Search for a resource-based trade-off between lifetime reproductive effort and women's post-reproductive survival in preindustrial Sweden

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ABSTRACT

A reduced survival as a potential cost of high lifetime reproductive effort in women has intrigued human evolutionary biologists for more than a century. However, we do not currently have compelling evidence for the delayed survival costs of reproduction. Reasons for this may include several methodological issues like environmental confounding, measurement of individuals' lifetime reproductive effort using demographic data, and the practice of mortality selection that are all likely to compromise our ability to reliably detect trade-offs at the phenotypic level. The current research aims to address all these issues by using structural equation modelling (SEM) to examine the potential trade-off between women's lifetime reproductive effort and their post-reproductive mortality in a large data set of 6,594 women from preindustrial northern Sweden that has not previously been used for this purpose. Despite this, the results showed only weak evidence for a trade-off between lifetime reproductive effort and post-reproductive mortality, one that was confined to only those women who had high lifetime reproductive effort and spend more than 20 years in widowhood. The socio-economic status of the family or mother's ethnic background did not moderate this association, with the general trend being one of higher, not lower, post-reproductive survival with high lifetime reproductive effort in women.

Keywords: Cost of reproduction, disposable soma, latent variable modeling, post-reproductive survival, structural equation modeling.

1. Introduction

One of the most enduring questions in human life-history evolution has been whether women, who invest more direct energetic resources in reproduction than men, sacrifice their long-term survival for higher reproductive success. These studies are often grounded on the evolutionary theories of senescence that predict reduced old-age survival as a cost of high reproductive effort at earlier ages (1,2). Despite over a century of research on the subject, evidence for the survival costs of reproduction in women at the phenotypic level remains mixed (reviewed in 3-7).

Why we have not seen such costs in most of the human populations studied so far is not well understood. It has long been acknowledged among evolutionary biologists that revealing underlying genetic life-history trade-offs using phenotypic data is very challenging (8,9). There are several methodological issues that may prevent us from detecting the underlying trade-offs. First, the analyses are likely confounded by the missing variables not included in the statistical model that are causally related to both the outcome and the predictor(s), known as environmental bias in the field of evolutionary biology (10-12). Owing to the dominant idea of resource-based trade-offs among the vital functions within organisms (2), perhaps the best-known example of this is the between-women heterogeneity in resource allocation and acquisition to reproduction (13,14). Because of the multitude of potentially important confounding environmental- and individual-level variables that can for example influence resource allocation and acquisition, it is almost impossible to fully account for such confounders in evolutionary research using correlative data in a long-lived species like humans.

Second, poor validity of measurements used to represent the traits or characteristics of interest (15) used as predictors in statistical models will bias the results (16). Recently, Helle (17) argued that demographic studies on reproduction-longevity trade-offs in humans are likely to suffer from such validity problems. This is because measuring lifetime reproductive effort in women as predicted by theory would entail recording their physiological energy allocation during every reproductive attempt proportional to the overall energy available over their whole reproductive life (6). It is clear that this is mission impossible using demographic data. Instead, what has been measured to date has generally been the total number of offspring born or surviving to adulthood, and, in some studies, the number of multiple births (e.g. 18) or the offspring sex ratio (e.g. 19,20). Such demographic variables cannot be used to accurately measure the total lifetime reproductive effort, even in concert, since they fail to consider parental energetic resources allocated to offspring in terms of e.g. lactation and care during childhood (6). Hence, the currently used proxies of women's lifetime reproduce effort are likely underestimated owing to measurement error (17).

Third, the great majority of demographic studies in this field have focused on the estimated post-menopausal survival of women only (3-7). That is, some pre-defined age for women entering menopause (e.g. age of 50 years) has been used as an inclusion-criteria, and for all women in the sample irrespective of their underlying true age at menopause. This leads to a non-random sampling of women included in the analysis, i.e., to mortality selection based on women's age at death. Thus, selection bias likely alters our biological inference regarding the potential underlying reproduction-survival trade-off. This is because it is likely that reproductive effort has been affecting women's survival during pre-menopausal period also, particularly during our evolutionary history when mortality rates were much higher than in contemporary populations (21). This suggests that mothers dying prematurely before menopause likely experienced fitness-costs. One solution to this problem without involving potentially complicated modeling of the mortality selection process would be to model post-reproductive survival instead of post-menopausal survival (21). This approach also allows for between-women variation in age when they enter post-reproductive period.

In this study, the above mentioned methodological shortcomings are addressed by applying structural equation modeling (SEM) with latent variables (22,23) to examine whether women who invest heavily in reproduction during their lifetime suffer from reduced post-reproductive mortality. Latent variables are existing traits or characteristics that are unmeasured (or measured with non-negligible measurement error) using the current data at hand. This approach can handle measurement error in variables when the researcher has recorded several indicators of a target latent trait and can simultaneously accommodate complex environmental confounding using structural equations. In addition, mortality selection is avoided by using the length of post-reproductive mortality, not post-menopausal mortality as commonly done in this field, as the fitness-component that is presumably traded-off for higher lifetime reproductive effort (20,21). Because the detection of trade-offs likely depends on the variability of between-women resource acquisition (13), we also test whether the resources available to the mother, measured by the socio-economic status of her family, the length of potential widowhood and her ethnic background, moderated the association between lifetime reproductive effort and post-reproductive mortality. Recent research has also shown that covariance between resource allocation and acquisition may further influence the detection of trade-offs and should thus be accounted for in the analysis (14). SEM framework provides a convenient way to incorporate such associations in the model. The data analysed here comes from a large demographic data base of populations from preindustrial northern Sweden (24) that, to our knowledge, has not been used in this context before.

2. Methods

Demographic data

The demographic data used here were compiled from historical parish registers kept by the Lutheran church, and they allow individuals to be followed from birth, through their reproductive history and adult life, to death (25). These data were collected from five parishes (Karesuando, Jukkasjärvi, Jokkmok, Vilhelmina and Jällivaara), located in northern Sweden in 1750-1900 and provided by the Demographic Data Base (DDB) at Umeå University (24). These data consist of two distinct ethnic groups: the indigenous Sami and the settlers coming mainly from southern Sweden (but also from Finland and Norway), who became a majority by the end of the 19th century in these areas (26,27). The ethnicity of individuals was based on their nomenclature, occupation, and place of residence (26,27). Their socio-economic status was based on their best lifetime occupation, classified into six groups from low to high status: workers, trained/skilled workers, lower officials, lower businessmen, higher officials and large-scale entrepreneurs (24). During the study period, Sami people practised nomadic reindeer herding, hunting, fishing, and small-scale farming, whereas settlers relied mainly on agriculture, forestry, trade, and mining (24-27). Agriculture in Northern Sweden was largely animal husbandry (or dairy farming) by involving cattle and sheep as well as small-scale, unsophisticated farming because environmental conditions were harsh and unfavourable for crop cultivation. Owing to the historical nature of the data, it contains individuals who lacked modern birth-control methods and advancements in modern medical care.

From these records, we selected those women who married once (*n* = 7593) and recorded the relevant variables for the current study. The rationale for selecting only women who married once was to avoid complexities arising from combining information on multiple successive husbands. As a measure of the socio-economic status of the family, we used the sum of the social status of both the wife and the husband. Furthermore, since widows likely had an increased risk of mortality (28,29) and lower family size if the husband died during the childbearing years, we recorded how many years a woman spent as a widow before she died. This variable was constrained to have a lower limit of zero years, as it makes little sense to include those years a husband outlived his spouse. Women's ethnicity predominantly accounts mainly for the potential cultural and genetic differences among women (26). Since post-reproductive mortality is definable only for women who gave birth, non-reproducing women were excluded from the analysis.

Statistical analyses

Structural equation modeling (SEM) with multiple-indicator latent variables (22,23) was used to examine how women's lifetime reproductive effort was associated with their post-reproductive mortality, and whether this association was moderated by their resource availability, measured here as the socio-economic status of the family, death of the husband during the post-reproductive period, and their ethnic background. Less than perfect validity of measurements representing women's lifetime reproductive effort causes measurement error for this key variable (15). In SEM, this measurement error can be managed by using an unobserved continuous latent variable instead of observed variables if one has recorded several variables conceptually linked with the target latent. Such latent variables accomplish this by partitioning the overall variance to the "true variance" of the construct of interest and to the "error variance", which contains errors of measurement in the observed variables (23). In this setup, the observed variables, called (reflective) indicators, are modelled as response variables since the indicators are thought to causally reflect the underlying latent variable (23). That is, in the current context, women's reproduction-related life-history traits can be assumed to causally reflect their total resource investment toward reproduction (17). Such indicators should thus show at least moderate intercorrelations (23). It is important to realize that the variable of interest here is the unmeasured latent variable and not its measured indicators. The disturbances, or errors, of latent variables represent the amount of unobserved omitted causes contributing to variation in those latents (23). Residual errors of the continuous reflective indicators, by contrast, represent the amount of unique measurement error specific to that indicator not accounted for by the underlying latent variable (23).

The observed indicators are connected to the unmeasured latent variable by linear regression weights called “loadings” (23). Because the latent variables are arbitrary constructs, they have no inherent metric. Typically, the most important indicator *a priori* (i.e., a referent indicator) is set to have a fixed loading of 1 in order to set the scale for the latent variable (23). Another option is to fix the latent variance to unity, so that all loadings of indicators can be estimated (note that this option also implies a standardization of the latent). Analytically, these two approaches produce identical results and model fit (23).

The SEM has two parts: the measurement model part that describes how the indicators load onto the latents and the structural model part that describes the association between the variables of interest, whether latent or observed. In SEM, these two are linked with simultaneous equations to accomplish unbiased estimation of structural parameters while accounting for the influence of measurement error (i.e., validity) in variables by the measurement model (23).

The continuous indicators reflecting women’s lifetime reproductive effort used here were the total number of biological offspring born to a woman, her age at last reproduction and total length of reproductive tenure. Furthermore, as a novel proxy of lifetime resources allocated in reproduction, we used the total number of child-years experienced by a mother during her lifetime. That is, we summed the years offspring and their mother co-survived together until the offspring reached adulthood, an age of 18 years. For example, if a mother had three offspring during her lifetime that lived to the ages of 2, 5, and 10, her child-years experienced before dying would be 17 years. Note that since we expect a reduction of care when offspring reached adulthood, a maximum value of co-living per offspring was set to 18 years. The total number of biological offspring born was used to set the scale for women’s lifetime reproductive effort because this variable is easy to comprehend and has been a widely-used proxy of lifetime reproductive effort in previous studies. For a correlation matrix of the indicators of women’s lifetime reproductive effort, please see the electronic supplementary materials (Table S1).

It should be noted that latent variables in SEM framework can be modelled more flexibly than described above (30). For example, although much less commonly used in SEM studies, the causal direction between the latent and its indicators can be reversed (30). Such an approach would have been the best choice here to model the resources available to women, determined by the socio-economic status of their family, the length of potential widowhood and ethnic background as causal indicators. However, a model including both reflective and causal indicators and an interaction between the resulting latent variables (note that the main aim here was to examine whether the magnitude of potential survival costs differed according to women's resource availability) would not have been identified (i.e., no unique solutions for unknown parameters would exist) using the data at hand (31). Therefore, we were forced to treat the socio-economic status of the family, the length of widowhood, and ethnicity as observed independent proxies of a women's resource availability that may include measurement errors.

The structural equation model used to examine how women's lifetime reproductive effort was associated with their post-reproductive mortality as well as whether this association was moderated by the socio-economic status of the family, the length of widowhood and ethnicity is shown in figure 1. The outcome variable of interest, the length of women's post-reproductive lifespan in years, was defined as the number of years from last childbirth until their age at death. We did not include only women living beyond some pre-defined age of estimated reproductive cessation (e.g. 50 years) as this likely would introduce selection bias and because reproductive costs are unlikely to be manifested solely after menopause (18, 19,32). Women's post-reproductive mortality was treated as an observed time-to-event variable, also predicted by age at last reproduction in order to control for differing ages among mothers in their entry into the risk set (33). Right-censoring of survival times was applied to those women for whom year of death was missing; in those cases, the year when a woman was last recorded alive in the population (if available) was used to replace the year of death. In addition, parish the family lived in and the women's birth cohort (1660-1710, 1710-1760, 1760-1810, 1810-1860, 1860-1910) were used to control for spatio-temporal variation in women's lifetime reproductive effort and their post-reproductive mortality. Descriptive statistics of the variables used are given in the electronic supplementary materials (Table S2).

Post-reproductive mortality was modelled as a semi-parametric continuous-time survival variable that approximates a non-parametric Cox model (34). Owing to missing data in the independent variables (i.e., parent's socio-economic status and the women's length of widowhood due to missing data in a husband's lifespan), we first applied multiple imputation with an unrestricted variance-covariance model using a Bayesian estimator. The number of imputed data sets needed, here 40, was determined following the methods described in von Hippel (35) and by accepting 5% change in the standard errors of the point estimates had the data been re-imputed. Owing to missing data in the outcome variable that were not imputed, women's post-reproductive lifespan, a final sample size after multiple imputation was 6,594 women per imputed data set. A full-information maximum likelihood estimator with robust standard errors using a Monte Carlo integration algorithm with 2,000 integration points was used to estimate the final model parameters where missing data in observed response variables (i.e., the indicators of lifetime reproductive effort) were assumed to be missing at random (36). Interactions between women's lifetime reproductive effort and the socio-economic status of the family, length of widowhood, and ethnicity were estimated using the latent moderated structural equations method (LMS) (37). To aid model interpretation, statistically non-significant interactions were sequentially removed from the final model. Because of the above mentioned statistical details, no commonly used chi-square test or fit indexes were available to assess model fit to the data because means, variances and covariances are not sufficient for the estimation of the current model. Instead, the model had to be fit to raw data. Analyses were conducted using Mplus version 8 (38).

3. Results

The results of the final SEM are shown in Table 1. Women's ethnic background did not moderate the influence of lifetime reproductive effort on their post-reproductive mortality (β ± s.e. = -0.024 ± 0.022, Wald χ^2_1 = -1.10, p = 0.27), and, thus, this interaction was the first to be removed from the model. Second, we removed the interaction between women's lifetime reproductive effort and the socio-economic status of the family (β ± s.e. = -0.003 ± 0.005, Wald χ^2_1 = -0.65, p = 0.51). That is, irrespective of the socio-economic status of their family, high lifetime reproductive effort in women was associated with reduced risk of death during the post-reproductive period (Figure 2). Instead, the influence of women's lifetime reproductive effort on their post-reproductive mortality was moderated by how many years they lived in widowhood after ceasing reproduction (Table 1). As shown in figure 3, the longer the time spent in widowhood, the higher the hazard ratio for death during the post-reproductive period if the women invested heavily in their lifetime reproductive effort. In particular, high lifetime reproductive effort increased women's post-reproductive mortality if a woman had spent 25 years or more as a widow before her death.

The measurement part of the model shows that all indicators loaded significantly onto the latent variable representing women's lifetime reproductive effort (Table 1). One unit increase in a woman's lifetime reproductive effort, scaled by the number of lifetime births, was associated with an increase of 14.4 (95% CIs = 14.1, 14.6) years in their total number of child-years experienced and with a 1.94 (95% CIs = 1.89, 2.00) later age at last reproduction (Table 1). Moreover, one unit increase in a woman's reproductive effort increased their reproductive tenure by 2.45 (95% CIs = 2.41, 2.48) years (Table 1). These indicators explained 84.6% (95% CIs = 0.838, 0.853) of variance in women's lifetime reproductive effort.

4. Discussion

The results from preindustrial northern Sweden do not provide strong support for the core prediction of life history theory that women should suffer from reduced post-reproductive survival as a cost of high lifetime reproductive effort, particularly if living in resource-poor environments. In contrast to some previous findings in this field (39-40), the association between women's post-reproductive mortality and their lifetime reproductive effort seemed not to strongly depend on resource availability: even mothers living in families with the poorest socio-economic status did not experience survival costs of reproduction during their post-reproductive period. Only those mothers who had spent more than 25 years in widowhood seemed to suffer from increased mortality had they invested heavily on reproduction during reproductive years. But such women were very few in these parishes since only 6.9% of women were widowed for more than 25 years before their death. Hence, the survival costs of high lifetime reproductive effort were confined to a very limited part of the population in these preindustrial Swedish parishes.

Revealing the predicted life-history trade-offs using phenotypic data is very challenging without an experimental approach (8,9) because several methodological issues may hide the underlying causal trade-offs (13,14,16). Owing to the infeasibility of an experimental approach in humans, we are forced to raise the methodological bar in phenotypic studies. In the current study, an attempt was made in this direction by simultaneously accounting for selection bias, validity issues related to the measurement of a woman's lifetime reproductive effort and environmental bias by including several potential confounders in the analysis. Moreover, our model allowed resource allocation to reproduction to be affected by between-family resource acquisition (14). The positive influence of resource abundance on reproductive allocation found in this population, and in humans in general (41), should have increased the probability of detecting reproduction-survival trade-offs in our species, which has a slow pace of life (14). Despite this, evidence for trade-offs and their resource-dependence was inconclusive at best in this large sample of preindustrial women. From a comparative perspective, studies on other mammals with similar-type of life histories living in the wild have generally also reported ambiguous evidence for survival-costs of reproduction in females (42,43).

It should be noted that one feature of the studies reporting a trade-off between reproduction and survival is a large sample size compared with studies reporting null or positive findings (17). A large sample size means high statistical power to uncover even small associations, which begs a rarely asked but crucial question in this field: What is the biological importance of the trade-offs reported of this magnitude? Do these survival costs, only commonly found during the post-menopausal period actually reduce the fitness of these mothers?

It would be hasty to claim that the effect sizes reported here represent true causal (genetic) effects of women's lifetime reproductive effort on their post-reproductive survival. This is because although we controlled for environmental bias using several resource-related variables as well as spatio-temporal factors, these variables unlikely fully captured all the causes affecting lifetime reproductive effort and post-reproductive survival in this population. On balance, the negative associations reported between reproduction and post-menopausal lifespan in some populations do not mean that the associations found are causal effects. Furthermore, to avoid the phenotypic gambit, future studies on life-history trade-offs should concentrate on exploring genetic correlations in addition to phenotypic ones. But even this does not guarantee that evidence for trade-offs will be observed: A recent study using a massive sample size and advanced statistical modeling did not find evidence for genetic trade-offs between reproduction and human post-menopausal lifespan (44).

It is important to recognize that the current model was designed to test within-individual resource-competition of energy between reproduction and post-reproductive mortality in the context of differential energy acquisition among women. However, if reproductive costs in women are mediated via pathways other than energetic ones responding to environmental resource availability (45), the current model is likely inappropriate. Previous research has found more detailed aspects of reproduction, such as the number of sons (17,18) and whether mothers produced multiple births or not (16), instead of the total number of offspring, to influence women's post-reproductive mortality, suggesting that other pathways (e.g. hormonal regulation) may also play a role in potential trade-offs. It has also been shown that adult offspring could improve their parents' old-age survival through caregiving and social support (46). All this makes the potential causal network connecting different aspects of reproduction to post-reproductive survival in humans complex, and appropriate data with which to contrast different hypotheses may be challenging to find and analyze.

Despite over a century-long research effort (47), evidence for the delayed survival costs of reproduction in humans remains surprisingly scarce. This is somewhat confusing because we now have better and bigger data sets and more advanced statistical tools to tease out the trade-offs, even at the genetic level. From a theoretical standpoint, we should not dismiss the possibility that we are not really asking the right questions of these data. Therefore, the future challenge is to derive more accurate predictions for human life history evolution and to better utilize the statistical tools developed to uncover true effects from non-experimental data.

Supplementary Material

Supplementary data is available at *The Journal of Gerontology, Series A: Biological Sciences* online.

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Competing interest

None.

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Table 1. Results of the final SEM examining the influence of women's lifetime reproductive effort on their post-reproductive mortality (*n* = 6,594) in northern Sweden and whether this association was moderated by ethnicity, the socio-economic status of the family, or the length of widowhood. Spatio-temporal controls of women's lifetime reproductive effort and post-reproductive mortality are omitted for simplicity (please see the electronic supplementary materials Table S3 for results of the full model). Note that structural coefficients for post-reproductive mortality are on the log-hazard scale. Distributional locations are given as intercepts for continuous response variables. The total number of parameters estimated was 37, combined from 40 imputed data sets.

	β	se	z	p
Loadings				
Lifetime reproductive effort				
Number of offspring born	1			
Child-years experienced	14.35	0.13	112.2	<0.0001
Age at last reproduction	1.94	0.03	68.3	<0.0001
Reproductive tenure	2.45	0.019	125.9	<0.0001
Structural path coefficients				
Post-reproductive mortality				
Lifetime reproductive effort (LRE)	-0.049	0.014	-3.54	<0.0001
LRE × WID	0.004	0.001	3.28	0.001
Socio-economic status	-0.037	0.014	-2.62	<0.0001

Age at last reproduction	0.185	0.049	3.81	<0.0001
Ethnicity	-0.060	0.060	-1.00	0.32
Years in widowhood (WID)	-0.075	0.006	-13.01	<0.0001
Lifetime reproductive effort				
Socio-economic status	0.206	0.025	8.305	<0.0001
Ethnicity	-0.197	0.104	-1.901	0.057
Years in widowhood	-0.008	0.006	-1.389	0.17
Intercepts				
Age at last reproduction	31.17	0.23	137.97	0.075
Number of offspring born	2.33	0.098	23.74	0.103
Child-years experienced	13.01	1.40	9.31	0.108
Reproductive tenure	3.7	0.236	15.79	0.107
Residual variances				
Age at last reproduction	2.27	0.05	44.11	<0.0001
Number of offspring born	1.59	0.05	31.67	<0.0001
Child-years experienced	50.78	1.27	40.13	<0.0001
Reproductive tenure	5.85	0.28	21.26	<0.0001
Lifetime reproductive effort	6.37	0.13	47.41	<0.0001

Figure legends

Figure 1. A graphical representation of the initial SEM used to examine the influence of women's lifetime reproductive effort (LRE), measured by their child-years experienced (CYE), the number of offspring born (OFF), age at last reproduction (ALR) and reproductive tenure (RTE), on their post-reproductive survival (PRS), and whether this association was moderated by the socio-economic status of the family (SES), the length of mother's widowhood (WID), and her ethinicity (ETH). Women's birth parish and birth cohort are also used to control for spatio-temporal variation in their lifetime reproductive effort and post-reproductive survival. Observed variables are represented as boxes and unobserved latent variables as circles. Single-headed arrows are used for three purposes: i) when pointing from a latent variable to observed indicators, they represent reflective loadings of the latent (λ's); ii) when pointing at observed or unobserved response variables, they represent structural path coefficients (β's) and; iii) when pointing at indicators, they represent their unique residual errors (ε). Double-headed arrows represent the error variances (i.e. disturbances) of latent variables (ζ). The single-headed arrows originating from SES, WID and ETH that intercept the arrow from LRE to PRS represent latent interactions (β_{int}), i.e., moderation. Please note that intercept parameters are omitted for simplicity.

Figure 2. Hazard ratios of the association between lifetime reproductive effort and post-reproductive mortality in women (regression line as a solid line and its 95% confidence intervals depicted as dotted lines), given for different levels of the socio-economic status of their family.

Figure 3. Hazard ratios of the association between lifetime reproductive effort and post-reproductive mortality in women (regression line as a solid line and its 95% confidence intervals depicted as dotted lines), given for different levels of years spent in widowhood.

Figure 1

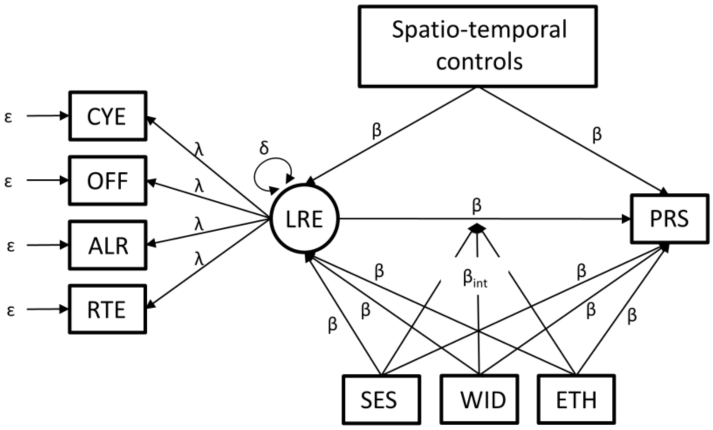

Spatio-temporal controls
ε
CYE
ε
OFF
ε
ALR
ε
RTE
λ
λ
λ
λ
δ
LRE
β
β
β
PRS
β_{int}
β
β
β
β
β
β
SES
WID
ETH

Figure 2.

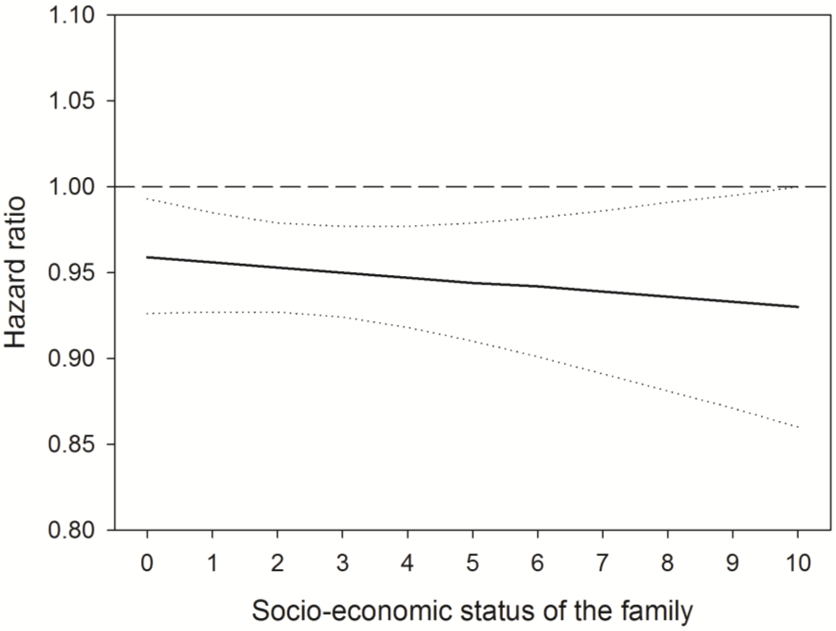
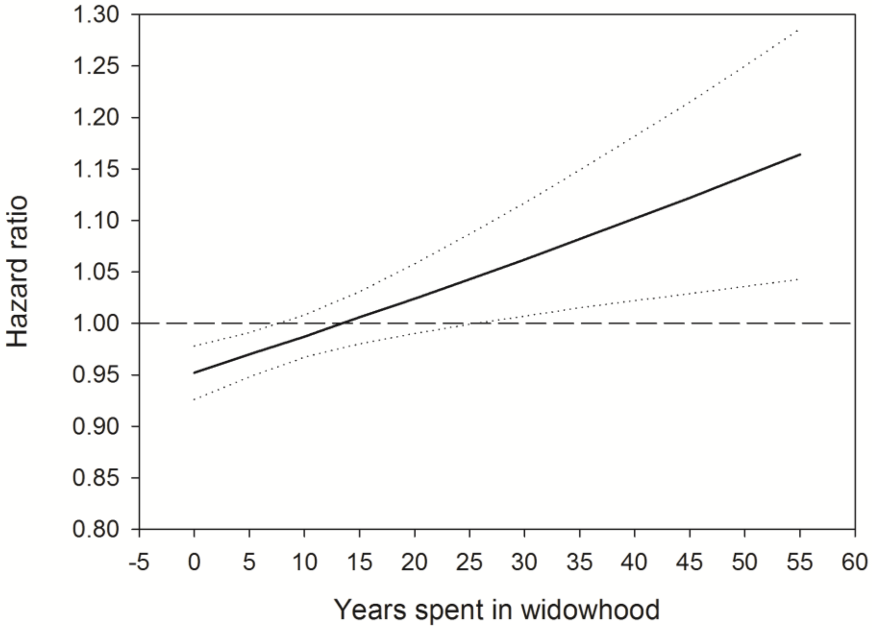

1.10
1.05
1.00
0.95
0.90
0.85
0.80
Hazard ratio
0
1
2
3
4
5
6
7
8
9
10
Socio-economic status of the family

Figure 3.


1.30
1.25
1.20
1.15
1.10
1.05
1.00
0.95
0.90
0.85
0.80
Hazard ratio
-5
0
5
10
15
20
25
30
35
40
45
50
55
60
Years spent in widowhood