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Be Fruitful and Multiply?
Moderate Fecundity and Long-Run Reproductive Success*

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Abstract

This research presents the first evidence that moderate fecundity maximized long-run reproductive success within the human species. Exploiting an extensive genealogy record for nearly half a million individuals in Quebec during the seventeenth and eighteenth centuries, the study traces the number of descendants of early inhabitants in the subsequent four generations. Using the time interval between the date of marriage and the first live birth as a measure of reproductive capacity, the research establishes that while a higher fecundity is associated with a larger number of children, an intermediate level maximizes long-run reproductive success. The finding further indicates that the optimal level of fecundity was below the population median, suggesting that the forces of natural selection favored individuals with a lower level of fecundity. The research lends credence to the hypothesis that during the Malthusian epoch, natural selection favored individuals with a larger predisposition towards child quality, contributing to the onset of the demographic transition and the evolution of societies from an epoch of stagnation to sustained economic growth.

Keywords Demography, Evolution, Natural Selection, Fecundity, Quantity-Quality Trade-Off, Long-Run Reproductive Success

JEL Classification Codes J10, O10

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1 Introduction

The transition from an epoch of stagnation to an era of sustained economic growth has triggered one of the most significant transformations in the course of human history. While living standards in the world economy stagnated during the millennia preceding the Industrial Revolution, income per capita has experienced an unprecedented tenfold increase over the past two centuries, profoundly altering the level and distribution of education, health, and wealth across the globe.[1]

Over most of human existence, the process of development was marked by Malthusian stagnation. The Malthusian pressure has governed the evolution of the size of the population, and conceivably, via the forces of natural selection, has shaped the composition of the population as well. Lineages of individuals whose traits were complementary to the economic environment generated higher income, and thus a larger number of surviving offspring. The gradual increase in the representation of these growth-enhancing traits in the population has contributed to the process of development and the take-off from stagnation to growth (Galor, 2011).[2]

In particular, as hypothesized by Galor and Moav (2002), during the epoch of Malthusian stagnation, traits associated with higher valuation of offspring quality generated an evolutionary advantage and their representation in the population had gradually increased.[3] This selection process, and its effect on investment in human capital, stimulated technological progress and ultimately initiated a reinforcing interaction between investment in human capital and technological progress that triggered the demographic transition and brought about the state of sustained economic growth.

This research provides the first evidence that the forces of natural selection have favored moderate levels of fecundity within the human species. It further suggests that individuals with lower levels of fecundity than the median in the population generated an evolutionary advantage in the pre-demographic transition era. These findings lend credence to the hypothesis that during the Malthusian epoch, natural selection favored individuals with a larger predisposition towards child

[1] The transition from stagnation to growth and the associated divergence of income per capita across the globe have been the subject of intensive research in the growth literature in recent years (Galor and Weil, 1999, 2000; Galor and Moav, 2002; Hansen and Prescott, 2002; Lucas, 2002; Galor, 2011).

[2] Evidence suggests that evolutionary processes in the composition of existing genetic traits may be rather rapid, and major evolutionary changes have occurred in the human population over a short time period. Voight et al. (2006) detected about 700 regions of the human genome where genes have been reshaped by natural selection within the last 5,000 to 15,000 years. Moreover, Mekel-Bobrov et al. (2005) reports that a variant of the gene ASPM (a specific regulator of brain size in the lineage leading to Homo sapiens) arose in humans merely about 5800 years ago and has since swept to high frequency under strong positive selection. Other notable evidence suggests that lactose tolerance was developed among Europeans and Near Easterners since the domestication of dairy animals in the course of the Neolithic revolution, whereas in regions that were exposed to dairy animals in later stages, a larger proportion of the adult population suffers from lactose intolerance. Furthermore, genetic immunity to malaria provided by the sickle cell trait is prevalent among descendants of Africans whose engagement in agriculture improved the breeding ground for mosquitoes and thereby raised the incidence of malaria, whereas this trait is absent among descendants of nearby populations that have not made the transition to agriculture (Livingstone, 1958; Wiesenfeld, 1967; Durham, 1982).

[3] For simulation of the theory see Collins et al. (2014). The theory is applicable to either social or genetic intergenerational transmission of entrepreneurial traits. Vertical and horizontal transmissions of preferences expedite the speed of selection (Bisin and Verdier, 2000; Cavalli-Sforza, 1981; Boyd, 1988). The evolution of preferences in a given economic environment is surveyed by Weibull (1997); Bowles (1998).

quality, contributing to the onset of the demographic transition and the evolution of societies from an epoch of stagnation to sustained economic growth.[4]

The influential life-history theory in the field of evolutionary biology suggests that the fecundity of organisms reflects a trade-off in reproductive success between the quantity and quality of offspring. Central to the theory is the supposition that there exists an optimal level of fecundity beyond which fitness diminishes.[5] A negative association between the quantity and the quality of offspring has been documented in a wide variety of species, ranging from plants to humans. In particular, researchers uncovered an inverse relationship between the number of seeds and their size as well as between the quantity and quality of offspring within and across mammals.[6] Moreover, a trade-off between fertility and offspring survival probability and education in pre-industrial human societies has been documented.[7] The exploration of the static trade-off between quantity and quality of offspring, while confirming an important building block of life-history theory, does not generate direct evidence about the effect of fecundity on long-run reproductive success.[8]

This research presents evidence of the effect of fecundity on long-run reproductive success within the human species. Exploiting an extensive genealogy record for nearly half a million individuals in Quebec between the 17th and the 18th centuries, the study traces the number of descendants of early inhabitants of this Canadian province in the subsequent four generations. Using the time interval between the date of marriage and the first live birth as measure of fecundity over this period, the research establishes that while higher fecundity is associated with a larger number of children, an intermediate level maximizes long-run reproductive success.

The research finds that the maximal reproductive success is attained by couples with a moderate level of time to first birth (i.e., those whose first delivery occurs 69 weeks after their marriage, in comparison to a sample median of 52 weeks). In particular, in comparison to highly fertile couples whose first child is born 38 weeks after the marriage, those individuals have on average 0.4 fewer children, but 2.8 more grandchildren, 17 additional great-grandchildren, and 24 added great-great-grandchildren.

In light of the heritability of fecundity, the finding that the optimal level of time to first birth is above the population median suggests that in pre-industrial Quebec, the representation of individuals with lower levels of fecundity has gradually increased in the population.[9] Thus, plausibly, the forces of natural selection favored individuals characterized by a lower level of fecundity, and hence a larger predisposition towards a quality strategy. These findings support the hypothesis that dur-

[4]The interaction between human evolution and the process of development has been further explored theoretically by Lagerlöf (2007); Galor (2005); Galor and Michalopoulos (2012). The long lasting effects of these historically determined genetic factors on comparative development have been establish by Galor and Moav (2007); Spolaore and Wacziarg (2009); Ashraf and Galor (2013).

[5]See Lack et al. (1954); Cody (1966); Roff (1992); Stearns (1992).

[6]See Salisbury et al. (1942); Harper et al. (1970); Roff (2002); Charnov and Ernest (2006); Walker et al. (2008).

[7]See Hill and Hurtado (1996); Strassmann and Gillespie (2002); Gillespie et al. (2008); Meij et al. (2009); Becker et al. (2010).

[8]Furthermore, few attempts to examine the related phenomenon of the effect of the number of children on fitness are largely inconclusive (Kaplan et al., 1995; Borgerhoff Mulder, 2000).

[9]For the heritability of fecundity, see Christensen et al. (2003); Pettay et al. (2005); Ramlau-Hansen et al. (2008); Kosova et al. (2009).

ing the Malthusian epoch, natural selection favored individuals with a larger predisposition towards child quality, contributing to the onset of the demographic transition and the evolution of societies from an epoch of stagnation to sustained economic growth.

2 Empirical Strategy

Two major obstacles affect the identification of the effect of fertility on long-run reproductive success. First, omitted correlates of offspring quantity may also be correlated with offspring quality, obscuring the effect of quantity on long-run reproductive success. For instance, if variations in resources across individuals (e.g., income, education) enable some parents to produce more offspring of higher quality, failing to account for the effect of resources will obscure the effect of child quantity on long-run reproductive success. In particular, an observed monotonically positive relationship between the number of children and that of grandchildren may misleadingly be interpreted as indicative of the lack of an optimal level of quantity beyond which fitness diminishes.

Second, reverse causality from offspring's quality to the aggregate quantity of offspring may obscure the presence or the absence of an optimal level of fecundity beyond which fitness diminishes. For instance, the adverse effect of low offspring quality on the offspring survival rate may contribute to the total number of offspring born (via the child replacement channel), generating a negative correlation between the long-run reproductive success and the quantity of offspring that has no bearing on the presence or the absence of an optimal level of quantity beyond which fitness diminishes.

This research mitigates these major hurdles by focusing on the effect of fecundity, rather than fertility, on reproductive success. Furthermore, it designs an empirical strategy that exploits the inherent uncertainty in the process of human reproduction to identify the effect of fecundity on reproductive success. In particular, in light of the social norm observed in pre-industrial Quebec, in which marriage marked the intention to conceive, the research exploits variation in the random component of the time interval between the date of first marriage and the first birth (TFB) to capture the effect of fecundity on fitness.

Indeed, as depicted in Figure 1, a marriage over this period signaled a deliberate attempt conceive. A sharp spike in birth rates occurs starting in the 35th week after marriage and nearly a third of births occurs within the 36–44 weeks time interval.[10] Furthermore, premarital conception is insignificant, reflecting possibly an adherence to the existing social and religious norms. In particular, only 7.9 percent of the births over this period occurred within 35 weeks of marriage, and the incidence of premature births suggests that even this small fraction overstates the share of babies conceived prior to marriage.[11]

[10]Full term babies are born upon 38 weeks of gestation. Nevertheless, pregnancy is considered at term if the gestation period is within the interval 36-40 weeks. However, since the marriage age may coincide with the ovulation period and may occur at most 4 weeks before it, time to first birth within the interval 36–44 weeks would correspond to babies born at term.

[11]In the sample of all 59,238 mothers, 3.2 percent of births occurred prior to the marriage date, 5.5 percent of the births occurred after two years and 38 weeks of marriage (i.e., two years after first conception), and 1.6 percent

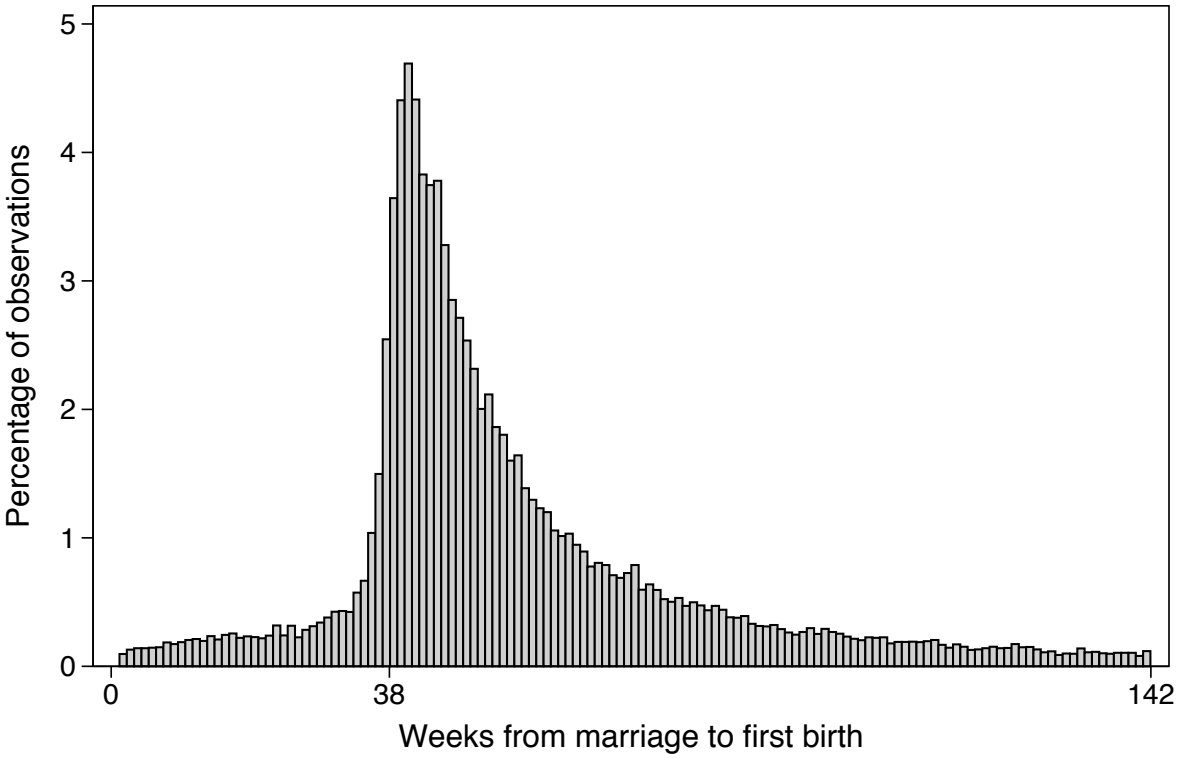

Figure 1: The histogram depicts the durations (in weeks) from first marriages to first births of 53,154 mothers in Quebec between the 17th and the end of the 18th century who gave birth between the 7th and 728th day of their marriage date.

Since fecundity reflects genetic and socio-environmental factors, TFB is affected by genetic predisposition, socio-environmental conditions, as well as the realization of random elements that affect conception. Accounting for a range of genetic and socio-environmental confounding factors that may affect the time to first birth, reproductive success, and the quality of offspring, the study attempts to isolate the effect the random variations in TFB across individuals. In particular, genetic, as well as cultural and socio-economic factors that may affect fecundity are accounted for by the inclusion of Maternal Founder fixed effects. Namely, the effect of fecundity on reproductive success is identified based on variations in reproductive success among siblings, capturing the similarities in the genetic predisposition of these genetically linked individuals, as well as their cultural and socio-economic proximity.

Additional confounding variations between siblings are accounted for by the inclusion of dummies for their marriage age, birth year, stoppage age, gender, and literacy. Furthermore, additional control variables include the geographic location at birth and death, birth order, month of birth,

of births occurred within one week of marriage (reflecting possibly a tendency of mothers who gave birth before marriage to baptize their firstborn at or shortly after their wedding date).

month of birth of the firstborn, number of marriages, and immigration and emigration status of the spouse, for each head of lineage.

3 Data and Main Variables

This section sets the stage for the empirical validity of the hypothesis that higher fecundity in the pre-demographic transition era was associated with a larger number of children, while an intermediate level maximized long-run reproductive success. Furthermore, the potential mechanisms that could generate the observed patterns are explored.

3.1 Data

The data is based on the demographic history of Quebec, using the reconstructed genealogy based on the entire parish registers of Quebec, covering 471,412 individuals from the beginning of the French colonization in the 17th century to the turn of the 19th century. The data covers all parishes of Quebec, and thus in light of negligible inter-provincial migration, intra-provincial migration does not prevent the tracking of reproductive success of individuals over several generations. Indeed, more than 94% of these individuals were born and died in Quebec. The analysis focuses on the reproductive success of individuals born in Quebec in the thirty-year period 1651–1680 and died in the province, whose TFB is at least 38 weeks.[12]

The focus on the reproductive success of heads of lineages born in the time period 1651–1680 permits tracing of descendants of these individuals in the subsequent four generations, while accounting for the Maternal Founder fixed effects.[13] Moreover, over this time interval, the identity of the mother is known for a sufficiently large number of individuals born, permitting the identification based on Maternal Founder fixed effects (i.e., identify the effect of fecundity on reproductive success based on variation across siblings, as opposed to the population as a whole).[14]

Furthermore, immigrants among heads of lineages are excluded from the sample for two reasons. First they may differ systematically from natives, reflecting the circumstances that led to their decision to immigrate as well as the effects of immigration on their socio-economic status and thus their reproductive success. Second, reproduction of immigrants prior to their arrival to Quebec is unknown. Similarly, emigrants are excluded as well since they may possess unique attributes and their subsequent marriages and births outside of Quebec are not observed.

[12] 11% of individuals in this subset of head of lineages whose first marriage date is unknown or whose firstborn's birth date is unknown are excluded from the sample.

[13] Since 91% of individuals born prior to 1650 were immigrants, whose maternal identity is unknown (in comparison to 29% (immigrants?) of those born in the thirty-year period 1651–1680), a focus on the previous 30-year interval, 1621-1650, will reduce the number of observations that satisfy the sample conditions to 71, as opposed to 2,657, which would not permit a meaningful statistical analysis.

[14] All children of heads of lineages, virtually all grandchildren, and most of the descendants in the third and the fourth generations are observed. In particular, fewer than 3% of the head of lineages that satisfy the sample selection criteria produced a birth after age 60, implying that fewer than 0.1% of lineages produced a grandchild after 120 years. Systematic association between the birth year of the head of the lineage and the number of unobserved descendants in the third and fourth generations are accounted for by the inclusion dummies for the birth year of the heads of lineages.

The study focuses on individuals whose time from first marriage to first birth is at least 38 weeks.[15] Finally, the study follow the convention in the literature (e.g. Milot et al. (2011)) and restricts the sample to individuals whose time to first conception is less than 2 years, excluding 11% of this subset.[16] This further restriction is designed to mitigate the effect of extreme values of time to first birth (some of which may reflect measurement errors), that could possibly distort the quadratic estimation. Thus the analysis focuses on the reproductive success of 2,657 heads of lineages in the thirty-year period 1651–1680 that satisfy the entire sample restrictions.[17]

3.2 Main Variables

3.2.1 Dependent and Independent Variables

In the main analysis that explores the effect of TFB on reproductive success, the dependent variable is the number of offspring of each head of lineage in the subsequent four generations (i.e., children, grandchildren, great-grandchildren and great-great-grandchildren). In the additional analysis that examines the mechanism through which TFB affects long-run reproductive success, the dependent variables are the number of children surviving to the average marriage age, and the fraction of literate children amongst children with known literacy status. The independent variable throughout the analysis is time interval between the first marriage date of the head of a lineage and the birth date of the individual's first child (TFB).[18]

3.2.2 Maternal Founder Fixed Effects

The effect of fecundity on reproductive success may be affected by variation in the genetic predisposition among genetically distinct individuals, as well as the variation in cultural and socio-economic background. Hence, similarities in the genetic, cultural, and socio-economic characteristics across siblings within each household are exploited to isolate the effect of random variation in TFB on reproductive success. Accounting for Maternal Founder fixed effects, as well as the confounding factors underlined below, the analysis explores the effect of random variation in TFB on long-run reproductive success within lineages headed by siblings, as opposed to variation across all heads of lineages.

[15] For 8.2 percent of the individuals in the sample of non-migrating heads of lineages whose first born date of birth is unknown, it is estimated to be one week prior to the date of baptism.

[16] The average time to first birth in the sample is about 62 weeks, exceeding the median of about 52 weeks, and thus reflecting a long right tail of the distribution of time to first birth.

[17] The summary statistics for this sample can be found in Table A.1. In addition, it should be noted that only 80 individuals that satisfy the sample selection criteria were born in Quebec before 1650.

[18] In couples where neither spouse remarried, TFB is identical for the husband and the wife. Nevertheless, given that the frequency of remarriage over this period is substantial, reflecting in part a considerable mortality rate, TFB and the number of offspring of each spouse often differ. The correlation in reproductive success between husband and wife sharing the same firstborn, and therefore the same TFB, is accounted for by clustering the standard errors for heads of lineages sharing the same firstborn.

3.2.3 Control Variables

The analysis accounts for the confounding effects of the marriage age, birth year, stoppage age, literacy, and the maternal identity, for each head of lineage. Furthermore, additional control variables include the geographic location at birth and death, birth order, month of birth, month of birth of the firstborn, number of marriages, and immigration and emigration status of the spouse, for each head of lineage.

The confounding effects of the marriage age on affluence, fecundity, and reproduction of the head of lineage is accounted for by the inclusion of dummy variables indicating the marriage age of heads of lineages. The marriage age is associated with reproductive success through three channels. First, fecundity is affected by age.Baird et al. (2005) Second, the marriage age affects the length of the reproductive period of the couple. Third, in the pre-demographic transition era that corresponds to our sample, marriage age was inversely related to the affluence of the individuals, and marriage age and its potential association with affluence could have an independent effect on long-run reproductive success.

The time-path of socioeconomic and demographic factors may differentially affect fecundity and reproductive success across cohorts of heads of lineages. These confounding factors are accounted for by the inclusion of dummy variables indicating the birth year of heads of lineages. The affluence, fecundity, and reproductive success of heads of lineages may be affected by the socioeconomic and demographic conditions during their lifetime, as partly captured by their birth year.[19]

Variations in socioeconomics and physiological factors across heads of lineages may generate variation in the length of the reproductive period that may obscure the effect of TFB on reproduction. In particular, conditional on the marriage age, the age at last delivery determines the length of the reproductive period. Hence, dummy variables indicating the stoppage age of heads of lineages, in addition to the marriage age, are introduced to account for this confounding factors, permitting the study to capture the effects of TFB on fertility, for a given length or reproductive period.[20]

The human capital attainment that may reflect the socioeconomic status of heads of lineages may affect their TFB and reproductive success. This confounding factor is partly accounted for by the inclusion of the literacy status of heads of lineages, inferred from the existence of a signature, in contrast to a mark, on the marriage certificate.

Additional confounding variations between head of lineages are accounted for by the inclusion of dummies capturing gender, geographic location at birth and death, birth order, month of birth, month of birth of the firstborn, number of marriages, and immigration and emigration status of the spouse.

[19] In addition, the inclusion of birth year dummies mitigates the potential systematic associations between the birth year and the number of unobserved descendants after three or four generations.

[20] As depicted in Figure A.1, the stoppage age over this period marked the decline in fecundity and onset of sterility associated with age-related infertility and onset of menopause, with a modal stoppage age of 41.

4 Empirical Analysis

This section examines the proposed hypothesis that higher fecundity in the pre-demographic transition era was associated with a larger number of children, while an intermediate level maximized long-run reproductive success. The examination proceeds in two stages. The empirical regularities that emerge from the data are examined initially semi-parametrically, using cubic spline regression models, followed by OLS regressions models.

4.1 Semi-Parametric Analysis

The proposed hypothesis is confirmed initially using restricted cubic spline regression models. It establishes that while a higher fecundity is associated with a larger number of children, an intermediate level maximizes long-run reproductive success.[21] The effect of TFB of heads of lineages on their number of descendants in the subsequent four generations, accounting for the marriage age, birth year, and the stoppage age of heads of lineages, is depicted in Figure 2. In line with the proposed hypothesis, panel A shows an approximately linear negative partial effect of TFB on the number of children, confirming the conventional presumption that *ceteris paribus*, a short time to first birth in the pre-demographic transition era increased the number of children. In contrast, as hypothesized, an intermediate TFB maximizes long-run reproductive success. In particular, panel B depicts a hump-shaped relation between TFB of the heads of the lineages and their number of grandchildren. The optimal TFB is 62 weeks and it is associated with 44 grandchildren. Panels C and D reveal a similar a hump-shaped relation between TFB of the heads of the lineages and their great-grandchildren and great-great-grandchildren. The optimal TFB of heads of lineages for reproductive success in the 3rd generation is 65 weeks and it is associated with 179 great-grandchildren, whereas the optimal TFB of heads of lineages for reproductive success in the 4rd generation is 67 weeks and is associated with 301 great-great-grandchildren.

Thus, Figure 2 shows that, in accordance with the proposed hypothesis, the TFB of the head of lineage has a monotonically negative effect on the number of children and a hump-shaped effect on the number of grandchildren, great-grandchildren and great-great-grandchildren.[22] Thus, heads of lineages with an intermediate level of TFB achieved the maximal number of descendants in the long run, despite having a smaller number of children relative to those with lowest TFB.

4.2 Econometric Model

The negative relationship between TFB of the head of lineage and the number of children as well as the hump-shaped relationship between TFB of the head of lineage and long-run reproductive success is further assessed by estimating a series of quadratic regression models. First, the effect of

[21] The use of multivariate LOWESS results in a similar qualitative pattern.

[22] Figure A.2 in the appendix depicts a scatterplot of the conditional means of the number of descendants by bins.

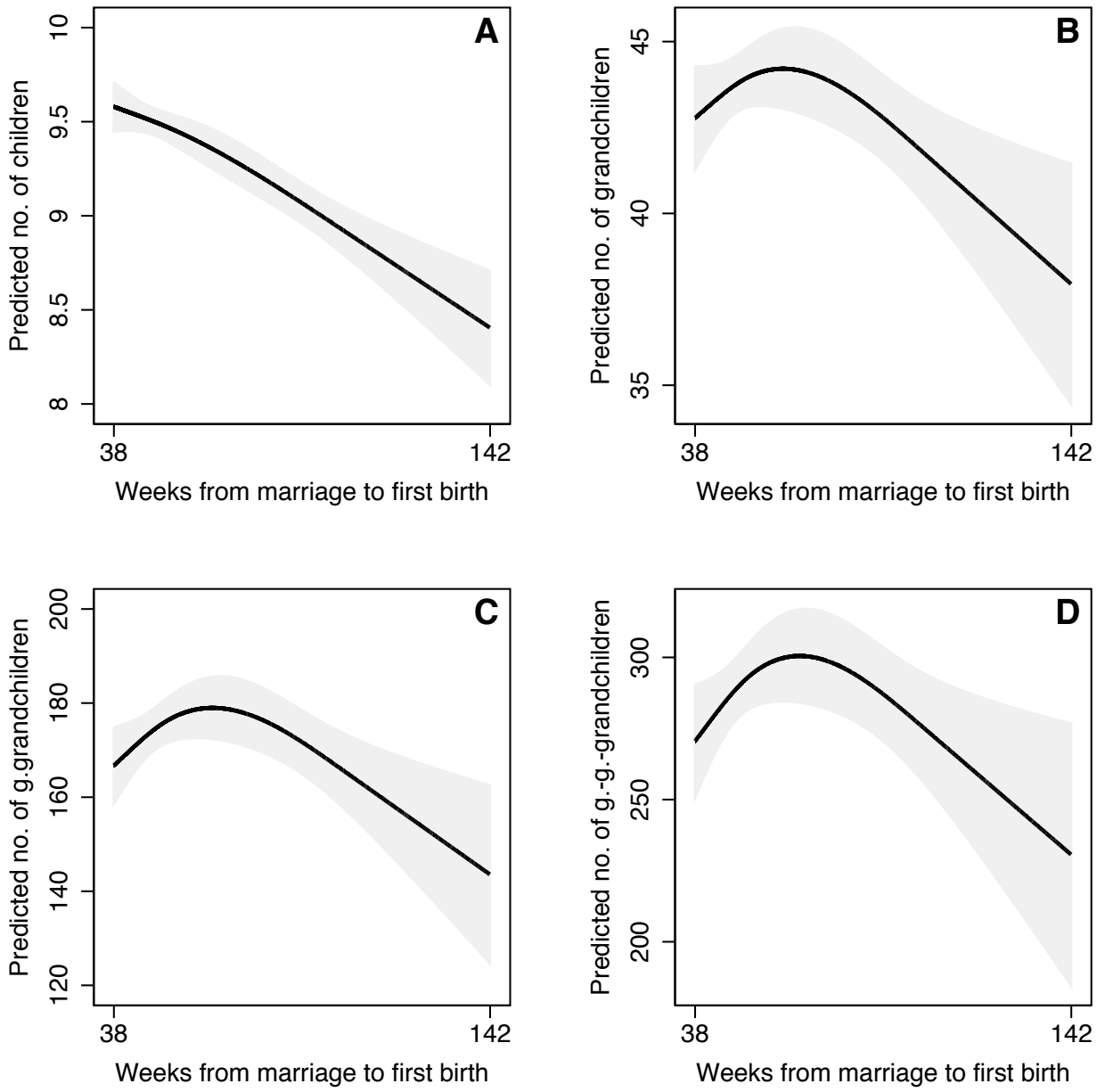

Figure 2: Predicted number of descendants with 90% confidence interval ($n = 2{,}657$) as a function of TFB based on restricted cubic splines with three knots (following the methodology of Harrell (2001)). Dummies indicating the marriage and stoppage age are included in the underlying regressions. (A) Number of children. (B) Number of grandchildren. (C) Number of great-grandchildren. (D) Number of great-great-grandchildren.

TFB of the head of lineage on the number of children is estimated using the OLS regression model:

$$\ln D_{i,1} = \beta_{0,1} + \beta_{1,1} TFB_i + Z_i \beta_{2,1} + \varepsilon_{i,1},$$

where $D_{i,1}$ is the number of children (i.e., offspring in generation 1) born to head of lineage i; TFB_i is the time from the first marriage to the first birth of the head of lineage i; Z_i is a vector of control variables capturing the characteristics of the head of lineage i; and $\varepsilon_{i,1}$ is an error term clustered at the level of heads of lineages sharing the same firstborn. The coefficient of interest is $\beta_{i,1}$. The tested hypothesis is that $\beta_{i,1} < 0$, i.e., TFB of the head of lineage negatively affects the number of children.

Second, the effect TFB of the head of lineage and long-run reproductive success is estimated using the OLS regression model:

$$\ln D_{i,t} = \beta_{0,t} + \beta_{1,t} TFB_i + \beta_{2,t} TFB_i^2 + Z_i \beta_{3,t} + \varepsilon_{i,t},$$

where $D_{i,t}$ is the number of descendants that the head of household i, has in the subsequent three generations t, $t = 2, 3, 4$; TFB_i is the time from the first marriage to the first birth of the head of lineage i; Z_i is a vector of control variables capturing the characteristics of the head of lineage i; and $\varepsilon_{i,t}$ is an error term clustered at the level of heads of lineages sharing the same firstborn.[23] The coefficients of interest are $\beta_{1,t}$ and $\beta_{2,t}$. The tested hypothesis is that $\beta_{1,t} > 0$ and $\beta_{2,t} < 0$, i.e., TFB has a hump-shaped effect on the number of grandchildren, great-grandchildren and great-great-grandchildren.

4.3 Estimation based on Variation across all Heads of Lineages

The baseline OLS estimates of the effect TFB of the head of lineage on reproductive success are presented in Tables 1 and 2, accounting for the marriage age, birth year, and the stoppage age of heads of lineages. The initial estimates in Tables 1 are based on variation in TFB across all head of lineages, whereas those in Table 2 accounts for Maternal Founder fixed effects fixed effects, and thus presents estimates based on variation in TFB within head of lineages that are originated from the same mother. The results are depicted in Figures A.3–A.4.

Consistently with the first element of proposed hypothesis, and the pattern depicted in Figure 2, panel A, column 1 establishes a highly significant negative association between TFB of heads of lineages and the number of children. An increase in the TFB by one year results in a reduction of 0.069 in the log number of children. In particular, an increase in TFB from 38 weeks to 1 year and 38 weeks would result in a reduction of approximately 0.65 children.[24]

[23] To ensure that the logarithmic transformation is defined for extinct lineages, 1 is added to the number of descendants in all generations. The results are robust to alternative methods that could account for extinct lineages. In particular, Table 3–4 demonstrates that the results are robust to the use of a GLM model with a negative binomial distribution and a logarithmic link function.

[24] Throughout the analysis, estimates on the original scale of numbers of descendants are corrected for retransformation bias in accordance with Duan (1983).

Table 1: The effect of the time to first birth (TFB) on the number of descendants – baseline analysis

ln(descendants) in:	(1) Gen. 1	(2) Gen. 2	(3) Gen. 3	(4) Gen. 4	(5) Gen. 1	(6) Gen. 2	(7) Gen. 3	(8) Gen. 4	(9) Gen. 1	(10) Gen. 2	(11) Gen. 3	(12) Gen. 4
TFB	-.069***	.493**	.955***	1.320***	-.066***	.424*	.821**	1.144**	-.067***	.372	.716**	1.012**
	(.011)	(.242)	(.370)	(.473)	(.011)	(.238)	(.360)	(.460)	(.011)	(.236)	(.356)	(.456)
TFB^2		-.173**	-.318***	-.441***		-.156**	-.286**	-.399***		-.143*	-.259**	-.365**
		(.078)	(.117)	(.150)		(.076)	(.114)	(.147)		(.076)	(.113)	(.145)
Literate					-.051***	.334***	.655***	.919***	-.051***	.329***	.644***	.906***
					(.012)	(.051)	(.081)	(.104)	(.012)	(.051)	(.080)	(.103)
Male									.007	.228***	.458***	.577***
									(.013)	(.048)	(.074)	(.090)
Number of observations	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657
Adjusted R^2	.823	.461	.357	.316	.825	.479	.390	.355	.824	.483	.399	.363
Joint sign. of TFB & TFB^2		.055	.02	.012	0	.049	.023	.013		.044	.024	.013
Maximizing TFB		1.422	1.5	1.496		1.355	1.436	1.432		1.300	1.384	1.385
Lower limit of 90% CI		.952	1.257	1.286		.491	1.075	1.137		-.407	.825	.967
Upper limit of 90% CI		1.63	1.673	1.657		1.571	1.616	1.596		1.532	1.577	1.559
Significance of hump-shape		.013	.003	.001		.02	.006	.003		.03	.011	.006

This table presents the results of a series of OLS regressions of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2. Birth year, marriage age and stoppage age dummies are included as controls. A dummy indicating unknown literacy is included in the regressions underlying column 5–12. Standard errors clustered at the level of the firstborn are reported in parentheses. * p <0.10, ** p <0.05, *** p <0.01.

The positive association of an intermediate level of TFB and long-run reproductive success is confirmed in columns 2–4, resembling the pattern depicted in Figure 2, panel A–D. Column 2 establishes a significant quadratic relationship between TFB of heads of lineages and the number of grandchildren. In particular, the first-order effect of the quadratic expression is positive and significant at the 5% level and the second-order effect of the quadratic expression is negative and significant at the 5% level. Moreover, an additional test establishes a significant hump-shaped relationship (p=0.013).[25]

Column 3 establishes a highly significant quadratic relationship between TFB of heads of lineages and the number of great-grandchildren. Moreover, an additional test establishes a significant hump-shaped relationship (p=0.003). Similarly, column 4 establishes a highly significant quadratic relationship between TFB of heads of lineages and the number of great-great-grandchildren. The first and second-order effects are both significant at the one percent level, and jointly significant (p=0.012). Moreover, an additional test establishes a significant hump-shaped relationship (p=0.001).

Columns 5–8 establish that the results are robust to the inclusion of parental literacy as a control variable. The highly significant negative association between TFB of heads of lineages and the number of children is maintained and the coefficient is rather stable (column 5). Furthermore, a significant quadratic relationship between TFB of heads of lineages and the number of descendants in the second, third, and fourth generations is stable, although somewhat less significant (column 6-8). Moreover, the test for the hump-shaped relationship remains significant. In particular, it is highly significant for great-great grandchildren (p=0.003). Literacy is negatively associated with the number of children (column 5), indicating a possible quality-bias of literate parents. Furthermore, literacy is positively associated with long-run reproductive success (columns 6–8). As will become apparent in Table 6, literacy (and its potential association with a quality bias) is positively associated with the number of surviving children, and is thus rewarding in the long run.

Furthermore, columns 9–12 establish that the results are robust to the inclusion of a control for gender. The highly significant negative association between TFB of heads of lineages and the number of children is maintained and the coefficient is rather stable (column 5). Furthermore, a quadratic relationship between TFB of heads of lineages and the number of descendants is only marginally significant in the second generation, but is stable and significant at the 5% level in the third and fourth generations (column 6-8). Moreover, the test for the significance of hump-shaped relationship remains significant in all configurations. In particular, it is highly significant for great-great grandchildren (p=0.006).

4.4 Estimation based on Variation within Head of Lineages traced to the same Maternal Founder

The effect of fecundity on reproductive success may be affected by variation in the genetic predisposition among genetically distinct heads of lineages, as well as the variation in cultural and

[25] See Lind and Mehlum (2010).

Table 2: The effect of the time to first birth (TFB) on the number of descendants – accounting for Maternal Founder fixed effects

ln(descendants) in:	(1) Gen. 1	(2) Gen. 2	(3) Gen. 3	(4) Gen. 4	(5) Gen. 1	(6) Gen. 2	(7) Gen. 3	(8) Gen. 4	(9) Gen. 1	(10) Gen. 2	(11) Gen. 3	(12) Gen. 4
TFB	-.064***	.537*	.966**	1.148**	-.063***	.529*	.950**	1.131**	-.063***	.505*	.886**	1.067**
	(.016)	(.282)	(.430)	(.530)	(.016)	(.283)	(.432)	(.533)	(.016)	(.284)	(.431)	(.533)
TFB^2		-.188**	-.339**	-.422**		-.186**	-.334**	-.418**		-.179*	-.318**	-.401**
		(.091)	(.138)	(.173)		(.092)	(.138)	(.174)		(.092)	(.138)	(.174)
Literate					-.027	.031	.103	.137	-.027	.034	.109	.144
					(.020)	(.073)	(.107)	(.134)	(.020)	(.073)	(.106)	(.133)
Male									.005	.127	.331***	.332**
									(.021)	(.078)	(.115)	(.144)
Number of observations	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657
Adjusted R^2	.833	.567	.530	.539	.833	.568	.531	.539	.833	.568	.534	.541
Joint sign. of TFB & TFB^2		.096	.030	.023		.104	.033	.024		.112	.036	.024
Maximizing TFB		1.426	1.424	1.359		1.425	1.421	1.354		1.407	1.394	1.330
Lower limit of 90% CI		.837	1.049	.918		.791	1.024	.888		.584	.893	.761
Upper limit of 90% CI		1.696	1.62	1.553		1.703	1.620	1.550		1.688	1.6	1.532
Significance of hump-shape		.019	.007	.007		.021	.007	.008		.025	.010	.010

This table presents the results of a series of OLS regressions of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2. Birth year, marriage age and stoppage age dummies are included as controls. A dummy indicating unknown literacy is included in the regressions underlying column 5–12. Furthermore, dummies for individuals sharing the same mother are also included. Standard errors clustered at the level of the firstborn are reported in parentheses. * p <0.10, ** p <0.05, *** p <0.01.

socio-economic background. The study attempts to further isolate the random variations in TFB across head of lineages by accounting for common characteristics across heads of lineages originated from the same mother. Hence, similarities in the genetic, cultural, and socio-economic characteristics across siblings within each household are exploited to isolate the effect of random variation in TFB on reproductive success. Accounting for Maternal Founder fixed effects, as well as additional confounding factors, the analysis explores the effect of random variation in TFB on long-run reproductive success within lineages headed by siblings, as opposed to variation across all heads of lineages.

As established in Table 2, the qualitative results established in Table 1 are unaffected by the inclusion of Maternal Founder fixed effects. In particular, consistently with the first element of proposed hypothesis, column 9 establishes a highly significant negative association between TFB of heads of lineages and the number of children, accounting for the marriage age, birth year, the stoppage age, literacy status and gender of the heads of lineages. An increase in the TFB by one year results in a reduction of 0.063 in the log number of children. In particular, an increase in TFB from 38 weeks to 1 year and 38 weeks would result in a reduction of approximately 0.59 children.

The beneficial effects of an intermediate level of TFB on long-run reproductive success is confirmed in columns 10–12. They establish a significant hump-shaped effect of TFB of heads of lineages on the number of descendants in the third and fourth generations, accounting for the marriage age, birth year, the stoppage age, literacy status and gender of the heads of lineages. In particular, the first and second order terms are jointly significant at the 5% level for great-grandchildren and great-great-grandchildren. Moreover, the hump-shaped relationship for great-great-grandchildren is p=0.010.

Interestingly, the estimated effect of literacy on reproductive success diminishes and is insignificant, indicating that the Maternal Founder fixed effects indeed account for some of the variation in socioeconomic conditions across siblings.

The analysis suggests that the maximal reproductive success is attained by heads of lineages with a moderate TFB (i.e., those whose first delivery occurs 69 weeks after their marriage, in comparison to a sample median of 52 weeks), suggesting that the forces of natural selection had a positive effect on the median TFB in the population over this time period. In particular, in comparison to highly fertile couples whose first child is born 38 weeks after the marriage, those individuals have on average 0.36 fewer children, but 2.8 more grandchildren, 17.2 additional great-grandchildren, and 24.4 added great-great-grandchildren.

Thus, the regression analysis presented in Table 2 confirms the hypothesis that higher fecundity in the pre-demographic transition era was associated with a larger number of children, while an intermediate level maximized long-run reproductive success.

5 Robustness to Additional Attributes of Heads of Lineages

This section establishes the robustness of the qualitative results to a wide range of potential confounding factors, accounting for geographic location at birth and death, birth order, month of birth, month of birth of the firstborn, number of marriages, and immigration and emigration status of the spouse, for each head of lineage.

5.1 Spousal migration

Immigrants may differ systematically from natives reflecting the circumstances that led to their decision to immigrate as well as the effects of immigration on their socio-economic status and thus their reproductive success. Thus, the migration status of the first spouse may have affected the reproductive success of heads of lineages. In the sample, heads of lineages were neither immigrants nor emigrants. Nevertheless, 26.7% of their first spouses were immigrants and 0.9% were emigrants. To account for the potential effect spousal migration, dummy variables indicating the immigration and emigration status of heads of lineages are included in the regressions analysis performed in Tables 1 and 2. As established in Table A.2–A.3, the qualitative results are unaffected by the migration status of the first spouse of the head of lineage.

5.2 Remarriages

Some head of lineages and their spouses, remarried, possibly multiple times, reflecting in part a considerable mortality rate over this period. The formation of additional unions may affect the reproductive success of heads of lineages via various channels, reflecting possibly the health and socioeconomic circumstances that led to these remarriages, as well as the potential differential treatment of previous and new children in the newly formed household. To account for the effect of remarriages, dummy variables indicating the number of marriages experienced by each head of lineage are included in the regressions performed in Tables 1 and 2. As established in Table A.2–A.3, the qualitative results are unaffected by accounting for remarriages.[26]

5.3 Gender

Reflecting an earlier marriage age of women relative to men, the sample of heads of lineages born in the period 1651-1680 is unbalanced across gender. Although men on average married at a later age than women (i.e., 27.2 for men versus 19.5 for women), their average age at last delivery was higher (i.e., 46.5 for men versus 37.4 for women), and they remarried more often, resulting in a higher number of children per male (i.e., 9.9 for men versus 8.96 for woman). The effect of gender is directly accounted for as a control in the regressions performed in Tables 1 and 2. As an additional

[26] Excluding remarriages of head of lineages would reduce the sample size considerably and thus would affect the significance of the estimations. Nevertheless, the qualitative results would not be altered and the significance of the hump-shaped relationship would be significant at the 5% level in the presence of birth and death location dummies and birth year, marriage age and stoppage age dummies measured over longer time intervals, as needed, given the reduction in the sample size.

robustness check, Table A.4–A.5 demonstrate that splitting the sample into a sample for male and female has not effect on the qualitative results.[27]

5.4 Birth and Death parish

The parish of birth and death may affect TFB of heads of lineages and their reproductive success due to the influence of cultural and socioeconomic factors in a parish on the resources and preferences of heads of lineages. To account for the effect of these confounding geographical factors, dummy variables indicating the parish of birth and death of each head of lineages are included in the regressions performed in Tables 1 and 2. As established in Table A.6–A.7, the qualitative results are unaffected by accounting for these parish fixed effects.

5.5 Month of Marriage and Month of Birth of Firstborn

The month of marriage may affect TFB and reproductive success of heads of lineages due to influence of climatic conditions on resources, nutrition and human physiology. In addition, the month of birth of the firstborn may affect the resources of heads of lineages and thus their reproductive success. To account for these confounding seasonal factors, dummy variables indicating the month of marriage for each head of lineage and the months of birth of the first born of each head of lineage are included in the regression performed in Tables 1 and 2. As established in Table A.6–A.7, the qualitative results are unaffected by accounting for these seasonal factors.

5.6 Birth Order

The birth order of heads of lineages may affect their TFB and reproductive success due to its effect of their nourishment as children, physiology, intergenerational transfers of wealth, and therefore resources as adults. To account for the potential effect of birth order, a dummy variable indicating if the head of lineage is the first birth among individuals sharing the same mother is included in the regressions performed in Tables 1 and 2. As established in Table A.8–A.9, the qualitative results are unaffected by accounting for the firstborn status of heads of lineages. Moreover, the firstborn status has no significant effect on reproductive success. Furthermore, accounting for the entire birth order of each head of lineage does not alter the qualitative results.

5.7 Alternative Estimation Method

The negative relationship between TFB of the head of lineage and the number of children as well as the hump-shaped relationship between TFB of the head of lineage and long-run reproductive success is established using quadratic OLS regression models. Table 3–4 demonstrate that the

[27] Since the division of the sample into males and females results in a small number of heads of lineages sharing the same mother in each sample (on average 1.6 for men and 1.7 for women, versus on average 3.3 for the combined sample), the use of Maternal Founder fixed effects is practically infeasible.

Table 3: Robustness to GLM regression

ln(descendants) in:	(1) Gen. 1	(2) Gen. 2	(3) Gen. 3	(4) Gen. 4	(5) Gen. 1	(6) Gen. 2	(7) Gen. 3	(8) Gen. 4	(9) Gen. 1	(10) Gen. 2	(11) Gen. 3	(12) Gen. 4
TFB	-.081***	.319*	.691***	.781***	-.078***	.277	.646***	.758***	-.078***	.233	.575**	.684**
	(.012)	(.171)	(.225)	(.282)	(.012)	(.172)	(.229)	(.290)	(.012)	(.171)	(.229)	(.290)
TFB^2		-.121**	-.246***	-.289***		-.110**	-.233***	-.283***		-.098*	-.215***	-.264***
		(.055)	(.071)	(.089)		(.055)	(.072)	(.091)		(.055)	(.072)	(.091)
Literate					-.061***	.203***	.314***	.351***	-.061***	.201***	.311***	.349***
					(.013)	(.036)	(.050)	(.062)	(.013)	(.036)	(.050)	(.062)
Male									.009	.179***	.279***	.314***
									(.014)	(.034)	(.047)	(.059)
Number of observations	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657
Joint sign. of TFB & TFB^2		.014	.000	.000	.000	.014	.000	.000	.000	.010	.000	.000
Maximizing TFB		1.319	1.404	1.351		1.265	1.384	1.337		1.186	1.337	1.292

This table presents the results of a series of GLM regressions with negative binomial distributions and logarithmic link functions of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2. Birth year, marriage age and stoppage age dummies are included as controls. Standard errors clustered at the level of the firstborn are reported in parentheses. * p <0.10, ** p <0.05, *** p <0.01.

Table 4: Robustness to GLM regression – accounting for Maternal Founder fixed effects

ln(descendants) in:	(1) Gen. 1	(2) Gen. 2	(3) Gen. 3	(4) Gen. 4	(5) Gen. 1	(6) Gen. 2	(7) Gen. 3	(8) Gen. 4	(9) Gen. 1	(10) Gen. 2	(11) Gen. 3	(12) Gen. 4
TFB	-.071***	.499**	.869***	.872**	-.070***	.495**	.858***	.868**	-.071***	.466**	.794***	.822**
	(.014)	(.208)	(.283)	(.353)	(.014)	(.209)	(.283)	(.354)	(.014)	(.209)	(.284)	(.354)
TFB^2		-.173***	-.302***	-.332***		-.171**	-.298***	-.331***		-.164**	-.281***	-.320***
		(.067)	(.090)	(.113)		(.067)	(.090)	(.113)		(.067)	(.091)	(.113)
Literate					-.030*	.025	.048	.063	-.029*	.030	.059	.072
					(.017)	(.055)	(.074)	(.094)	(.017)	(.055)	(.075)	(.094)
Male					-.012	.085	.118	.115	.011	.135**	.272***	.260**
					(.018)	(.058)	(.077)	(.097)	(.018)	(.056)	(.078)	(.104)
Number of observations	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657
Joint sign. of TFB & TFB^2		.022	.002	.001		.025	.002	.001		.029	.003	.001
Maximizing TFB		1.44	1.439	1.312		1.444	1.440	1.310		1.420	1.411	1.283

This table presents the results of a series of GLM regressions with negative binomial distributions and logarithmic link functions of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2. Birth year, marriage age and stoppage age dummies are included as controls. Furthermore, dummies for individuals sharing the same mother are also included. Standard errors clustered at the level of the firstborn are reported in parentheses. * p <0.10, ** p <0.05, *** p <0.01.

qualitative results are robust to an alternative estimation method, using a generalized linear model (GLM) with a negative binomial distribution and a logarithmic link function.

6 Mechanism

There are two related mechanisms that could generate the observed the hump-shaped effect of TFB on reproductive success in the long run. First, the number of surviving offspring of heads of lineages may not be monotonic in the number of children born, reflecting an adverse effect of the number of children on their survival probability of each child. Second, the number of children may come on the account of their human capital, and thus conditional on survivability, it may affect their standard of living and ultimately their reproductive success.

6.1 Surving Offspring

The survival probability channel is explored in Table 5. As established in column 1, the number of children surviving to the mean marriage age of 23 is indeed associated non-monotonically with

Table 5: The effect of time to first birth (TFB) on the number of children surviving to the average marriage age

	(1)	(2)	(3)	(4)	(5)	(6)
ln(children surviving to average marriage age)						
TFB	.197*	.175*	.161	.275**	.268*	.253*
	(.106)	(.106)	(.105)	(.139)	(.140)	(.140)
TFB^2	-.088***	-.083**	-.079**	-.111**	-.110**	-.106**
	(.034)	(.034)	(.034)	(.045)	(.045)	(.045)
Literate		.079***	.078***		.044	.046
		(.023)	(.023)		(.036)	(.036)
Male			.062***			.080**
			(.022)			(.036)
Lineage fixed effects	No	No	No	Yes	Yes	Yes
Number of observations	2,657	2,657	2,657	2,657	2,657	2,657
Adjusted R^2	.611	.617	.618	.650	.651	.652
Joint sign. of TFB & TBF^2	.000	.000	.000	.003	.003	.003
Maximizing MFCI	1.112	1.059	1.018	1.231	1.223	1.196
Lower limit of 90% CI	.327	.030	-.256	.586	.518	.344
Upper limit of 90% CI	1.327	1.299	1.279	1.431	1.428	1.412
Significance of hump-shape	.005	.008	.010	.007	.008	.010

This table presents the results of a series of OLS regressions of the number of children surviving to the average marriage age (23 years) in generation t on time to first birth, i.e. TFB and TFB^2. Birth year, marriage age and stoppage age dummies are included as controls. A dummy indicating unknown literacy is included in the regressions underlying column 2, 3, 5 and 6. Furthermore, dummies for individuals sharing the same mother are also included in column 4–6. Standard errors clustered at the level of the firstborn are reported in parentheses. * p <0.10, ** p <0.05, *** p <0.01.

Table 6: The effect of time to first birth (TFB) on the fraction of literate children

	(1)	(2)	(3)	(4)	(5)	(6)
Share of literate children						
TFB	.392***	.317***	.294***	.347***	.323**	.305**
	(.106)	(.108)	(.108)	(.133)	(.133)	(.135)
Literate		1.376***	1.376***		.699***	.710***
		(.109)	(.109)		(.172)	(.172)
Male			.521***			.334
			(.122)			(.219)
Maternal Founder fixed effects	No	No	No	Yes	Yes	Yes
Number of observations	2,322	2,322	2,322	2,322	2,322	2,322

This table presents the results of a series of GLM regressions with binomial distributions and logit link functions of the fraction of literate children among children with known literacy status on time to first birth, i.e. TFB and TFB^2. Birth year, marriage age and stoppage age dummies are included as controls. A dummy indicating unknown literacy is included in the regressions underlying column 2, 3, 5 and 6. Furthermore, dummies for individuals sharing the same mother are also included in column 4–6. Standard errors clustered at the level of the firstborn are reported in parentheses. * p <0.10, ** p <0.05, *** p <0.01.

TFB of heads of lineages.[28] In particular, accounting for the marriage age, birth year, the stoppage age of heads of lineages, as well as gradually for their literacy status, gender, and Maternal Founder fixed effects, there is a significant and rather stable quadratic relationship between the TFB and the number of children surviving to the average marriage age. Moreover, the hump-shaped relationship is statistically significant ($p \leq 0.01$).

6.2 Education of Offspring

The education channel is investigated in Table 6. As established in column 1 and 2, TFB of heads of lineages has a highly significant positive association with the fraction of literate children, accounting for the marriage age, birth year, and the stoppage age of heads of lineages. As controls are gradually introduced to account for the confounding effects of the literacy status, gender, and Maternal Founder fixed effects of heads of lineages the positive coefficient remains stable and significant at the 5% level. Moreover, literacy of heads of lineages has a highly significant positive effect on the literacy of their children.[29]

7 Concluding Remarks

This research presents the first evidence that moderate fecundity maximized long-run reproductive success within the human species. Exploiting an extensive genealogy record for nearly half a

[28] The use of the number of married children as dependent variable generates qualitatively similar results.

[29] The estimated effect of the literacy of heads of lineages on their children's literacy diminishes by nearly 50%, one Maternal Founder fixed effects are accounted for, indicating the fixed effects account for some of the variation in socioeconomic conditions across siblings.

million individuals in Quebec during the seventeenth and eighteenth centuries, the study traces the number of descendants of early inhabitants in the subsequent four generations. Using the time interval between the date of marriage and the first live birth as a measure of reproductive capacity, the research establishes that while a higher fecundity is associated with a larger number of children, an intermediate level maximizes long-run reproductive success.

The research further indicates that the optimal level of fecundity was below the population median, suggesting that the forces of natural selection favored individuals with a lower level of fecundity. The research lends credence to the hypothesis that during the Malthusian epoch, natural selection favored individuals with a larger predisposition towards child quality, contributing to the onset of the demographic transition and the evolution of societies from an epoch of stagnation to sustained economic growth.

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A Distribution of stoppage ages

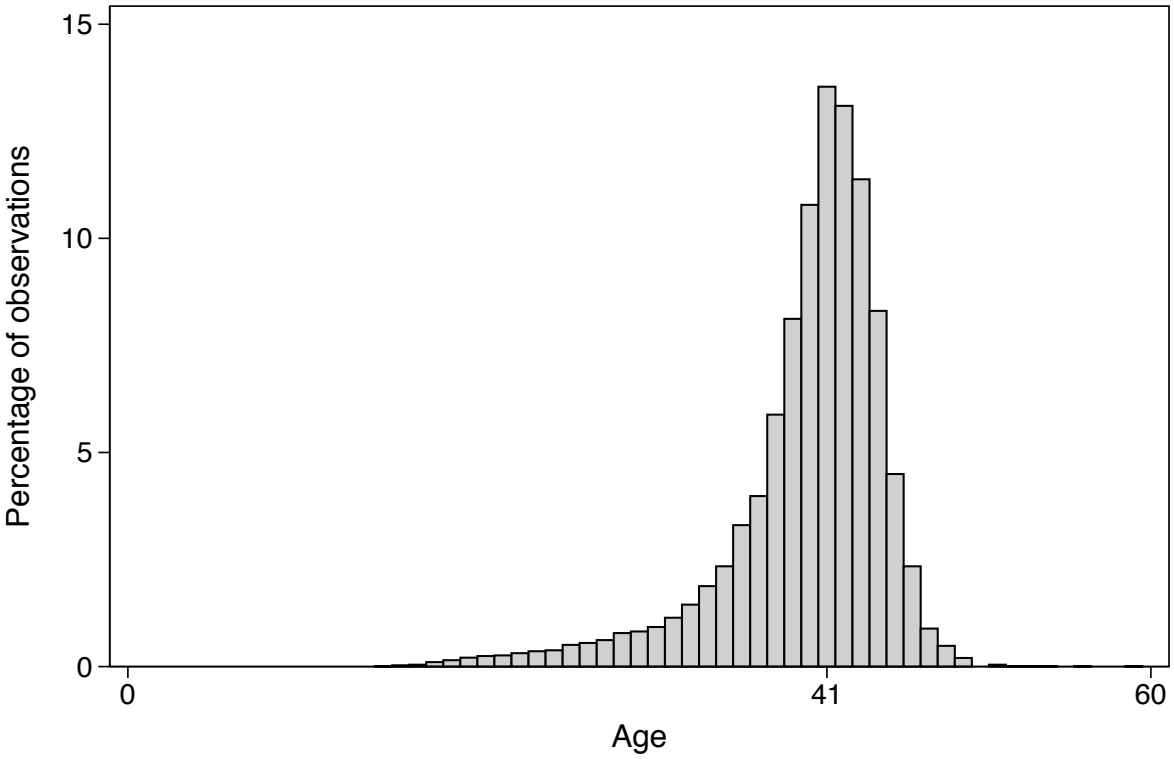

Figure A.1: The histogram depicts the age at last delivery of 13,411 once-married non-migrant mothers in Quebec born born before 1749 (and after 1624) who survived to age 50 and whose husband survived to age 50.

B Conditional means by bins

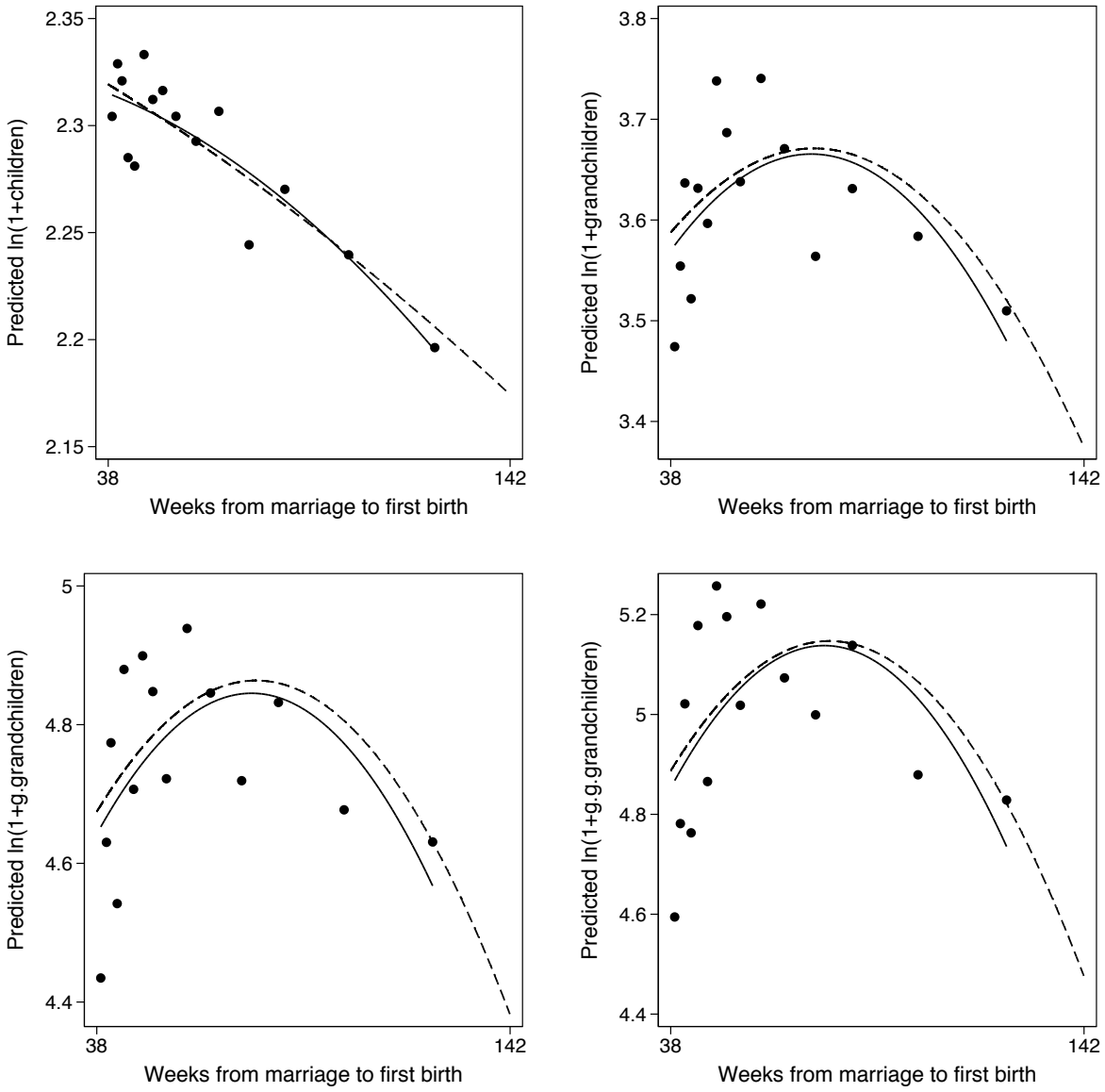

Figure A.2: Conditional means by bins ($n = 2{,}657$)

The figure depicts estimates of the mean of the transformed number of descendants conditional on the marriage age, the stoppage age and the birth year of the head of lineage. The sample is sorted by TFB and successively divided into 15 bins of approximately equal numbers of head of lineages. The median TFB in for each bin b, TFB_b is obtained. The figure depicts the expected value of $\ln(D_{b,t})$, where $D_{b,t}$ is the number of descendants in generation t by head of household bin b, $b = 1, 2, \ldots, 15$, conditional on marriage age, stoppage age and birth year dummies on the individual level, plotted against TFB_b. The median marriage age, stoppage age and birth year dummies are set to 1 and the rest of the dummies are set to zero. The solid line represents the OLS fit of a quadratic regression of $\ln(D_{b,t})$ on TFB_b and the dashed line represents the estimated equation in Table 1 evaluated with median marriage age, stoppage age and birth year dummies set to 1 and the rest of the dummies set to zero.

C Plot of Regression Analysis

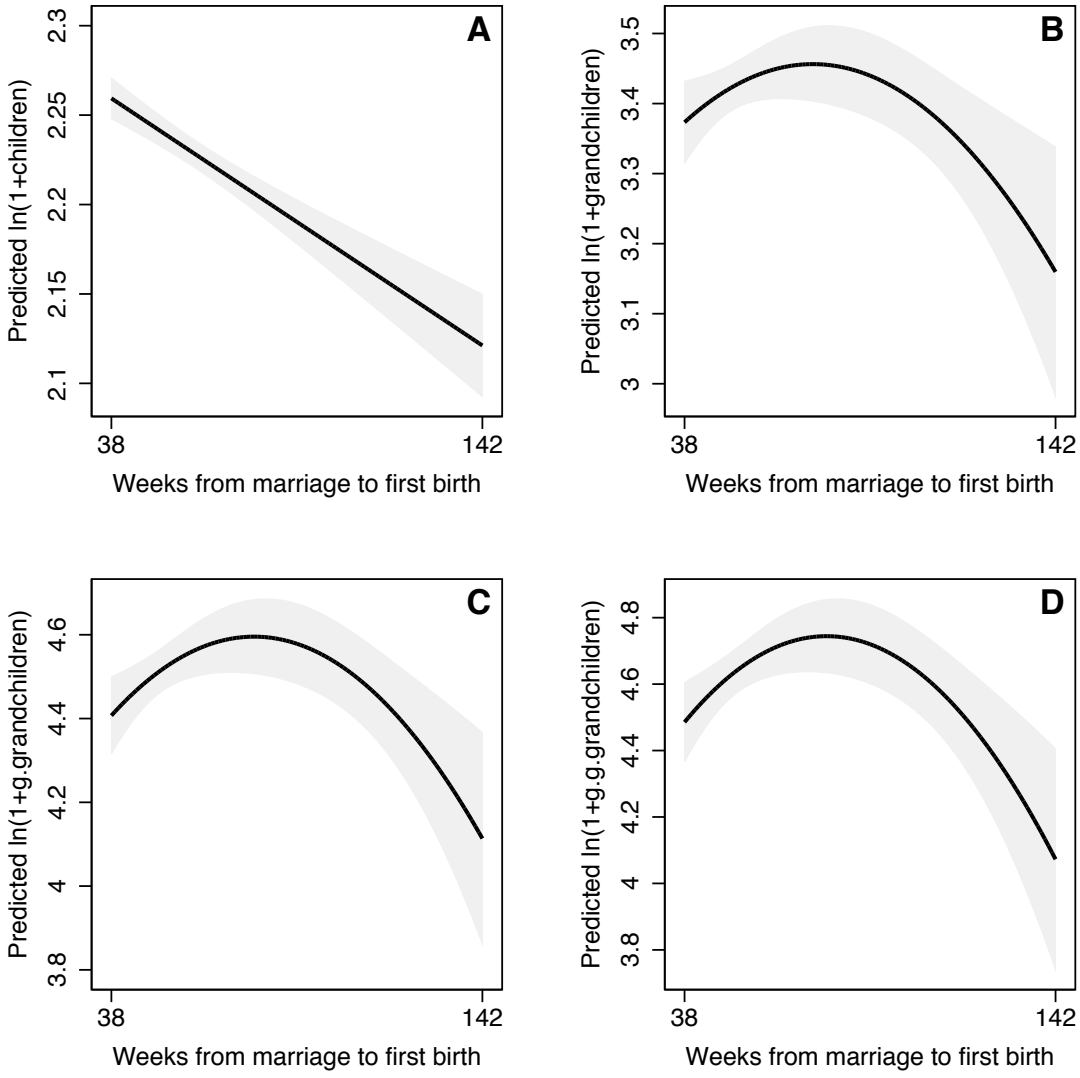

Figure A.3: Predicted number of descendants in logs with 90% confidence interval (n = 2,657) in generation t, based on the regressions in column 1–4 of Table 1.

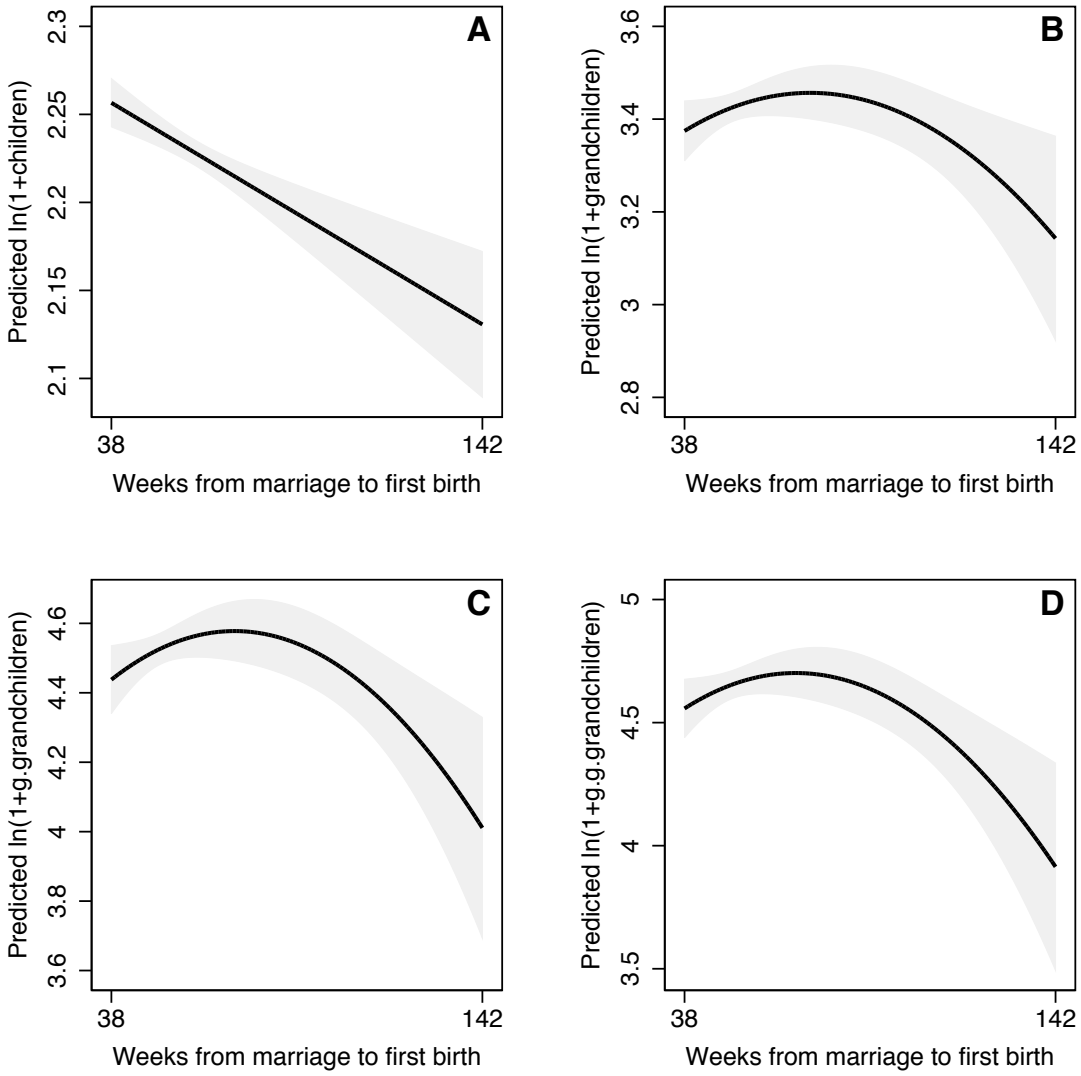

Figure A.4: Predicted number of descendants in logs with 90% confidence interval (n = 2,657) in generation t, based on the regressions in column 9–12 of Table 2, accounting for Maternal Founder fixed effects.

D Summary statistics for heads of lineages

Table A.1: Summary statistics of heads of lineages

	(1) Mean	(2) Median	(3) S.D.	(4) Count
Females				
Children	8.96	9	3.91	1,467
Grandchildren	41.13	38	28.62	1,467
Great-grandchildren[a]	167.91	141	145.58	1,467
Great-great-grandchildren[a]	324.87	209	372.72	1,467
Years from marriage to first birth	1.22	1.02	0.49	1,467
Literate	0.64	1	0.48	925
Fraction of literate children	0.69	0.88	0.38	1,267
Fraction of surviving children with known literacy[b]	0.63	0.60	0.41	1,388
Fraction of surviving children[b]	0.55	0.56	0.24	1,467
Age at first marriage	19.53	18.8	3.98	1,467
Age at last delivery	37.41	39.9	7.07	1,467
Males				
Children	9.85	10	4.50	1,190
Grandchildren	45.75	42	29.94	1,190
Great-grandchildren[a]	176.76	153.5	141.64	1,190
Great-great-grandchildren[a]	234.53	147.5	270.92	1,190
Years from marriage to first birth	1.15	0.98	0.43	1,190
Literate	0.62	1	0.49	760
Fraction of literate children	0.73	1	0.36	1,055
Fraction of surviving children with known literacy[b]	0.59	0.56	0.38	1,145
Fraction of surviving children[b]	0.57	0.58	0.23	1,190
Age at first marriage	27.15	26.3	5.17	1,190
Age at last delivery	46.49	46.8	9.12	1,190
All				
Children	9.36	10	4.21	2,657
Grandchildren	43.20	40	29.30	2,657
Great-grandchildren[a]	171.88	147	143.87	2,657
Great-great-grandchildren[a]	284.41	175	334.00	2,657
Years from marriage to first birth	1.19	0.46	1.00	2,657
Literate	0.63	1	0.48	1,685
Fraction of literate children	0.71	1	0.37	2,322
Fraction of surviving children with known literacy[b]	0.61	0.60	0.40	2,533
Fraction of surviving children[b]	0.56	0.57	0.24	2,657
Age at first marriage	22.94	22.2	5.92	2,657
Age at last delivery	41.47	41.9	9.23	2,657

[a] The moderate increase in the mean and median number of descendants from the third to the fourth generation (i.e. from great-grandchildren to great-great-grandchildren) reflects the fact that these cohorts are less fully observed. Furthermore, since men produce children at lager ages than women, this effect is more pronounced among men.

[b] Survival is recorded at the average marriage age, i.e. 23 years.

E Robustness: Number of Marriages and Spousal Migration

Table A.2: Robustness to additional control variables: number of marriages and spousal migration

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
	Controlling for number of marriages				Controlling for spousal migration			
ln(descendants) in:	Gen. 1	Gen. 2	Gen. 3	Gen. 4	Gen. 1	Gen. 2	Gen. 3	Gen. 4
TFB	-.065***	.373	.705**	.985**	-.066***	.360	.685*	.973**
	(.011)	(.236)	(.357)	(.457)	(.011)	(.236)	(.355)	(.454)
TFB^2		-.143*	-.254**	-.355**		-.137*	-.245**	-.348**
		(.076)	(.113)	(.146)		(.076)	(.112)	(.144)
Literate	-.048***	.334***	.650***	.905***	-.050***	.331***	.644***	.907***
	(.012)	(.051)	(.080)	(.103)	(.012)	(.051)	(.080)	(.103)
Male	.005	.227***	.455***	.573***	-.006	.153***	.321***	.385***
	(.013)	(.048)	(.074)	(.090)	(.013)	(.049)	(.074)	(.091)
Number of observations	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657
Adjusted R^2	.828	.485	.402	.366	.825	.487	.406	.372
Joint sign. of TFB & TBF^2		.046	.029	.018		.059	.038	.021
Maximizing TFB		1.303	1.387	1.386		1.308	1.397	1.398
Lower limit of 90% CI		-.399	.800	.939		-1.018	.769	.950
Upper limit of 90% CI		1.536	1.584	1.566		1.549	1.600	1.579
Significance of hump-shape		.030	.012	.007		.035	.014	.008

This table presents the results of a series of OLS regressions of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2. Birth year, marriage age and stoppage age dummies are included as controls. Furthermore, in column 1-4, dummies for individuals having experienced the same total number of marriages during their lifetime, as well as dummies for individuals having spouses that experienced the same total number of marriages during their lifetime are included. In column 5-9, dummies indicating if the spouse is an immigrant and dummies indicating if the spouse is an emigrant are included. In column 10-13, dummies indicating the birth (or baptism) parish and dummies indicating the death (or burial) parish are included. Standard errors clustered at the level of the firstborn are reported in the parentheses. * p <0.10, ** p <0.05, *** p <0.01.

Table A.3: Robustness to additional control variables: number of marriages and spousal migration – accounting for Maternal Founder fixed effects

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
	Controlling for number of marriages				Controlling for spousal migration			
ln(descendants) in:	Gen. 1	Gen. 2	Gen. 3	Gen. 4	Gen. 1	Gen. 2	Gen. 3	Gen. 4
TFB	-.062***	.519*	.896**	1.071**	-.063***	.495*	.863**	1.044**
	(.016)	(.283)	(.429)	(.532)	(.016)	(.282)	(.427)	(.529)
TFB^2		-.183**	-.320**	-.401**		-.174*	-.305**	-.388**
		(.091)	(.137)	(.173)		(.091)	(.136)	(.172)
Literate	-.026	.040	.114	.147	-.026	.034	.105	.142
	(.020)	(.073)	(.106)	(.132)	(.020)	(.072)	(.105)	(.132)
Male	.002	.115	.316***	.317**	-.002	.047	.191	.158
	(.020)	(.079)	(.116)	(.144)	(.021)	(.081)	(.121)	(.151)
Number of observations	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657
Adjusted R^2	.834	.570	.536	.543	.833	.572	.541	.547
Joint sign. of TFB & TFB^2	0	.102	.035	.025	0	.131	.049	.032
Maximizing TFB		1.415	1.4	1.334		1.423	1.413	1.344
Lower limit of 90% CI		.709	.921	.776		.551	.898	.756
Upper limit of 90% CI		1.687	1.604	1.537		1.728	1.629	1.552
Significance of hump-shape		.022	.01	.01		.028	.012	.012

This table presents the results of a series of OLS regressions of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2. Birth year, marriage age and stoppage age dummies are included as controls. Furthermore, in column 1-4, dummies for individuals having experienced the same total number of marriages during their lifetime, as well as dummies for individuals having spouses that experienced the same total number of marriages during their lifetime are included. In column 5-9, dummies indicating if the spouse is an immigrant and dummies indicating if the spouse is an emigrant are included. In column 10-13, dummies indicating the birth (or baptism) parish and dummies indicating the death (or burial) parish are included. Furthermore, dummies for individuals sharing the same mother are also included. Standard errors clustered at the level of the firstborn are reported in the parentheses. * p <0.10, ** p <0.05, *** p <0.01.

F Robustness: Gender

Table A.4: Robustness to gender distinction – sample restricted to females

ln(descendants) in:	(1) Gen. 1	(2) Gen. 2	(3) Gen. 3	(4) Gen. 4	(5) Gen. 1	(6) Gen. 2	(7) Gen. 3	(8) Gen. 4
TFB	-.070***	.392	.815*	1.203**	-.068***	.358	.747*	1.109**
	(.012)	(.280)	(.431)	(.544)	(.012)	(.278)	(.422)	(.532)
TFB^2		-.144	-.286**	-.415**		-.137	-.273**	-.397**
		(.091)	(.138)	(.174)		(.091)	(.135)	(.170)
Literate					-.071***	.383***	.761***	1.073***
					(.015)	(.066)	(.106)	(.136)
Number of observations	1,467	1,467	1,467	1,467	1,467	1,467	1,467	1,467
Adjusted R^2	.838	.487	.389	.330	.841	.505	.425	.373
Joint sign. of TFB & TFB^2		.213	.082	.043		.179	.066	.034
Maximizing TFB		1.363	1.423	1.45		1.303	1.367	1.396
Lower limit of 90% CI		–	.789	1.074		–	.468	.916
Upper limit of 90% CI		–	1.675	1.662		–	1.608	1.599
Significance of hump-shape		.058	.019	.008		.066	.022	.010

This table presents the results of a series of OLS regressions of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2. Birth year, marriage age and stoppage age dummies are included as controls. A dummy indicating unknown literacy is included in the regressions underlying column 5–9. Furthermore, dummies for individuals sharing the same mother are also included. Standard errors clustered at the level of the firstborn are reported in parentheses. * p <0.10, ** p <0.05, *** p <0.01.

Table A.5: Robustness to gender distinction – sample restricted to males

ln(descendants) in:	(1) Gen. 1	(2) Gen. 2	(3) Gen. 3	(4) Gen. 4	(5) Gen. 1	(6) Gen. 2	(7) Gen. 3	(8) Gen. 4
TFB	-.066***	.650**	1.164**	1.575**	-.065***	.545*	.979**	1.330**
	(.016)	(.315)	(.471)	(.618)	(.015)	(.312)	(.470)	(.618)
TFB^2		-.222**	-.375**	-.525***		-.194*	-.327**	-.464**
		(.102)	(.150)	(.201)		(.101)	(.151)	(.202)
Literate					-.011	.272***	.514***	.736***
					(.019)	(.069)	(.104)	(.135)
Number of observations	1,190	1,190	1,190	1,190	1,190	1,190	1,190	1,190
Adjusted R^2	.829	.443	.343	.348	.829	.460	.372	.378
Joint sign. of TFB & TFB^2		.079	.044	.032		.101	.087	.055
Maximizing TFB		1.465	1.553	1.499		1.401	1.495	1.432
Lower limit of 90% CI		1.081	1.348	1.285		.511	1.143	1.071
Upper limit of 90% CI		1.682	1.76	1.687		1.629	1.72	1.627
Significance of hump-shape		.014	.006	.004		.027	.015	.010

This table presents the results of a series of OLS regressions of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2. Birth year, marriage age and stoppage age dummies are included as controls. A dummy indicating unknown literacy is included in the regressions underlying column 5–9. Furthermore, dummies for individuals sharing the same mother are also included. Standard errors clustered at the level of the firstborn are reported in parentheses. * p <0.10, ** p <0.05, *** p <0.01.

G Robustness: Location and Season of Marriage and Birth

Table A.6: Robustness to additional control variables: location and season of marriage and birth

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
	Controlling for birth and death parish				Controlling for month of marriage and month of birth of firstborn			
ln(descendants) in:	Gen. 1	Gen. 2	Gen. 3	Gen. 4	Gen. 1	Gen. 2	Gen. 3	Gen. 4
TFB	-.061***	.250	.617*	.932**	-.065***	.527**	.980***	1.260***
	(.011)	(.231)	(.343)	(.437)	(.011)	(.239)	(.363)	(.470)
TFB^2		-.102	-.228**	-.340**		-.188**	-.335***	-.434***
		(.074)	(.109)	(.140)		(.077)	(.115)	(.150)
Literate	-.052***	.242***	.482***	.674***	-.048***	.329***	.650***	.910***
	(.013)	(.050)	(.077)	(.099)	(.012)	(.051)	(.080)	(.103)
Male	.006	.195***	.369***	.448***	.005	.212***	.427***	.540***
	(.013)	(.049)	(.074)	(.089)	(.013)	(.049)	(.075)	(.091)
Number of observations	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657
Adjusted R^2	.826	.525	.473	.455	.825	.488	.405	.370
Joint sign. of TFB & TFB^2		.106	.032	.015		.024	.009	.008
Maximizing TFB		1.226	1.353	1.370		1.398	1.462	1.450
Lower limit of 90% CI		–	.499	.903		.997	1.218	1.204
Upper limit of 90% CI		–	1.562	1.549		1.581	1.618	1.604
Significance of hump-shape		.210	.065	.034		.026	.007	.007

This table presents the results of a series of OLS regressions of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2. Birth year, marriage age and stoppage age dummies are included as controls. Furthermore, in column 1-4, dummies for individuals having experienced the same total number of marriages during their lifetime, as well as dummies for individuals having spouses that experienced the same total number of marriages during their lifetime are included. In column 5-9, dummies indicating if the spouse is an immigrant and dummies indicating if the spouse is an emigrant are included. In column 10-13, dummies indicating the birth (or baptism) parish and dummies indicating the death (or burial) parish are included. Standard errors clustered at the level of the firstborn are reported in the parentheses. * p <0.10, ** p <0.05, *** p <0.01.

Table A.7: Robustness to additional control variables: location and season of marriage and birth – accounting for Maternal Founder fixed effects

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
		Controlling for birth and death parish				Controlling for month of marriage and month of birth of firstborn		
ln(descendants) in:	Gen. 1	Gen. 2	Gen. 3	Gen. 4	Gen. 1	Gen. 2	Gen. 3	Gen. 4
TFB	-.055***	.470	1.042**	1.305**	-.057***	.642**	1.140***	1.291**
	(.017)	(.298)	(.443)	(.558)	(.016)	(.287)	(.427)	(.539)
TFB^2		-.159*	-.359**	-.470**		-.219**	-.395***	-.468***
		(.097)	(.142)	(.182)		(.093)	(.137)	(.175)
Literate	-.023	.012	.056	.057	-.021	.035	.117	.149
	(.021)	(.074)	(.106)	(.132)	(.020)	(.074)	(.107)	(.135)
Male	.009	.106	.255**	.210	.004	.120	.311***	.314**
	(.022)	(.082)	(.119)	(.148)	(.021)	(.079)	(.115)	(.143)
Number of observations	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657
Adjusted R^2	.833	.576	.556	.571	.835	.574	.540	.546
Joint sign. of TFB & TFB^2	.001	.251	.034	.020	.000	.054	.010	.013
Maximizing TFB		1.475	1.452	1.388		1.463	1.442	1.380
Lower limit of 90% CI		-21.215	1.132	1.045		1.115	1.181	1.036
Upper limit of 90% CI		2.57	1.659	1.57		1.701	1.613	1.560
Significance of hump-shape		.071	.016	.019		.020	.008	.018

This table presents the results of a series of OLS regressions of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2. Birth year, marriage age and stoppage age dummies are included as controls. Furthermore, in column 1-4, dummies for individuals having experienced the same total number of marriages during their lifetime, as well as dummies for individuals having spouses that experienced the same total number of marriages during their lifetime are included. In column 5-9, dummies indicating if the spouse is an immigrant and dummies indicating if the spouse is an emigrant are included. In column 10-13, dummies indicating the birth (or baptism) parish and dummies indicating the death (or burial) parish are included. Furthermore, dummies for individuals sharing the same mother are also included. Standard errors clustered at the level of the firstborn are reported in the parentheses. * p <0.10, ** p <0.05, *** p <0.01.

H Robustness: Birth Order

Table A.8: Robustness to additional control variable: birth order

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
		Controlling for firstborn status				Controlling for birth order		
ln(descendants) in:	Gen. 1	Gen. 2	Gen. 3	Gen. 4	Gen. 1	Gen. 2	Gen. 3	Gen. 4
TFB	-.067***	.367	.706**	.996**	-.069***	.366	.697*	.969**
	(.011)	(.236)	(.356)	(.457)	(.011)	(.236)	(.358)	(.459)
TFB^2		-.141*	-.255**	-.360**		-.141*	-.252**	-.349**
		(.076)	(.113)	(.145)		(.076)	(.113)	(.146)
Literate	-.051***	.329***	.645***	.908***	-.051***	.337***	.654***	.915***
	(.012)	(.051)	(.080)	(.103)	(.012)	(.051)	(.080)	(.104)
Male	.008	.226***	.454***	.571***	.008	.227***	.463***	.582***
	(.013)	(.048)	(.074)	(.090)	(.013)	(.048)	(.075)	(.091)
Firstborn	-.027**	.054	.118*	.179**				
	(.012)	(.044)	(.066)	(.082)				
Number of observations	2657	2657	2657	2657	2657	2657	2657	2657
Adjusted R^2	.825	.484	.399	.364	.825	.486	.400	.364
Joint sign. TFB & TFB^2	0	.046	.027	.015	0	.044	.029	.02
Maximizing TFB		1.298	1.383	1.384		1.295	1.381	1.385
Lower limit of 90% CI		-.582	.796	.948		-.626	.761	.91
Upper limit of 90% CI		1.534	1.579	1.562		1.53	1.58	1.57
Significance of hump-shape		.031	.012	.006		.032	.013	.008

This table presents the results of a series of OLS regressions of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2. Birth year, marriage age and stoppage age dummies are included as controls. In column 5-9, dummies indicating the birth order of the head of lineage are included. In column 10-13, dummies indicating the birth (or baptism) parish and dummies indicating the death (or burial) parish are included. Standard errors clustered at the level of the firstborn are reported in the parentheses. * p <0.10, ** p <0.05, *** p <0.01.

Table A.9: Robustness to additional control variable: birth order – accounting for Maternal Founder fixed effects

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
	Controlling for firstborn status				Controlling for birth order			
ln(descendants) in:	Gen. 1	Gen. 2	Gen. 3	Gen. 4	Gen. 1	Gen. 2	Gen. 3	Gen. 4
TFB	-.063***	.502*	.881**	1.059**	-.068***	.498*	.864**	.997*
	(.016)	(.284)	(.431)	(.533)	(.016)	(.286)	(.435)	(.538)
TFB^2		-.179*	-.316**	-.399**		-.178*	-.311**	-.379**
		(.092)	(.138)	(.174)		(.093)	(.139)	(.175)
Literate	-.027	.034	.109	.144	-.028	.028	.106	.141
	(.020)	(.073)	(.106)	(.133)	(.020)	(.074)	(.107)	(.133)
Male	.008	.124	.325***	.322**	.008	.124	.338***	.348**
	(.021)	(.078)	(.115)	(.144)	(.021)	(.080)	(.117)	(.147)
Firstborn	-.032*	.037	.078	.135				
	(.020)	(.068)	(.101)	(.126)				
Birth order fixed effects	No	No	No	No	Yes	Yes	Yes	Yes
Number of observations	2,657	2,657	2,657	2,657	2,657	2,657	2,657	2,657
Adjusted R^2	.833	.568	.534	.541	.833	.567	.531	.538
Joint sign. of TFB & TFB^2	0	.113	.037	.025	0	.112	.041	.034
Maximizing TFB		1.406	1.393	1.328		1.396	1.387	1.317
Lower limit of 90% CI		.562	.883	.745		.465	.824	.574
Upper limit of 90% CI		1.689	1.6	1.531		1.674	1.598	1.535
Significance of hump-shape		.026	.011	.011		.027	.013	.015

This table presents the results of a series of OLS regressions of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2. Birth year, marriage age and stoppage age dummies are included as controls. In column 5-9, dummies indicating the birth order of the head of lineage are included. In column 10-13, dummies indicating the birth (or baptism) parish and dummies indicating the death (or burial) parish are included. Furthermore, dummies for individuals sharing the same mother are also included. Standard errors clustered at the level of the firstborn are reported in the parentheses. * p <0.10, ** p <0.05, *** p <0.01.