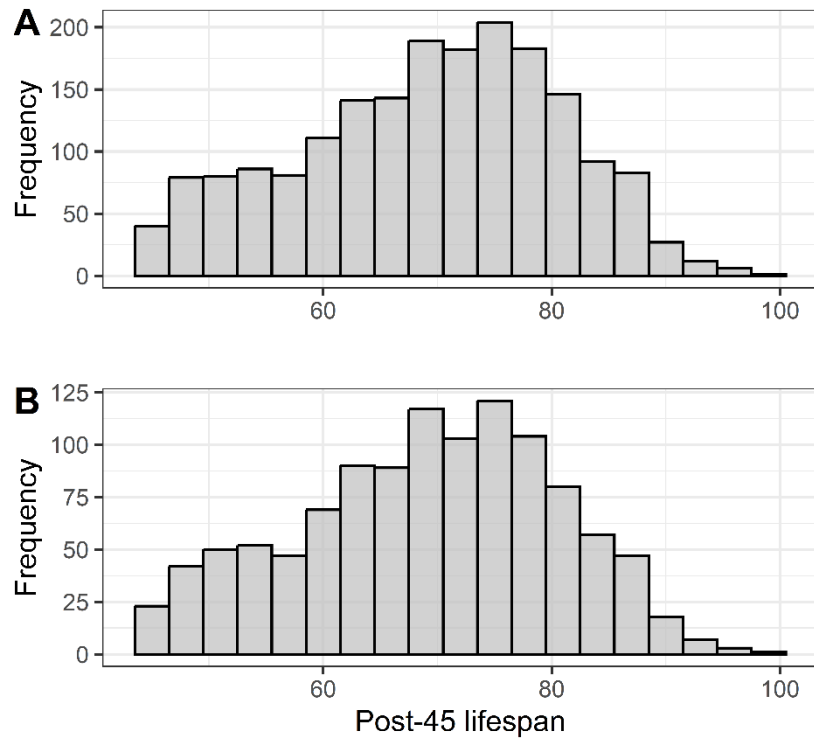


Fig. S3: Distribution of the post-menopausal lifespan in the cohorts 1621-1754 (A) and in the cohorts 1621-1713 (B)

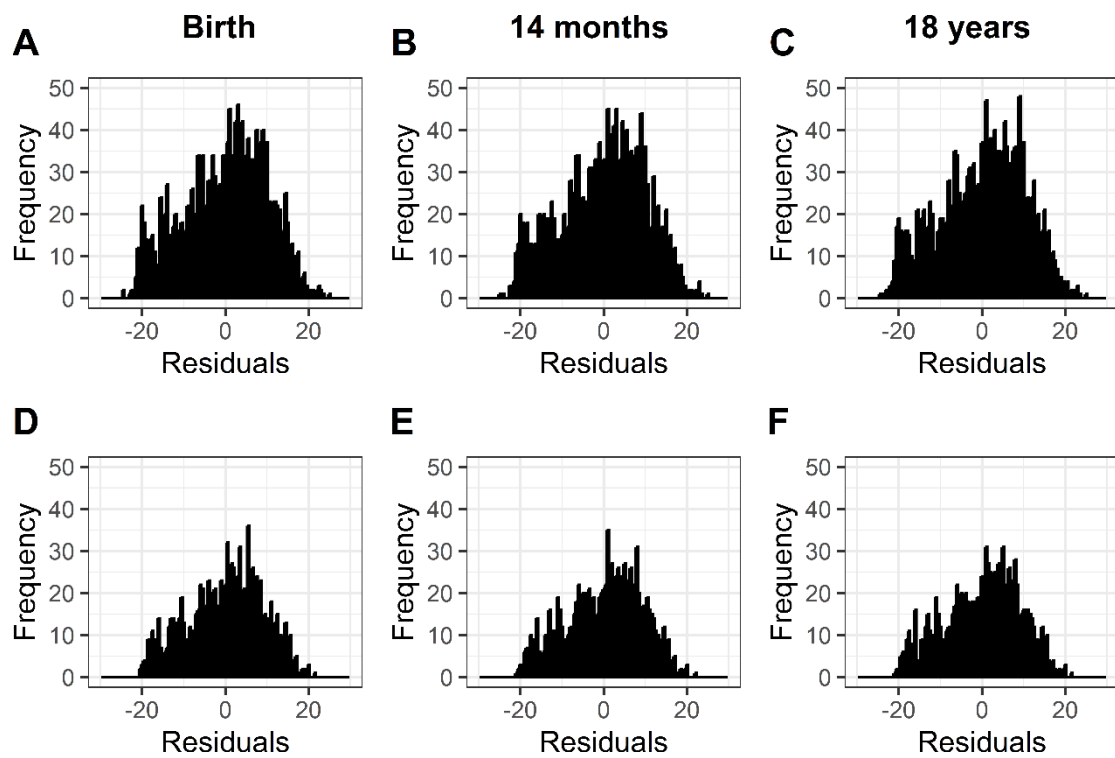


Fig. S4: Distribution of residuals of models considering women as homogenous. Each column represents the stage of development at which sons and daughters were considered. Graphs A to C corresponds to the models performed in the 1621-1754 birth cohorts, while graphs D to F corresponds to the models performed in the 1621-1713 birth cohorts.

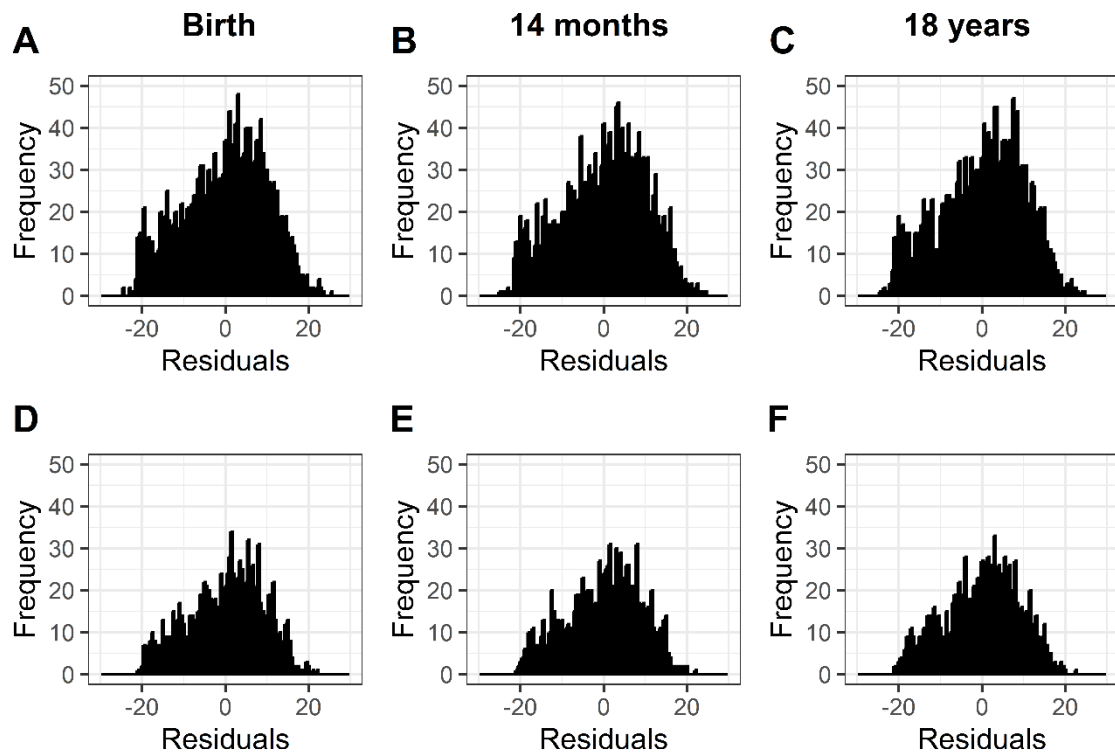


Fig. S5: Distribution of residuals of models considering women as heterogenous using infant mortality. Each column represents the stage of development at which sons and daughters were considered. Graphs A to C corresponds to the models performed in the 1621-1754 birth cohorts, while graphs D to F corresponds to the models performed in the 1621-1713 birth cohorts

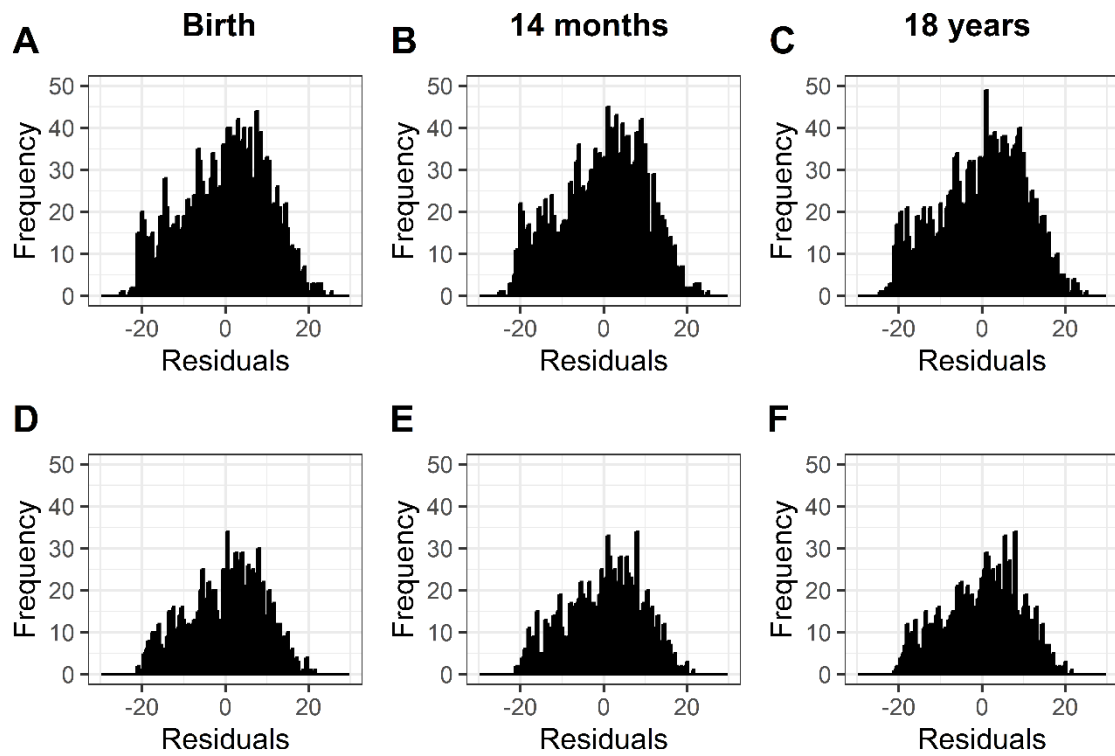


Fig. S6: Distribution of residuals of models considering women as heterogenous using the shore. Each column represents the stage of development at which sons and daughters were considered. Graphs A to C corresponds to the models performed in the 1621-1754 birth cohorts, while graphs D to F corresponds to the models performed in the 1621-1713 birth cohorts

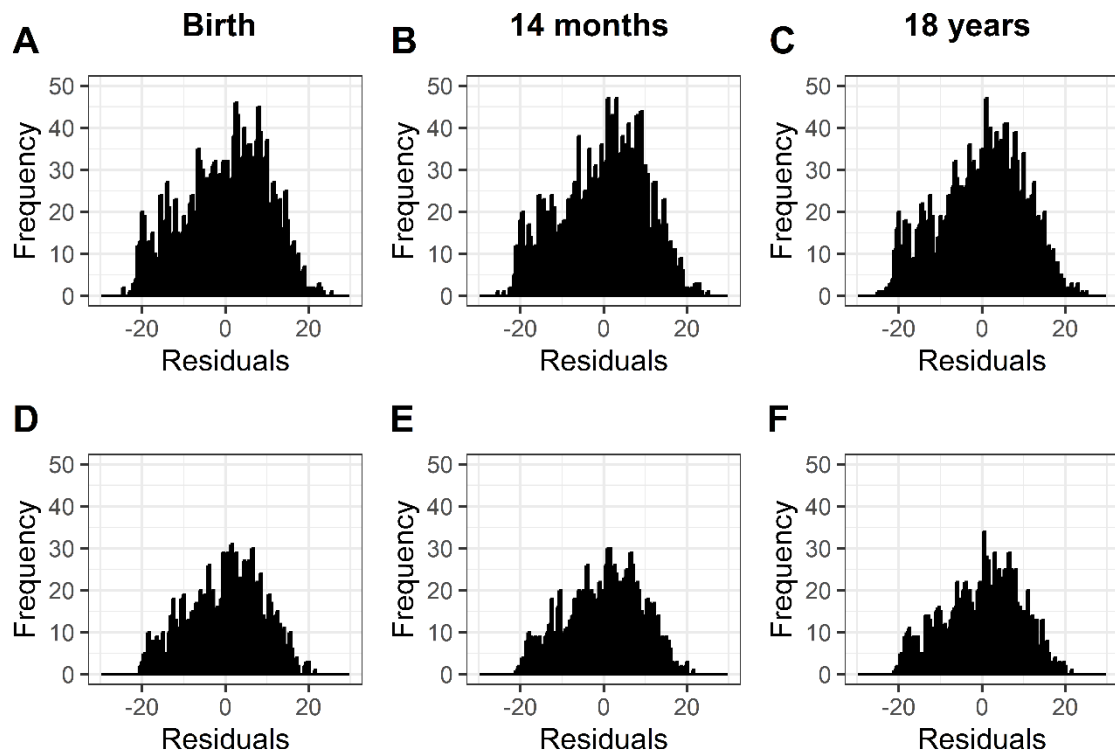


Fig. S7: Distribution of residuals of models considering women as heterogeneous using the age of last birth. Each column represents the stage of development at which sons and daughters were considered. Graphs A to C corresponds to the models performed in the 1621-1754 birth cohorts, while graphs D to F corresponds to the models performed in the 1621-1713 birth cohorts

Table S2: Parameters estimates from linear mixed models of the association between post-menopausal lifespan and the number of sons born, surviving to 14 months and 18 years in pre-industrial Québec women born between 1621 and 1754 (N=1886 women).

	Born			Surviving to 14 months			Surviving to 18 years		
Fixed effect:	Estimates	SE	p-value	Estimates	SE	p-value	Estimates	SE	p-value
Intercept	68.415	2.033	<0.001	68.778	2.008	<0.001	68.815	2.003	<0.001
Infant mortality	-1.902	0.888	0.032	-2.156	0.981	0.028	-2.103	0.960	0.029
Number of sons	-0.231	0.133	0.082	-0.226	0.167	0.175	-0.144	0.180	0.422
Number of daughters	0.012	0.134	0.931	0.083	0.163	0.610	-0.002	0.179	0.993
Husband lifespan	0.031	0.019	0.108	0.031	0.019	0.103	0.031	0.019	0.104
Age of last birth	0.008	0.050	0.873	-0.012	0.049	0.799	-0.015	0.047	0.757
Geographic location (South)	0.021	0.542	0.969	-0.002	0.542	0.998	0.002	0.543	0.998
Urbanity (yes)	-1.788	0.863	0.038	-1.878	0.860	0.029	-1.862	0.859	0.030
Wave front	0.002	0.011	0.844	0.003	0.011	0.747	0.003	0.011	0.766
Random effect:	Variance			Variance			Variance		
Family ID	15.000			15.100			15.100		
Mother birth year	0			0			0		
Model residual variance:	115.000			114.800			114.900		

Table S3: Parameters estimates from linear mixed models of the association between post-menopausal lifespan and the number of sons born, surviving to 14 months and 18 years in pre-industrial Québec women born between 1621 and 1713 (N=1120 women).

	Born			Surviving to 14 months			Surviving to 18 years		
Fixed effect:	Estimates	SE	p-value	Estimates	SE	p-value	Estimates	SE	p-value
Intercept	67.995	2.794	<0.001	68.448	2.749	<0.001	68.432	2.734	<0.001
Infant mortality	-3.274	1.433	0.022	-3.448	1.528	0.024	-3.461	1.515	0.023
Number of sons	-0.189	0.166	0.255	-0.102	0.200	0.611	-0.120	0.214	0.575
Number of daughters	0.024	0.167	0.887	0.060	0.196	0.758	0.062	0.213	0.772
Husband lifespan	0.052	0.026	0.044	0.052	0.026	0.045	0.052	0.026	0.045
Age of last birth	-0.013	0.072	0.858	-0.039	0.072	0.588	-0.037	0.069	0.586
Geographic location (South)	0.242	0.710	0.734	0.275	0.712	0.700	0.272	0.711	0.702
Urbanity (yes)	-0.496	1.210	0.682	-0.592	1.209	0.624	-0.595	1.204	0.621
Wave front	-0.011	0.018	0.541	-0.009	0.018	0.629	-0.009	0.018	0.623
Random effect:	Variance			Variance			Variance		
Family ID	26.500			26.500			26.600		
Mother birth year	0			0			0		
Model residual variance:	101.500			101.700			101.600		

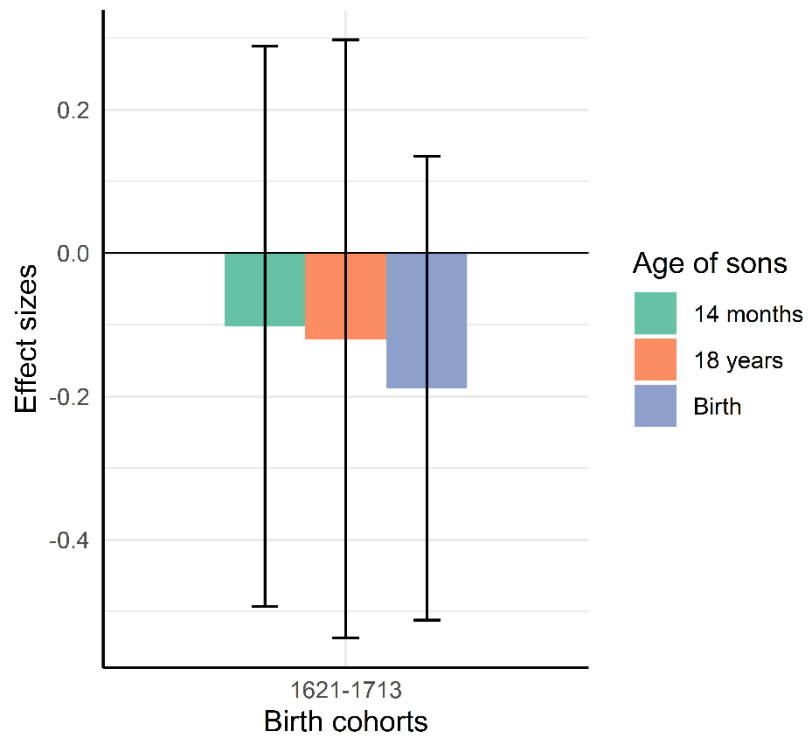


Fig. S8: The slopes between the number of sons and post-menopausal lifespan considering the three ages at which the number of sons were considered. Black bars represent SE and p-values are display in brackets. These slopes were extracted from models shown in Table S3.

Table S4: Parameters estimates from linear mixed models of the association between post-menopausal lifespan and the number of sons born, surviving to 14 months and 18 years in pre-industrial Québec women born between 1621 and 1713 when integrating the infant mortality as an indicator of heterogeneity of women (N=1120 women).

	Born			Surviving to 14 months			Surviving to 18 years		
Fixed effect:	Estimates	SE	p-value	Estimates	SE	p-value	Estimates	SE	p-value
Intercept	67.511	2.833	<0.001	67.568	2.815	<0.001	67.784	2.796	<0.001
Infant mortality	-1.035	2.117	0.625	-1.946	1.838	0.290	-2.336	1.798	0.194
Number of sons	0.114	0.240	0.634	0.218	0.261	0.405	0.217	0.277	0.433
Number of daughters	-0.020	0.236	0.933	-0.016	0.255	0.949	-0.064	0.274	0.815
Husband lifespan	0.053	0.026	0.041	0.053	0.026	0.040	0.053	0.026	0.043
Age of last birth	-0.024	0.072	0.738	-0.028	0.072	0.695	-0.029	0.069	0.681
Geographic location (South)	0.322	0.714	0.652	0.330	0.713	0.644	0.299	0.712	0.675
Urbanity (yes)	-0.564	1.210	0.641	-0.592	1.209	0.624	-0.656	1.204	0.586
Wave front	-0.007	0.018	0.674	-0.008	0.018	0.665	-0.008	0.018	0.664
Infant mortality x Number of sons	-1.310	0.780	0.093	-2.018	1.051	0.055	-2.184	1.131	0.054
Infant mortality x Number of daughters	0.361	0.766	0.638	0.493	1.030	0.632	0.771	1.127	0.494
Random effect:	Variance			Variance			Variance		
Family ID	26.300			26.500			26.600		
Mother birth year	0			0			0		
Model residual variance:	101.700			101.400			101.400		

Table S5: Parameters estimates from linear mixed models of the association between post-menopausal lifespan and the number of sons born, surviving to 14 months and 18 years in pre-industrial Québec women born between 1621 and 1713 when integrating the shore as an indicator of heterogeneity of women (N=1120 women).

	Born			Surviving to 14 months			Surviving to 18 years		
Fixed effect:	Estimates	SE	p-value	Estimates	SE	p-value	Estimates	SE	p-value
Intercept	68.366	2.837	<0.001	68.405	2.794	<0.001	68.410	2.778	<0.001
Geographic location (South)	-0.769	1.427	0.590	0.216	1.357	0.874	0.039	1.289	0.976
Number of sons	-0.312	0.223	0.163	-0.172	0.259	0.508	-0.250	0.283	0.378
Number of daughters	-0.008	0.235	0.973	0.118	0.265	0.655	0.134	0.286	0.639
Husband lifespan	0.052	0.026	0.044	0.052	0.026	0.045	0.052	0.026	0.044
Age of last birth	-0.006	0.073	0.932	-0.037	0.072	0.605	-0.034	0.069	0.628
Infant mortality	-3.286	1.434	0.022	-3.428	1.530	0.025	-3.436	1.517	0.024
Urbanity (yes)	-0.433	1.214	0.721	-0.600	1.213	0.621	-0.576	1.207	0.634
Wave front	-0.012	0.018	0.494	-0.009	0.018	0.630	-0.009	0.018	0.604
Geographic location x Number of sons	0.249	0.309	0.420	0.156	0.357	0.662	0.274	0.386	0.479
Geographic location x Number of daughters	0.032	0.307	0.916	-0.126	0.351	0.719	-0.164	0.384	0.669
Random effect:	Variance			Variance			Variance		
Family ID	26.000			26.300			26.300		
Mother birth year	0			0			0		
Model residual variance:	102.000			102.100			102.100		

Table S6: Parameters estimates from linear mixed models of the association between post-menopausal lifespan and the number of sons born, surviving to 14 months and 18 years in pre-industrial Québec women born between 1621 and 1713 when integrating the age of last birth as an indicator of heterogeneity of women (N=1120 women).

	Born			Surviving to 14 months			Surviving to 18 years		
Fixed effect:	Estimates	SE	p-value	Estimates	SE	p-value	Estimates	SE	p-value
Intercept	71.513	3.860	<0.001	72.075	3.719	<0.001	70.781	3.606	<0.001
Age of last birth	-0.098	0.096	0.307	-0.123	0.092	0.180	-0.093	0.088	0.291
Number of sons	0.569	1.557	0.715	-0.414	1.819	0.820	-0.274	1.968	0.889
Number of daughters	-2.789	1.444	0.054	-2.316	1.683	0.169	-1.823	1.847	0.324
Husband lifespan	0.052	0.026	0.048	0.050	0.026	0.055	0.051	0.026	0.049
Geographic location (South)	0.195	0.711	0.784	0.235	0.715	0.743	0.244	0.715	0.732
Infant mortality	-3.583	1.441	0.013	-3.936	1.561	0.012	-3.776	1.544	0.015
Urbanity (yes)	-0.367	1.215	0.763	-0.553	1.216	0.649	-0.583	1.211	0.630
Wave front	-0.011	0.018	0.547	-0.008	0.018	0.650	-0.009	0.018	0.624
Age of last birth x Number of sons	-0.019	0.038	0.620	0.007	0.045	0.873	0.003	0.048	0.944
Age of last birth x Number of daughters	0.069	0.035	0.051	0.058	0.041	0.158	0.046	0.045	0.307
Random effect:	Variance			Variance			Variance		
Family ID	27.000			26.748			26.800		
Mother birth year	0			<0.001			<0.001		
Model residual variance:	101.000			101.372			101.472		

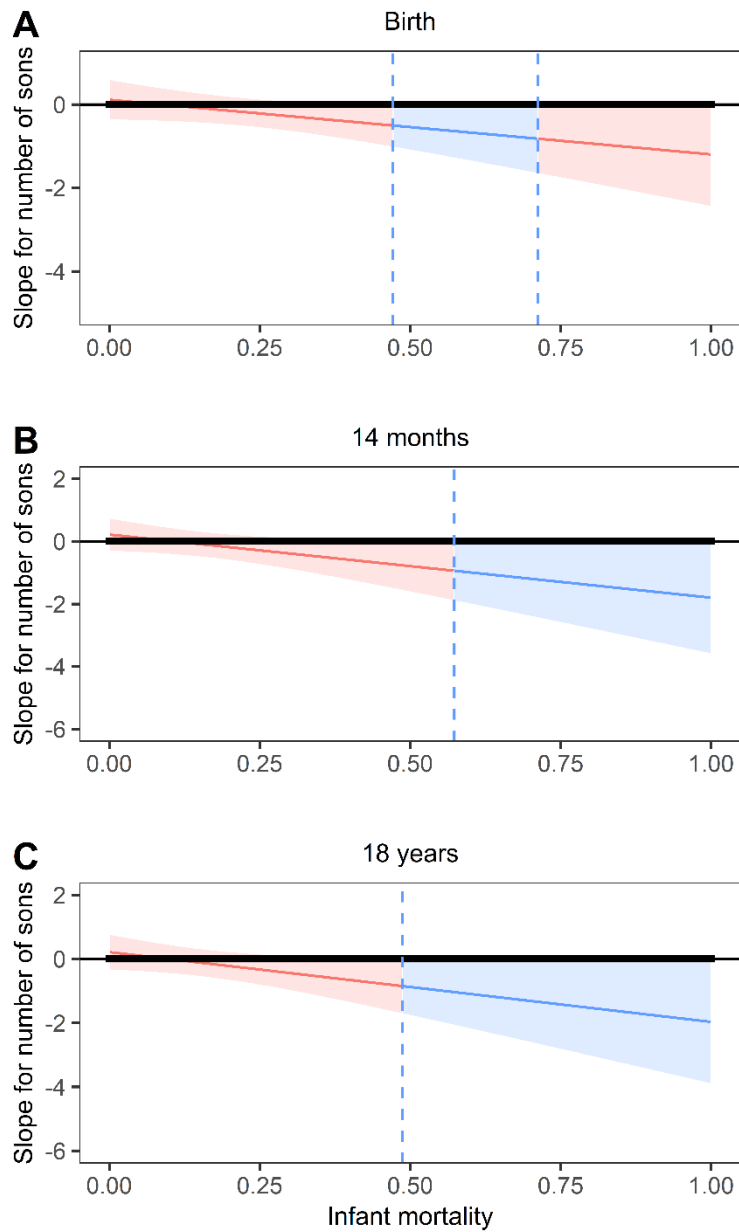


Fig. S9: Johnson-Neyman plot assessing how the relationship between the number of sons and the post-menopausal lifespan in Québec mothers (Y axis) varies depending on infant mortality (X axis) when sons were considered at birth (A), surviving to 14 months (B) or surviving to 18 years (C) in the 1621-1713 cohorts. Blue dashed lines represent the infant mortality threshold at which the relationship between the number of sons and post-menopausal lifespan becomes significant ($p < 0.05$).

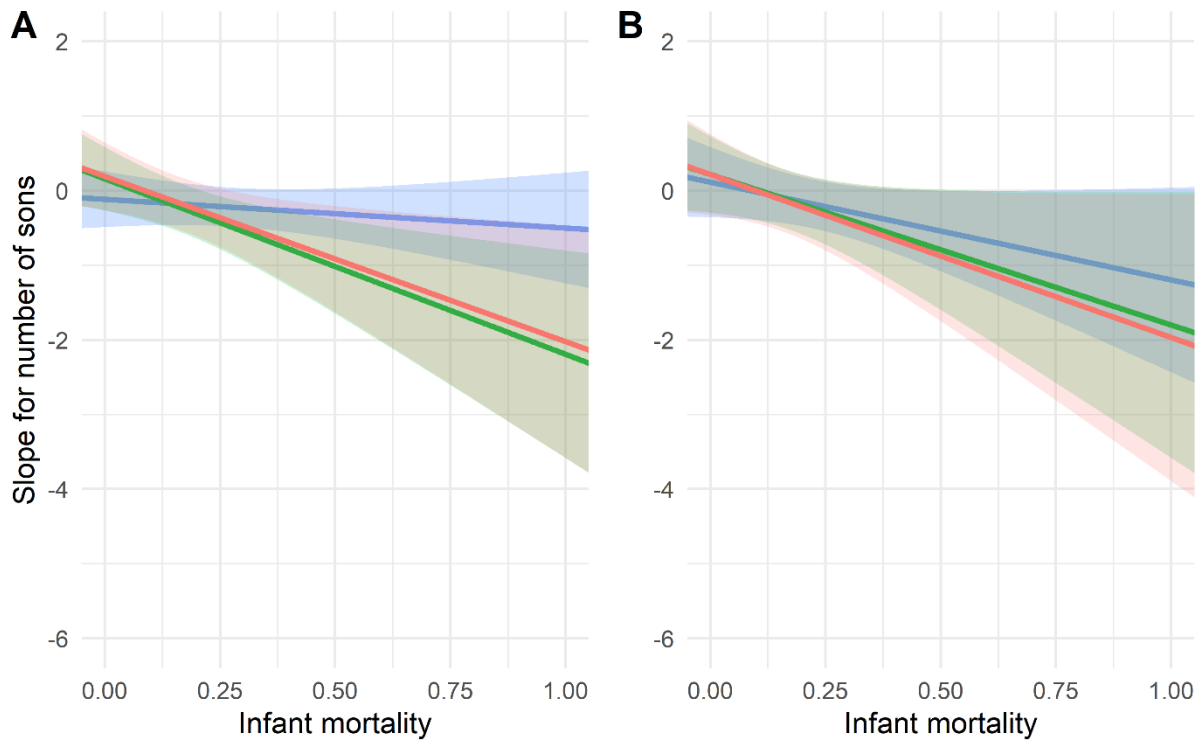


Fig. S10: Superposition of Johnson-Neyman plots, shown in Figure 2 for the 1621-1754 cohorts and in Figure S9 for the 1621-1713 cohorts when sons were considered at birth (blue curve), surviving to 14 months (green curve) or surviving to 18 years (orange curve). We represented these relationships in the 1621-1754 cohorts (A) and in the 1621-1713 cohorts (B). Curves indicate the predicted slope of the number of sons for each value of infant mortality and are surrounded by the 95% confidence interval.