**Early-life environment and differences in costs of reproduction in a preindustrial human population**

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**Abstract (max. 350 words)**

1. The measurable costs of reproduction on maternal survival vary between individuals, birth cohorts and populations. One potential factor creating such variation is differences in the early developmental conditions. The early-life environment can alter later-life health and body condition through permanent changes in body structure, physiology and metabolism, and thereby modify resource acquisition and the trade-off between reproduction and survival. However, the effect of early-life environmental conditions on the survival costs of reproduction has rarely been investigated before.
2. We quantified the effect of early environmental conditions on the trade-off between female reproduction and survival in humans. We predicted that women born during poor environmental conditions, as measured by climatic conditions, food availability and infant mortality rate, would show stronger survival costs of reproduction in adulthood compared to women born in better conditions. Moreover, we expected the effect to be strongest in women from poor socio-economic class and generally with lower resource access.
3. We analysed individual-based life-history data collected from Finnish church records on 1,751 pre-industrial women born between 1751 and 1850. We used historical records of annual spring temperature, rye yields and infant mortality in their birth parish as proxies of their early developmental conditions. We tested the effect of poor birth conditions on the survival cost of both the number of offspring born (costs of pregnancy) and the number of offspring raised to maturity (costs of parental care) using Cox proportional hazard models.
4. We found considerable variation between the 100 female birth cohorts in the correlation between reproduction and longevity, as well our measures of their developmental conditions. However, spring temperature, rye yields, and infant mortality around birth did not significantly modify the relationship between a women’s reproduction and survival. Moreover, the survival of women from the poor socio-economic class was not affected by the early-life environment.
5. Our results do not provide evidence that poor early-life conditions lead to higher cost of reproduction on adulthood survival in our population. Future studies are needed to increase our understanding of the causes of variation in reproduction-survival trade-offs, and any role of the early-life developmental conditions therein.

**Introduction**

Life-history theory predicts that investments in reproduction come at the cost of future reproduction and survival because they share a pool of finite resources [[1](#_ENREF_1)]. In support of such predictions, classic studies showed that mothers that skipped reproduction or produced smaller broods in a given year had higher chance of survival to the next breeding season [[2-4](#_ENREF_2)]. Yet due to variation in resource access between individuals or seasons [[5](#_ENREF_5)], the best evidence comes from experimental studies which have been able to manipulate either the reproductive effort or resource access during reproduction and link this to reduced maternal survival [[6-8](#_ENREF_6)]. Nevertheless, even such studies often demonstrate large variation between populations, cohorts or individuals in the magnitude of reproductive costs on survival. Such heterogeneity could be explained by variation between individuals in acquisition and allocation of available resources generating variable sized resource pools [[9](#_ENREF_9)] and by interactions between genotype and environment [[10](#_ENREF_10)] that can lead to positive relationships between fitness traits.

Similarly, results from studies in humans testing for costs of reproduction remain variable. While some studies have shown a negative relationship between number of children and maternal lifespan e.g. [[11](#_ENREF_11), [12](#_ENREF_12)], some have shown positive [[13](#_ENREF_13), [14](#_ENREF_14)], or no association at all e.g.[[15](#_ENREF_15), [16](#_ENREF_16)]. Two lines of evidence support this. First, some studies on humans have only found the predicted negative association between reproduction and survival among the poorest mothers in the population, whereas wealthier women show no or positive associations [[17](#_ENREF_17), [18](#_ENREF_18)]. Second, Wang et al. [[19](#_ENREF_19)] found that the relationship between the number of children born and lifespan differed among cohorts from the same population born in different years: historical data from Framingham, USA, showed generally positive correlations in cohorts born in years 1893 to 1907 and negative ones in those born from 1908 to 1913. Wang et al. suggest that environmental perturbations experienced by the latter group such as the Great Depression and Second World War may explain the differences among cohorts, but the specific factors leading to differential cost of reproduction experienced by different cohorts were not studied on a cohort level basis.

One potential key factor creating differences between cohorts and individuals in their ability to cope with the cost of reproduction not studied so far [[20](#_ENREF_20)] is variation in environmental conditions experienced during early development. Variation in early-life environmental conditions such as season of birth [[21](#_ENREF_21)], population density [[22](#_ENREF_22)], drought [[23](#_ENREF_23)], spring temperature and body mass [[24](#_ENREF_24)], or nutrition [[25](#_ENREF_25)] have been related to between-individual differences in survival and/or reproductive performance in many species [[26](#_ENREF_26), [27, including humans (Lummaa & Clutton-Brock 2002). Potential physiological mechanisms for such relationships between early-life natal conditions and later-life fitness include effects of poor early-life conditions on rate of telomere loss {Hall, 2004 #1385](#_ENREF_27)], metabolic rate [[28 and resistance to oxidative stress {Alonso-Alvarez, 2006 #1386](#_ENREF_28)]. However, to our knowledge there is only one study in which variation in early-life conditions was analysed in relation to survival costs of reproduction. Experiments performed by Oksanen and colleagues (2007) determined that smaller size and high breeding density in bank voles (*M. glareolus*) increased survival costs of reproduction in adulthood.

Such effects of early-life conditions on the ability to cope with the cost of reproduction are plausible, because their effects can extend into the whole length of adult life [[29](#_ENREF_29)] through changes in body structure, physiology and metabolism. Note also that these effects do not only include severe deprivation (e.g. famine in humans), but early environment effects on later health can also be detected within the ‘normal’ range of weight at birth [[30](#_ENREF_30)]. In humans, a favourable early-life environment has been shown to have a positive impact on lifetime reproductive success [[31](#_ENREF_31), [32](#_ENREF_32)] and longevity [[33](#_ENREF_33), [34](#_ENREF_34)]. Meanwhile, a poor early-life environment increases the risk of dying from infectious diseases in early adulthood [[35](#_ENREF_35)] and from complications of childbirth [[36](#_ENREF_36)], increases the risk of developing cardiovascular diseases, obesity, and non-insulin dependent diabetes mellitus [[29](#_ENREF_29), [37](#_ENREF_37), [38](#_ENREF_38)], and reduces late-life reproduction and survival [[39](#_ENREF_39)]. However, although such previous studies have highlighted early-life environment impacts on both reproduction and longevity in humans, no studies have investigated its impact on the interaction between early-life environment and reproduction on survival. It has therefore yet to be determined whether the between-individual variation in the trade-off between reproductive effort and survival is related to poor early developmental conditions leading to higher apparent cost of reproduction, or to other unknown factors.

In this study we test the hypothesis that individuals with poor early developmental conditions express stronger survival costs of reproduction than those experiencing better early conditions. To this end, we used individual based life-history data collected from church records for 1,751 Finnish women born 1751-1850, combined with historical records of annual rye yields, spring temperature and infant mortality in their birth parish as proxies for their early-life developmental conditions. First, we quantify variation in the relationship between reproduction and survival among the 100 birth cohorts included in this study. Second, we determine whether variation in the cost of reproduction among cohorts can be explained by the early developmental conditions experienced by individuals. We test the effect of both the number of born and raised offspring on maternal survival in order to include the costs incurred from pregnancy (born offspring) and parental care to those offspring (raised offspring). We further test whether the socio-economic status of the studied women modified such effects, predicting that women from the lowest socio-economic group should be most adversely affected by poor developmental conditions and should thus exhibit the largest cost of reproduction. Our analyses control for confounding factors such as shared family effects and variation due to birth order, geographic location and year. This is, to our knowledge, one of the first examinations of associations between early-life environmental conditions and costs of reproduction in humans or other species.

**Material and Methods**

**Study population and data collection**

We used demographic data collected by the Lutheran church in Finland from the eighteenth century onwards. Our database was compiled using church registers of births, movements, marriages and deaths in five Finnish parishes: Hiittinen, Kustavi, Tyrvää, Rymättylä and Ikaalinen. The population was strictly monogamous, women may have remarried only if their husband died, and both divorce and adultery were outlawed [[40](#_ENREF_40)] and extra-marital paternity was very low [[41](#_ENREF_41)]. The main source of livelihood was farming, with around 60% of the energy consumed by working people contributed by rye alone, 20% from potatoes and barley [[42](#_ENREF_42)], and the remainder from meat, fish and dairy products [[43](#_ENREF_43)]. In general, the standard of living was low in the studied population and climatic conditions in Finland were challenging, resulting in immense between-year variation in food availability (Turpeinen 1973). We used data collected on women born between 1751 and 1850. Women included in the study were therefore at least 50 years old in 1900 and experienced natural fertility during their reproductive lifespan. The demographic transition to lower child mortality rates and female fertility began from the 1880s onwards but largely occurred only in the 1900s [[44](#_ENREF_44)]. These women gave birth on average to 5·33 children (SD = 2·89) and 65% of these children survived until 15 years of age; 50% of the women in the sample lived for at least 63 years, and all reproduced at least once in their life. This selection resulted in a total of 1751 women for whom we knew their socio-economic status and their lifetime number of children born. The individuals were classified into two socio-economic classes based on their husband’s occupation: a rich class included farm owners and merchants, craftsmen and tenant farmers, and a poor class consisted of crofters and labourers [[41](#_ENREF_41)]. Three proxies of the quality of the early-life environment were used: annual spring temperature, rye yield, and yearly infant mortality in the population around the time of each individual’s birth.

1. **Spring temperature**

Firstly, we used spring temperature as a measure of conditions around the time of birth, which is associated with the severity of the winter: higher spring temperature is associated with a less severe winter and a more successful rye harvest [[45](#_ENREF_45)]. It was reconstructed using standard multiproxy techniques from historical data including sea ice break-up and plant phenology which explained a large proportion of the variance in observed February–June temperatures in south-west Finland [[46](#_ENREF_46)] and is available for the entire study period that our demographic records of the population cover. We have previously shown in the pre-industrial Finnish population studied here that spring temperature is negatively related to child and adulthood mortality [[47](#_ENREF_47)].

1. **Rye yield**

Second, rye yield was used as a proxy of quality of the early-life environment. Annual harvest success was quantified as the amount of grain harvested as a multiple of the quantity sown (‘yield’ from herein), a measure which is unbiased by variation in planting effort and population size. In addition, low grain yields have been found to be associated with documented famines [[48](#_ENREF_48)]. Although grain yields do not directly reflect individual food availability, this measure is relative to the success compared to other years and reflects year-to-year variation in harvest quality, which varied considerably during the study period [[49](#_ENREF_49)]. Birth year grain figures in the study population predict later-life survival [[39](#_ENREF_39)], reproduction success [[31](#_ENREF_31)], and reproductive rate [[50](#_ENREF_50)].

1. **Infant mortality**

Finally, mean infant mortality was calculated as the proportion of infants born in each parish each year who died in their first year of life. This constitutes a demographic measure of environmental quality and has been used in the context of environmental quality in ecological studies of animals [[51](#_ENREF_51), [52](#_ENREF_52)], other study on humans four northern European countries [[53](#_ENREF_53)], and a previous study on the Finnish population studied here [[47](#_ENREF_47)], which showed that individuals born in years with high infant mortality experienced higher mortality later in life. In this study, data were taken from census records but gaps in such record-keeping meant that the data were not available for all years in each parish that the demographic records cover (analyses included 1615 women born over 99 years).

**Statistical analysis**

First, we calculated the correlation between number of children born and longevity in each birth cohort separately (birth cohorts with <10 individuals excluded, total N = 80 cohorts) to quantify variation in the cost of reproduction to survival over our entire study period. We included women with known date of death and who survived at least to 50 years of age.

Second, to test whether environmental conditions experienced in early life modify the cost of reproduction to individual survival (i.e. the hazard between the number of children born and mortality at a given time step) we used mixed effects Cox right-censored regression models with number of children born as a time dependent covariate and survival as response variable using the packages ‘*survival*’ [[54](#_ENREF_54)] and *‘coxme’* [[55](#_ENREF_55)] in R-3.1.0*.* We tested whether the effect of the number of children on survival at each time interval was modified by the early-life conditions of the individual by fitting an interaction between the measure of early-life environment (see below) and the number of children either born or raised. This method combines a few important strengths. First of all it allowed us to take into account time-independent and time-dependent variables (i.e. socio-economic status, number of children born up to each stage). Second, the method allows for inclusion of censored data, that is, individuals that have not been followed until the end of the study period (for example, because of migration). Third, it allowed us to control for random effects, by accounting for the dependency owing to shared family or the same year.

We also tested whether early developmental conditions modified the cost of reproduction on survival when the cost of parental care (in addition to production of offspring) was included in the total cost of reproduction. To this end, the effect of lifetime proportion of children who survived to fifteen years of age on maternal survival was analysed with Cox right-censored regression models in order to also test for costs of parental care involved in raising children, which could be much higher than costs of bearing children. By including the proportion of children surviving instead of the total amount we effectively test for differential cost of parental care over child bearing. If costs of parental care are disproportionally large compared to child bearing we also expect these two terms to interact, given that when half the children survive of two versus four children born, the full costs of parental care for two children is likely disproportionally higher than caring for a single child if costs of parental care are high.

Finally, we repeat our analyses for only those women surviving to age 50 (end of reproductive lifespan, in order to determine whether the effects of early conditions on the cost of reproduction are exhibited as reduced post—reproductive survival.

**Early-life environment and children–survival relationship**

1. **Spring temperature**

The data contained 1751 women (1461 with known date of death and 290 censored) excluding individuals who had unknown parental identity or socio-economic status. The data were encoded using (start, stop] form of the model [[54](#_ENREF_54)]. The first interval in the dataset for a woman started with 0 (date of birth) and finished with age at first reproduction which corresponds with 1 in the variable number of children born. Therefore we had 10924 intervals analysed from 1751 women. Consequently each interval stopped when another child was born and the last record stopped with age at death. For those individuals with unknown age at death, date of last appearance was used in the models and those individuals were considered as right censored. Information about spring temperature was available for all five parishes: Hiittinen, Kustavi, Tyrvää, Rymättylä, Ikaalinen for the period 1751-1850. We tested whether spring temperature modified the relationship between number of children born up to the age at which survival was being assessed and subsequent survival. Spring temperature is highly correlated with harvest quality [[45](#_ENREF_45)], therefore mean spring temperature during pregnancy and first year of life was calculated taking into account that harvest time was in September. We calculated mean spring temperature from a period which covers pregnancy and first year of life. Thus, for women born in January to May, the three-year mean was calculated from the values in the two years previous to the year of birth and the year of birth; for women born between June and August, the two-year mean was calculated from the year before and year of birth; for women born between September and December, the three year mean was calculated from the year before birth, the year of birth, and the year after birth.

We tested the relationship between the number of children born up to the age at which survival was being assessed as linear and quadratic terms in a model with potential confounding factors as: twin status (as a categorical variable with two levels [[56](#_ENREF_56)]); birth order (as a categorical variable with two levels: firstborns vs. laterborns [[57](#_ENREF_57)]; birth parish (as a categorical variable with five levels); social status as categorical variable with two levels [[41](#_ENREF_41)] and mean spring temperature around birth as a linear covariate. In addition, we fitted a three-way interaction between spring temperature, number of children born and social class and all two-way interactions between those variables to test the prediction that the negative effect of poor early conditions on the cost of reproduction was largest among the poorest socio-economic class. Non-significant terms were removed in sequential order of least significance from the maximal model, as assessed by p-values derived from z statistics, on the appropriate number of degrees of freedom. Maternal identity and birth year were fitted as random effects to account for the dependency owing to shared family or the same year, and retained in the model whenever significant, as assessed by p-value. We are aware that backward selection is prone to type I error and following recommendation from [[58](#_ENREF_58)] according to this type of analysis we limited number of explanatory variables to those which were the most important for the survival (as shown by previous studies in this population). Further, we provide information of the structure of the full model and statistic with standard errors for all parameters.

In order to test the costs of parental care on survival, the lifetime proportion of children survived to 15 years of age was analysed in separate models using mixed effects Cox regression models. Due to different intervals in between children who survived until 15 years of age this variable was not tested as time varying covariate. Instead we used proportion of children survived to 15 years of age which was divided into two groups according to median (0.67) and considered *‘high’* when was above median and *‘low’* when was below or equal to median. The procedure of getting a minimal model was the same as in models with number of children born.

1. **Rye yield**

Rye yields were available for Hiittinen, Kustavi, Rymättylä for the period 1756-1800 and for Ikaalinen and Tyrvää for 1804-1850. Data contained 5935 intervals from 887 women (632 with known date of death and 255 censored). Rye was harvested in autumn [[59](#_ENREF_59)] therefore women were assumed to eat rye from previous year during January-August and from current year since September. The method of calculating mean of rye yields and model selection procedure is similar to the one outlined in section (i).

1. **Infant mortality**

Models were repeated with population infant mortality as a measure of early-life environment. The three-year mean centered value of infant mortality around the individual’s year of birth was calculated to capture environmental quality around pregnancy and the first year of life for every woman. Information about infant mortality was available for all five parishes: Hiittinen, Kustavi, Tyrvää, Rymättylä, Ikaalinen for the period 1752-1850 with some years missing due to damage of the records [[47](#_ENREF_47)]. Data comprised 10095 intervals from 1615 women (1337 with known date of death and 278 censored). Model selection proceeded as in section (i).

**Results**

As illustrated in Fig. 1a, considerable variation existed between birth cohorts in the correlation between reproduction and longevity: while 55 % of all cohorts show the predicted negative relationship ranging from none (r = -0·003) in 1810 to strong (r = -0·43) in 1840, some cohorts reach highly positive correlations between reproduction and longevity (above r = 0·4 in 1812, 1815 and 1820). No clear time trend in the direction of the relationship was obvious, but rather both positive and negative correlations throughout the 100 years study period.

Similarly, spring temperature, annual crop yields and population infant mortality all also varied widely during the study period (Fig. 1b-d) without clear time trends (respectively: r= -0.27, p<0.001;, r= 0.13, p<0.001; r= -0.13, p<0.001). For example, spring temperature different by over 6°C between the coldest (1845) and warmest (1822) years (Fig 1c); annual rye yield varied by 5-fold between years; and whilst 97% of all infants born in 1835 survived to age 1 in Hiittinen, there were years during the study period when more than 50% of the infants born died before their first birthday (Fig 1b).

We therefore investigated whether the variation in the cost of reproduction across cohorts is associated with different early conditions experienced by those individuals. We found no support for the prediction that those experiencing poor early developmental conditions as measured by spring temperature around the year of birth would pay higher cost of reproduction in terms of lower probability of survival following each reproduction (children born\*spring temperature β = 0·0135 ± 0·0096, z = 1·41, p = 0·16, Table 1). We also tested whether any such effects of early conditions would be most pronounced among women from the poor class. However, although poor women had significantly lower overall survival probability than rich women (β = 0·2014 ± 0·0792, z = 2·54, p = 0·011) representing a hazard ratio of 1·22 for poor women compared to rich women (Fig. 2), the effect of spring temperature on the association between number of children and age-specific survival did not differ between the poor and the rich women (children born\*poor\*spring temperature β = 0·0255 ± 0·0288, z = 0·88, p = 0·38). Overall, neither early-life spring temperature (β = 0·0358 ± 0·0335, z = 1·07, p = 0·28) nor the number of children born (β = - 6·033×10-5 ± 0·0112, z = -0·01, p = 0·99) were significantly associated with maternal survival probability in later life, and such effects remained similar for both poor and rich women (poor\*spring temperature β = 0·0497 ± 0·0728, z = 0·68, p = 0·49; children born\*poor β = 0·0137 ± 0·0318, z = 0·43, p = 0·67).

Next, we tested whether between-year variation in the cost of parental care was related to different early conditions experienced by individuals (Table 1). We did not find evidence for higher cost of parental care for women born in low quality early-life environment (high proportion of children 15 years of age\*spring temperature β = -0·0580±0·0567, z = -1·02, p = 0·31). Further, we tested whether poor women suffer more from cost of parental care. There was no effect of spring temperature on the association between parental care and survival (proportion of children 15 years of age\*poor\*spring temperature β = 0·183±0·198, z = 0·924, p = 0·36), yet poor women having high proportion of children who survived to 15 years of age had lower mortality (high proportion of children 15 years of age\*poor β = -0·3560±0·1571, z = -2·27, p = 0·023). Generally, there was no main effect of spring temperature on survival (β = 0·0315±0·0332, z = 0·95, p = 0·34) and the effect remained similar for women from both social groups (poor\*spring temperature β = 0·0080±0·0725, z = 0·11, p = 0·91).

All these results remained qualitatively unchanged when either infant mortality rate or rye yields was used as indicator of early-life environment instead of spring temperature (supplementary materials). Moreover, repeating analyses only for women who survived at least to 50 years of age did not change the results (results not shown).

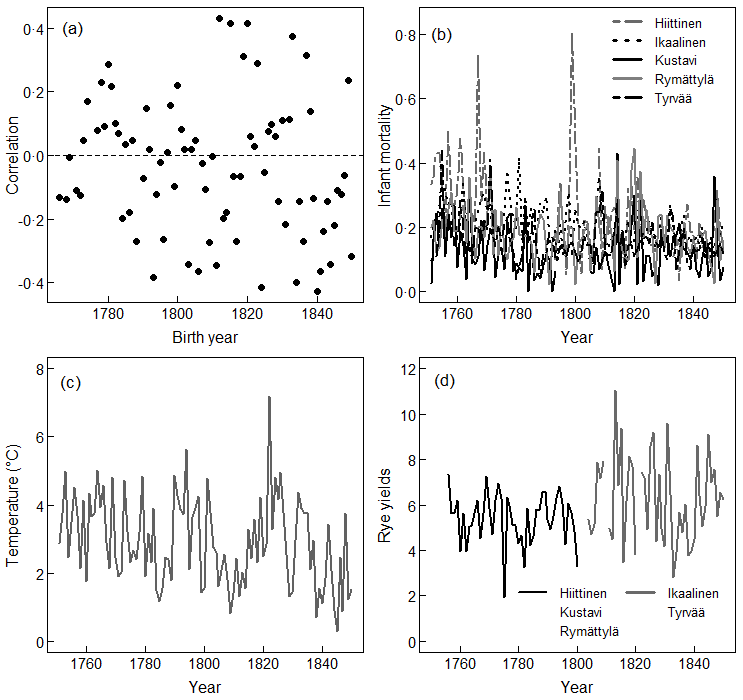


Fig.1. Variation in relationship between children born and lifespan, and environmental conditions in the study period (1751-1850); (a) the relationship between number of children born and post-reproductive lifespan among 100 birth cohorts (1751-1850) varied between r = -0·43 and r = 0·4; (b) the proportion of children who were born in a given year and died before the age of 1 (infant mortality) varied between years in the five studied parishes between 0·0 and 0·81; (c) spring temperature estimated using multiproxy reconstruction varied substantially between years during the studied period; (d) rye yields varied between years across the study period in all parishes.

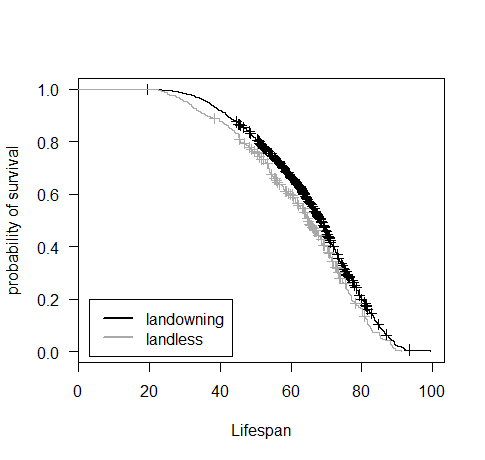


Fig. 2. Differences in the probability of survival between women from different socio-economic groups. The Poor women had a lower probability of survival compared to rich women in a model in which the number of children born up to a certain moment in life was tested.

**Discussion**

In this study, we tested whether individuals experiencing poor early-life environmental conditions displayed a stronger trade-off between investment in reproduction and survival compared to individuals experiencing more favourable developmental conditions. We used detailed demographic data collected from a preindustrial Finnish population experiencing natural fertility and mortality, combined with three measures of early-life environmental quality: spring temperature, infant mortality and rye yields. Early-life conditions did not modify the relationship of maternal survival with either the number of children produced by a female or the number of children raised to adulthood. Additionally, we did not find evidence that women from the lowest socio-economic class were most adversely affected by poor early-life conditions. Below, we discuss these results in relation to demographic, anthropological and reproductive ecology literature.

Although poor early-life environmental conditions have been related to reduced survival and/or reproductive performance in many species [[26](#_ENREF_26), [27, including humans (Lummaa & Clutton-Brock 2002), only one previous study in any species has investigated whether poor early-life conditions increase the survival costs of reproduction in females {Oksanen, 2007 #1288](#_ENREF_27)]. We hypothesized that such effects of early-life conditions on the ability to cope with the cost of reproduction would be likely, as an increasing number of studies have shown that early conditions can permanently alter body structure, physiology and metabolism in a way that decreases both reproductive success and longevity in adulthood [[32](#_ENREF_32), [33](#_ENREF_33)] (but see [[60](#_ENREF_60)]). Furthermore, such reductions in both reproductive success and survival have also been reported in the population studied here [[31](#_ENREF_31), [39](#_ENREF_39)]. In contrast to these predictions, however, we found no evidence to support the hypothesis that poor early developmental conditions increased the survival costs of reproduction in pre-industrial women. This contradicts with findings from the only other species studied in this respect before, bank voles, in which poor early developmental conditions measured by smaller size and high breeding density at birth increased survival costs of reproduction in adulthood [[61](#_ENREF_61)]. A possible explanation for this discrepancy could be that whereas bank voles are short-lived and thus usually give birth up to four litters during the season [[62](#_ENREF_62)], women may more carefully adjust their reproductive output to their condition and only reproduce when “they can afford to do so”. Ovarian function is very sensitive to energy supply and this sensitivity is thought to protect maternal condition and to optimize a woman’s lifetime reproductive output [[63](#_ENREF_63)]. Therefore, reproductive suppression through ovarian function can lengthen the inter-birth intervals and allows women to improve their own nutritional status before their next pregnancy. Thus, it is possible that we did not detect effects of developmental conditions on the relationship between reproductive output and survival, because pregnancy only happened at a time when energy conditions were good enough to handle both – maintaining good maternal condition and pregnancy. This strategy may also enhance child fitness since good maternal condition is associated with higher birth weight and increased child survival probability [[64](#_ENREF_64)]. Hence, the apparent lack of a negative relationship between the total number of children born and maternal lifespan observed in many populations [[65](#_ENREF_65)] could be due to the fact that the number of pregnancies is adjusted to environmental conditions without detrimental effects on mothers. Nevertheless, this explanation is not completely satisfactory as women in some populations [[12](#_ENREF_12), [66](#_ENREF_66)] or in some cohorts (this study; [[19](#_ENREF_19)]) exhibit reproductive rates that bear costs on their survival, and our findings therefore call for further investigation in other populations and ecologies.

We showed that poor women having a higher proportion of children who survived until adulthood had a higher probability of survival themselves as compared to women whose offspring tended to die. This could potentially be explained by both biological and social factors. From a biological perspective, raising a higher proportion of children to independence may be a sign of the quality of maternal care and/or high child fitness. It has been shown that insufficient nutrition is related to overall mortality as well as with cause-specific mortality from diarrhea, pneumonia, malaria, and measles [[67](#_ENREF_67)]. From the social point of view, a larger completed family size would mean more hands to work which especially in agricultural populations like the preindustrial Finns, might be needed. Raised children may help in the household as well in childcare for younger siblings [[68-70](#_ENREF_68)]. Additionally, women with a larger number of surviving children may have help from them in older ages which was shown to have an effect on survival [[71](#_ENREF_71), [72](#_ENREF_72)].

Several limitations must be considered when assessing our results. Firstly, our results could have been strengthened if individual access to resources rather than population-level annual differences had been used as a measure of early-life environment, but such information does not exist for historical population. Here we used three different measures of early-life conditions, all of which have been used in previous studies [[31](#_ENREF_31), [39](#_ENREF_39), [47](#_ENREF_47)]. Lower spring temperature around birth has been shown to be associated with higher mortality in childhood and adulthood in our study population [[47](#_ENREF_47)]. High infant mortality around birth is associated with increased mortality in childhood in our population, but the effect apparently does not persist into adulthood [[47](#_ENREF_47)]. Finally, rye yields around birth were shown to have an effect on reproductive success especially in women from the poorest socio-economic class [[31](#_ENREF_31)]. Landless women exposed to higher rye yields around birth had higher probability of reproducing in their lifetime and had higher proportion of children surviving to adulthood comparing to landless women born in low rye yields. Overall, taking into account the above findings, we would argue that spring temperature, infant mortality, and grain-yield data do reflect meaningful variation in environmental conditions around birth which have significant effects on fitness in our population, although they apparently do not mediate between-individual differences in the costs of reproduction on maternal survival. Second, our analyses controlled for other factors potentially associated with mortality risk, as suggested by previous studies of this population. We took into account socio-economic class because women from the poor socio-economic class had lower survival rates comparing to women from better off families [[41](#_ENREF_41)]. We also controlled for birth order [[57](#_ENREF_57)] and twin status [[56](#_ENREF_56)] as they were shown to have an effect on survival in the studied population.

In conclusion, despite using a detailed database on individual reproductive histories on several hundreds of women experiencing natural fertility we did not find evidence that environmental conditions experienced during early life modified the relationship between reproduction and survival. Many previous studies measuring the cost of reproduction on survival have used lifetime reproductive success as a measure of reproductive investment, and contrasted this with post-reproductive survival (e.g. [[11](#_ENREF_11), [18](#_ENREF_18), [73](#_ENREF_73)]). Potential problems with this approach are that (i) longer lifespan during the reproductive years means more opportunities to have children leading to reverse-causality between the number of children born and longevity, and (ii) this approach does not consider the contrasting effects of bearing children versus raising them to independence. We addressed these issues by fitting the number of children born as a time-varying covariate and analysing the effects of both the number of births and child survival rate on maternal survival at each age. Despite apparent variation between cohorts in the trade-off between reproduction and survival, in both the current study and that of Wang et al. (2013), neither study has been able to determine the drivers of this variation. Therefore, we hope that such variation as well as the predictions of the hypothesis studied here continue to be tested using a broad range of approaches and making use of available data, since only then we will increase our understanding of the causes of between-individual differences in reproduction-survival trade-offs, and any role of the early-life developmental conditions therein.

Table 1. Results from Cox right-censored regression models with *(a)* number of children born as a time dependent covariate (10 924 events from 1751 women); *(b)* proportion of surviving children to adulthood (n = 1751) and maternal survival as response. Spring temperature was used as indicator of early-life environment. Minimal model (in bold) was obtained, by excluding step by step the least significant term, is shown.

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| --- | --- | --- | --- |
| **Models of spring temperature** |  |  |  |
| 1. **Children born** |  |  |  |
| *Fixed effects* | Coefficient ± se | z - value | p - value |
| Children born2 | 0.0007±0.0034 | 0.22 | 0.83 |
| Children born \*Social class (rich) \* Temperature | 0.0000 |  |  |
| Children born \*Social class (Poor) \* Temperature | 0.0255±0.0288 | 0.88 | 0.38 |
| Children born \*Social class (Rich) | 0.0000 |  |  |
| Children born \*Social class (Poor) | 0.0137±0.0318 | 0.43 | 0.67 |
| Social class (rich) \* Temperature | 0.0000 |  |  |
| Social class (poor) \* Temperature | 0.0497±0.0728 | 0.68 | 0.49 |
| Twin status (Single) |  |  |  |
| Birth status (Twin) | -0.0997±0.1353 | -0.74 | 0.46 |
| Children born \* Temperature | 0.0136±0.0096 | 1.41 | 0.16 |
| Temperature | 0.0358±0.0335 | 1.07 | 0.28 |
| Birth Order (0) | 0.0000 |  |  |
| Birth Order (1) | -0.1016±0.0673 | -1.51 | 0.13 |
| **Children born** | **-6.0326×10-5±0.0112** | **-0.01** | **0.99** |
| **Social class (Rich)** | **0.0000** |  |  |
| **Social class (Poor)** | **0.2014±0.0792** | **2.54** | **0.01** |
| **Parish(Hiittinen)** | **0.000** |  |  |
| **Parish(Ikaalinen)** | **0.1212±0.0891** | **1.36** | **0.17** |
| **Parish(Kustavi)** | **0.3231±0.1057** | **3.06** | **0.002** |
| **Parish(Rymättylä)** | **0.2711±0.1162** | **2.33** | **0.02** |
| **Parish(Tyrvää)** | **0.2521±0.1031** | **2.45** | **0.01** |
| *Random effects* |  |  |  |
| **Birth year** | **0.0290±0.0170** |  |  |
| **Maternal identity** | **0.1350±0.0105** |  |  |
| 1. **Children 15 years old** |  |  |  |
| *Fixed effects* |  |  |  |
| Twin status (Single) | 0.0000 |  |  |
| Birth status (Twin) | -0.928±0.1377 | -0.67 | 0.50 |
| Proportion of children survived (Low) \*Social class (Rich) \* Temperature | 0.0000 |  |  |
| Proportion of children survived (High) \*Social class (Poor) \* Temperature | 0.0965±0.1467 | 0.66 | 0.51 |
| Social class (Rich) \* Temperature | 0.0000 |  |  |
| Social class (Poor) \* Temperature | 0.0080±0.0725 | 0.11 | 0.91 |
| Proportion of children survived (Low) \* Temperature | 0.0000 |  |  |
| Proportion of children survived (High) \* Temperature | -0.0580±0.0567 | -1.02 | 0.31 |
| Temperature | 0.0315±0.0332 | 0.95 | 0.34 |
| Birth order (0) | 0.0000 |  |  |
| Birth order (1) | -0.1079±0.0681 | -1.58 | 0.11 |
| **Proportion of children survived (Low)** | **0.0000** |  |  |
| **Proportion of children survived (High)** | **-0.1159±0.0660** | **-1.76** | **0.079** |
| **Social class (Rich)** | **0.000** |  |  |
| **Social class (Poor)** | **0.3926±0.1148** | **3.42** | **0.0006** |
| **Parish (Hittinen)** | **0.0000** |  |  |
| **Parish (Ikaalinen)** | **0.1153±0.0905** | **1.27** | **0.2** |
| **Parish (Kustavi)** | **0.3218±0.1076** | **2.99** | **0.003** |
| **Parish (Rymättylä)** | **0.2641±0.1183** | **2.23** | **0.026** |
| **Parish (Tyrvää)** | **0.2591±0.1048** | **2.47** | **0.013** |
| **Proportion of children survived (Low) \* Social class (Rich)** | **0.0000** |  |  |
| **Proportion of children survived (High) \* Social class (Poor)** | **-0.3560±0.1571** | **-2.27** | **0.023** |
| *Random effects* | *Variance ±se* |  |  |
| **Birth year** | **0.0261±0.0162** |  |  |
| **Maternal identity** | **0.1599±0.0114** |  |  |

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