Mothers facing greater environmental adversity experience increased costs of reproduction

Short title: Costs of reproduction and environmental adversity

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ABSTRACT

Evolutionary theory of aging predicts that women with increased reproductive effort live shorter lives, but evidence is inconsistent. These inconsistencies could be because environmental conditions influence how much a mother's life span is reduced when having more children, i.e. their life-span cost of reproduction. Using a structural equation measurement model, we compare how reproductive effort affects the life span of 4,684 women exposed across different life-stages, or not at all, to the Great Finnish Famine. We find that life span costs of reproduction became higher in mothers exposed to the famine during reproduction, and for these mothers amounted to lower life expectancy of ~0.5 years per child. Conversely, reproduction did not shape the life spans of mothers not exposed to the famine, or exposed post-reproduction or during development. This natural experiment reveals how environmental adversity can influence reproductive costs, providing a biological explanation for previous inconsistent findings, while showing how reproductive behavior has shaped the evolution of aging in humans.

TEASER

Mothers with more children had shorter lives during a famine, suggesting that harsh conditions increase costs of reproduction.

KEYWORDS: disposable soma theory of aging, reproduction-survival trade-off, early-life adversity, resource acquisition-allocation, human life-history, maternal lifespan

INTRODUCTION

Understanding why we age – defined as a physiological decline in later-life – and why some of us undergo this aging process faster than others, are vital foundations for improving human health-spans (1). One theory – the disposable soma hypothesis – predicts that aging is a consequence of natural selection honing our physiology to maximize reproduction at the cost of other organismal functions, resulting in an accumulation of damage through life that limits lifespans (2,3). Consequently, researchers have tested if individuals who devote more resources to reproduction have shorter lifespans (4). However, expected negative associations between reproduction and lifespans are rarely found (5,6) and typically only when using experimental manipulations (e.g., (7)). For humans, the bearing and raising of even one child is energetically demanding for women (8), but – despite over 100 years of research (9) – evidence of a reproduction-survival trade-off is inconsistent (10–12) and the role that human reproductive behavior plays in shaping aging remains unclear.

One potential explanation for these inconsistencies is that the reproduction-survival trade-off does not manifest itself in the same way when measured across a heterogeneous set of individuals (13). First, individual heterogeneity will weaken the observed slope of the regression of survival against reproduction (i.e. the estimate of the reproduction-survival trade-off *function*) because among-individual variation in resource acquisition introduces a positive association between reproductive effort and lifespan that can mask the within-individual reproduction-survival trade-off (i.e., the big house and big car syndrome (14,15)). Thus, the *estimated* trade-off function quantifies how important reproductive behavior versus individual heterogeneity is in shaping human lifespans, and studies aim to account for such individual heterogeneity in their analyses (16). Second, among-individual variation (e.g., in frailty or quality), due to intrinsic or environmental differences, may mean that some women will manifest costs of reproduction more than others (12,13,17–19). Previously, the reproduction-survival trade-off has been found to be stronger in lower socioeconomic status women (20,21) and women experiencing higher levels of infant mortality (22). However, we still have a poor understanding of which biological factors drive these changes in the reproduction-survival trade-off, with studies showing considerable variation in the estimated trade-off within the same populations over time, in line with environmental causes playing a role (23–25). Understanding these drivers can give us insight into the mechanisms underlying this fundamental trade-off, how it manifests itself, and under what circumstance human reproductive behavior is an important factor in shaping aging.

Although the role of reproductive effort in shaping aging is uncertain, examples of environmental effects on human health are numerous (26,27). In humans, experiencing periods of extreme environmental adversity, such as famines, can accelerate the biological aging process (28). In fact, famine can have an array of effects, from long-term individual effects on human health, such as prenatal famine exposure increasing risk of type-2 diabetes and schizophrenia later in life (29,30), to social and economic consequences (31). Although widely used as natural experiments in other fields, the role that famine

exposure plays in shaping estimated lifespan costs of reproduction has not to our knowledge been studied.

Given the well-documented adverse effects of famines, mothers exposed to famines could show greater reductions in lifespan for a given increase in reproductive effort. However, this reduction may depend upon the life-history stage of the mother during the famine exposure. Firstly, even short-term fluctuations in early-life environmental conditions can lead to physiological differences (32) that influence the overall lifespan and realized reproduction of individuals (33,34). Thus, women experiencing famines during development may show increased costs of reproduction. However, Nenko et al. (24) found no evidence that crop yields, spring temperatures, or infant mortality rates at birth modified the reproduction-lifespan trade-off in mothers. Instead, mothers may be especially vulnerable to resource limitations while raising children (24), due to both the calorific demands of pregnancy and lactation, and increased vulnerability to disease (8). Indeed, Wang et al. (25) proposed that some individuals experiencing the Great Depression and Second World War while raising and bearing offspring caused the variation in costs of reproduction in the Framingham cohort study. Finally, women in post-reproductive life are particularly at risk of mortality under lower food availability (34). Thus, mothers could suffer increased frailty due to high reproductive effort, but perhaps only when combined with famine exposure during post-reproductive life would this result in reduced lifespans. However, no study has examined how a period of environmental adversity affects lifespan costs of reproduction in humans and whether this might vary across life-stages.

Rigorous tests of these hypotheses require detailed individual-level life-history data for a period encapsulating a major famine event. Here, we use individual life-history data across 250 years from rural Finland to quantify lifespan costs of reproduction and compare how they changed across mothers exposed to the Great Finnish Famine in different life-stages, and those not exposed at all. In the 1860s, Finland experienced several harsh winters resulting in a series of low harvests, which in 1867 dropped to catastrophic levels, resulting in a major loss of employment (35). Widespread migration then followed as people went in search of work, which in turn triggered a large spike in infectious diseases, such as typhoid fever, typhus, and dysentery (35). This led to an excess mortality of 110,000 (or 5-10% of Finland's population (36)) making it one of the most devastating famines in recent European history, and the worst in Finland since the 17th century (37).

Here we capitalize on the fact that this famine occurred in the middle of our study period, allowing us to estimate the lifespan costs of reproduction before, during, and after a famine. Specifically, we compare mothers exposed to the famine during three life-stages (during their development [ages 0-19], while reproductively active [ages 19-45], and while in post-reproductive life [ages 45+]) to mothers dying before the famine and those born in the years after using a structural equation measurement model (N = 4,868, Fig. 1). We follow Helle (38) and use a measurement model using multiple indicator variables to obtain a comprehensive measure of lifetime reproductive effort. Within this structural

equation model framework, we estimate the association between reproductive effort and lifespan (i.e., the reproduction-survival trade-off function) in each famine exposure group and how these lifespan costs of reproduction differed across groups, accounting for the changes in reproductive effort and lifespan in relation to famine exposure. Broadly we expected mothers exposed to the famine to show an increased lifespan cost of reproduction, but that this cost would depend upon the life-stage of mothers during this famine exposure. Showing such a dependency would shed light on why the estimated costs of reproduction are so variable both among and within studies.

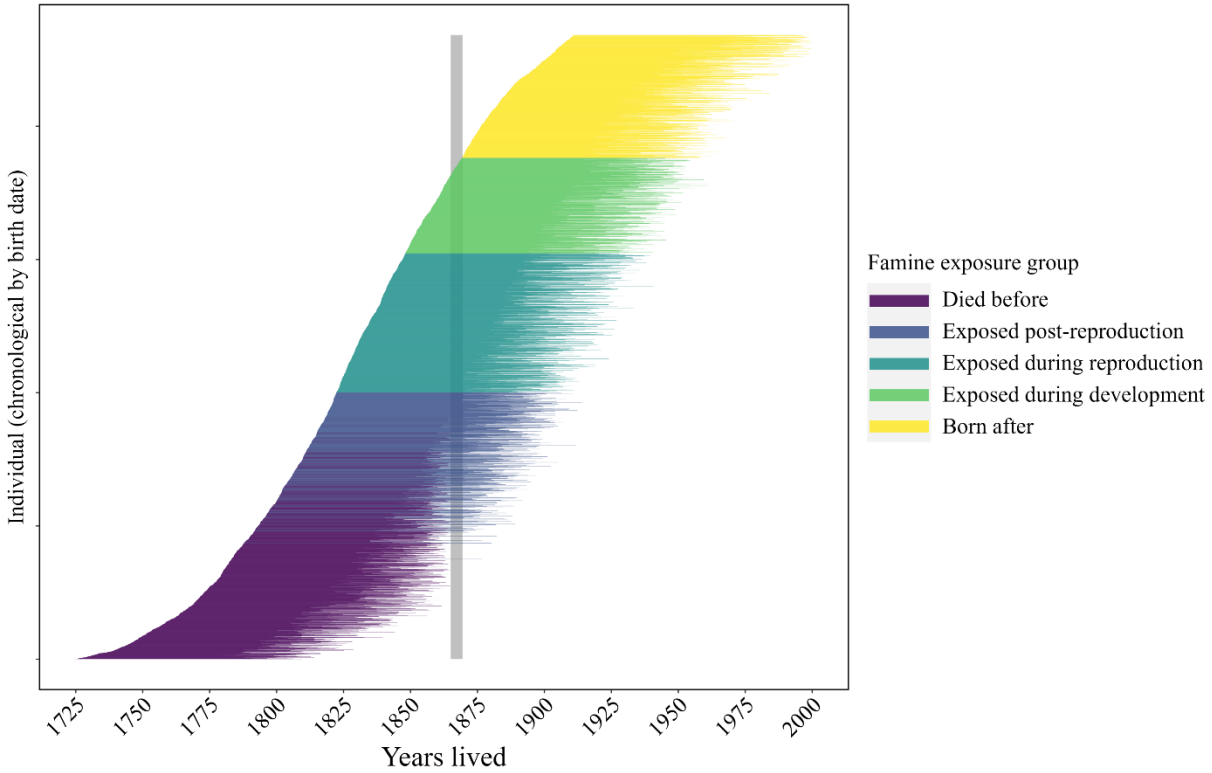

Fig. 1: Line graph showing the years lived for each mother included in the analyses, sorted chronologically by their birth date (N = 4,684). Colors indicate their exposure to the Great Finnish Famine (grey bar) and groupings in the analyses: died before (n = 1,297), exposed post-reproduction (n = 705), exposed during reproduction (n = 1,044), exposed during development (n = 716), and born after (n = 922).

RESULTS

Lifespan costs of reproduction

Exposure to the Great Finnish Famine shaped the estimated reproduction-survival trade-off (Fig. 2, Tables 1 and 2). Specifically, increases in reproductive effort were associated with a reduction in

lifespan in mothers exposed to the famine while reproductively active, but not among other groups (Fig. 2; Table 2). Mothers exposed to the famine who had one child would be expected to live to age 71.6 (95% CIs 69.2 – 74.6), whereas a mother with 15 children would only be expected to live to age 64.3 (61.7-68.3), or a reduction in lifespan of half a year per child (Fig. 2, Table S1). In line with this, pairwise comparisons of the five groups showed that the association between reproductive effort and lifespan in mothers exposed during reproduction was also higher than in mothers dying before the famine, mothers born after the famine, and mothers exposed to the famine in post-reproductive life ($p < 0.05$), and marginally higher than those exposed to the famine during development ($p = 0.087$, Table 2, Fig. 2).

These results were confirmed in a complementary mixed model analysis that accounted for significant variation in lifespan amongst birth years, families, and 13 geographical regions (Table S2). Mothers again varied in the reproduction-survival trade-off function according to famine exposure, with the statistically significant association between reproductive effort and lifespan only found in mothers exposed to the famine during reproduction, and similar in magnitude as estimated in the previous model (Tables S3 and S4). The association between reproductive effort and lifespan in mothers exposed to the famine while reproductively active was also higher than in all other groups, except for those exposed during development (Table S4).

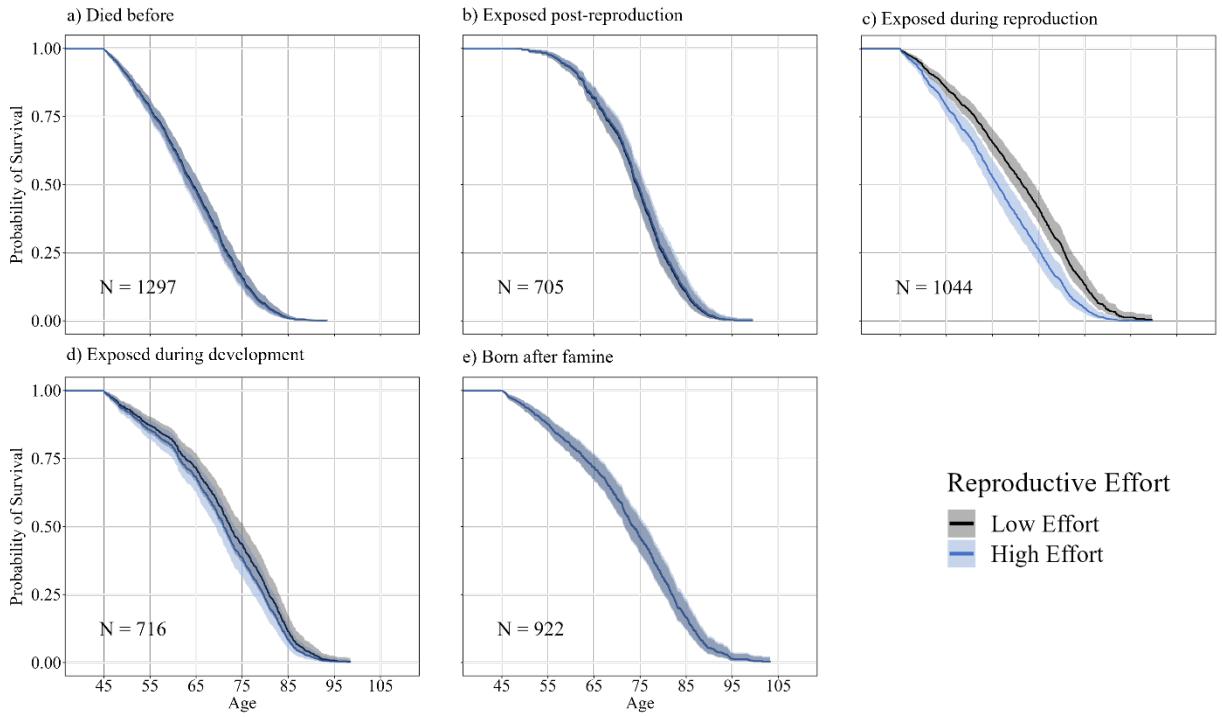

Fig. 2: Predicted survival curves for low and high reproductive effort across five famine exposure groups. Curves were generated using Cox proportional hazards models on each famine exposure group separately (see Table S1). Each panel represents a different famine exposure group: (a) died before famine, (b) exposed during post-reproduction, (c) exposed during reproduction, (d) exposed during

development, and (e) born after famine. Survival curves are shown for low (5th percentile, -3.8) and high (95th percentile, 6.5) reproductive effort levels. All curves are calculated for individuals of intermediate socioeconomic status and median relative birth date within each famine group. Shaded areas represent 95% confidence intervals.

Temporal changes in lifespan

There were differences *among* famine exposure groups in mean lifespan, and in how lifespan changed over time *within* each group (Table 1, Table S1). Life-expectancy for mothers dying before the famine was 66 years for those born in 1777 but declined over time to 55 years for mothers born in 1819 (Table 1, Table S1). Similarly, for mothers exposed to the famine post-reproduction, life-expectancy was 79 years for those born in 1796 but declined overtime to 70 years for mothers born in 1822 (Table 1, Table S1). These trends reflect the classification of these groups: within mothers who died before the start of the famine, those born later must have lived shorter lives. Similarly, by focusing only on famine survivors, mothers born earlier among those exposed to the famine during post-reproduction cannot have had short lives, with the higher life-expectancies overall likely reflecting the loss of higher frailty women during the famine itself. Mothers exposed to the famine during reproduction had a life expectancy of 71 years, which stayed similar for mothers exposed during development and did not change through time in either group (Table 1, Table S1). However, life-expectancies then increased for mothers born after the famine from 71 years in mothers born in 1869 to 78 years for mothers born in 1910 (Table 1, Table S1).

Temporal changes in reproductive effort

Mean reproductive effort did not differ between mothers dying before the famine and those exposed to the famine post-reproduction, and it remained constant overtime within each group (Table 1, Fig. S1). However, for mothers exposed during reproduction, reproductive effort increased from being similar to prefamine levels for mothers born in 1822 to being 0.8 children higher in mothers born in 1848 in this group (Table 1). Reproductive effort then remained similarly high for mothers exposed during development who had on average 0.6 children more than pre-famine levels, which did not change over time (Table 1). Reproductive effort then declined rapidly in mothers born after the famine going from mothers born in 1869 having 0.8 children more than mothers dying before the famine, to mothers born in 1911 having 1.8 children fewer than prefamine levels (Table 1).

Socioeconomic status effects

Socioeconomic status did not modify the association between reproductive effort and lifespan (Table S5). However, there were differences in both lifespan and reproductive effort across socioeconomic status groups, with the magnitude of these differences changing according to famine exposure (Table 1, Table S1). No differences in lifespans were found in mothers dying before the famine between higher and middle socioeconomic statuses, and these effects did not change across famine exposure groups (Table 1). However, lower socioeconomic status mothers had lower life-expectancies of around three years compared with intermediate socioeconomic status mothers (Table 1). This difference in life-expectancies between lower and intermediate socioeconomic status mothers remained similar across famine exposure groups, except in lower socioeconomic status mothers exposed to the famine during development who did not have lower lifespans than mothers of intermediate socioeconomic status (Table 1).

Upper socioeconomic status mothers dying before the famine had higher reproductive effort than mothers of intermediate socioeconomic status, amounting to 0.6 more children (Table 1). These differences gradually decreased through time until mothers born after the famine, where upper and intermediate socioeconomic status mothers had identical reproductive effort (Table 1). Mothers from lower socioeconomic statuses had lower reproductive effort amounting to 0.6 fewer children in mothers dying before the famine than those from intermediate socioeconomic status. This difference in reproductive effort between lower and intermediate socioeconomic status mothers remained stable, except for mothers exposed during reproduction, where the difference increased to 1.2 fewer children.

DISCUSSION

Using life-history records for 4,684 Finnish women, we find evidence supporting adverse environmental conditions increasing the importance of reproductive behavior in shaping a mother's lifespan (Fig. 2, Table 2). Specifically, mothers exposed to the Great Finnish Famine (1866-68) while reproductively active showed reduced lifespans of approximately 0.5 years per child as estimated through a structural equation measurement model. On the other hand, mothers not exposed to the famine (i.e., mother who died before, or were born after) or those exposed to the famine in post-reproductive life or during development did not pay a lifespan cost of reproduction. Although the effects of famines on human health and aging are well documented (28), with some evidence for environmentally-dependent costs of reproduction in animals (13,19), this is, to the best of our knowledge, the first evidence of a famine event modifying the reproduction–survival trade-off function in humans. These findings therefore add a biological explanation – to previously highlighted methodological explanations (detailed in: Helle et al. (39); Helle (40)) – for why several studies have shown variation in costs of reproduction across cohorts (23–25): fluctuations in environmental conditions experienced by mothers while reproductively active impact the trade-off function. This strengthens the evidence for the existence of lifespan costs of

217 reproduction and gives insight into under what circumstances human reproductive behavior is an
218 important driver of aging.

219 These results align with other studies showing variation in the estimated reproduction-survival trade off
220 amongst mothers in human populations. For instance, one recent study using data for preindustrial
221 Canada showed that only mothers having both high reproductive effort (i.e., a high number of sons) and
222 high lifetime infant mortality showed increased lifespan costs of reproduction (22). While this change
223 in the reproduction-survival function across mothers is in line with our findings, Invernizzi et al. (22)
224 did not explore how environmental conditions drive variation in infant mortality among mothers beyond
225 showing an effect of a mother's birth year (see (22), Supplementary Table 1). These results also show
226 parallels with studies showing that women of lower socioeconomic status showed a stronger trade-off
227 (20,21). However, while these results align with some previous findings, we present the first evidence
228 suggesting that environmental adversity influences the reproduction-survival trade-off across women.

229 Our finding that only mothers exposed to the famine while reproductively active showed lifespan costs
230 of reproduction could be due to the increased energetic demands of bearing and raising children during
231 a period of high environmental adversity, as previously suggested (41). When pregnant, mothers must
232 increase their caloric consumption by on average 300 kcal/d to sustain a healthy pregnancy, which rises
233 to 460-630 kcal/d during breastfeeding (42). If the mother's pregnancy or breastfeeding coincides with
234 a famine it could mean that these increases in metabolic demands are paid by themselves through
235 lowering basal metabolism, and thus slowing or shutting down other important functions, such as
236 immunity (11,43), resulting in a decline in health and shorter lifespans. Specifically, circulating estrogen
237 levels – which are important for cardiovascular health (44) – are very low during breastfeeding (45).
238 These levels are even lower in mothers with poor nutrition (46), which could mean that cardiovascular
239 disease risk (which is already a risk factor of high parity (47)) could be even higher in mothers of high
240 reproductive effort experiencing poor nutrition while reproducing. Although we can speculate,
241 ultimately the underlying mechanisms are difficult to disentangle in genealogical data, but we hope that
242 these results may help guide future human biobank studies or experiments on model species where
243 unravelling underlying mechanisms is more attainable.

244 In addition to famine exposure, we found that demographic and cultural factors were important drivers
245 of reproductive effort, lifespan, and their association. Differences across socioeconomic groups were
246 pronounced, with lower socioeconomic status mothers having lower realized reproduction (37) and
247 shorter lives (48), but not increased lifespan costs of reproduction (Supplementary Table S5, Helle (38),
248 but see (21)). We also found that mothers exposed to the famine during reproduction lived shorter lives
249 than those exposed during development, and those exposed during development lived shorter lives than
250 mothers born after the famine. Rather than being a direct effect of famine exposure, this is probably a
251 symptom of increased industrialization, which, in line with country-wide trends, started during this
252 period (49). These improvements in lifespan through, for example, vaccination (50), combined with a

253 reduction in overall reproductive effort, are potential additional reasons why the importance of the
254 reproductive-survival trade-off decreased in mothers born after the famine. This is analogous to results
255 from the Netherlands, where the reductions in lifespan for mothers having more children found in 1850
256 had disappeared by 1910 (51). However, these results require replication outwith northern European
257 countries.

258 Although high reproductive effort during the famine may have affected individual health directly,
259 among-individual processes, such as selective disappearance, may still have influenced the
260 reproduction–survival trade-off function. Because the association between reproduction and survival
261 will weaken with higher individual heterogeneity (14,15,17), higher mortality rates during the Great
262 Finnish Famine may have driven higher mortality of frailer individuals (as suggested by a previous study
263 (52)), reducing the overall amount of individual heterogeneity in mothers sampled after completing
264 reproduction, and increasing the strength of the association. However, because our study necessarily
265 included only survivors of the famine, selective disappearance due to the famine could have occurred in
266 all of the famine exposure groups. Moreover, given that the effects of the famine on mortality were
267 biased towards the very young and old, and lowest amongst reproductive age individuals (53), the
268 selective disappearance should have been highest in the development and post-reproductive famine
269 exposure groups – even after accounting for adverse conditions potentially increasing maternal death
270 during childbirth (54). However, we found that the trade-off function was strongest and significant only
271 in mothers reproducing during the famine, further suggesting that our results reflect a direct negative
272 within-individual effect of famine exposure on reproducing mothers. Thus, while it is possible that
273 among individual factors, such as selective disappearance, may have shaped some of our findings, the
274 evidence suggests that it is not the primary cause of the stronger reproduction-survival trade-off in
275 mothers exposed to the famine during reproduction.

276 However, higher selective disappearance in the mothers exposed during development may help explain
277 why no moderating effects of the early-life environment have been found here and elsewhere (24). For
278 instance, if selective disappearance removes the frailest mothers who are most susceptible to the trade-
279 off, leaving a more robust subset of mothers for whom reproduction is less costly, the trade-off function
280 may become weaker with greater selective disappearance. Some evidence of increased selective
281 disappearance in the mothers exposed during development may be visible in our results, with women of
282 lower socioeconomic status in general having lower lifespan, except if they have been exposed to the
283 famine during development where selective disappearance may be larger. While evidence for cohorts in
284 gestation during the Great Finnish Famine having shorter lives is lacking (55), given the importance of
285 the early-life environment on human health (56), and in modifying the reproduction–survival trade-off
286 function in wild animal populations (57), future studies should aim to better account for selective
287 disappearance when studying how environmental adversity may modify lifespan costs of reproduction,
288 in particular when looking for early-life effects.

We emphasize that our findings should be interpreted within the context of this being an observational study occurring over a single famine event that will have coincided with other historical events that may have shaped reproduction and lifespan. Albeit the largest (as measured by death rates (37)), the Great Finnish Famine is only one of many societal perturbations faced by Finns between the 18th century and present day. Principally, the Finnish War (1808-1809), severe epidemics and crop failures (1832–1833), the Finnish Civil War (1918), and World War II may all have shaped the reproduction and longevity of individuals in our study population (58). Although we were able to account for some demographic trends in reproductive effort and lifespan both within and among famine groups, including expanding analyses to account for correlations among birth years, regions, and families, which did not affect results, there are limitations. Most importantly, because Finland began to industrialize soon after the famine (i.e. in the 1870s), we had no group of women born after the famine whose demography was comparable to the time preceding the start of industrialization. Thus, proving the causality of the Great Finnish Famine (1866-68) shaping the trade-off function is difficult within our system, but it may be possible in other datasets.

After over 100 years of research, human observational studies have provided mixed evidence for lifespan costs of reproduction, leading some to believe that reproductive behavior is not important in shaping human aging. Contrary to this, we provide evidence for a life-history trade-off between reproductive effort and lifespan and demonstrate that – under harsh conditions – reproductive effort is an important driver of individual variation in lifespan. These findings suggest that famines can provide fitness costs to mothers in the form of reduced lifespan, but may also include reduced reproduction of the children born from pregnancies during famine, although whether early-life environmental effects cause positive or negative effects fitness effects in humans remains debated (59,60). Although reproductive behavior may shape the lifespans of mothers exposed to adverse environments while reproducing, it appears less important in contemporary Finland where investment in reproduction is far lower, and modern medicine may alleviate many potential costs. Finally, we would like to acknowledge that due to unaccounted variation in individual heterogeneity, our study will still underestimate the underlying trade-off, and future research should focus on the underlying mechanisms or within-individual measures of aging (e.g., (61)). Lifespan is the ultimate outcome of many underlying factors, and reproductive behavior in particular can have different effects on different diseases: for example, high reproductive effort increases the risk of cardiovascular disease (47) but very low reproductive effort may increase the risk of breast cancer (62). Therefore, future studies focusing on specific diseases or using biomarkers would be best placed to study how individual reproductive behavior shapes aging.

MATERIALS AND METHODS

Study population

To investigate how a mother's reproductive behavior affects her lifespan, we used long-term individual life-history data from rural Finland. Data were adapted from Parish records across rural Finland dating back to the 16th century. These records were maintained by the Lutheran Church and include birth, marriage, and death certificates, but also yearly attendances of religious services, which from 1749 onwards were required by law to be recorded for tax purposes. This allows complete life-histories to be precisely constructed, including the migration of individuals between parishes. These individual records were then linked across generations resulting in a genealogical dataset of 100,598 people born from 1536 to 2012.

The majority of individuals in these data were born in a preindustrial period where agriculture employed 90% of the population (35). Preindustrial farming techniques, combined with particularly tough crop growing conditions in Finland, meant that during this period yearly yields of the two main crops, rye and barley, varied a lot with the climatic conditions (33). Consequently, the population was characterized by high birth and death rates due to limited access to healthcare and contraception, and infectious diseases such as smallpox, typhus, and typhoid fever (58). In our records, mothers on average had 4 children, but 38% of children died before their 15th birthday. On average, women had their first child at age 25 and 95% had their last child before age 45. Like other pre-industrial European populations, the mating system was patrilocal and highly monogamous. Divorce was forbidden (63) and infidelity severely punished (64), with recent genetic studies showing that ~1% of children were born outside of marital ties (65,66).

Industrialization began in Finland in the 1870s – relatively late by European standards – and developed gradually, with manufacturing still employing only 20% of the population by 1910 (35). Throughout this period, access to healthcare improved and vaccination of children against smallpox was relatively common by the 1880s (50). Consequently, life expectancy in Finland increased from 32 years at birth in 1865 to 70 for those born in 1965 and is now above the European average (67). In this period, access to contraception also improved and cultural preferences changed, with the fertility transition beginning around 1910 where birth rates declined from ~30 births per 1000 people to ~12 by the 1970s (49).

Quantification of lifespans

All data handling was performed in R 4.3.2 (68) within RStudio 2023.12.1 (69), using *tidyr* 1.3.1 (70). We calculated the lifespan of all individuals with a recorded birth (99%) and death (43%). For those with recorded years but missing months and/or days the middle value was used (1% and 2% of recorded births and deaths, respectively). Individuals with missing death dates were then assigned a last-seen date of the final year they were known to have been alive in the data (available for 97% of individuals missing death dates), which could include a last-known birth of child or attendance of religious services. As the

357 precise date of these services was often unknown, we standardized the date across individuals and treated
358 all individuals as at least being alive on January 1st of their year of last appearance. Lifespans were then
359 calculated in decimal years using the *lubridate* package 1.9.2 (71) giving a median of 24 (range = 0-
360 108). We also recorded whether this lifespan was calculated from known death dates or dates of last
361 appearance which would be accounted for using a survival analysis (see *Statistical analyses*).

362 **Quantification of reproductive traits**

363 We recorded six aspects of a woman's reproductive history thought to capture a mother's reproductive
364 effort, defined as the total amount of resources devoted to bearing and raising offspring to independence
365 (38). These variables included the four variables that Helle (38) used to measure reproductive effort:
366 number of children born, number of child-years experienced, ages at last reproduction, and reproductive
367 tenure (i.e., the time between first and last reproduction). Additionally, we included the number of sons
368 born, and the number of children born that were twins or triplets (hence multiple births), which may be
369 associated with increased reproductive effort (72). We also modified the definition of child-years
370 experienced from the cumulative time that a mother co-survived with her children while they were
371 younger than age 18 to age 5, because the effort of bearing and raising offspring is relatively low and
372 children are more independent after age 5 (73), even helping to raise younger siblings thereafter (74).
373 Thus, if a mother survived at least 5 years after her last birth and had 3 children, one of which died at
374 age 1, another age 10, and another age 60, her child years experienced would be (1+5+5=) 11.

375 The median number of children for known mothers in our population was 3, ranging from 1 to 18. We
376 estimated the ages at last reproduction and reproductive tenure for all mothers with a known child-birth
377 date, which had medians of 35 (range, 16–51) and 8 (0–31), respectively. Sex of children was known in
378 99.4% of children, with mothers having 0–12 sons, with population-level birth sex ratios approximately
379 50:50. Multiple birth status was assigned to 99.3% of cases. Six percent of mothers had at least one set
380 of twins or triplets, but one mother had 3 sets of twins. In cases where children or mothers had unknown
381 death dates before age 5 (81%), the year of last appearance was used to calculate the child-years
382 experienced. Median child years experienced were 12 (0-75).

383 **Assigning famine exposure groups**

384 All individuals were grouped according to whether – and in what life stage – they were exposed to the
385 Great Finnish Famine. We first assigned the start and end dates of the famine as February 1st 1865 and
386 May 31st 1869 which is the period of elevated excess mortality observed country-wide in Finland due to
387 the famine (35). Based on these dates we categorized all women surviving to adulthood (19.1yr, 5th
388 percentile for age at first reproduction) into 3 groups: individuals dying before the famine (n = 3,694),
389 individuals exposed to the famine at some point in their live (n = 9,337), and individuals born after the
390 famine (n = 15,036). We then further divided individuals exposed to the famine into three groups based
391 on when they were exposed to the famine: when they were developing, reproductively active, or post-

392 reproductive. We defined women as reproductively active during the famine if – at the midpoint of the
393 famine (i.e., March 31st 1867) – they were older than the 5th percentile of age at first reproduction (19.1
394 yr) but younger than the 95th percentile of age at last reproduction (44.9 yr) calculated from mothers
395 reproducing before the fertility transition in 1911 (49). Individuals younger than 19.1 years at the
396 famine's midpoint were assigned the developing group (n = 4,231) and individuals older than 44.9 at
397 the midpoint were assigned the post-reproductive group (n = 1,612), with those aged in between assigned
398 to the reproductively active group (n = 3,494). 1,052 women could not be assigned a famine category,
399 due to missing birth or last seen dates.

400 **Assigning socioeconomic status groups**

401 To account for a source of individual heterogeneity that can influence the lifespan and reproductive
402 effort of women (48), we grouped women surviving to adulthood into three socioeconomic status
403 groups: upper, including mostly landowners and merchants (n = 6,591); intermediate, including mostly
404 craftsmen, such as smiths, and fishermen (n = 7,764); and lower, consisting of landless families and
405 servants (n = 6,750). In cases where a woman's occupation was missing but the husband's occupation
406 was present, we assigned it based on the husband's occupation (n = 2,357). If both were present but
407 different (n = 590), the highest socioeconomic status was used. In total, socioeconomic status could be
408 determined for 76% of adult women.

409 **Data selection**

410 The data selection is summarized in Fig. S2. For women surviving to adulthood, we first excluded
411 childless women (n = 9,275) because of the substantial differences in health of childless females in
412 preindustrial populations that make comparisons to reproductive females (henceforth mothers)
413 challenging (12). We then excluded mothers that had not been tracked throughout their entire
414 reproductive period (n = 6,658) to ensure the precise estimation of reproductive effort. We further
415 excluded mothers who died before completing their reproductively active period (age 44.9, as defined
416 above) because we wanted to estimate the long-term lifespan costs of reproduction and minimize frailty
417 heterogeneity (n = 2,204). However, we accept that this may lead to an underestimation of the total costs
418 of reproduction by excluding those who died directly after reproducing and by including only the most
419 robust mothers that survived to post-reproductive life (23,40). This left 9,930 women. Before 1725 the
420 coverage of the data was very low and after 1911 there were increasing numbers of missing individuals
421 because they are still alive, both of which could bias lifespans, so were removed (n = 1,906). We were
422 also only interested in the long-term effects of the famine and so excluded those dying during the famine
423 period itself (n = 478). We further controlled for individual heterogeneity by excluding mothers who
424 were twins or triplets (n = 119), multiple marriers (n = 612), and women without recorded childbirth
425 dates (n = 4) or socioeconomic statuses (n = 410) as done in other studies (75).

Finally, prior to analyses we examined the proportion of individuals with known death dates versus those that had only a last seen date (i.e. were censored) across the years lived for each of our famine exposure groups. Survival analyses (as used here) allow the combining of censored and uncensored data to estimate lifespans but can become biased if the proportion of censoring is biased with respect to lifespan across predictors in a survival model (76). We found that the percentage of censored individuals was much higher in the groups of individuals exposed to the famine while reproductively active (43%), while developing (51%), and those born after the famine (35%), compared with those exposed post-reproduction (4%) and dying before the famine (3%; Fig. S3a), due to two spikes in the number of censored individuals between the years of 1898-1904 and 1910-11 (Fig. S3b). Because of the temporal nature of our famine exposure groups, these resulted in systematic structuring of censoring across lifespans (Fig. S4), which would result in biased lifespans. Removing lifespans censored during those two periods (n = 1717) removed these biases (Fig. S4) and resulted in a relatively even percentage of censored to non-censored individuals across famines exposure categories for analyses (2-11%; Fig. S5).

This resulted in 4684 mothers with a median lifespan of at least 68 years (range 45-103) and 5 children (1-17) (Table S6). These values are slightly higher than the full dataset (see Table S6) but remained comparable to other similar populations (22,75).

Statistical analysis

Following Helle (38) we used a confirmatory factor analysis measurement model to estimate the *latent* lifetime reproductive effort from the six indicator variables that are hypothesized to be components of a woman's reproductive effort (77–79). Measurement models use simultaneous equations to separate the correlation between these indicator variables into the true variance in reproductive effort, and the error variance which captures the measurement error for each specific indicator variable (80). As indicator variables we used the number of children born, number of child-years experienced, ages at last reproduction, and reproductive tenure, number of sons born, and number of children that were part of multiple births. Indicators with factor loading p-values < 0.05 contributed to estimating lifetime reproductive effort. The number of children born was used to scale the *latent* reproductive effort so that each unit increase in reproductive effort could be interpreted as equivalent to the total resources used in raising one child. The latent reproductive effort was mean centered at 0 so values could be negative, and indicate lower than average reproductive effort.

All reproductive variables significantly contributed to estimating reproductive effort (p-value < 0.001, *loadings*, Table 1). Specifically, increases in one unit of reproductive effort was associated with 0.536 (95% CIs = 0.523-0.548) more sons, 1.238 (1.187-1.289) years increase in ages at last reproduction, 2.131 (2.092-2.170) years longer reproductive tenures, 3.878 (3.811-3.945) years increase in child-years experienced, and 0.052 (0.044-0.059) more multiple births (Table 1). The number of children was

clearly the most important component of the reproductive effort variable and showed a correlation with the estimated reproductive effort of 0.99 (see Fig. S6).

This measurement model was incorporated within a structural equation model (SEM) estimated using simultaneous equations and restricted maximum likelihood in the software *Mplus* 8.8 (81). This model was used to examine how reproductive effort, lifespan, and the direct effect of reproductive effort on lifespan changed across mothers exposed to the Great Finnish Famine. Lifespan was estimated using a semiparametric continuous-time survival model which approximates a Cox-proportional hazards model (82). This combines the number of years individuals were known to have lived and whether these individuals had a recorded death date or had been censored. By using a survival analysis, the SEM estimates how the log-hazard mortality risk changes according to each covariate. Hence, positive coefficients indicate an increased risk of mortality with an increase in the covariate, and thus a reduction in survival probability or lifespan. The model included the direct effects of reproductive effort on lifespan while simultaneously estimating the differences in reproductive effort and lifespan across predictors. Separating these effects is a key strength of the SEM, which cannot be done in other models (such as linear mixed models). We also modelled the differences in lifespan and reproductive effort across socioeconomic statuses and temporal changes occurring in each famine exposure group by including a birth year effect relative to the middle birth year in each famine exposure group, and by allowing the effects of relative birth year to vary across groups. We also tested if the effect of reproductive effort on lifespan depended on socioeconomic status. P-values less than 0.05 were deemed significant and non-significant interactions were removed from final models, least significant first, to aid interpretation of lower-order effects. Pairwise comparisons between categories were done by swapping the reference groups in the SEM. Collinearity of between variables used in models was checked using *corvif ()* from *Highstat* 10 (83). The variance inflation factors were all < 1.5. For illustration and quantification purposes, we extracted the estimated reproductive effort for mothers and ran Cox proportional hazard models with the same predictors for each famine exposure group separately, allowing us to estimate and present the predicted effect of changing reproductive effort on lifespan under a given famine exposure.

Mplus does not allow for the inclusion of random effects if some groups only have one sample (81). Therefore, we also used the extracted reproductive effort estimates for each mother from the SEM in mixed effect Cox proportional hazard models using *Coxme* 2.2-20 (84) to see if our results were robust when accounting for shared family, region, and birth year effects among mothers. For these analyses we retained all but four individuals of unknown region. Mothers with unknown parents were assumed to have come from different families (44%) as sisters would have been identifiable in the data. *Coxme* models cannot model the direct effects of factors such as famine exposure on reproductive effort, but they represent a useful robustness check and still account for such dependencies when estimating the

marginal effects. For *Coxme* models, we used likelihood ratio chi-squared tests comparing models with and without a given predictor to test for the significance of predictors with a threshold of $p < 0.05$.

The SEMs were run in *Mplus* (81), implemented in R 4.3.0 (68) using *MplusAutomation* 1.1.0 (85). *ggplot2* 3.3.5 (86) and *ggpubr* 0.4.0 (87) were used for plotting, *ggeffects* 1.5.1 (88) was used for estimating marginal effects. *survival* 3.5.7 (89) was used for estimating life-expectancies which were calculated as the predicted age at which survival probability was 50%, using median values for variables and an intermediate socioeconomic status if not otherwise specified.

COMPETING INTERESTS

The authors declare no competing interests.

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DATA AVAILABILITY STATEMENT

Code and data necessary for reproducing results are available at: https://doi.org/10.34894/HEWSRP

AUTHOR CONTRIBUTION

Conceptualization and methodology: EAY, EP, VL, HLD

Data collection: VL

Data wrangling and analysis: EAY

Writing—original draft: EAY

Writing—review & editing: EAY, EP, VL, HLD

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Fig. 1: Line graph showing the years lived for each mother included in the analyses, sorted chronologically by their birth date (N = 4,684). Colors indicate their exposure to the Great Finnish Famine (grey bar) and groupings in the analyses: died before (n = 1,297), exposed post-reproduction (n = 705), exposed during reproduction (n = 1,044), exposed during development (n = 716), and born after (n = 922).

Fig. 2: Predicted survival curves for low and high reproductive effort across five famine exposure groups. Curves were generated using Cox proportional hazards models on each famine exposure group separately (see Table S1). Each panel represents a different famine exposure group: (a) died before famine, (b) exposed during post-reproduction, (c) exposed during reproduction, (d) exposed during development, and (e) born after famine. Survival curves are shown for low (5th percentile, -3.8) and high (95th percentile, 6.5) reproductive effort levels. All curves are calculated for individuals of intermediate socioeconomic status and median relative birth date within each famine group. Shaded areas represent 95% confidence intervals.

Table 1: Structural equation model showing effects on lifetime reproductive effort and lifespan (as measured by log-hazard mortality risk) from 4,684 mothers. Factor loadings, mean values (*Intercept*), and residual variance for indicator variables used to estimate lifetime reproductive effort in the measurement model are shown. Estimates are shown with 95% confidence intervals and p-values. Significant effects ($p < 0.05$) are in bold. Effects of famine exposure are compared to women who died before the famine. Socioeconomic statuses are compared to intermediate statuses. Relative birth date is scaled by year and centered by the middle birth date for each group.

Variable	Estimate (95% CI)	P-value
Lifetime reproductive effort loadings		
Number of children born	1 (1-1)	-
Number of sons born	**0.536 (0.523-0.548)**	**<0.001**
Age at last reproduction	**1.238 (1.187-1.289)**	**<0.001**
Reproductive tenure	**2.131 (2.092-2.17)**	**<0.001**
Child-years experienced	**3.878 (3.811-3.945)**	**<0.001**
Number of multibirth children born	**0.052 (0.044-0.059)**	**<0.001**
Effects on reproductive effort		

Exposure group (exposed post-reproduction)	0.125 (-0.442-0.691)	0.666
Exposure group (exposed during reproduction)	*0.386 (-0.006-0.778)*	*0.054*
Exposure group (exposed during development)	**0.551 (0.080-1.022)**	**0.022**
Exposure group (born after)	**-0.504 (-0.922--0.086)**	**0.018**
Relative birth date	-0.004 (-0.013-0.004)	0.343
Relative birth date x Exposure group (exposed post-reproduction)	0.022 (-0.005-0.049)	0.108
Relative birth date x Exposure group (exposed during reproduction)	**0.033 (0.008-0.057)**	**0.010**
Relative birth date x Exposure group (exposed during development)	0.019 (-0.018-0.057)	0.308
Relative birth date x Exposure group (born after)	**-0.061 (-0.078--0.044)**	**<0.001**
Socioeconomic status (lower)	**-0.541 (-1.020--0.062)**	**0.027**
Socioeconomic status (lower) x Exposure group (exposed post-reproduction)	-0.470 (-1.228-0.287)	0.224
Socioeconomic status (lower) x Exposure group (exposed during reproduction)	**-0.653 (-1.299--0.008)**	**0.047**
Socioeconomic status (lower) x Exposure group (exposed during development)	-0.132 (-0.875-0.611)	0.728
Socioeconomic status (lower) x Exposure group (born after)	-0.335 (-1.010-0.339)	0.330
Socioeconomic status (upper)	**0.609 (0.243-0.975)**	**0.001**
Socioeconomic status (upper) x Exposure group (exposed post-reproduction)	-0.010 (-0.594-0.574)	0.974
Socioeconomic status (upper) x Exposure group (exposed during reproduction)	-0.113 (-0.655-0.429)	0.683
Socioeconomic status (upper) x Exposure group (exposed during development)	-0.265 (-0.890-0.359)	0.405

Socioeconomic status (upper) x Exposure group (born after)	**-0.583 (-1.157--0.008)**	**0.047**
Effects on mortality risk		
Exposure group (exposed post-reproduction)	**0.333 (0.283-0.392)**	**<0.001**
Exposure group (exposed during reproduction)	**0.694 (0.593-0.812)**	**<0.001**
Exposure group (exposed during development)	**0.600 (0.508-0.711)**	**<0.001**
Exposure group (born after)	**0.462 (0.397-0.538)**	**<0.001**
Lifetime reproductive effort	1.003 (0.985-1.021)	0.733
Lifetime reproductive effort x Exposure group (exposed post-reproduction)	0.994 (0.966-1.023)	0.682
Lifetime reproductive effort x Exposure group (exposed during reproduction)	**1.041 (1.009-1.073)**	**0.011**
Lifetime reproductive effort x Exposure group (exposed during development)	1.009 (0.977-1.041)	0.599
Lifetime reproductive effort x Exposure group (born after)	0.996 (0.964-1.028)	0.794
Relative birth date	**1.026 (1.022-1.029)**	**<0.001**
Relative birth date x Exposure group (exposed post-reproduction)	1.005 (0.998-1.012)	0.161
Relative birth date x Exposure group (exposed during reproduction)	**0.970 (0.962-0.980)**	**<0.001**
Relative birth date x Exposure group (exposed during development)	**0.972 (0.961-0.984)**	**<0.001**
Relative birth date x Exposure group (born after)	**0.960 (0.954-0.967)**	**<0.001**
Socioeconomic status (lower)	**1.305 (1.095-1.553)**	**0.003**
Socioeconomic status (lower) x Exposure group (exposed post-reproduction)	1.027 (0.811-1.303)	0.822
Socioeconomic status (lower) x Exposure group (exposed during reproduction)	1.130 (0.878-1.455)	0.342

Socioeconomic status (lower) x Exposure group (exposed during development)	**0.752 (0.579-0.976)**	**0.032**
Socioeconomic status (lower) x Exposure group (born after)	0.866 (0.674-1.113)	0.260
Socioeconomic status (upper)	1.110 (0.974-1.264)	0.118
Socioeconomic status (upper) x Exposure group (exposed post-reproduction)	0.967 (0.801-1.165)	0.720
Socioeconomic status (upper) x Exposure group (exposed during reproduction)	0.873 (0.715-1.066)	0.183
Socioeconomic status (upper) x Exposure group (exposed during development)	0.872 (0.705-1.078)	0.206
Socioeconomic status (upper) x Exposure group (born after)	1.121 (0.91-1.381)	0.282
Intercepts		
Number of children born	**5.265 (4.978-5.552)**	**<0.001**
Number of sons born	**2.695 (2.539-2.852)**	**<0.001**
Age at last reproduction	**38.133 (37.762-38.504)**	**<0.001**
Reproductive tenure	**11.872 (11.254-12.49)**	**<0.001**
Child-years experienced	**21.131 (20.016-22.245)**	**<0.001**
Number of multibirth children born	**0.211 (0.187-0.235)**	**<0.001**
Residual variances		
Number of children born	**0.344 (0.276-0.411)**	**<0.001**
Number of sons born	**1.348 (1.283-1.412)**	**<0.001**
Age-at-last reproduction	**19.315 (18.463-20.166)**	**<0.001**
Reproductive tenure	**10.771 (10.128-11.415)**	**<0.001**
Child-years experienced	**27.365 (24.856-29.875)**	**<0.001**
Number of multibirth children born	**0.439 (0.397-0.481)**	**<0.001**
Lifetime reproductive effort	**8.298 (7.995-8.602)**	**<0.001**

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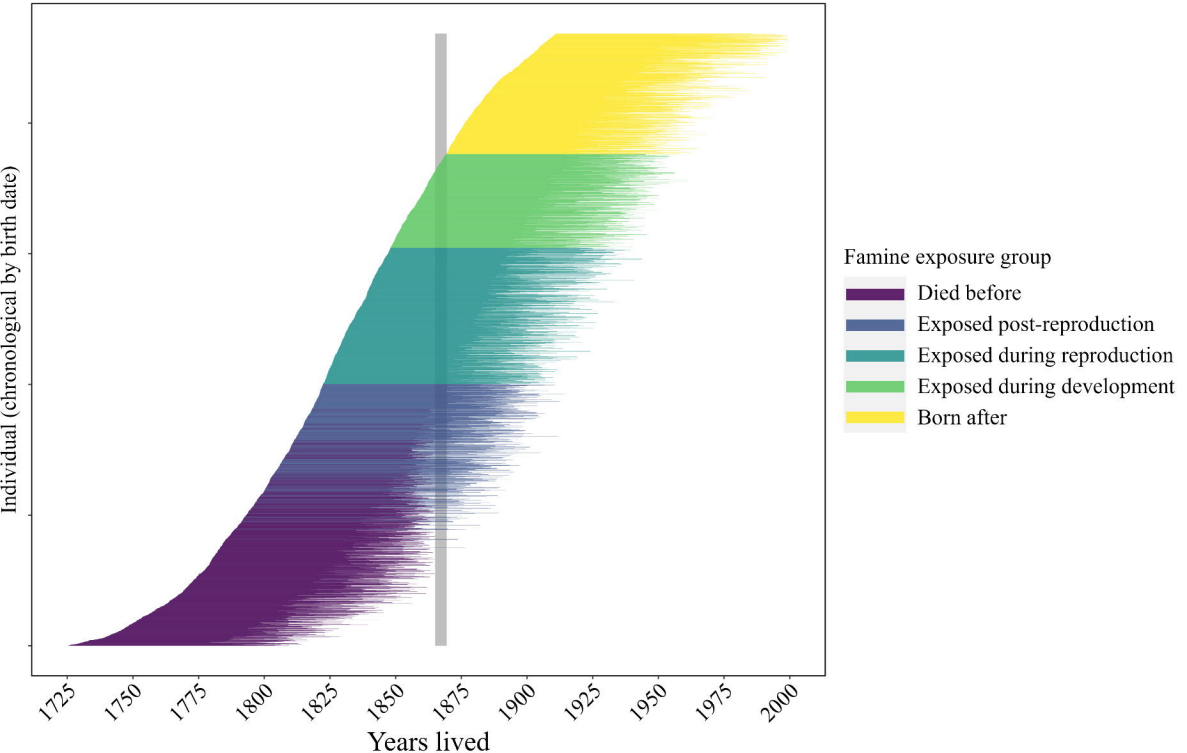
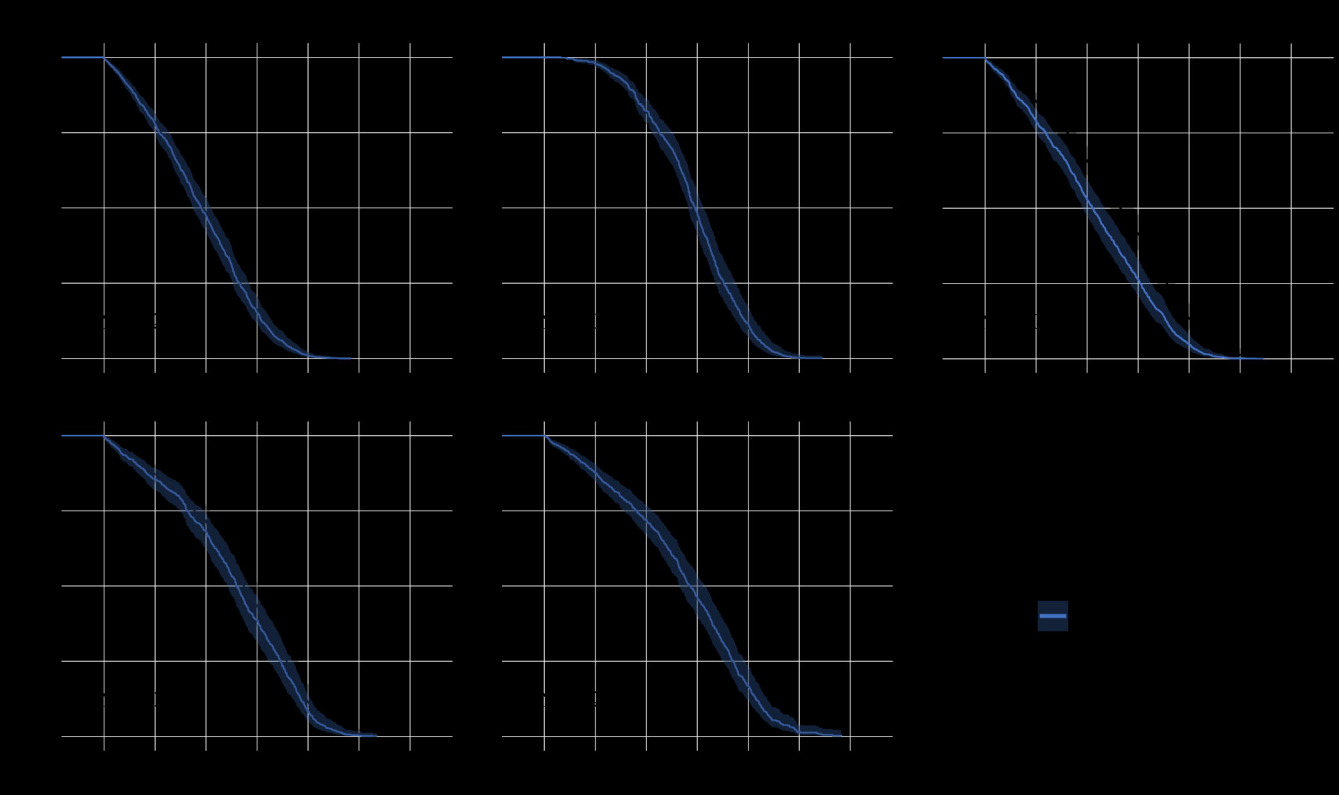
Table 2: Pairwise comparisons of the association between reproductive effort and mortality risk across famine exposure groups. Diagonal values show the hazard ratio (95% Confidence Intervals) for the effect of reproductive effort on mortality within each group. Off-diagonal values show p-values for pairwise differences in this association between groups. Significant differences or associations ($p < 0.05$) are highlighted in bold; marginally significant associations ($p > 0.05$ and < 0.10) are italicized. Results are from a structural equation model of the same structure as Table 1 but with different reference groups to estimate p-values and associations.

	Died before famine	Exposed post-reproduction	Exposed during reproduction	Exposed during development	Born after famine
Died before famine	1.003 (0.985 - 1.021)				
Exposed post-reproduction	0.682	0.997 (0.975 - 1.019)			
Exposed during reproduction	**0.011**	**0.007**	**1.044 (1.018 - 1.069)**		
Exposed during development	0.599	0.404	*0.087*	1.012 (0.986 - 1.039)	
Born after famine	0.794	0.926	**0.018**	0.5	0.999 (0.972 - 1.026)


Individual (chronological by birth date)
1725
1750
1775
1800
1825
1850
1875
1900
1925
1950
1975
2000
Years lived
Famine exposure group
Died before
Exposed post-reproduction
Exposed during reproduction
Exposed during development
Born after