Social and biological determinants of reproductive success in Swedish males and females born 1915-1929

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Abstract

Studying biological and social determinants of mortality and fertility provides insight into selective pressures in a population and the possibility of trade-offs between short- and long-term reproductive success. Limited data is available from post-demographic transition populations. We studied determinants of reproductive success using multi-generational data from a large, population-based cohort of 13 666 individuals born in Sweden between 1915 and 1929. We studied the effects of birthweight for gestational age, preterm birth, birth multiplicity, birth order, mother's age, mother's marital status and family socio-economic position upon reproductive success, measured as total number of children and grandchildren. We further tested the hypothesis that number of grandchildren would peak at intermediate family size, as predicted by some life history explanations for fertility limitation.

Reproductive success was associated with both social and biological characteristics at birth. In both sexes, a higher birthweight for gestational age, a term birth and a younger mother were independently associated with a greater number of descendants. A married mother and higher family socio-economic position were also associated a greater number of descendants in males (but not females), while in females (but not males) higher birth order was associated with higher reproductive success. These effects were mediated by sex-specific effects upon the probability of marriage. Marriage was also affected by other early life characteristics including birthweight, indicating how 'biological' characteristics may operate via social pathways.

Number of grandchildren increased with increasing number of children in both sexes, providing no evidence for a trade-off between quantity of offspring and their subsequent reproductive 'quality'.

Introduction

1.1 Studying reproductive success in humans

The central driving force of evolution through natural selection is differential mortality and fertility among individuals. Together these determine an individual's reproductive success, usually defined as number of children or grandchildren. Reproductive success, in turn, influences an individual's long-term genetic contribution to future generations, this being at the core of the concept of 'fitness' in evolutionary biology [1]. Investigating the biological and social characteristics associated with individual reproductive success in humans provides insight into the nature and magnitude of selective pressures operating in a particular society at a particular time. In combination with observations from different populations, hypothesis testing and evolutionary theory, this can clarify the selective pressures which shaped human evolution in the past, and the contexts in which these pressures become most evident [2]. Understanding social and biological determinants of mortality, fertility and reproductive success is also of much interest from a public health perspective as it can illuminate how systematic differences in health between social groups reappear in each subsequent generation and why social inequalities in health tend to persist across generations.

Yet studying reproductive success is challenging in humans because of the long generation time. Studies of contemporary populations usually use short-term and partial outcomes such as death during childhood e.g. [3] or the probability of giving birth within an observation period e.g. [4] rather than direct and detailed measurements of survival and reproduction over the whole life-course. Using historical data can preserve the ability to trace long-term outcomes [2], but tends to be compromised by poor data quality as there is often substantial uncertainty regarding the completeness and accuracy with which mortality and/or fertility was recorded. Furthermore, such data is generally only available for pre-demographic transition populations; that is, populations predating the radical declines in family sizes observed across Western Europe in the 18th and 19th centuries and coinciding with increased urbanisation, industrialisation and material prosperity [5]. Historical populations therefore cannot be used to address the challenges which, as discussed in more detail below, are posed for evolutionary theory by the demographic transition. Finally, it is rare in both contemporary and historical studies for information to be available for different stages of an individual's life. This makes it difficult to apply a lifecourse approach in exploring how childhood characteristics are mediated by adult experiences in affecting survival and reproduction.

We had a unique possibility to explore social and biological determinants of reproductive success in Sweden during the 20th century, using multi-generational data from a large, population-based cohort born 1915-1929. This cohort was born at a time when the Swedish demographic transition was largely concluded: completed family size had fallen from over four for cohorts born 1736-1856 to under three in the 1886 cohort and to under two in the 1901 cohort [6]. Most unusually for a cohort this old, high-quality data was collected at birth on a number of characteristics including birthweight and gestational age; birth multiplicity and birth order; mother's age and marital status at the time of birth; and family socio-economic position (SEP). Socio-demographic and socio-economic information was collected about cohort members during their adult lives, as was their number of descendants.

Two questions which relate to subcomponents of reproductive success have previously been examined in this cohort, specifically the role of birthweight for gestational age upon the probability of marriage [7] and the role of birth order upon mortality [8]. Reproductive success has not, however, previously been examined explicitly, in detail, and over more than one generation. The aims of the current study were to investigate whether early life characteristics predict subsequent reproductive success; to ascertain the pathways mediating any observed effects; to examine the relationship between number of children and number of grandchildren; to investigate intergenerational effects upon number of grandchildren independent of number of children; and to examine whether any of the above effects are gender-specific.

1.2 Existing evidence on how early life circumstances affect an individual's reproductive success

In the medical literature, recent years have seen some attention to how low birth weight, premature birth and other indicators of adverse health in early life predict long-term health outcomes, including a reduced probability of reproduction [4, 9]. The effects such biological markers of early development have received less attention from evolutionary anthropologists. While effects have been demonstrated in animal studies [10] little research has addressed this question in human populations, particularly with regards to reproduction [11].

More attention has been paid to factors such as sibling composition and the attendant consequences for parental investment and sibling resource competition. A number of studies of historical and traditional societies support the predictions of a life history theory in finding that having more siblings, particularly older siblings, has negative consequences for individual development, survival and long-term fertility [12-15]. In post-transitional populations, the implications for reproductive success are less clear-cut. There is some evidence that adverse effects on health and development persist [8, 16, 17] but some studies have also found that larger natal family size and/or higher birth order is associated with higher fertility [18-21]. Not all study populations born in the early 20th century show this relationship [22, 23] and several report it to be stronger in women than in men [18, 19]. The mechanisms of the association are also unclear, although they may result from a large natal family increasing an individual's own fertility preferences. It is plausible that this increase in fertility could compensate for any deleterious effects of high birth order on health and lead to higher reproductive success overall. To our knowledge no study has explicitly tested this.

Evolutionary anthropologists have also paid considerable attention to how reproductive success is influenced by social status or socio-economic position in early and adult life. A strong positive correlation is consistently observed in traditional and hunter-gatherer populations [24, 25], but in modern post-demographic transition populations this association is often greatly attenuated or even reversed [2]. In part this is because the fertility reductions associated with demographic transition usually occurred first and fastest in richer areas and among social elites [26].

1.3 Quality-quantity tradeoffs in post-demographic transition populations

Post-demographic transition populations therefore show substantial society-wide fertility limitation at a time of unsurpassed affluence, and often also feature a within-society levelling of reproductive success. Both features pose important theoretical challenges to the neo-Darwinian assumption that humans evolved to use their available resources to maximise reproductive success [27]. Various theories have been proposed which try to account for these observations within an evolutionary framework reviewed in [28]. Some theories suggest that fertility limitation is maladaptive in the current environment e.g. [29, 30] or reflects behaviour designed to maximise some other aspect of fitness e.g. [31]. A prominent alternative argument, however, is that fertility limitation *may* optimise reproductive success in post-transition populations through a life history trade-off between offspring 'quality' and 'quantity' [15, 23]. The central hypothesis is that because total parental resources are limited, offspring quality will decrease with larger total family sizes. This in turn leads to each additional child making a smaller marginal contribution to the parent's long-term fitness (often operationalised as number of grandchildren). If at some point this marginal return becomes negative then reproductive success will be maximised at intermediate family sizes in which each child receives more investment.

A key prediction of this hypothesis is that the average number of grandchildren will peak at an intermediate family size [23, 32]. The limited empirical work conducted in pre-transition populations provides support for such a relationship in some cases [13, 33] but not others [34]. There is no support for this prediction in any of the studies we know of which test this hypothesis in a post-transition populations. Rather in range of 20th century populations from the US [23, 32] and Germany [23] the number of grandchildren increased across the range of number of children. Moreover, there was not even any suggestion of a reduction in the *marginal* fitness return of additional children in larger family sizes. Instead, number of grandchildren either increased in an approximately linear fashion with increasing number of children or, if anything, increased somewhat more rapidly at higher numbers of children.

Methods

2.1 Study population

The Uppsala Birth Cohort (UBCoS) includes all live births at the Uppsala University Hospital from 1915 to 1929 (N=14 193). Of these, 13 811 (97.3%) subjects were successfully traced through parish archives until death, emigration or until their unique personal registration number was assigned, usually in 1947 further details in [35].

Information about descendants of the cohort was obtained through linkage to the Swedish Multigeneration Registry for the 12 168 (85.7%) individuals who were still alive and resident in Sweden in 1947 (i.e. the year when Swedish citizens were assigned personal identification numbers) (Koupil 2007). To be included in the Multigenerational registry, these descendants had to be born in 1932 or later (i.e. when the UBCoS cohort was aged 3-17 years) and to survive to at least 1961 [36]. The resulting UBCoS multigenerational data base (Koupil [37] and http://www.chess.su.se/ubcosmg/) contains information about families spanning up to five generations.

In the current analysis, of the total 14 193 live born cohort members born in Uppsala between 1915 and 1929, we excluded the 382 infants (2.7%) who were never traced. We also excluded the 145 (1.0%) subjects who emigrated permanently between age 0-60, and who were therefore most likely to have had children born abroad and never registered in Sweden. This left a study population of 13 666 cohort members (96.3%), of whom 7176 were male and 6490 female.

The study was approved by the regional Ethics Committee in Stockholm.

2.2 Explanatory and outcome variables

2.2.1 Social and biological characteristics at birth

Information on social and biological characteristics of the cohort members at birth was obtained from archived obstetric records. As presented in Table 1, these characteristics were birth weight and length of gestation (used to generate standardised birthweight for gestational age); preterm birth; birth multiplicity; birth order; mother's age at the child's birth; mother's marital status; and family socio-economic position (SEP). We calculated birthweight for gestational age by standardising birthweight on a week-by-week basis, standardising separately for males and females. We used the means and standard deviations observed in UBCoS for the 13 599 infants born at 30 or more completed weeks (i.e. an internal reference). For the 86 children born at 22-29 weeks we used external reference data [38] adjusted for birth weight distributions observed within our cohort; full details available in the Supplementary Material. Family SEP was defined based upon father's occupation or, if the mother was unmarried, mother's occupation. Unfortunately, we did not have data on the number of younger siblings for each cohort member, and were therefore unable to calculate total family size.

The characteristics of males and females at birth were very similar (see Table 1) with no variables showing evidence of an association with sex ($p>0.05$).

2.2.2 Mortality, marriage and adult SEP

Information on mortality was obtained from the Swedish death registry [39] or, for those who died before being assigned a personal identification number, from parish archives. Information on the adult social characteristics of the cohort members in adulthood was obtained by linkage to the Swedish censuses of 1960 and 1970 [40]. These were highest educational level in 1960, marital status in 1970 and equivalised household income in 1970 (see Table 1). When household income was measured in 1970 the UBCoS cohort was 41-55 years old, an age range during which annual and lifetime incomes have been shown to be highly correlated in Sweden in this time period [41]. We equivalised the household income between married cohabiting couples and single-adult households by dividing the former by 1.7, in accordance with the OECD standard [42].

There was strong evidence ($p<0.001$) that men had higher levels of education than women (7.5% educated to senior level and 6.5% to post-senior level, vs. 2.5% in each category for women) and were less likely to have ever been married by 1970 (89.6% vs. 92.5% for women). There was no evidence of a sex difference in equivalised household incomes.

2.2.3 Total number of children and grandchildren

Total number of biological children and biological grandchildren in 2002 were obtained from the Multigenerational registry [43]. These data were available for all of the 11 563 individuals who survived until age 50 and for 505/720 (70.1%) of those who died ages 15-49. For the 215 cohort members who died aged 15-49 before being assigned a personal number, their number of children and grandchildren was imputed using multiple imputation (see below); these individuals represent 1.5% of the total UBCoS cohort. Number of children and grandchildren was assumed to be zero for the 1383 individuals who died aged 0-14.

Table 1: Social and biological characteristics of the Uppsala Birth Cohort (UBCoS) members

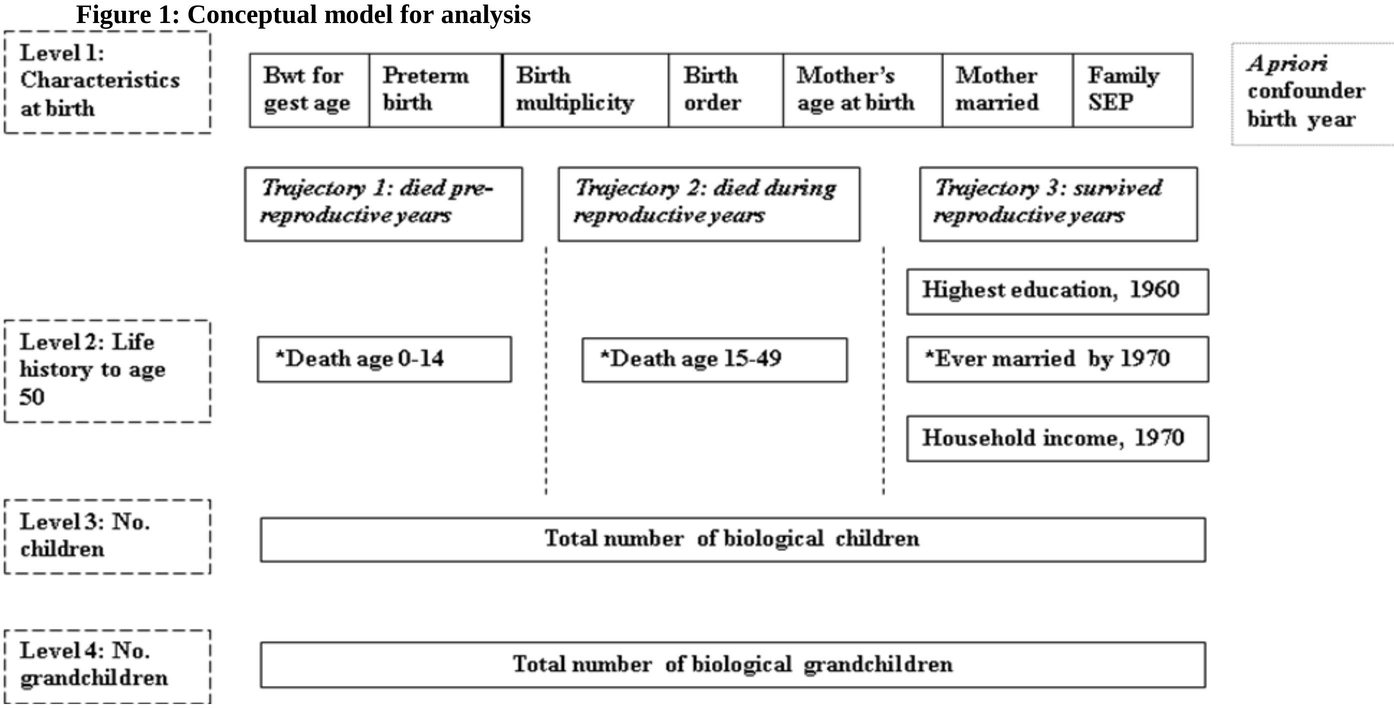
Independent variables	Range/categories	Percentage Males	Percentage Females
Early life characteristics for full cohort (7176 males, 6490 females)			
Standardised birthweight for gestational age (standardised separately by sex)	Quintile 1 (smallest), n=2682	20.2	20.4
	Quintile 2, n=2606	19.8	19.6
	Quintile 3, n=2647	20.7	19.3
	Quintile 4, n=2640	19.2	20.9
	Quintile 5 (largest), n=2646	20.2	19.9
Preterm birth	Term (≥37 weeks), n=11 995	90.1	90.8
	Pre-term (32-36 weeks), n=1065	8.4	7.6
	Very pre-term (≤31 weeks), n=209	1.5	1.6
Birth multiplicity	Singleton, n=13 241	97.1	96.7
	Twin/triplet, n=425	2.9	3.3
Birth order (mother's parity)	1, n=5313	38.9	38.8
	2-3, n=3200	23.3	23.5
	4-5, n=1815	13.1	13.5
	6-18, n=3336	24.7	24.1
Mother's age at birth	15-19 years, n=788	5.9	5.7
	20-24 years, n=3627	26.2	26.9
	25-29 years, n=3800	28.4	27.2
	30-34 years, n=2766	19.9	20.7
	35-39 years, n=1847	13.8	13.2
	40-49 years, n=831	5.9	6.3
Mother's marital status	Ever married, n=10 957	80.6	80.1
	Never married, n=2681	19.4	19.9
Family socio-economic position (SEP) at birth	Higher non-manual, n=1055	8.2	7.7
	Medium/low non-manual or self-employed, n=2732	20.8	20.4
	Skilled manual, n=1925	14.2	14.9
	Semi or unskilled manual, n=4863	36.5	36.8
	Farmer, n=1953	15.0	14.4
	House son/daughter, n=730	5.2	5.8
Adult characteristics for cohort members who survived to age 50 (5954 males, 5609 females)			
Highest educational level, 1960	Elementary (≤10 years), n=10 329	86.0	95.1
	Secondary (11-12 years), n=577	7.5	2.5
	Post-secondary (13+ years) n=523	6.5	2.5
Marital status, 1970	Ever married, n=10 486	89.6	92.5
	Never married, n=1040	10.4	7.5
Equivalised household disposable income, 1970	0-9999 SEK, n=1591	14.1	13.7
	10000-14999 SEK, n=3084	26.2	27.7
	15000-19999 SEK, n=3657	32.1	31.6
	20000-29999 SEK, n=2460	21.2	21.7
	30000+ SEK, n=679	6.5	5.4

SEK = Swedish Krona

2.3 Conceptual models and statistical analysis

To investigate the direct and indirect pathways whereby social and biological characteristics at birth influence mortality and fertility across the life course we adopted a conceptual model with three different life history ‘trajectories’: 1) dying before reaching the reproductive years (N=1383), 2) dying during the reproductive years (N=720) and 3) surviving throughout the reproductive years (N=11 563); see Fig. 1. We defined the reproductive years as ages 15-49 for both men and women. Among those who survived to adulthood, we hypothesised that marriage would be a central determinant of fertility and that education and household income might mediate some of the effects of childhood characteristics upon adult reproductive behaviours. Analyses of the effects of adult social characteristics were restricted to a subsample of subjects who survived to age 50 (trajectory 3).

Figure 1: Conceptual model for analysis



Abbreviations in Fig. 1: ‘Bwt for gest age’ = standardised birthweight for gestational age, ‘SEP’ = Socio-economic position. The Level 2 events marked with a * were hypothesised to be central determinants of an individual’s total number of children.

The frequency of missing data for the variables presented in Fig. 1 ranged from 0%-3.4%. We used multiple imputation to impute missing values under an assumption of missing at random [44], using the MICE command in Stata10 [45, 46]. We used five imputations for these models, including in our imputation models all explanatory and outcome variables which we ever use in our substantive models of interest (i.e. all those in Levels 1 to 4 of Fig. 1).

We first conducted univariable analyses to investigate the effect of each biological and social variable measured at birth upon number of children and number of grandchildren. We then fitted multivariable models, using a hierarchical modelling strategy guided by the Levels in our conceptual model. We used forced entry to enter all variables into each model, and adjusted all models for year of birth as a categorical variable by one-year age band.

In fitting multivariable models, we adopted a hierarchical modelling strategy guided by the Levels in our conceptual model. We present multivariable models created through linear/logistic regression with the forced entry of all variables measured at birth. Clearly this involved substantial multiple testing, and we therefore concentrate in our results upon main effects which were significant at the 1% level. Our conceptual model includes four continuous variables (birthweight for gestational age, birth order, mother's age and equivalised household income). In order to facilitate comparisons across models, we present the results from these variables after grouping them as categorical variables. This did not affect our substantive conclusions regarding which variables were or were not associated with any mortality or fertility outcome. The p-values presented for all ordered categorical variables are p-values for heterogeneity rather than for trend. When investigating intergenerational effects, we used the adjusted R-squared from ANOVA analyses to calculate the proportion of variance in number of grandchildren which was explained by number of children.

As one of our key objectives is to investigate whether any observed pathways are gender-specific, we tested all models for interactions between sex and each of the other characteristics measured at birth. We also believed it plausible that some of these variables might differ in their effect depending on an individual's socio-economic position, and we therefore additionally tested for interactions with family SEP.

Results

3.1 Determinants of total number of children and grandchildren

In total, 22 376 children and 41 153 grandchildren are registered for the 13 666 cohort members. This includes biological descendants given away for adoption (1.6% of children, 0.6% of grandchildren), and excludes non-biological descendants adopted into the families of cohort members (1.6% of children and grandchildren). 99.4% of the children had fathers aged 15-49 at the time of their birth, and 99.9% had mothers aged 15-49, providing justification for our choice of this age range as defining the reproductive years. Indirect evidence from the co-parents of cohort members suggests that underestimation of reproductive success due to missing data on parent identity on birth certificates will have been rare; father's identity was unrecorded in 2.3% of children of UBCoS females and mother's identity was unrecorded in 0.4% of the children of UBCoS males.

As judged by the distribution of birth years, by 2002 the number of children of cohort members was complete and the number of grandchildren was almost complete (see Fig. 2). As Fig. 3 shows, males and females had similar distributions of number of descendants, although men were more likely to have no children (30.0% vs. 25.6%

in women, χ^2_1=32.2, p<0.001) and no grandchildren (36.0% vs. 31.1% in women, χ^2_1=36.4, p<0.001). Univariable analyses also revealed considerable uniformity in the number of children and grandchildren across groups with different characteristics at birth; for all groups except those born very preterm, the mean number of children was 1.5 to 2.0 and the mean number of grandchildren was 2.5 to 3.5 (see the Supplementary Material).

Figure 2: Distribution of year of birth for cohort members, children and grandchildren

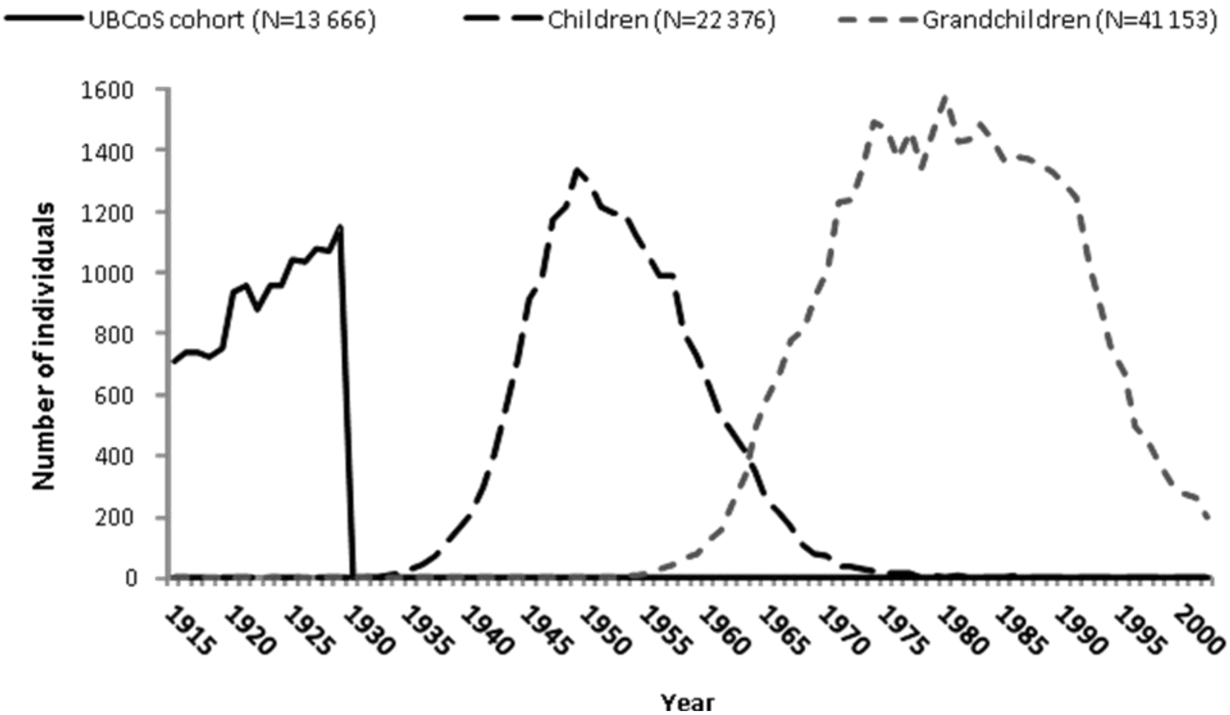


Figure 3: Total number of children and grandchildren for the full UBCoS cohort of 7176 males and 6490 females

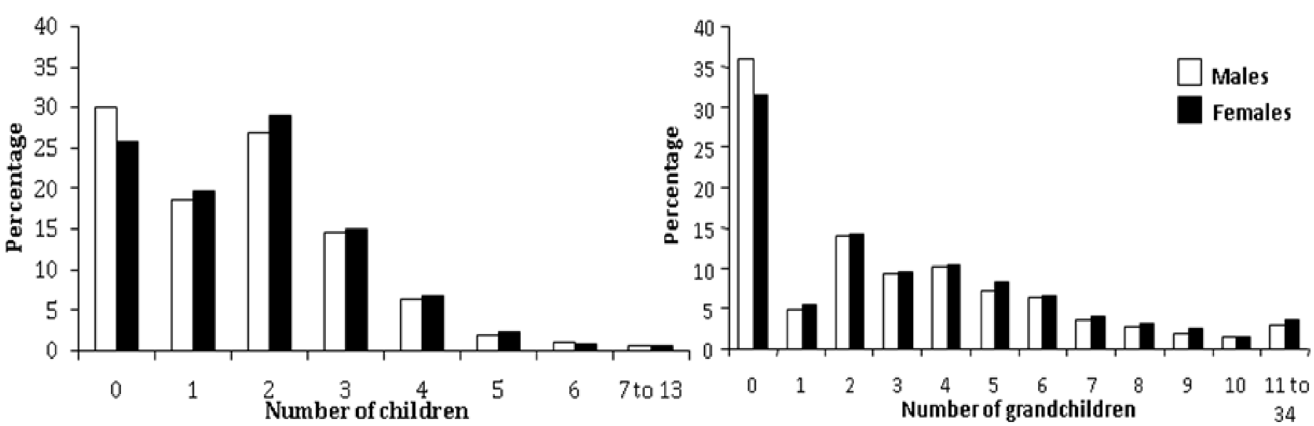


Table 2: Predictors of reproductive success, and pathways to reproductive success in the Uppsala Birth Cohort (UBCoS)

		Total effects on reproductive success		Pathways to reproductive success				
		No. children in full cohort[a]	**No. grand-children in full cohort[a]**	**Survived to age 15 in full cohort [b]**	**Survived to age 50 if survived to age 15 [b]**	**Ever married if survived to age 50 [b]**	**No. children if survived to 50 & married[a]**	**No. grand-children if ever had children, adjusting for no. children[a]**
N		13666	13666	13666	12283	11563	10510	9694
Sex	Male	**0*****	**0*****	**1****	**1*****	**1*****	0	**0*****
	Female	**0.09**	**0.30**	**1.22**	**1.47**	**1.43**	0.00	**0.18**
Standardised birthweight for gestational age	Quintile 1 (smallest)	**0*****	**0*****	**1*****	1	**1****	0	0
	Quintile 2	**0.08**	**0.17**	**1.36**	1.16	**1.08**	0.02	0.02
	Quintile 3	**0.18**	**0.39**	**1.90**	1.26	**1.52**	0.01	0.07
	Quintile 4	**0.15**	**0.24**	**2.10**	1.16	**1.23**	-0.01	-0.04
	Quintile 5 (largest)	**0.21**	**0.44**	**2.31**	1.09	**1.31**	0.03	0.07
Preterm birth	Term	**0*****	**0*****	**1*****	1	[1]	0	0*
	Preterm	**-0.23**	**-0.29**	**0.39**	0.82	[0.83]	0.01	0.21
	Very preterm	**-1.04**	**-1.92**	**0.05**	0.80	[0.59]	-0.07	-0.09
Birth multiplicity	Singleton	0	0	1	1	1	0	0
	Twin/triplet	-0.07	-0.10	0.81	0.68	0.94	0.00	0.05
Birth order (mother's parity)	1	[0]	**0****	**1*****	1*	[1]	**0****	**0****
	2-3	[0.03]	**0.10**	**0.79**	0.78	[1.15]	**0.05**	**0.07**
	4-5	[0.06]	**0.28**	**0.69**	0.70	[1.18]	**0.14**	**0.23**
	6-18	[0.07]	**0.39**	**0.55**	0.92	[1.38]	**0.16**	**0.33**
Mother's age at birth	15-19 years	**0****	**0*****	1	1	**1*****	0	**0*****
	20-24 years	**-0.03**	**-0.08**	1.17	1.10	**0.68**	-0.03	**-0.06**
	25-29 years	**-0.10**	**-0.33**	1.16	1.22	**0.48**	-0.05	**-0.21**
	30-34 years	**-0.11**	**-0.44**	1.20	1.08	**0.47**	-0.07	**-0.34**
	35-39 years	**-0.23**	**-0.66**	1.06	1.13	**0.39**	-0.16	**-0.33**
	40-49 years	**-0.23**	**-0.64**	1.06	1.17	**0.35**	-0.14	**-0.32**
Mother's marital status	Ever married	[0]	[0]	**1****	1	[1*]	0*	0
	Never married	[-0.01]	[-0.06]	**0.72**	0.84	[0.77]	0.10	-0.08
Family SEP at birth	Higher non-manual	**[0***]**	0*	1	1	[1]	**0*****	0
	Med/low non-man/self-empl	**[-0.19]**	-0.26	0.90	1.12	[1.00]	**-0.22**	0.15
	Higher manual	**[-0.21]**	-0.35	1.07	0.97	[1.11]	**-0.29**	0.10
	Lower manual	**[-0.25]**	-0.37	0.89	1.21	[0.97]	**-0.30**	0.16
	Farmer	**[-0.14]**	-0.20	0.90	1.37	[0.78]	**-0.13**	0.12
	House son/daughter	**[-0.24]**	-0.39	0.94	1.09	[0.81]	**-0.28**	0.13

*p<0.05, **p<0.01, ***p<0.001, with bold font used for variables significant at p<0.01. SEP = socio-economic position. [a =] Regression coefficients from linear regression [b =] Odds ratio from logistic regression. All analyses adjust for year of birth by one-year age band, and all p-values are from tests for heterogeneity. Variables presented in square brackets showed significant or near-significant evidence (p<0.06) of an interaction with sex: see text for details, and see Supplementary Material for models presented stratified by gender.

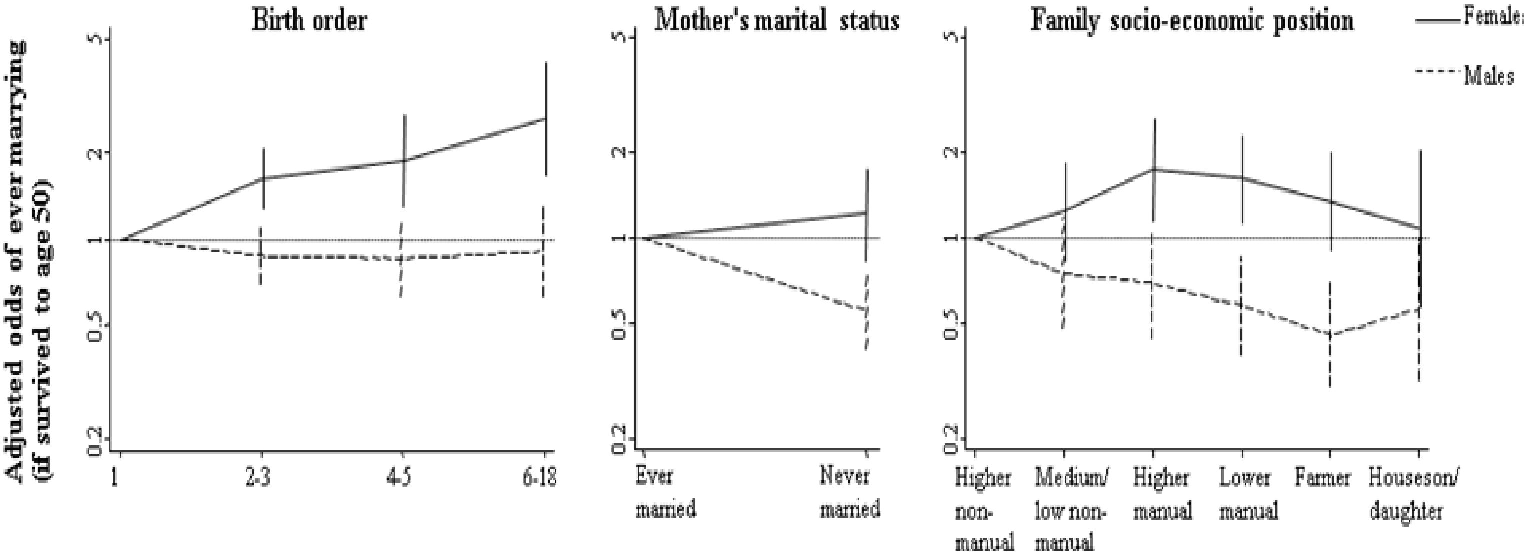
The results of multivariable analyses of the predictors of number of children and number of grandchildren in the full cohort are presented in the first two columns of Table 2. In both sexes, a higher birthweight for gestational age, a term birth and a younger mother at birth were independently associated with a greater number of descendants. None of these variables showed any evidence of an interaction with gender. By contrast, there was significant or near-significant evidence of an interaction upon number of children for birth order (p=0.06), mother's marital status (p=0.004) and family SEP at birth (p=0.06). As shown in the sex-specific models presented in the Supplementary Material, higher birth order was associated with a greater number of children in females (but not males), while a married mother and higher family SEP were associated with a greater number of children in males (but not females). Except for this interaction with gender, we did not find evidence of family SEP interacting with any other characteristic measured at birth in their effect on reproductive success.

3.2 The role of survival, marriage, and fertility among those who married, in mediating the relationship between characteristics at birth and number of children

The importance of mortality is indicated by the fact that 784 males (10.9%) and 599 females (9.23%) died between ages 0 and 14, over 60% in both sexes dying before the age of 1. These cohort members were all assumed to die childless which, in perspective, makes up over a third of the childless individuals in the full cohort. A further 438 males (6.1%) and 282 females (4.5 %) died between ages 15 and 49. For both sexes, this had a strong effect in curtailing their child-bearing, with the mean number of children decreasing by 0.1-0.5 per 5-year decrease in age of death. The importance of marriage is likewise demonstrated by the fact that among those who survived to age 50, the mean number of children among the ever married was 2.05 (95%CI 2.02 – 2.09) in both men and women vs. 0.10 (95%CI 0.07 – 0.14) for never married men and 0.21 (95%CI 0.16 – 0.27) for never married women.

As shown in Table 2, the higher reproductive success of women compared to men resulted from both a survival advantage in both child and adulthood and a greater probability of marriage. The positive effect of higher birthweight for gestational age operated via both childhood survival and marriage. There was some suggestion that in males the same might be true of being born closer to term, although in females preterm birth was only associated with higher mortality in childhood and had no association with marriage (p-value for interaction 0.03). Higher birth order was associated with poorer childhood survival but a greater number of children within marriage. In females (but not males) higher birth order was also associated with a greater probability of marriage (p-value for interaction 0.001; see Fig. 4). By contrast, males (but not females) were more likely to marry if their own mothers were ever married or if they were of higher SEP while women of the highest SEP category were less likely to marry than other groups (p-values for interaction with sex 0.008 and 0.0001, respectively; see Fig. 4). In addition, in both sexes a married mother was associated with greater childhood survival while higher family SEP was associated with a greater number of children within marriage. Finally, the negative effect of increasing mother's age upon number of children appeared to be entirely mediated through a lower likelihood of marriage, and being a twin had no effect upon reproductive success at any stage of the pathway.

Figure 4: Sex-specific models of the effect of birth order, mother's marital status, and family SEP upon the odds marriage among those who survived to age 50



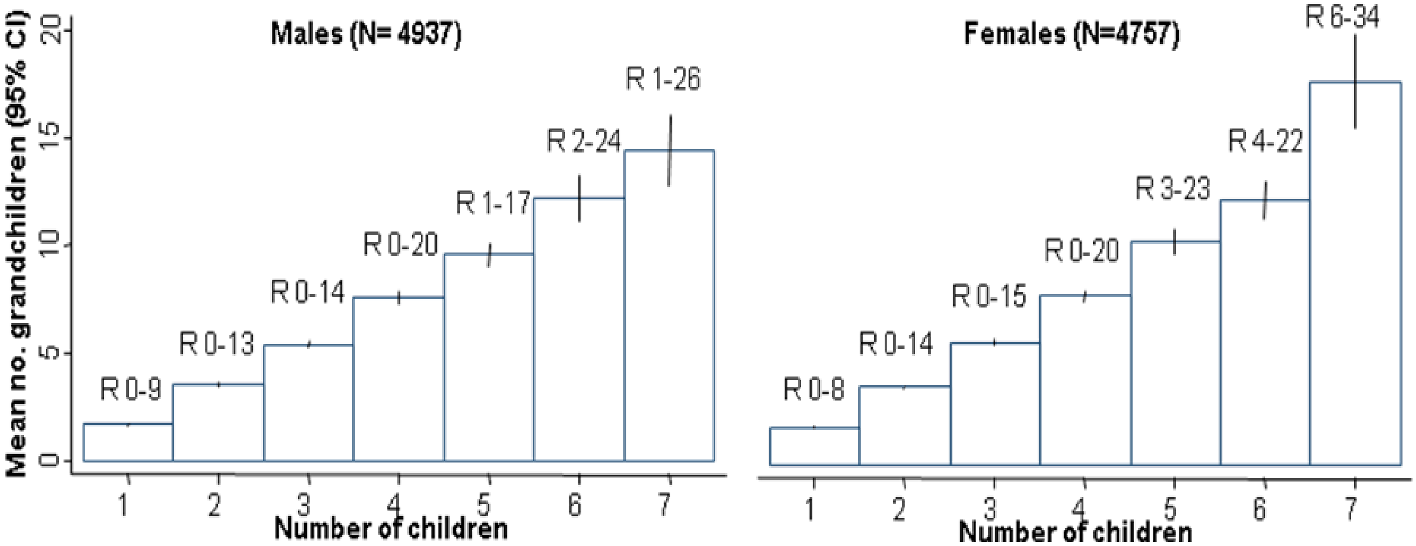
All models adjusted for standardised birthweight for gestational age, preterm birth, multiplicity, birth order, mother's marital status and family SEP at birth. Full results of sex-specific models in Supplementary Material.

These results therefore suggested substantial variation in how the social and biological characteristics measured at birth affect total number of children. They also indicate that the interactions between sex and birth order, mother's marital status and family SEP in predicting total number of children all seemed to be mediated exclusively via effects on probability of marriage. The effects observed upon fertility among those who married did not seem to be mediated by age of marriage; after adjusting for the year of marriage in the 90% of men and women for whom this data was available, the estimated effect sizes either remained the same or, for family SEP, became stronger.

3.3 Relationship between number of children and number of grandchildren, and intergenerational effects.

Very similar characteristics predicted number of children and number of grandchildren, suggesting that variation in number of children may explain a large part of the variation observed in number of grandchildren (Table 2). We confirmed that this was indeed the case in ANOVA analyses where, among those who had at least one child, number of children explained 60% of the observed variation (58% in men and 63% in women), based on adjusted R-squared values. In contrast to the hypothesis that intermediate family sizes maximise long-term reproductive success, we observed that number of grandchildren increased across the range for number of children in both men and women (Fig. 5).

Figure 5: Mean number of grandchildren (and 95% CI) for a given number of children



Range (R) given above bars

Given a certain number of children, individuals of both sexes had more children if they were of a higher birth order or if their mother was younger when they were born (Table 2). In exploratory analyses to investigate whether this was mediated via earlier first child-bearing, we adjusted for the age at which cohort members first became parents. In both sexes, this adjustment caused the effect sizes of mother's age and birth order to reduce substantially towards the null and rendered the associations only weakly significant (p=0.03 and 0.02 respectively). The effect sizes were reduced even further and became entirely non-significant (p>0.1), when we instead adjusted for the mean age at which the children of cohort members themselves became parents, in the 92% of non-childless men and women who also had at least one grandchild. These two variables were highly correlated (0.77 in men, 0.76 in women), indicating a high degree of intergenerational continuity in age of first child-bearing. Thus in both sexes it seems possible that the positive effects of a younger mother and a higher birth order upon a greater number of grandchildren are mediated by a shorter generation time.

3.4 The role of adult socio-economic position in mediating the relationship between characteristics at birth and number of children

With the exception of family SEP, the estimated effect sizes for the effect of early life characteristics on reproductive success changed very little upon adjustments for adult social characteristics (see Supplementary Material). We therefore conclude that the effects of early life circumstances on reproduction are unlikely to be mediated by social conditions in later life. The results were little changed when analyses of predictors of fertility among those who married were restricted to 87% of the ever-married sample (90% males and 85% females) who were living in a currently-cohabiting married couple in 1970. This indicates that the observed effects of equivalised household income do not simply reflect confounding by couple-status through use of an inappropriate equivalence scale.

Adult education and income were nonetheless important independent predictors of marriage and of fertility among those who married, with marked gender differences: higher education was associated with substantially higher probability of marriage in men (88% for elementary education, 96% for senior and 96% for post-senior) but a lower probability of marriage in women (93% for elementary, 82% for senior, 81% for post-senior; $p<0.001$ for interaction). This lower probability of marriage among more educated women offsets a higher fertility among those highly educated women who did marry, resulting in similar mean number of children in women from different education categories in univariable analyses (mean number of children 1.91, 1.92 and 1.92 for the three educational levels, p-value 0.96; see Supplementary Material). In the adjusted model, higher equivalised household income showed a U-shaped relationship with number of children within marriage, which was highest in the top and bottom groups. There was borderline evidence of an interaction ($p=0.05$) such that this pattern was particularly marked in males, but in the context of multiple testing this may represent a chance finding.

In both sexes, there was strong evidence that increasing education predicted fewer grandchildren for a given number of children, but no evidence of any effect from household income (see Supplementary Material). Adjustment for the mean age of first childbearing of a cohort member's children reduced the effect size of higher education substantially and made the strong association only borderline significant ($p=0.05$).

Discussion

To our knowledge, our study of 13 666 infants born in Uppsala between 1915 and 1929 is unique in providing a detailed investigation of the determinants of reproductive success over three generations. It demonstrates that an individual's social and biological characteristics at birth do predict long-term reproductive success even in a post-demographic transition population. In both sexes, a higher birth weight for gestational age, a term birth and a younger mother were independently associated with a greater number of descendants. A married mother and higher family social class were also associated a greater number of descendants in males (but not females), while in females (but not males) higher birth order was associated with higher reproductive success. These differences were mediated by gender-specific effects upon probability of marriage. Childhood survival, marriage and fertility among those who married seemed more important than adult survival or age of marriage in explaining how these early life characteristics affect number of children.

Number of grandchildren increased progressively with increasing number of children in both sexes, and most associations between early life characteristics and number of grandchildren seemed to operate through number of children. For a given number of children, however, cohort members of both sexes had more grandchildren if their own mother was younger, if they had a higher birth order and if they had a lower educational level.

4.1 Strengths and limitations of the study

Our study has several strengths, including its use of a well-defined population-based cohort with prospective data collection; the availability of both social and biological variables at birth, with data of high quality and high completeness; the use of data from adult life to give a lifecourse perspective; the greater time-depth offered by using a cohort born several decades before most registers were established; and the consequent availability of near-complete data from across three generations.

There are, however, several important limitations to our analyses. One of the most important is that we did not have data on the number of younger siblings of our original cohort members. We were therefore not able to calculate total family size or to distinguish its effects from those of higher birth order *per se*. As such, as discussed in more detail below, it is very possible that the effects of higher birth order observed in these analyses in fact reflect the effects of larger total family size.

Another set of limitations relate to children and grandchildren who were missing or inappropriately included in our analyses because of limitations of the multigenerational registry. The multigenerational registry excludes all those who died before 1961 and a small proportion who died in 1961-67 [36]. This will underestimate somewhat the number of children born, but as almost all unrecorded children will have died aged less than 30 years the effect on number of grandchildren should be minimal. Number of descendants will also be underestimated because of missing data on parent identity on birth certificates, although indirect evidence from the co-parents of cohort members suggested this will have been rare in men and very rare in women. The biological parenthood of some offspring may have been misattributed, and this is again expected to be more common in men. If some groups of men were particularly likely to have unrecorded or misattributed offspring, this could bias our results.

Finally, the distribution of birth years indicates that not all grandchildren who will ever be born to this cohort were born as of 2002. Those grandchildren yet to be born are likely to be disproportionately drawn from families in which the original cohort member and/or their child delayed child-bearing until an older age. This is important because, as described above, exploratory analyses indicated that a longer generation time seemed to mediate the finding that (for a given number of children) number of grandchildren was lower than expected for cohort members with older mothers, a lower birth order or a higher educational level. It is therefore plausible that these groups will 'catch up', at least to some extent, once the full cohort of grandchildren is born. Even if this were the case, however, this would not render these characteristics irrelevant to Darwinian fitness, given that such slower breeding would still be expected to be detrimental to long-term contribution to the gene pool.

4.2 Consistency of findings with previous research and directions for future investigations

One striking finding of our study is that the probability of marriage was associated with a large number of characteristics at birth and that this was the only stage of the pathway to reproductive success in which highly gender-specific effects were observed. The predictors of marriage included the biological variables of lower birthweight for gestational age and (in males only) premature birth. Both variables were associated with a substantially lower probability of marrying, showing a dose response relationship and neither appearing to be mediated by adult SEP. For birthweight, this had already been described in the male sample of this cohort [7] and in cohorts of men born at a similar time in the UK and Finland [47]. Our analyses expand upon this previous work by including results for women and in demonstrating that the effect in men persists after adjusting for a large number of factors at birth; that birthweight for gestational age has no effect upon fertility among those who married, and therefore does not seem likely to have its effect through biological fecundity; and that premature birth may have the same effect as birthweight.

What is particularly intriguing about these results is that they appear to provide an example of biological characteristics at birth having an effect upon total reproductive success which is partly mediated by the *social* fact of adult marital status. This provides an interesting counterpoint to the concept of 'embodiment', which highlights how the health effects of detrimental aspects of the social environment are manifested through biological characteristics [48]. Far less attention has been paid to effects in the opposite direction, but our results suggest that low birthweight and preterm birth not only had negative implications for physical health but also constrained the life chances of individuals in our cohort in other ways by making them less attractive marriage partners. The fact that adjustment for child and adult SEP leaves the effects of birthweight and prematurity virtually unchanged suggests that they are not simply markers for general social adversity. Beyond this, it is not clear whether poor early growth has a direct role (e.g. as mediated by adult height) or is a marker for other adverse health experiences *in utero* (e.g. as mediated by adult health or cognitive abilities). Investigating these mechanisms further may shed light onto why preterm birth appears to reduce the probability of giving birth in more recent cohorts of males [9] and perhaps (although the evidence is more conflicting) also in females [4, 9].

One unexpected and, to our knowledge, novel finding was that having a younger mother was associated with a higher probability of marriage in both men and women. The effect of higher birth order in women has somewhat more support [21], although one important limitation of our data is the absence of information on number of younger siblings. This makes it very possible that the 'higher birth order' effects we observed are due to a more general effect of larger family size. Such an association between the family sizes of mothers and their daughters has been observed in many cohorts born before 1950 from Scandinavia and elsewhere [18, 19]. Our inability to distinguish the effects of birth order *per se* from larger family size therefore represents an important limitation. Nevertheless, our findings are still of interest on several counts. First, previous studies have often been restricted to married mothers and married daughters. The fact that we show higher rates of *marriage* as well as fertility within marriage is therefore of interest in indicating that greater biological fecundity or a greater desired family size within the context of marriage cannot be the sole explanations. Secondly, our analyses demonstrate that the positive effects of higher birth order/larger family size upon total reproductive success via higher fertility did indeed outweigh their negative effects via higher mortality in the context of 20th

century Sweden. Finally, our study is unusual in including a male sample [19]. The absence of a birth order effect on the probability of marriage for men is consistent with previous studies of cohorts born early in the 20th century which have often found the effects of birth order to be weaker or absent in men than in women [18, 19], although again we are limited by our inability to distinguish the effects of birth order from family size.

The effect of socio-economic position is interesting in highlighting the potential both for continuity and for historical contingency in the determinants of reproductive success. The continuity is illustrated by the positive correlation in both sexes between higher SEP and a greater number of descendents. This is consistently observed in traditional populations [24, 25] and, although evidence in modern populations is more variable [2], our study adds to the evidence that the demographic transition does not necessarily erase the relationship between access to resources and reproductive advantage. Yet in females this advantage exists only because of higher fertility within marriage; unlike males, females of higher SEP are no more likely to secure a marriage partner. Indeed, when it came to adult SEP, the probability of marriage was much *lower* in more highly educated females. This contrasts with the earlier marriage among the daughters of wealthier men in historical Sweden [49, 50]. It also contrasts with more recent trends in from Sweden and elsewhere, whereby women of higher education are more likely to intend to get married, to get married and to stay married [51-54]. This cohort also belongs to a generation which was unusual in the rarity of unmarried cohabitation. This had been somewhat more widespread at the turn of the 20th century in Sweden, but then grew much rarer for several decades before becoming extremely common since the 1960s [54]. With over half of Swedish children now born to unmarried parents, marriage is no longer as strong a determinant of reproductive success. For example, while in our cohort the difference in number of children between ever-married and never-married women was almost two, in a cohort of Swedish women born in 1955-59 it fell to only one, and in more recent cohorts it is likely to fall further still [55].

In this paper, we found no evidence to support the existence of a quality-quantity trade-off in which number of grandchildren peak at an intermediate family size. Instead, number of grandchildren increased progressively with an increasing number of children in both sexes. This suggests that fertility limitation in this population cannot be explained as an optimal strategy for maximising parent’s long-term reproductive success in this population, thereby replicating previous studies of cohorts born at a similar time in Germany and the US [23, 32]. We also extend this previous work by examining whether any early life characteristics of our cohort members predict number of grandchildren independently of their effect on number of children. Our results suggested that intergenerational effects were largely absent in this cohort, and that what comparatively small effects were observed seemed to relate to a cohort member’s family composition (mother’s age and higher birth order/family size) and to be mediated by an earlier age of first childbearing among a cohort member’s children. This may reflect the way in which intergenerational continuities in fertility preferences regarding timing and number of children appear to be strengthening in more recent cohorts, and to represent an increasing important determinant of completed family size [18].

4.3 Conclusion

The Uppsala Birth cohort is representative of the Uppsala region and Sweden in 1915-1929 in terms of infant mortality [56-58]. The fertility of the cohort is also similar to that reported from large nationally-representative Swedish cohorts from the same period [59]. This suggests that it may be possible to generalise our observations from this cohort to the Swedish native-born cohort of 1915-1929. One implication is that our findings can potentially inform other analyses of reproductive career as a determinant of health and survival in later life in this and other similar populations. The importance of reproductive history in the aetiology of breast cancer has been recognised for a long time [60-62]. There is also a growing interest in studying the long-term effects of childbearing and childrearing on subsequent health of both parents more generally and with respect to circulatory disease in particular [63-66]. Better understanding of what determines the reproductive career can certainly add to pinpointing the most relevant underlying mechanisms and indirectly, suggest new ways of disease prevention.

By characterising in unusual detail the determinants of reproductive success, our study adds to understanding of contemporary variations in mortality and reproduction in our particular population. Clearly much of what we have described for this cohort will be context-specific to an important degree. Sweden, for example, has experienced a substantial increase in childhood survival and childbearing outside of marriage across the 20th century, and the childhood survival and marriage pathways are therefore unlikely to explain as much variation in reproductive success in more recent cohorts. Yet the effect of variables such as low birthweight may nonetheless continue to manifest themselves through closely related pathways such as poor adult health or a lower probability of forming a long-term romantic partnership. The greater our understanding of precisely how these factors operate – for example, whether and to what extent these may be expressions of a genetic predisposition to particular patterns of foetal growth – the greater our ability to predict which factors will have more persistent effects across time and space. As such, we believe that our study not only describes past selective pressures in a particular population, but also generates hypotheses about the potential long-term consequences of adverse environment and impaired foetal growth on future health and reproduction of concurrent cohorts around the world.

Conflict of interest

None

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APPENDIX 1 - SUPPLEMENTARY MATERIAL

Standardised birthweight for gestational age

We first cleaned the data to identify infants with implausibly large birthweights given their gestational age. Following Ekholm *et al.* (2005) these were defined as gestational age ≤28 completed weeks and birthweight >2000g, gestational age 29-30 weeks and birthweight >2500g, gestational age 31-32 weeks and birthweight >3000g, and gestational age 33 or 34 weeks and birthweight >3500g. We also added a further exclusion category of gestational age ≤25 weeks and birthweight >1500g. This identified a total of 83 children with incompatible birthweights and gestational ages, for whom we recoded both birthweight and gestational age as missing.

We then calculated standardised birthweight for gestational age on week-by-week basis separately for males and females. This was done using the observed mean and standard deviation for that week within the UBCoS cohort for the 13 599 infants born at 30 or more completed weeks (i.e. an internal reference). For the 86 children born at 22-29 completed weeks, there were insufficient numbers of children in each category to use this internal reference method and we therefore used external reference data. Because no normative data for this range of gestational lengths exists for this historical population we instead used data from a large population-based sample of Canadian births from 1994-6 (Kramer et al., 2001). This was selected as the only reference data we could find which presents means and standard deviations for as low as 22 weeks; by contrast the youngest reference data we could find from Swedish reference data was 28 weeks (Niklasson et al., 1991). The Canadian data also has the advantaged of presenting the results separately by sex and in tables (and not just in graphs) and of having used sophisticated techniques to clean and smooth the data. The infants in this Canadian reference data weighed an average of 162g less than the Uppsala sample, however, with no evidence of a difference in the size of this offset across the 22-29 week range or between boys and girls (p-values for interaction>0.7). We therefore again followed the methodology of Ekholm *et al*. (2005) in always adding 162g to the mean of the Canadian reference data before calculating birthweight for gestational age in our cohort, but leaving the value of the standard deviations unchanged. For the six infants born at 21 completed weeks or less, we left their birthweight for gestational age as missing.

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Supplementary Table 1: Social and biological characteristics of UBCoS cohort, and univariable association with number of children and grandchildren

Full UBCoS cohort		**Total population**			**Males**			**Females**		
		N	**Mean no. children**	**Mean no. grandchildren**	**N**	**Mean no. children**	**Mean no. grandchildren**	**N**	**Mean no. children**	**Mean no. grandchildren**
Full sample		13666	1.64	3.02	7176	1.60	2.88	6490	1.69	3.18
Sex	Male	7176	1.60	2.88	6965	1.61	2.90	6276	1.70	3.19
	Female	6490	1.69	3.18	211	1.22	2.27	214	1.53	2.86
	p-value for heterogeneity		***<0.001***	***<0.001***		***<0.001***	***0.006***		***0.09***	***0.16***
Standardised birthweight for gestational age	Quintile 1 (smallest)	2682	1.52	2.77	1403	1.46	2.68	1279	1.58	2.87
	Quintile 2	2606	1.60	2.93	1378	1.56	2.77	1228	1.64	3.11
	Quintile 3	2647	1.71	3.16	1439	1.64	2.94	1208	1.78	3.43
	Quintile 4	2640	1.68	3.03	1333	1.65	2.91	1307	1.70	3.16
	Quintile 5 (largest)	2646	1.73	3.22	1401	1.70	3.12	1245	1.76	3.33
	p-value for heterogeneity		***<0.001***	***<0.001***		***<0.001***	***0.004***		***0.03***	***<0.001***
	p-value for linear plus quadratic terms		***<0.001***	***<0.001***		***<0.001***	***<0.001***		***<0.001***	***<0.001***
Preterm birth	Term	11995	1.68	3.08	6279	1.64	2.94	5716	1.72	3.23
	Preterm	1065	1.44	2.76	588	1.40	2.67	477	1.48	2.88
	Very preterm	209	0.65	1.19	106	0.48	0.95	103	0.83	1.44
	p-value for heterogeneity		***<0.001***	***<0.001***		***<0.001***	***<0.001***		***<0.001***	***<0.001***
Birth multiplicity	Singleton	13241	1.65	3.04	6965	1.61	2.90	6276	1.70	3.19
	Twin/triplet	425	1.37	2.57	211	1.22	2.27	214	1.53	2.86
	p-value for heterogeneity		***<0.001***	***0.004***		***<0.001***	***0.006***		***0.09***	***0.16***
Birth order (mother's parity)	1	5313	1.64	2.98	2793	1.62	2.89	2520	1.66	3.07
	2-3	5015	1.66	3.03	2608	1.61	2.88	2407	1.71	3.19
	4-5	1877	1.65	3.09	1006	1.61	2.88	871	1.70	3.33
	6-18	1459	1.63	3.09	767	1.53	2.88	692	1.74	3.33
	p-value for heterogeneity		***0.86***	***0.52***		***0.49***	***0.99***		***0.44***	***0.15***
	p-value for linear trend		***0.99***	***0.14***		***0.21***	***0.95***		***0.16***	***0.03***
Mother's age at birth	15-19 years	788	1.66	3.11	420	1.64	3.02	368	1.68	3.22
	20-24 years	3627	1.68	3.15	1881	1.61	2.95	1746	1.76	3.37
	25-29 years	3800	1.65	3.00	2033	1.62	2.90	1767	1.67	3.12
	30-34 years	2766	1.66	3.00	1426	1.61	2.87	1340	1.71	3.13
	35-39 years	1847	1.56	2.85	992	1.59	2.87	855	1.53	2.82
	40-49 years	831	1.58	2.95	420	1.42	2.45	411	1.74	3.45

	p-value for heterogeneity		***0.06***	***0.04***		***0.20***	***0.11***		***0.006***	***0.002***
	p-value for linear trend		***0.008***	***0.002***		***0.09***	***0.02***		***not linear***	***not linear***
Mother's marital status	Ever married	10957	1.65	3.03	5772	1.63	2.93	5185	1.68	3.15
	Never married	2681	1.62	2.99	1390	1.51	2.71	1291	1.74	3.28
	p-value for heterogeneity		***0.38***	***0.52***		***0.008***	***0.03***		***0.14***	***0.22***
Family SEP at birth	Higher non-manual	1055	1.84	3.27	570	1.90	3.29	485	1.77	3.25
	Medium/low non-manual or self-employed	2732	1.64	3.03	1445	1.61	2.90	1287	1.67	3.17
	Higher manual	1925	1.64	2.96	988	1.59	2.81	937	1.66	3.11
	Lower manual	4863	1.59	2.96	2539	1.51	2.76	2324	1.68	3.17
	Farmer	1953	1.70	3.13	1042	1.69	3.06	911	1.72	3.22
	House son/daughter	730	1.62	2.97	364	1.52	2.72	366	1.73	3.22
	p-value for heterogeneity		***<0.001***	***0.06***		***<0.001***	***0.004***		***0.72***	***0.98***
UBCoS cohort members who survived to age 50										
Full sample		11563	1.88	3.46	5954	1.85	3.33	5609	1.91	3.60
Highest educational Level, 1960	Elementary (<10 years)	10329	1.86	3.45	5057	1.80	3.28	5272	1.91	3.61
	Secondary (11-12 years)	577	1.94	3.40	441	1.94	3.34	136	1.92	3.59
	Post-secondary (13+ years)	523	2.28	3.73	385	2.41	3.95	138	1.92	3.14
	p-value for heterogeneity		***<0.001***	***0.16***		***<0.001***	***<0.001***		***0.96***	***0.28***
Marital status, 1970	Ever married	10486	2.05	3.78	5314	2.05	3.71	5172	2.05	3.86
	Never married	1040	0.15	0.23	619	0.10	0.14	421	0.21	0.37
	p-value for heterogeneity		***<0.001***	***<0.001***		***<0.001***	***<0.001***		***<0.001***	***<0.001***
Equivalised household disposable income, 1970	0-9999 SEK	1591	1.73	3.27	830	1.56	2.80	761	1.92	3.73
	10000-14999 SEK	3084	1.83	3.34	1543	1.77	3.12	1541	1.89	3.56
	15000-19999 SEK	3657	1.87	3.47	1895	1.84	3.39	1762	1.89	3.55
	20000-29999 SEK	2460	1.95	3.58	1252	1.98	3.56	1208	1.93	3.60
	30000+ SEK	679	2.27	4.02	381	2.42	4.18	298	2.08	3.81
	p-value for heterogeneity		***<0.001***	***<0.001***		***<0.001***	***<0.001***		***0.61***	***0.59***
	p-value for linear trend		***<0.001***	***<0.001***		***<0.001***	***<0.001***		***not linear***	***not linear***

Note the frequency of missing data ranged from 0 to 3.4%, and therefore the number of individuals observed in each category is sometimes less than the total sample. SEP = socio-economic position. SEK = Swedish Krona.

Supplementary Table 2: Predictors of reproductive success, and pathways to reproductive success in males

		Total effects on reproductive success		Pathways to reproductive success				
		No. children in full cohort[a]	**No. grand-children in full cohort[a]**	**Survived to age 15 in full cohort [b]**	**Survived to age 50 if survived to age 15 [b]**	**Ever married if survived to age 50 [b]**	**No. children if survived to 50 & married[a]**	**No. grand-children if had children, adjusting for no. children[a]**
N		7176	7176	7176	6392	5954	5328	4937
Standardised birthweight for gestational age	Quintile 1 (smallest)	**0*****	0*	**1*****	1	**1*****	0	0
	Quintile 2	**0.09**	0.08	**1.40**	1.15	**1.29**	0.06	-0.13
	Quintile 3	**0.16**	0.23	**1.62**	1.24	**1.87**	0.07	-0.11
	Quintile 4	**0.17**	0.19	**1.95**	1.06	**1.50**	0.10	-0.18
	Quintile 5 (largest)	**0.24**	0.43	**2.16**	1.10	**1.57**	0.17	-0.02
Preterm birth	Term	**0*****	**0*****	**1*****	1	**1****	**0****	0
	Preterm	**-0.21**	**-0.22**	**0.42**	0.78	**0.74**	**-0.15**	0.25
	Very preterm	**-1.12**	**-1.93**	**0.05**	0.70	**0.35**	**-1.13**	0.38
Birth multiplicity	Singleton	0	0	**1****	1	1	0	0
	Twin/triplet	-0.17	-0.29	**0.62**	0.68	1.02	-0.22	0.07
Birth order (mother's parity)	1	0	0	1*	1	1	0	**0****
	2-3	-0.04	-0.03	0.77	0.81	0.87	-0.03	**0.06**
	4-5	-0.02	0.05	0.77	0.80	0.85	0.01	**0.10**
	6-18	-0.04	0.22	0.64	0.84	0.91	-0.03	**0.45**
Mother's age at birth	15-19 years	0*	**0*****	1	1	1*	0	0*
	20-24 years	-0.10	**-0.21**	1.15	0.72	0.84	-0.06	-0.04
	25-29 years	-0.14	**-0.39**	1.20	0.87	0.59	-0.04	-0.17
	30-34 years	-0.17	**-0.49**	1.05	0.85	0.66	-0.10	-0.26
	35-39 years	-0.20	**-0.57**	1.05	0.83	0.52	-0.09	-0.27
	40-49 years	-0.38	**-1.07**	0.95	0.90	0.47	-0.25	-0.57
Mother's marital status	Ever married	0*	0*	1*	1	**1*****	0	0
	Never married	-0.15	-0.33	0.74	0.87	**0.56**	-0.07	-0.08
Family SEP at birth	Higher non-manual	**0*****	**0****	1	1	**1****	**0*****	0
	Med/low non-man/self-empl	**-0.21**	**-0.29**	0.81	1.09	**0.75**	**-0.19**	0.16
	Higher manual	**-0.27**	**-0.46**	1.20	0.96	**0.70**	**-0.26**	0.09
	Lower manual	**-0.35**	**-0.53**	0.84	1.28	**0.58**	**-0.30**	0.21
	Farmer	**-0.20**	**-0.26**	0.92	1.61	**0.46**	**-0.09**	0.17
	House son/daughter	**-0.30**	**-0.47**	0.92	1.03	**0.56**	**-0.22**	0.15

*p<0.05, **p<0.01, ***p<0.001, with bold font used for variables significant at p<0.01. SEP = socio-economic position. [a =] Regression coefficients from linear regression [b =] Odds ratio from logistic regression. All analyses adjust for year of birth by one-year age band, and all p-values are from tests for heterogeneity.

Supplementary Table 3: Predictors of reproductive success, and pathways to reproductive success in females

		Total effects on reproductive success		**Pathways to reproductive success**				
		No. children in full cohort[a]	**No. grand-children in full cohort[a]**	**Survived to age 15 in full cohort [b]**	**Survived to age 50 if survived to age 15 [b]**	**Ever married if survived to age 50 [b]**	**No. children if survived to 50 & married[a]**	**No. grand-children if had children, adjusting for no. children[a]**
N		6490	6490	6490	5891	5609	5182	4757
Standardised birthweight for gestational age	Quintile 1 (smallest)	**0****	**0****	**1*****	1	1	0	0
	Quintile 2	**0.07**	**0.27**	**1.34**	1.21	0.82	0.03	0.17
	Quintile 3	**0.20**	**0.56**	**2.38**	1.28	1.11	0.05	0.24
	Quintile 4	**0.12**	**0.28**	**2.33**	1.34	0.91	-0.02	0.10
	Quintile 5 (largest)	**0.17**	**0.44**	**2.61**	1.11	0.98	0.02	0.15
Preterm birth	Term	**0*****	**0*****	**1*****	1	1	0	0
	Preterm	**-0.25**	**-0.36**	**0.35**	0.91	1.04	-0.04	0.17
	Very preterm	**-0.91**	**-1.83**	**0.05**	1.03	1.62	-0.04	-0.34
Birth multiplicity	Singleton	0	0	1	1	1	0	0
	Twin/triplet	0.03	0.09	1.14	0.70	0.82	0.10	0.02
Birth order (mother's parity)	1	0*	**0*****	**1*****	1*	**1*****	**0****	0*
	2-3	0.10	**0.26**	**0.83**	0.73	**1.62**	**0.09**	0.07
	4-5	0.15	**0.56**	**0.60**	0.56	**1.88**	**0.22**	0.35
	6-18	0.22	**0.60**	**0.45**	1.05	**2.63**	**0.28**	0.22
Mother's age at birth	15-19 years	**0*****	**0*****	1	1	**1*****	0*	0**
	20-24 years	**0.06**	**0.08**	1.21	2.04	**0.45**	0.07	-0.10
	25-29 years	**-0.05**	**-0.26**	1.10	1.89	**0.32**	0.01	-0.28
	30-34 years	**-0.05**	**-0.37**	1.48	1.46	**0.27**	0.01	-0.44
	35-39 years	**-0.26**	**-0.77**	1.08	1.72	**0.23**	-0.19	-0.40
	40-49 years	**-0.07**	**-0.21**	1.18	1.72	**0.22**	0.02	-0.17
Mother's marital status	Ever married	0*	0	1*	1	1	0**	0
	Never married	0.14	0.22	0.68	0.79	1.21	0.20	-0.10
Family SEP at birth	Higher non-manual	0	0	1	1	1	0*	0
	Med/low non-man/self-empl	-0.15	-0.22	1.03	1.15	1.24	-0.24	0.13
	Higher manual	-0.13	-0.22	0.92	0.98	1.72	-0.24	0.09
	Lower manual	-0.12	-0.20	0.93	1.08	1.61	-0.25	0.08
	Farmer	-0.08	-0.15	0.84	1.07	1.34	-0.14	0.04
	House son/daughter	-0.18	-0.31	0.94	1.10	1.08	-0.27	0.07

*p<0.05, **p<0.01, ***p<0.001, with bold font used for variables significant at p<0.01. SEP = socio-economic position. [a =] Regression coefficients from linear regression [b =] Odds ratio from logistic regression. All analyses adjust for year of birth by one-year age band, and all p-values are from tests for heterogeneity.

Supplementary Table 4: Pathways to reproductive success after adjusting for adult education and household income

		Total population			Males			Females		
		Ever married if survived to age 50 [b]	**No. children if survived to 50 & married**[a]	**No. grand-children if ever had children, adjusting for no. children**[a]	**Ever married if survived to age 50** [b]	**No. children if survived to 50 & married**[a]	**No. grand-children if ever had children, adjusting for no. children**[a]	**Ever married if survived to age 50** [b]	**No. children if survived to 50 & married**[a]	**No. grand-children if ever had children, adjusting for no. children**[a]
N		11563	10510	9694	5954	5328	4937	5609	5182	4757
Sex	Male	**1*****	0	**0*****						
	Female	**1.48**	0.02	**0.15**						
Standardised birthweight for gestational age	Quintile 1 (smallest)	**1****	0	0	**1*****	0	0	1	0	0
	Quintile 2	**1.08**	0.02	0.02	**1.28**	0.01	-0.14	0.84	0.02	0.18
	Quintile 3	**1.51**	0.01	0.07	**1.85**	-0.02	-0.11	1.15	0.04	0.24
	Quintile 4	**1.22**	-0.02	-0.03	**1.48**	-0.01	-0.17	0.93	-0.03	0.11
	Quintile 5 (largest)	**1.30**	0.02	0.08	**1.52**	0.03	-0.01	1.02	0.01	0.16
Preterm birth	Term	[1]	0	0	**1****	0	0	1	0	0
	Preterm	[0.83]	0.01	0.21	**0.74**	0.07	0.25	1.05	-0.03	0.17
	Very preterm	[0.59]	-0.06	-0.11	**0.36**	-0.05	0.34	1.61	-0.04	-0.34
Birth multiplicity	Singleton	1	0	0	1	0	0	1	0	0
	Twin/triplet	0.95	0.00	0.05	1.03	-0.12	0.06	0.81	0.09	0.02
Birth order (mother's parity)	1	[1]	**0****	**0****	1	0	0*	**1*****	**0*****	0*
	2-3	[1.17]	**0.07**	**0.05**	0.91	0.03	0.04	**1.57**	**0.10**	0.06
	4-5	[1.21]	**0.17**	**0.19**	0.92	0.11	0.06	**1.77**	**0.23**	0.33
	6-18	[1.44]	**0.20**	**0.28**	1.03	0.12	0.37	**2.40**	**0.30**	0.20
Mother's age at birth	15-19 years	**1*****	0	**0****	**1****	0	0	**1*****	**0*****	**0****
	20-24 years	**0.68**	-0.03	**-0.05**	**0.84**	-0.12	-0.04	**0.45**	**0.07**	**-0.09**
	25-29 years	**0.47**	-0.06	**-0.19**	**0.57**	-0.12	-0.14	**0.33**	**0.01**	**-0.27**
	30-34 years	**0.47**	-0.08	**-0.31**	**0.63**	-0.16	-0.22	**0.28**	**0.01**	**-0.43**
	35-39 years	**0.38**	-0.18	**-0.29**	**0.48**	-0.16	-0.22	**0.24**	**-0.20**	**-0.38**
	40-49 years	**0.35**	-0.16	**-0.28**	**0.44**	-0.34	-0.52	**0.23**	**0.02**	**-0.15**
Mother's marital status	Ever married	[1*]	0*	0	**1****	0	0	1	**0****	0
	Never married	[0.79]	0.13	-0.11	**0.61**	0.04	-0.12	1.13	**0.20**	-0.12
Family SEP at birth	Higher non-manual	[1]	**0*****	0	1	**0****	0	1	0	0
	Medium/low non-manual or self-employed	[1.12]	**-0.09**	-0.01	1.10	**-0.04**	-0.03	0.93	-0.16	0.00
	Higher manual	[1.27]	**-0.15**	-0.08	1.07	**-0.16**	-0.12	1.24	-0.16	-0.04
	Lower manual	[1.12]	**-0.15**	-0.02	0.91	**-0.15**	-0.01	1.13	-0.16	-0.06

	Farmer	[0.91]	**0.02**	-0.07	0.74	**0.07**	-0.05	0.94	-0.06	-0.10
	House son/daughter	[0.93]	**-0.15**	-0.05	0.87	**-0.11**	-0.06	0.78	-0.19	-0.07
Highest educational level, 1960	Elementary	[1*]	**0*****	**0*****	**1*****	**0****	**0*****	**1*****	0*	0*
	Senior	[1.42]	**0.05**	**-0.18**	**2.65**	**-0.06**	**-0.24**	**0.41**	0.31	-0.08
	Post-senior	[1.42]	**0.32**	**-0.56**	**2.89**	**0.26**	**-0.53**	**0.40**	0.28	-0.65
Equivalised household disposable income, 1970	0-9999 SEK		**[0***]**	0		**0*****	0		**0****	0
	10000-14999 SEK		**[-0.19]**	-0.11		**-0.16**	-0.14		**-0.23**	-0.08
	15000-19999 SEK		**[-0.20]**	-0.02		**-0.15**	0.05		**-0.25**	-0.08
	20000-29999 SEK		**[-0.19]**	-0.02		**-0.10**	0.06		**-0.25**	-0.07
	30000+ SEK		**[0.08]**	-0.09		**0.29**	-0.03		**-0.15**	-0.10

*p<0.05, **p<0.01, ***p<0.001, with bold font used for variables significant at p<0.01. SEP = socio-economic position. SEK = Swedish Krona. Shaded cells represent variables not entered into the analysis. All analyses adjust for year of birth by one-year age band, and all p-values are from tests for heterogeneity. Variables presented in square brackets showed significant evidence (p<0.05) of an interaction with sex.