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The Biocultural Origins of Human Capital Formation*

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August 27, 2014

Abstract

This research explores the biocultural origins of human capital formation. It presents the first evidence that moderate fecundity and thus predisposition towards investment in child quality was conducive for long-run reproductive success within the human species. Using an extensive genealogical record for nearly half a million individuals in Quebec from the sixteenth to the eighteenth centuries, the study explores the effect of fecundity on the number of descendants of early inhabitants in the subsequent four generations. The research exploits variation in the random component of the time interval between the date of first marriage and the first birth to establish that while higher fecundity is associated with a larger number of children, an intermediate level maximizes long-run reproductive success. Moreover, the observed hump-shaped effect of fecundity on long-run reproductive success reflects the negative effect of higher fecundity on the quality of each child. The finding further indicates that the optimal level of fecundity was below the population median, lending credence to the hypothesis that during the Malthusian epoch, the forces of natural selection favored individuals with lower fecundity and thus larger predisposition towards child quality, contributing to human capital formation, the onset of the demographic transition and the evolution of societies from an epoch of stagnation to sustained economic growth.

Keywords Demography, Evolution, Human Capital Formation, Natural Selection, Fecundity, Quantity-Quality Trade-Off, Long-Run Reproductive Success, Economic Growth

JEL Classification Codes J10, N30, 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 twelvefold 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 higher reproductive success. The gradual increase in the representation of these growth-enhancing traits in the population presumably has contributed to the process of development and the take-off from stagnation to growth (Galor, 2011).²

In particular, it was hypothesized that during the Malthusian epoch, natural selection brought about a gradual increase in the representation of traits associated with predisposition towards offspring quality in the population. The effect of this evolutionary process on investment in human capital stimulated technological progress and contributed to the reinforcing interaction between investment in human capital and technological progress that triggered the demographic transition and brought about a state of sustained economic growth (Galor and Moav, 2002).

This research explores the biocultural origins of human capital formation. It presents the first evidence that moderate fecundity and thus predisposition towards investment in child quality was conducive for long-run reproductive success 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 lower fecundity and thus larger predisposition towards child quality, contributing to human capital formation, the onset of the demographic transition and the evolution of societies from an epoch of stagnation to sustained economic growth.³

¹The 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).

²Evidence suggests that the composition of existing genetic traits may experience rapid evolutionary processes. 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. 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).

³The interaction between human evolution and the process of development, as was further explored theoretically by Galor (2005); Lagerlöf (2007); Dalgaard and Strulik (2011); Galor and Michalopoulos (2012), is applicable to either cultural or genetic intergenerational transmission of entrepreneurial traits (Cavalli-Sforza, 1981; Boyd, 1988; Weibull,

The influential life-history theory in the field of evolutionary biology suggests that observed fecundity of organisms reflects a trade-off in reproductive success between the quantity and quality of offspring, given the evolutionary history of the organism. Central to the theory is the supposition that there exists an optimal level of fecundity beyond which fitness diminishes.⁴ 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.⁵ Moreover, a trade-off between fertility on the one hand and offspring survival probability and education on the other hand has been documented for pre-industrial human societies.⁶

Nevertheless, the presence of a static trade-off between the quantity and quality of offspring is merely a necessary but not a sufficient condition for the presence of an adverse effect of fecundity on reproductive success in the long run. In particular, a priori, during the Malthusian epoch individuals with the highest level of fecundity could have had the largest reproductive success if for any feasible number of children, an additional child would have contributed directly to the number of offspring in the long-run more than the adverse indirect effect of this additional child on the quality of hence the reproductive success of these children.⁷

This research explores the effect of fecundity on long-run reproductive success within the human species. Using an extensive genealogical record for nearly half a million individuals in Quebec between the 16th and the 18th centuries, the study examines the effect of fecundity on the number of descendants of early inhabitants of this Canadian province in the subsequent four generations. 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 during this time period to capture the effect of fecundity on fitness. The research establishes that while higher fecundity is associated with a larger number of children, an intermediate level of fecundity is conducive for 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 65 weeks after their marriage, in comparison to a sample median of 53 weeks). In particular, in comparison to highly fertile couples whose first child is born 38 weeks after the marriage, those individuals have on average 0.3 fewer children, but 0.6 more grandchildren, 9.5 additional great-grandchildren, and 15 added great-great-grandchildren (in comparison to a sample mean of 294). In light of the heritability of fecundity, the

^{1997;} Bowles, 1998; Bisin and Verdier, 2000). The long lasting effects of these historically determined genetic factors on comparative development have been established by Galor and Moav (2007); Spolaore and Wacziarg (2009); Ashraf and Galor (2013); Ashraf et al. (2014).

⁴See Lack et al. (1954); Cody (1966); Roff (1992); Stearns (1992).

⁵See Salisbury et al. (1942); Harper et al. (1970); Roff (2002); Charnov and Ernest (2006); Walker et al. (2008).

⁶See Lee (1993); Hill and Hurtado (1996); Strassmann and Gillespie (2002); Gillespie et al. (2008); Meij et al. (2009): Becker et al. (2010).

⁷Furthermore, 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).

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, and thus higher pre-disposition towards child quality, has gradually increased in the population.⁸

The research identifies several mechanisms that had contributed to the trade-off associated with higher fecundity and to the observed hump-shaped effect of fecundity on reproductive success in the long run. While individuals with lower fecundity had fewer children, the observed hump-shaped effect of fecundity on long-run reproductive success reflects the adverse effect of fecundity on the quality of each child. In particular individuals with lower fecundity were more likely to have children that: (i) survived and got married, (ii) married at an earlier age, and (iii) were educated. Thus, despite the positive effect of fecundity on the number of children, the adverse effect of fecundity on child quality and the reproductive success of each child, generated the observed hump shaped relationship between fecundity and long-run reproductive success.

The evidence from pre-industrial Quebec suggests that the forces of natural selection favored individuals characterized by moderate fecundity,, increasing the population's predisposition towards investment in child quality. Interestingly, the conditions that were faced by the founder population of Quebec during this high fertility time period resemble the environment that anatomically modern humans confronted during their migration out of Africa, as they settled new territories where the carrying capacity of the new environment was an order of magnitude greater than the size of the founder population. Thus, the findings support the hypothesis that during the Malthusian epoch, natural selection favored individuals with a larger predisposition towards child quality, contributing to human capital formation, 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 fecundity on long-run reproductive success. First, omitted correlates of the quantity of children may also be correlated with their quality, obscuring the effect of the nubmer of children on long-run reproductive success. For instance, if variations in resources across individuals (e.g., income) enable some parents to produce more children as well as higher quality children, 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 a lack of an optimal level of quantity beyond which fitness diminishes.

Second, reverse causality from the quality of children to their aggregate quantity may obscure the presence or the absence of an optimal level of fecundity beyond which fitness diminishes. For instance, the adverse effect of low child quality on the child survival rate may contribute to the total number of children born (via the child replacement channel), generating a negative correlation

⁸For the heritability of fecundity, see Christensen et al. (2003); Pettay et al. (2005); Ramlau-Hansen et al. (2008); Kosova et al. (2009). In the Quebec sample the time from marriage to first birth is heritable ($h^2 = 0.04$).

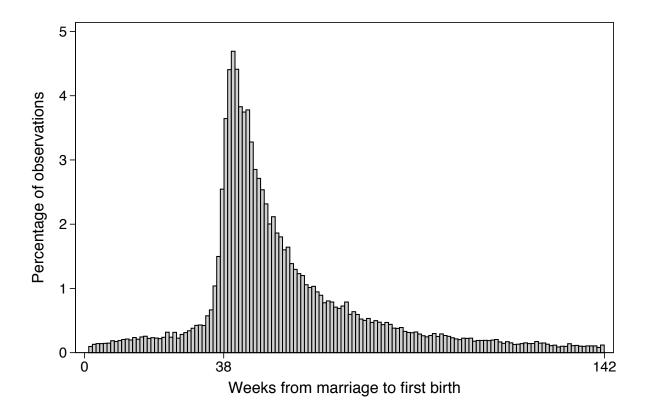


Figure 1: The histogram depicts the durations (in weeks) from first marriages to first births of 53,154 mothers in Quebec between the 16th and the end of the 18th century who gave birth between the 7th and 728th day of their marriage date.

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 to capture the effect of fecundity on fitness.

As depicted in Figure 1, a marriage over this period signaled a deliberate attempt to 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.⁹ Furthermore, premarital conception is insignificant, reflecting possibly an adherence to the social and religious norms existing at the time.

⁹Full 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.

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.¹⁰

Since fecundity reflects genetic and socio-environmental factors, the time interval between the date of first marriage and the first birth (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 of 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, gender, and literacy. 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.

Finally, to assure the external validity of the empirical analysis for significant evolutionary patterns in fecundity during most of human existence, the research focuses on this evolutionary process among the founder population of Quebec during the pre-industrial, pre-demographic transition era – a high fertility environment that had naturally led to rapid evolutionary changes in the composition of the population. The conditions that were faced by the founder population of Quebec during that time period capture the environment that anatomically modern humans confronted during their migration out of Africa, as they settled new territories where the carrying capacity of the new environment was an order of magnitude greater than the size of the founder population. Thus, the evolution in fecundity in Quebec during this time period is likely to capture the dominating trend in this evolutionary process during the Malthusian epoch as a whole.

3 Data and Main Variables

This section sets the stage for the empirical examination of the hypothesis that higher fecundity in the pre-demographic transition era was associated with a larger number of children, while an intermediate level of fecundity maximized long-run reproductive success.

¹⁰In 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 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).

3.1 Data

The data is based on the demographic history of Quebec, using the reconstructed genealogy of the entire parish registers of Quebec, covering 471,412 individuals born between 1572 and 1799, spanning the French settlement and colonization of Quebec.¹¹ 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 who were born in Quebec prior to and including 1685, died in the province, and had at least one great-great grandchild.¹² The focus on the reproductive success of heads of lineages born prior to and including 1685 permits tracing of most descendants of these individuals in the subsequent four generations, while accounting for the Maternal Founder fixed effects.¹³

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.

The study focuses on individuals whose time from first marriage to first birth is at least 38 weeks. Horover, 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 (i.e., TFB less than 2 years and 38 weeks), excluding 10.9% of this subset. This further restriction is designed to mitigate the effect of extreme values of time to first birth which may reflect measurement errors or underlying biological conditions that may directly affect long-run reproductive success. Thus the analysis focuses on the reproductive success of 3,798 heads of lineages in the pre-1685 period that satisfy the entire sample restrictions. Horover, whose time from first marriage to first birth is at least 38 weeks. Horover, which is a least 38 weeks. Horover, wh

¹¹The data is provided by Le Programme de recherche en démographie historique at the University of Montreal.

¹²All children of these heads of lineages, virtually all grandchildren, and most of the descendants in the third and the fourth generations are observed. In particular, fewer than 2.5% 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 115 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.

¹³The use of alternative time intervals would not affect the qualitative results. In particular, as established in Tables 3 and 4, the main results are qualitatively unchanged if the analysis focuses on the reproductive success of heads of lineages born: (i) in 1660–1685 or (ii) over the entire sample period.

¹⁴For the 8.2 percent of the individuals in the sample of non-migrating heads of lineages whose firstborn's date of birth is unknown, it is estimated to be one week prior to the date of baptism.

¹⁵The use of alternative cut-offs would not affect the qualitative results. In particular, focusing on individuals whose time from first marriage to first birth is at least 36 weeks, the hump-shaped relationship remains highly significant. Likewise, focusing on individuals whose time from first marriage to first birth is at least 40 weeks, the hump-shaped relationship remains significant. Furthermore, exploiting alternative estimation methods that do not rely on a quadratic specification reveals qualitatively similar patterns in the presence of observations with TFB exceeding 2 years and 38 weeks.

¹⁶The summary statistics for this sample can be found in Table A.1.

3.2 Main Variables

3.2.1 Dependent and Independent Variables

In the main analysis that explores the effect of the time interval between the first marriage date of the head of a lineage and the birth date of the individual's first child (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 fraction of ever-married children among children observed to have survived to age 40, the average marriage age of children with observed marriage age, and the fraction of literate children among children with observed literacy status (recorded at marriage). The independent variable throughout the analysis is the time interval between the first marriage date of the head of a lineage and the birth date of the individual's first child (TFB).¹⁷

3.2.2 Maternal Founder Fixed Effects

The effect of fecundity on reproductive success may be affected by variation in genetic predisposition among genetically distinct individuals, as well as 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 across all heads of lineages.¹⁸

3.2.3 Control Variables

The analysis accounts for the confounding effects of the marriage age, birth year, 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 associations between the marriage age of heads of lineages and their affluence, fecundity, and reproduction is accounted for by the inclusion of dummy variables indicating the

¹⁷In 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 parents 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.

¹⁸Accounting for the family characteristics of the spouse of the head of dynasties would restrict the sample for siblings who married siblings from a different household. Accounting for these fixed effects would reduce the sample size by more than 90%, and more importantly, would introduce biases associated with the unique characteristics of these families and their matching technology. Reassuringly however, the Maternal Founder fixed effects do accounts for the characteristics of the spouses of heads of households in the likely scenario of non-random (assortative) mating. Moreover, since the regression analysis is nearly unaffected by the introduction of Maternal Founder fixed effects, the potential effect of random mating does not compromise the analysis and further control for fixed factors in the family of the spouse of the head of lineage are unlikely to alter the results.

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, the marriage age was inversely related to the affluence of individuals, and marriage age and its potential association with affluence could have had 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. In particular, 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. These confounding factors are accounted for by the inclusion of dummy variables indicating the birth year of heads of lineages.¹⁹

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 (rather than a mark) on the marriage certificate. Additional confounding variations between heads 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.

Finally, variations in socioeconomic 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, to account for the potential effect of the stoppage age, the analysis is shown to be robust to the inclusion of 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

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 of fecundity 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 an examination using OLS regressions models.

¹⁹In 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.

²⁰As 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.

4.1 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 of fecundity 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 birth year and the marriage and stoppage age of heads of lineages, with confidence intervals based on standard errors clustered for heads of lineages sharing the same firstborn is depicted in Figure 2.

The correlation in reproductive success between parents 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.

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 heads of the lineages and their number of grandchildren. The TFB of heads of lineages that maximizes the number of grandchildren is associated with 48 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 TFB of heads of lineages that maximizes the number of great-grandchildren is associated with 194 great-grandchildren, whereas the optimal TFB of heads of lineages for reproductive success in the 4rd generation (62 weeks) is associated with 306 great-great-grandchildren.

Figure 2 shows that, in accordance with the proposed hypothesis, TFB of heads of lineages has a monotonically negative effect on the number of children and a hump-shaped effect on the number of grandchildren, great-grandchildren and 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 lower TFB.

4.2 Econometric Model

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

First, the effect of TFB of the head of lineage on the number of children born to the head of lineage is estimated using the OLS regression model:

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

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

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

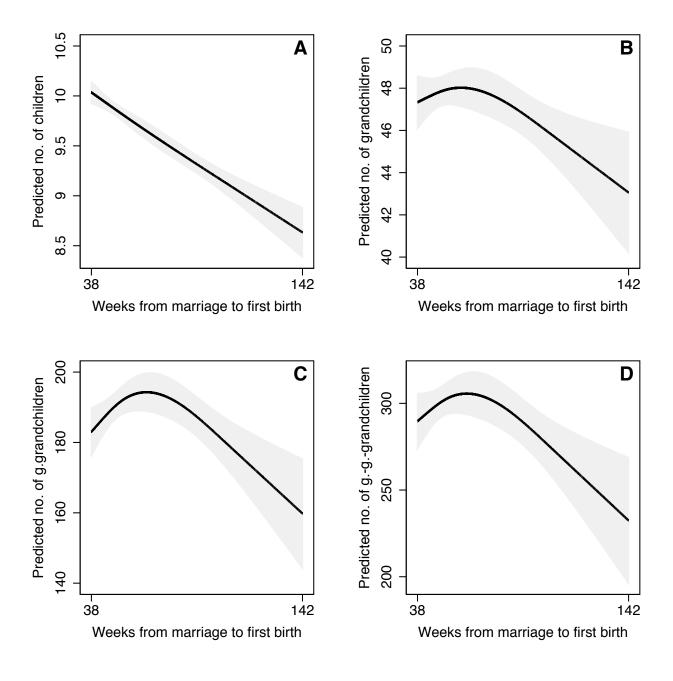


Figure 2: Predicted number of descendants with 90% confidence interval as a function of TFB based on restricted cubic splines with three knots, for 3,798 heads of lineages. Dummies indicating birth year and marriage and stoppage age are included in the underlying regressions. (A) Number of children. (B) Number of grandchildren. (C) Number of great-grandchildren. (D) Number of great-grandchildren.

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 $\beta_{1,1}$ and it is predicted to be negative, i.e., TFB of heads of lineages negatively affects the number of children.

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

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

where $D_{i,t}$ is the number of descendants that the head of household i, has in the subsequent 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 prediction 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-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 and the birth year of heads of lineages. The initial estimates in Table 1 are based on variation in TFB across all head of lineages, whereas those in Table 2 accounts for Maternal Founder fixed effects, and thus presents estimates based on variation in TFB within heads of lineages that are originated from the same mother. The correlation in reproductive success between parents 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.

Consistently with the first element of proposed hypothesis, and the pattern depicted in Figure 2, panel A, column 1 of Table 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 0.068 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 0.72 children.²⁴

The positive association of an intermediate level of TFB and long-run reproductive success is confirmed in columns 2–3, resembling the pattern depicted in Figure 2, panel C–D. Column 2 establishes a significant quadratic relationship between TFB of heads of lineages and the number of

²³To 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 5 and Table A.5 demonstrates that the results are robust to the use of a GLM model with a negative binomial distribution and a logarithmic link function.

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

Table 1: The association between the time to first birth (TFB) and the number of descendants for head of lineages born prior to and including 1685

					Log	number of	descendant	s in:				
	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
TFB	068***	.498**	.788***	068***	.403*	.674**	083***	.314	.596**	079***	.359*	.626**
	(.020)	(.228)	(.299)	(.020)	(.225)	(.295)	(.019)	(.222)	(.293)	(.009)	(.200)	(.288)
$\mathrm{TFB^2}$		171**	276***		145**	246***		125*	229**		138**	238***
		(.073)	(.095)		(.073)	(.094)		(.072)	(.094)		(.064)	(.092)
Literate				.015	.373***	.497***	.010	.364***	.489***	049***	.297***	.442***
				(.022)	(.049)	(.066)	(.022)	(.048)	(.066)	(.010)	(.044)	(.065)
Male							.240***	.475***	.420***	007	.193***	.270***
							(.021)	(.041)	(.050)	(.010)	(.039)	(.052)
Stoppage age fixed effects	No	No	No	No	No	No	No	No	No	Yes	Yes	Yes
Number of observations	3,798	3,798	3,798	3,798	3,798	3,798	3,798	3,798	3,798	3,798	3,798	3,798
Adjusted R^2	.019	.027	.307	.021	.052	.324	.052	.081	.334	.801	.291	.370
Joint signlevel of TFB & TFB ²	.001	.055	.007	.001	.084	.009	.000	.050	.006	.000	.012	.003
Maximizing TFB		1.458	1.427		1.389	1.369		1.254	1.302		1.297	1.314
Lower limit of 90% CI		1.095	1.158		.568	.970		-3.172	.718		.427	.825
Upper limit of 90% CI		1.678	1.585		1.632	1.543		1.513	1.491		1.501	1.490

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 for heads of lineages born prior to 1685. Birth year and marriage age dummies are included as controls. Furthermore, stoppage age dummies are included in columns 10–12. A dummy indicating unknown literacy is included in the regressions underlying column 4–12. Standard errors clustered at the level of the firstborn are reported in parentheses. * p < 0.10, *** p < 0.05, *** p < 0.01.

great-grandchildren.²⁵ 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. Similarly, column 3 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 highly significant (p=0.007). Moreover, an additional test (not reported in the table) establishes a highly significant hump-shaped relationship under this specification (p=0.009).²⁶

Columns 4–6 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 4). 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 5–6). Moreover, a test of the joint significance of the two coefficient estimates related to the fourth generation establishes that they are jointly highly significant (p = 0.009). Additionally, literacy is positively associated with long-run reproductive success (columns 5–6). As will become apparent in Table 6 and 7, literacy (and its potential association with a quality bias) is positively associated with the fraction of surviving children that got married as well as their average marriage age, and is thus rewarding in the long run.

Furthermore, columns 7–9 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 7). Moreover, a quadratic relationship between TFB of heads of lineages and the number of descendants is stable and significant at the 5% level in the third and fourth generations (column 8–9). In addition, a test of the joint significance of the two coefficient estimates related to the fourth generation establishes that they are jointly highly significant (p = 0.006).

Finally, columns 10-12 establish that the results are robust to the inclusion of a control for the stoppage age. 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 10). Furthermore, the quadratic relationship between TFB of heads of lineages and the number of descendants in the 3rd and the 4th generations is rather stable and significant (column 11-12). In addition, a test of the joint significance of the two coefficient estimates related to the fourth generation establishes that they are jointly highly significant (p = 0.003).

Table 2: The effect of the time to first birth (TFB) on the number of descendants for head of lineages born prior to and including 1685 – accounting for Maternal Founder fixed effects

					Log	g number o	f descendar	nts in:				
	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
TFB	043**	.499**	.751***	044**	.492**	.755***	052***	.457**	.740***	064***	.528***	.775***
TFB^2	(.020)	(.201) 191*** (.066)	(.253) 298*** (.083)	(.020)	(.201) 189*** (.066)	(.253) 301*** (.083)	(.020)	(.200) 181*** (.066)	(.253) 297*** (.083)	(.009)	(.178) 207*** (.058)	(.247) 312*** (.081)
Literate		(.000)	(.000)	005	.141***	.135**	003	.144***	.137**	019	.121***	.108*
				(.026)	(.050)	(.064)	(.025)	(.050)	(.064)	(.012)	(.045)	(.063)
Male							.200***	.293***	.132**	016	.082*	.043
							(.026)	(.046)	(.058)	(.012)	(.042)	(.060)
Stoppage age fixed effects	No	No	No	No	No	No	No	No	No	Yes	Yes	Yes
Number of observations	3,798	3,798	3,798	3,798	3,798	3,798	3,798	3,798	3,798	3,798	3,798	3,798
Adjusted R^2	.015	.039	.310	.016	.041	.310	.035	.052	.311	.806	.299	.360
Joint signlevel of TFB & TFB ²	.031	.002	.000	.026	.002	.000	.008	.002	.000	.000	.000	.000
Maximizing TFB		1.307	1.257		1.304	1.256		1.264	1.245		1.272	1.242
Lower limit of 90% CI		.966	.994		.954	.995		.835	.97		1.016	.997
Upper limit of 90% CI		1.466	1.395		1.465	1.393		1.434	1.384		1.402	1.372

This table presents the results of a series of fixed-effects regressions of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2 . All regressions account for Maternal Founder fixed effects. Birth year and marriage age dummies are included as controls. Furthermore, stoppage age dummies are included in columns 10-12. A dummy indicating unknown literacy is included in the regressions underlying column 4-12. Standard errors clustered at the level of the firstborn are reported in parentheses. *p < 0.10, **p < 0.05, ***p < 0.01.

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 their variation in cultural and socio-economic background. Thus, 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. In particular, similarities in the genetic, cultural, and socio-economic characteristics across siblings, as opposed to across the population as a whole, are exploited to isolate the effect of random variation in TFB on reproductive success. Accounting for these Maternal Founder fixed effects, as well as additional confounding factors and clustering of standard errors on the level of the firstborn, the analysis explores the effect of random variation in TFB on long-run reproductive success.

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 7 establishes a highly significant negative association between TFB of heads of lineages and the number of children, accounting for the marriage age, birth year, literacy status and gender of the heads of lineages. An increase in the TFB by one year results in a reduction of 0.052 in the log number of children. Hence, an increase in TFB from 38 weeks to 1 year and 38 weeks would result in a reduction of approximately 0.76 children.

The beneficial effects of an intermediate level of TFB on long-run reproductive success is confirmed in columns 8–9. 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, literacy status and gender of the heads of lineages. In particular, the first and second order terms are highly significant for great-great-grandchildren. In addition, the first-order coefficient and second-order coefficient estimates are jointly highly significant. Furthermore, as established in columns 10-12 the findings are robust to the inclusion of control for the stoppage age. In particular, the first and second order terms are highly significant for great-great-grandchildren and the additional test for a hump-shaped relationship for great-great-grandchildren is highly significant (p=0.007).

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 65 weeks after their marriage, in comparison to a sample median of 53 weeks), suggesting that the forces of natural selection may have 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 0.3 fewer children, but 0.6 more grandchildren, 9.5 additional great-grandchildren, and 15 added great-grandchildren.

²⁵The analysis focus on the effect on long-run reproductive success and hence on the 3rd and the 4th generations. As is apparent from Figure 2, the effect on the 2nd generation is similar qualitatively but somewhat less significant.

²⁶See Lind and Mehlum (2010).

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 of fecundity maximized long-run reproductive success.

5 Robustness

This section establishes the robustness of the qualitative results to (i) alternative sample periods, (ii) 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, and (iii) alternative estimation method (GLM).

5.1 Alternative Sample Periods

While the analysis accounts for cohort effects by the inclusion of birth year dummies, the economic and ecological environment may have changed over the sample period, shifting the costs and benefits of investment in offspring and thus affecting the existence or the nature of a long-run reproductive trade-off. Therefore, it might be a concern whether the baseline regression analysis is representative of alternative sample periods. Reassuringly, the main results are qualitatively unchanged if the analysis focuses on the reproductive success of heads of lineages born over a significantly shorter period, for example the period 1660–1685 (Table 3), as well as over a longer period, for example the entire sample period (Table 4).

5.2 Additional Attributes of Heads of Lineages

5.2.1 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 TFB and reproductive success. Thus, the migration status of the first spouse may have affected the TFB and the reproductive success of heads of lineages. In the sample, heads of lineages were neither immigrants nor emigrants. Nevertheless, 23.5% of their first spouses were immigrants and 0.5% were emigrants. To account for the potential effect of spousal migration, dummy variables indicating the immigration and emigration status of heads of lineages are included in the regression analysis performed in Table 2. As established in Table A.2, the qualitative results are unaffected by the migration status of the first spouse of the head of lineage.

5.2.2 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

Table 3: The effect of the time to first birth (TFB) on the number of descendants for head of lineages born 1660–1685 – accounting for Maternal Founder fixed effects

					Log	number of	f descendan	ts in:				
	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
TFB	053**	.537**	.788***	054***	.529**	.788***	063***	.480**	.760***	065***	.491***	.730***
$\mathrm{TFB^2}$	(.021)	(.212) 211***	(.267) 322***	(.021)	(.213) 209***	(.268) 322***	(.021)	(.212) 197***	(.268) 315***	(.010)	(.188) 200***	(.264) 307***
		(.070)	(.088)		(.070)	(.088)		(.070)	(.088)		(.062)	(.087)
Literate				022	.121**	.116*	024	.117**	.114*	025**	.107**	.086
				(.028)	(.054)	(.067)	(.027)	(.053)	(.067)	(.012)	(.048)	(.067)
Male							.199***	.309***	.176***	023*	.113***	.119*
							(.027)	(.048)	(.060)	(.012)	(.044)	(.063)
Stoppage age fixed effects	No	No	No	No	No	No	No	No	No	Yes	Yes	Yes
Number of observations	3,376	3,376	3,376	3,376	3,376	3,376	3,376	3,376	3,376	3,376	3,376	3,376
Adjusted R^2	.018	.043	.339	.019	.045	.339	.039	.059	.341	.811	.309	.385
Joint signlevel of TFB & TFB ²	.011	.001	.000	.01	.001	.000	.002	.000	.000	.000	.000	.000
Maximizing TFB		1.27	1.224		1.269	1.224		1.22	1.206		1.225	1.187
Lower limit of 90% CI		.926	.95		.914	.948		.767	.906		.887	.871
Upper limit of 90% CI		1.426	1.363		1.426	1.363		1.392	1.35		1.374	1.335

This table presents the results of a series of fixed-effects OLS regressions of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2 for heads of lineages born in the period 1660–1685. All regressions account for Maternal Founder fixed effects. Birth year and marriage age dummies are included as controls. Furthermore, stoppage age dummies are included in columns 10–12. A dummy indicating unknown literacy is included in the regressions underlying column 4–12. Standard errors clustered at the level of the firstborn are reported in parentheses. * p < 0.10, *** p < 0.05, **** p < 0.01.

Table 4: The effect of the time to first birth (TFB) on the number of descendants for entire sample period – accounting for Maternal Founder fixed effects

					Log	number of	descendant	s in:				
	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
TFB	054***	.311**	.392**	055***	.302**	.384**	061***	.286**	.377**	076***	.369***	.438**
$\mathrm{TFB^2}$	(.014)	(.138) 130***	(.185) 182***	(.014)	(.138) 127***	(.185) 180***	(.014)	(.137) 123***	(.185) 178***	(.007)	(.123) 155***	(.184) 202***
Literate		(.046)	(.061)	.006	(.046) .128***	(.061) .123***	.006	(.045) .129***	(.061) .123***	011	(.041) .105***	(.060) .110**
Literate				(.019)	(.036)	(.046)	(.019)	(.036)	(.046)	(.009)	(.032)	(.045)
Male				, ,	` /	, ,	.201***	.187***	.083**	005	.018	.018
							(.015)	(.026)	(.033)	(.007)	(.025)	(.035)
Number of observations	7,664	7,664	7,664	7,664	7,664	7,664	$7,\!664$	7,664	7,664	7,664	7,664	7,664
Adjusted R^2	.027	.068	.420	.027	.071	.421	.053	.078	.422	.795	.284	.440
Joint signlevel of TFB & TFB ²	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
Maximizing TFB		1.194	1.074		1.192	1.069		1.160	1.058		1.191	1.086
Lower limit of 90% CI		.727	.516		.693	.487		.588	.452		.916	.644
Upper limit of 90% CI		1.371	1.272		1.373	1.271		1.350	1.264		1.329	1.265

This table presents the results of a series of fixed-effects OLS regressions of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2 for heads of lineages born in the entire sample period. All regressions account for Maternal Founder fixed effects. Birth year and marriage age dummies are included as controls. Furthermore, stoppage age dummies are included in columns 10–12. A dummy indicating unknown literacy is included in the regressions underlying column 4–12. Standard errors clustered at the level of the firstborn are reported in parentheses. * p < 0.10, *** p < 0.05, **** p < 0.01.

19

Table 5: Robustness to GLM regression – accounting for Maternal Founder fixed effects

					N	Number of o	descendants	s in:				
	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
TFB	041**	.412**	.547**	042**	.414**	.557***	052***	.387**	.547**	073***	.468***	.595***
TFB^2	(.020)	(.179) 162***	(.215) 234***	(.020)	(.178) 163***	(.215) 238***	(.020)	(.177) 158***	(.215) 236***	(.010)	(.160) 191*** (.052)	(.216) 256***
Literate		(.058)	(.068)	006 (.026)	(.058) .121*** (.045)	(.069) .119** (.056)	006 (.025)	(.058) .124*** (.045)	(.068) .121** (.056)	020 (.013)	.118*** (.040)	(.069) .104*
Male				(.020)	(.045)	(.050)	.248***	.282*** (.044)	.127** (.054)	015 (.014)	.040) .083** (.040)	(.055) .072 (.055)
Stoppage age fixed effects	No	No	No	No	No	No	(.027) No	(.044) No	(.034) No	Yes	Yes	(.055) Yes
Birth year FE	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Number of observations Joint signlevel of TFB & TFB ²	3,798 .045	3,798 .001	3,798 .000	3,798 .037	3,798 .001	3,798 .000	3,798 .009	3,798 .000	3,798 .000	3,798 .000	3,798 .000	3,798 .000

This table presents the results of a series of GLM regressions, with a negative binomial distribution and a logarithmic link function, of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2 . All regressions include dummies for Maternal Founder fixed effects (the results without the Maternal Founder Fixed Effects is presented in Table A.6). Birth year and marriage age dummies are included as controls. Furthermore, stoppage age dummies are included in columns 10–12. A dummy indicating unknown literacy is included in the regressions underlying column 4–12. Standard errors clustered at the level of the firstborn are reported in parentheses. * p < 0.10, *** p < 0.05, *** p < 0.01.

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 Table 2. As established in Table A.2, the qualitative results are unaffected by accounting for remarriages.²⁷

5.2.3 Gender

Reflecting an earlier marriage age of women relative to men, the sample of heads of lineages is unbalanced across gender. Although men on average married at a later age than women (i.e., 26.6 for men versus 19.4 for women), their average age at last delivery was higher (i.e., 46.3 for men versus 38.3 for women), and they remarried more often, resulting in a higher number of children per male (i.e., 10 for men versus 9.4 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 robustness check, Table A.3 demonstrate that the results are qualitatively similar in a sample that includes only females.

5.2.4 Birth and Death Parishes

The parishes 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 parishes of birth and death of each head of lineages are included in the regressions performed in Tables 2. As established in Table A.4, the qualitative results are unaffected by accounting for these parish fixed effects.

5.2.5 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.4, the qualitative results are unaffected by accounting for these seasonal factors.

5.2.6 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

²⁷Excluding 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 existence of the hump-shaped relationship would be significant at the 1% level.

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 2. As established in Table A.5, 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.

5.3 Alternative Estimation Method

The negative relationship between TFB of heads of lineages and the number of children, as well as the hump-shaped relationship between TFB of heads of lineages and long-run reproductive success, is established using quadratic OLS regression models. Table 5 and A.6 demonstrate that these negative relationships 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

The section identifies several mechanisms that had contributed to the trade-off associated with higher fecundity. In particular, it establishes the observed hump-shaped effect of TFB on reproductive success in the long run reflects the positive effect of reduced fertility and thus higher child quality on the reproductive success of each child. While higher TFB reduced the number of children, it contributed to the quality of each child, as reflected by health, survivability, education, and earning capacity, and had therefore affected the long-run reproductive success of the lineage.²⁸

The findings suggest that child quality enhanced the likelihood that: (i) a child would reach the reproductive age and would have the qualities that would permit a success in the marriage market – preconditions for reproductive success, (ii) a child would have the qualities and the necessary income to be able to marry and start the process of reproduction earlier in life, and (iii) a child would become educated and thus would have higher earning capacity and reproductive success.

In particular, the fraction of children that survived till the end of their reproductive age, and succeeded to get married determined the fraction of offspring that contributed to the number of descendants and thus long-run reproductive success. Moreover, among children that got married, the average marriage age determined their average age of onset of reproductive activity and therefore the long-run reproductive success of the heads of lineages.

These marriage channels are explored in Table 6 and 7. The effect of TFB on the likelihood that a child married is explored in Table 6.²⁹ As established in column 1, the negative association

²⁸The interaction between demography and human capital formation is at the center of Unified Growth Theory (Cervellati and Sunde, 2005; Boucekkine et al., 2007; Galor, 2011).

²⁹Due to the fact that the outcome variable is a fraction, the estimates presented in this table are based on the fractional logit model (Papke and Wooldridge, 1996). The results are robust to the inclusion of marriage age, birth year and stoppage age as continuous variables. In particular, the coefficient on TFB in the first, second, third and fourth column would all increase in size to 0.316 (p = 0.005), 0.268 (p = 0.015), 0.255 (p = 0.020), and 0.256 (p = 0.020), respectively. Furthermore, the results are robust to the use of a linear probability model. In particular,

Table 6: The effect of time to first birth (TFB) on the fraction of children surviving to age 40 that got married

	Fraction of children surviving to age 40 that got married								
	(1)	(2)	(3)	(4)					
TFB	.299*** (.113)	.256** (.112)	.235** (.111)	.232** (.110)					
Literate	` '	.770*** (.110)	.763*** (.110)	.779*** (.109)					
Male		,	.396*** (.112)	.365*** (.120)					
Stoppage age fixed effects	No	No	No	Yes					
Number of observations	3,727	3,727	3,727	3,727					

This table presents the results of a series of fractional logit regressions of the fraction of children surviving to age 40 that got married on time to first birth, i.e. TFB and TFB^2 for heads of lineages with at least one child surviving to age 40. Birth year and marriage age dummies are included as controls. Furthermore, stoppage age dummies are included in column 4. A dummy indicating unknown literacy is included in the regressions underlying column 2–4. Standard errors clustered at the level of the firstborn are reported in parentheses. * p < 0.10, ** p < 0.05, *** p < 0.01.

between the fraction of children surviving to age 40 that got married and the TFB of heads of lineages is highly statistically significant.³⁰ In particular, accounting for the marriage age and birth year of heads of lineages, as well as gradually for their literacy status as well as gender, there is a significant negative effect of TFB on the fraction of children surviving to age 40 that got married. Thus, it appears that the marriage success channel plays a role in accounting for the established hump-shaped pattern between TFB and long-run reproductive success.³¹

The effect of TFB on the average marriage age of married offspring is explored in Table 7. As established in column 1, the association between the average marriage age among offspring that got married and TFB of heads of lineages is negative and highly significant statistically. In particular,

the coefficient on TFB in the first, second, third and fourth column would be 0.018 (p < 0.005), 0.015 (p < 0.016), 0.014 (p = 0.029), and 0.013 (p = 0.035), respectively. Since the Maternal Founder fixed effects constitute an unbalanced panel, the fractional logit model does not account for these fixed effects (Papke and Wooldridge, 2008). However, accounting for these fixed effects in a fixed-effects linear probability model yields similar results, although less precisely estimated. In particular, the estimate in column 4 would be 0.10 (p = 0.127). Under an alternative age criteria of 30 years instead of 40 years the estimate the estimate would be 0.011 (p = 0.087)).

 $^{^{30}}$ This finding is robust to the use of alternative age cut-offs. In particular, the effect of TFB on the fraction of surviving children that got married is statistically significant at the 5% level in all specifications when using 30, 35 or 45 as the surviving cut-off age.

 $^{^{31}}$ Underlying, in part, this positive effect of TFB on the marriage probability of offspring surviving to age 40 may be a positive association between TFB and the average longevity of offspring. Indeed, OLS regressions on the basis of the entire sample period, i.e., the regression sample underlying Table 4, suggests there is a positive association between TFB and the average longevity of offspring. In particular, measuring average longevity in years, the coefficient on TFB in the first, second, third and fourth column would be 1.063 (p = 0.038), 0.963 (p = 0.060), 0.980 (p = 0.056), and 1.033 (p = 0.043), respectively. It should be noted that this results depend on the abscence of control for Maternal Founder fixed effects and the larger sample period.

Table 7: Time to first birth (TFB) and the average marriage age

	Avera	age marria	ge age of ch	nildren
	(1)	(2)	(3)	(4)
TFB	430***	400***	376**	339**
	(.005)	(.008)	(.013)	(.023)
Literate		629***	621***	705***
Male		(.001)	(.001) 406***	(.000) 720***
Stoppage age fixed effects	No	No	(.009) No	(.000) Yes
Number of observations Adjusted \mathbb{R}^2	3,796 .006	3,796 .010	3,796 .011	3,796 .036

This table presents the results of a series of OLS regressions of the average marriage age of offspring on time to first birth, i.e. TFB and TFB^2 . Birth year and marriage age dummies are included as controls. Furthermore, stoppage age dummies are included in column 4. A dummy indicating unknown literacy is included in the regressions underlying column 2–4. Standard errors clustered at the level of the firstborn are reported in parentheses. * p < 0.10, *** p < 0.05, *** p < 0.01.

Table 8: The effect of time to first birth (TFB) on the fraction of literate children

	I	Fraction of I	literate child	dren
	(1)	(2)	(3)	(4)
TFB	.401***	.351***	.322***	.337***
	(.090)	(.090)	(.091)	(.091)
Literate		1.308***	1.307***	1.305***
		(.094)	(.094)	(.095)
Male			.563***	.407***
			(.090)	(.098)
Stoppage age fixed effects	No	No	No	Yes
Number of observations	3,448	3,448	3,448	3,448

This table presents the results of a series of fractional logit regressions of the share of children obtaining literacy on time to first birth, i.e. TFB and TFB^2 for heads of lineages with at least one surviving child with observed literacy status. Birth year and marriage age dummies are included as controls. Furthermore, stoppage age dummies are included in column 4. A dummy indicating unknown literacy is included in the regressions underlying column 2–4. Standard errors clustered at the level of the firstborn are reported in parentheses. * p < 0.10, ** p < 0.05, *** p < 0.01.

accounting for the marriage age and birth year of heads of lineages, as well as gradually for their literacy status and gender, there is a significant negative relationship between TFB and the average marriage age of children that got married.³² Thus, it appears that the marriage success channel plays a role in accounting for the established hump-shaped pattern between TFB and long-run reproductive success.

The education channel is investigated in Table 8. As established in column 1, TFB of heads of lineages has a highly significant positive association with the fraction of literate children, accounting for the marriage age and birth year of heads of lineages. As controls are gradually introduced to account for the confounding effects of the literacy status, gender, and stoppage age of heads of lineages, the positive coefficient remains stable and significant at the 1% significance level.³³ Moreover, literacy of heads of lineages has a highly significant positive effect on the literacy of their children.

7 Concluding Remarks

This research explores the biocultural origins of human capital formation. It presents the first evidence that moderate fecundity and thus predisposition towards investment in child quality was conducive for long-run reproductive success within the human species. Using an extensive genealogical record for nearly half a million individuals in Quebec from the sixteenth to the eighteenth centuries, the study explores the effect of fecundity on the number of descendants of early inhabitants in the subsequent four generations. The research exploits variation in the random component of the time interval between the date of first marriage and the first birth to establish that while higher fecundity is associated with a larger number of children, an intermediate level maximizes long-run reproductive success. Moreover, the observed hump-shaped effect of fecundity on long-run reproductive success reflects the negative effect of higher fecundity on the quality of each child.

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

 $^{^{32}}$ In fixed-effects regressions accounting for Maternal Founder fixed effects, the coefficient estimate drops somewhat resulting in decreased statistical significance. However, the finding remains statistically significant at the 10% significance level in the entire sample period, i.e., the regression sample underlying Table 4. In particular, in the regression corresponding to that underlying column 4, controlling for Maternal Founder fixed effects in the entire sample period, the effect of TFB on the average marriage age of offspring is -0.181 (p = 0.082).

 $^{^{3\}bar{3}}$ As in Table 6, the regressions underlying Table 8 are based on fractional logit models. The results are robust to the inclusion of marriage age, birth year and stoppage age as continuous variables. In particular, the coefficient on TFB in the first, second, third and fourth column would be 0.392 (p < 0.001), 0.334 (p < 0.001), 0.314 (p < 0.001), and 0.311 (p < 0.001), respectively. Furthermore, the results are robust to the use of a linear probability model. In particular, the coefficient on TFB in the first, second, third and fourth column would be 0.071 (p < 0.001), 0.060 (p < 0.001), 0.054 (p < 0.001), and 0.055 (p < 0.001), respectively. Since the Maternal Founder fixed effects constitute an unbalanced panel, the fractional logit model does not account for these fixed effects (Papke and Wooldridge, 2008). Accounting for the fixed effects in a fixed-effects linear probability model on the baseline sample also yields positive estimates of the coefficient on TFB, although the estimates are insignificant. However, focusing on heads of lineages born prior to and including 1660, the positive effect of TFB on the average literacy of offspring is statistically significant. In particular, the estimate in column 4 would be 0.137 (p = 0.002). Thus, the statistical evidence of the positive effect of lower TFB based on variation within siblings sharing the same Maternal Founder on offspring literacy is strongest for the first part of the baseline period.

fecundity and thus higher predisposition towards investment in child quality. 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 human capital formation, the onset of the demographic transition and the evolution of societies from an epoch of stagnation to sustained economic growth.

A Distribution of stoppage ages

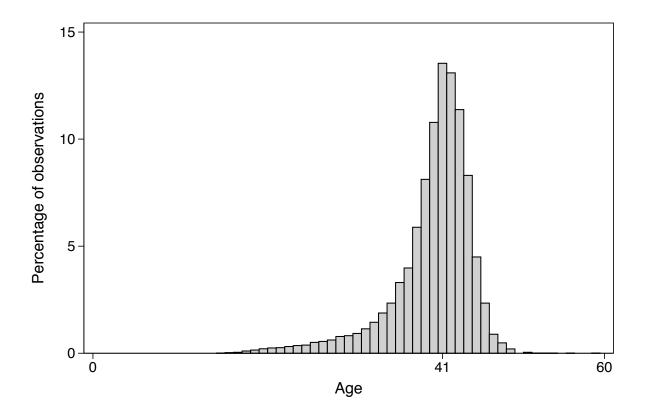


Figure A.1: The histogram depicts the age at last delivery of 13,411 once-married, non-migrant mothers in Quebec born born before 1749 (and after 1624) who survived to age 50 and whose husband survived to age 50.

B Conditional means by bins

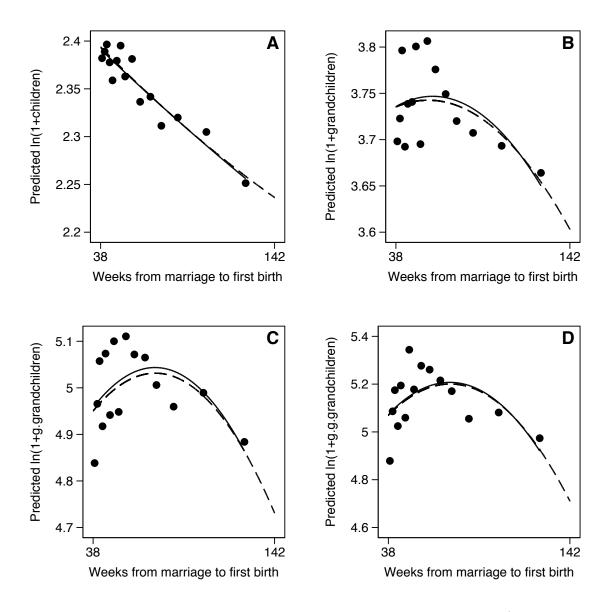


Figure A.2: Conditional means by bins for 3,798 heads of lineages)

The figure depicts estimates of the mean of the transformed number of descendants conditional on the marriage 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, where TFB_b is the median TFB in for each bin b. The figure depicts the expected value of $\ln(1 + D_{b,t})$, where $D_{b,t}$ is the number of descendants in generation t by head of household bin b, b = 1, 2, ..., 15, conditional on birth year, marriage age and stoppage age dummies on the individual level, plotted against TFB_b . The solid line represents the OLS fit of a quadratic regression of $\ln(1 + D_{b,t})$ on TFB_b and the dashed line represents the estimated equation in Table 1 evaluated with median marriage age and birth year dummies set to 1 and the rest of the dummies set to 0.

C Summary statistics for heads of lineages

Table A.1: Summary statistics of heads of lineages born before 1685

	Mean (1)	Median (2)	S.D. (3)	Count (4)
Females				
Children	9.42	10	3.66	2,058
Grandchildren	45.99	43	27.40	2,058
Great-grandchildren	187.65	159	142.74	2,058
Great-great-grandchildren	341.04	206.5	408.07	2,058
Years from marriage to first birth (TFB)	1.23	1.04	0.49	2,058
Literate	0.68	1	0.47	1,192
Fraction of literate children	0.72	1	0.36	1,872
Fraction of surviving children b	0.48	0.50	0.21	2,058
Fraction of surviving children with known literacy b	0.79	0.75	0.57	2,016
Age at first marriage	19.34	18.7	3.79	2,058
Age at last delivery	38.27	40.3	6.46	2,058
Males				
Children	10.03	10	4.32	1,740
Grandchildren	48.94	45	28.77	1,740
Great-grandchildren	187.53	159	137.10	1,740
Great-great-grandchildren	238.38	136.5	293.17	1,740
Years from marriage to first birth (TFB)	1.16	0.99	0.44	1,740
Literate	0.64	1	0.48	1,030
Fraction of literate children	0.76	1	0.34	1,576
Fraction of surviving children b	0.49	0.50	0.21	1,740
Fraction of surviving children with known literacy b	0.73	0.67	0.54	1,711
Age at first marriage	26.62	25.9	4.41	1,740
Age at last delivery	46.31	46.9	8.81	1,740
All				
Children	9.70	10	3.99	3,798
Grandchildren	47.35	44	28.07	3,798
Great-grandchildren	187.59	159	140.17	3,798
Great-great-grandchildren	294.01	171	363.58	3,798
Years from marriage to first birth (TFB)	1.20	1.02	0.47	3,798
Literate	0.66	1	0.47	2,222
Fraction of literate children	0.74	1	0.35	3,448
Fraction of surviving children b	0.49	0.50	0.21	3,798
Fraction of surviving children with known literacy b	0.76	0.67	0.56	3,727
Age at first marriage	22.67	22.2	5.46	3,798
Age at last delivery	41.95	42.1	8.61	3,798

^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-grandchildren) reflects the fact that these cohorts are less fully observed. Furthermore, since men produce children at later ages than women, this effect is more pronounced among men.

 $[^]b$ Survival is recorded at age 40.

D Robustness: Number of Marriages and Spousal Migration

Table A.2: Robustness to additional control variables: number of marriages and spousal migration – accounting for Maternal Founder fixed effects

		Log r	number of o	descendan	ts in:	
	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4
	(1)	(2)	(3)	(4)	(5)	(6)
TFB	049***	.583***	.794***	050**	.418**	.688***
TFB^2	(.019)	(.197) 222***	(.252) 315***	(.020)	(.200) 166**	(.253) 278***
Literate	008	(.065) .139***	(.083) .134**	003	(.066) .144***	(.083) .139**
Male	(.023) .156***	(.049) .250***	(.063) .117**	(.025) .182***	(.050) .227***	(.064) .041
	(.023)	(.045)	(.058)	(.026)	(.046)	(.058)
Total number of marriages fixed effects	Yes	Yes	Yes	No	No	No
Total number of marriages of spouse fixed effects	Yes	Yes	Yes	No	No	No
Immigration status of spouse fixed effects	No	No	No	Yes	Yes	Yes
Emigration status of spouse fixed effects	No	No	No	Yes	Yes	Yes
Number of observations	3,798	3,798	3,798	3,798	3,798	3,798
Adjusted R^2	.194	.098	.316	.038	.062	.319
Joint signlevel of TFB & TFB ²	.008	.000	.000	.012	.004	.000
Maximizing TFB		1.311	1.258		1.26	1.239
Lower limit of 90% CI		1.067	1.02		.728	.927
Upper limit of 90% CI		1.446	1.389		1.445	1.388

This table presents the results of a series of fixed-effects regressions of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2 . All regressions account for Maternal Founder fixed effects. Birth year, marriage age and stoppage age dummies are included as controls. A dummy indicating unknown literacy is also included in the regressions. In columns 1–3, dummies for the total number of marriages experienced during the lifetime of the heads of lineages, as well as dummies for the total number of marriages experienced by the first spouses of the heads of lineages, are included. In columns 4–6, dummies indicating the immigration and emigration statuses of the head of the first spouses of the heads of lineages are included. Standard errors clustered at the level of the firstborn are reported in parentheses. * p < 0.10, *** p < 0.05, **** p < 0.01.

E Robustness: Gender

Table A.3: Robustness to gender distinction – sample restricted to females – accounting for Maternal Founder fixed effects

		Log	number of	descendan	ts in:	
	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4
	(1)	(2)	(3)	(4)	(5)	(6)
TFB	065***	.972***	1.521***	065***	.980***	1.534***
TFB^2	(.025)	(.272) 343***	(.336) 545***	(.025)	(.272) 345***	(.336) 549***
		(.086)	(.106)		(.086)	(.106)
Literate				030	.117	.144
				(.037)	(.082)	(.103)
Number of observations	2,058	2,058	2,058	2,058	2,058	2,058
Adjusted R^2	.094	.092	.272	.093	.093	.272
Joint signlevel of TFB & TFB ²	.009	.000	.000	.008	.000	.000
Maximizing TFB		1.416	1.397		1.420	1.398
Lower limit of 90% CI		1.240	1.261		1.247	1.264
Upper limit of 90% CI		1.535	1.495		1.539	1.496

This table presents the results of a series of fixed-effects regressions of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2 for female heads of lineages. All regressions account for Maternal Founder fixed effects. Birth year, marriage age and stoppage age dummies are included as controls. A dummy indicating unknown literacy is also included in the regressions. Standard errors clustered at the level of the firstborn are reported in parentheses. * p < 0.10, *** p < 0.05, *** p < 0.01.

F Robustness: Location and Season of Marriage and Birth

Table A.4: Robustness to additional control variables: location and season of marriage and birth
– accounting for Maternal Founder fixed effects

		Log	number of	descendar	nts in:	
	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4
	(1)	(2)	(3)	(4)	(5)	(6)
TFB	053***	.334*	.548**	040**	.537***	.784***
	(.020)	(.198)	(.247)	(.020)	(.206)	(.265)
TFB^2		137**	228***		206***	313***
		(.065)	(.081)		(.067)	(.086)
Literate	012	.090*	.074	003	.151***	.141**
	(.026)	(.051)	(.064)	(.025)	(.050)	(.064)
Male	.183***	.223***	.044	.204***	.289***	.123**
	(.026)	(.045)	(.057)	(.026)	(.047)	(.058)
Birth parish fixed effects	Yes	Yes	Yes	No	No	No
Death parish fixed effects	Yes	Yes	Yes	No	No	No
Month of marriage fixed effects	No	No	No	Yes	Yes	Yes
Month of birth of firstborn fixed effects	No	No	No	Yes	Yes	Yes
Number of observations	3,798	3,798	3,798	3,798	3,798	3,798
Adjusted R^2	.070	.130	.375	.036	.056	.312
Joint signlevel of TFB & TFB ²	.007	.012	.000	.044	.001	.000
Maximizing TFB		1.218	1.200		1.301	1.251
Lower limit of 90% CI		.116	.707		.984	.978
Upper limit of 90% CI		1.441	1.382		1.453	1.39

This table presents the results of a series of fixed-effects regressions of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2 . All regressions account for Maternal Founder fixed effects. Birth year, marriage age and stoppage age dummies are included as controls. A dummy indicating unknown literacy is also included in the regressions. In columns 1–3, dummies for the birth (or baptism) parish of the heads of lineages, as well as dummies for the death (or burial) parish of the heads of lineages are included. In columns 4–6, dummies indicating the months of marriage of the heads of lineages, as well as dummies for the months of birth of the the firstborns of the heads of lineages, are 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: Birth Order

Table A.5: Robustness to additional control variable: birth order – accounting for Maternal Founder fixed effects

	Log number of descendants in:								
	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4			
	(1)	(2)	(3)	(4)	(5)	(6)			
TFB	052***	.458**	.740***	050**	.450**	.710***			
TFB^2	(.020)	(.200) 181***	(.253) 297***	(.020)	(.201) 177***	(.254) 288***			
Literate	003	(.066) .145***	(.083) .137**	002	(.066) .152***	(.083) .143**			
Male	(.025) .200***	(.050) .290***	(.064) .130**	(.025) .197***	(.050) .282***	(.064) .126**			
Firstborn	(.026) $.004$	(.046) $.039$	(.058) $.017$	(.026)	(.046)	(.058)			
Birth order fixed effects	(.021) No	(.039) No	(.047) No	Yes	Yes	Yes			
Number of observations	3,798	3,798	3,798	3,798	3,798	3,798			
Adjusted R^2	.035	.052	.311	.036	.053	.311			
Joint signlevel of TFB & TFB ²	.008	.002	.000	.012	.002	.000			
Maximizing TFB		1.265	1.245		1.269	1.232			
Lower limit of 90% CI		.838	.971		.823	.929			
Upper limit of 90% CI		1.435	1.385		1.442	1.378			

This table presents the results of a series of fixed-effects regressions of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2 . All regressions account for Maternal Founder fixed effects. Birth year, marriage age and stoppage age dummies are included as controls. A dummy indicating unknown literacy is also included in the regressions. In columns 1–3, a dummy for the firstborn status of the heads of lineages is included. In columns 4–6, dummies the birth order of the heads of lineages are included. Standard errors clustered at the level of the firstborn are reported in parentheses. * p < 0.10, *** p < 0.05, *** p < 0.01.

H Robustness: GLM Regression

Table A.6: Robustness of GLM regression to the exclusion of Maternal Founder fixed effects

	Number of descendants in:											
	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4	Gen. 1	Gen. 3	Gen. 4
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
TFB	063***	.371**	.616***	063***	.324*	.573**	081***	.260	.525**	090***	.346**	.573**
TFB^2	(.018)	(.185) 133**	(.230) 232***	(.018)	(.186) 119*	(.231) 219***	(.017)	(.184) 106*	(.231) 209***	(.010)	(.167) 137**	(.227) 224***
T		(.060)	(.074)	000	(.061)	(.074)	000	(.060)	(.074)	0 = 0 + 4 +	(.054)	(.073)
Literate				002 (.020)	.222*** (.038)	.227*** (.046)	009 $(.019)$.219*** (.038)	.225*** (.046)	056*** (.011)	.180*** $(.035)$.195*** (.047)
Male							.295*** (.019)	.402*** (.035)	.306*** (.041)	004 (.011)	.150*** (.032)	.194*** (.042)
Stoppage age fixed effects	No	No	No	No	No	No	No	No	No	Yes	Yes	Yes
Number of observations Joint signlevel of TFB & TFB ² Maximizing TFB	3,798 .000	3,798 .059 1.399	3,798 .000 1.328	3,798 .000	3,798 .086 1.363	3,798 .001 1.306	3,798 .000	3,798 .041 1.229	3,798 .000 1.255	3,798 .000	3,798 .001 1.262	3,798 .000 1.277

This table presents the results of a series of GLM regressions, with a negative binomial distribution and a logarithmic link function, of the number of descendants in generation t on time to first birth, i.e. TFB and TFB^2 . Birth year and marriage age dummies are included as controls. Furthermore, stoppage age dummies are included in columns 10–12. A dummy indicating unknown literacy is included in the regressions underlying column 4–12. Standard errors clustered at the level of the firstborn are reported in parentheses. * p < 0.10, *** p < 0.05, **** p < 0.01.

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