

Behavioral Ecology (2013), 00(00), 1–8. doi:10.1093/beheco/art091

Original Article

An evolutionary approach to change of status–fertility relationship in human fertility transition

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Received 16 April 2013; revised 24 July 2013; accepted 22 August 2013.

The change in benefits of high socioeconomic status to fertility in humans during the demographic transition from high to low fertility has interested both demographers and evolutionary biologists. Evolutionary analyses add to demographic analyses by considering also males and status-related differential in male mating success, but they have been limited to time cross-sections and have not linked this differential to differentials in other determinants of male fertility. We use life-history records of males ($n = 3791$) entering marriage market before (1810s–1880s) and during (1890s–1960s) the Finnish fertility transition to investigate associations between socioeconomic status and chance and timing of marriage, choice for spouse, and lifetime fertility. Low status invariably brought a lower marriage chance throughout these 160 years, which partly explained why ever-married high-status men lost advantage at early marriage when the system of achieving a high status shifted from inheritance to self-effort. The loss, coupled with assortative mating by age, promoted disappearance of differential in wife's age at marriage and thus, disappearance of differential in fertility between ever-married high- and low-status men in the Finnish fertility transition. Consequently, among all men (married and unmarried), status-related differential in lifetime fertility—not selection coefficient—declined over the transition. This study is among the first to show the interrelated dynamics of status-related differentials in male mating and reproductive traits; by doing so, it contributes to an evolutionary understanding of change of status–fertility relationship in human fertility transition and confirms continuing phenotypic selection on male status/wealth in modern societies.

Key words: age at marriage, assortative mating, female choice, marital fertility, mating success, phenotypic selection.

INTRODUCTION

The demographic transition in fertility was a major event in the modern history of human population (Coale 1986; Livi-Bacci 2012) and, consequently, has been a leading research topic among demographers since the 1940s (Kirk 1996). This transition refers to the transformation of reproductive pattern from one characterized by natural fertility to one characterized by family limitation (Knodel 1988). For most European countries, the transition started in the second half of the 19th century and lasted until around 1970; during this process, fertility in terms of total fertility rate, a measure of average number of children per woman, declined from a level of more than 4 offspring to a level around two (Livi-Bacci 2012). For African countries, the transition just started about 3 decades ago (Cohen 1998). The fertility transition also began

to attract attention of evolutionary biologists when Vining (1986) challenged a sociobiological approach to human behaviors in contemporary societies with his observation that high-status families did not translate their advantage in resources into more offspring in transitional or posttransitional societies. Consequently, there have been many evolutionary analyses on the fertility transition since the mid-1980s (Borgerhoff Mulder 1998).

The demographic analyses investigating the relationship between fertility and socioeconomic status within the same population indicated that the change of status-related fertility differential followed the pace of fertility transition/limitation, because high-status families reduced their family size earlier than low-status families, for example, in urban (Bardet 1983) and rural (Cummins 2013) populations of France. Skirbekk (2008) showed that in general, a neutral or negative relationship between status and fertility was established in European and North American countries before 1900 and in developing countries before 1975. Such demographic analyses considered only women or at least, men were not separated from

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women. However, the status–fertility relationship differs between men and women (Trivers 1985; Low 2000; Hopcroft 2006; Weeden et al. 2006; Fieder and Huber 2007; Nettle and Pollet 2008), and in pre-fertility transition societies, men rather than women controlled resources vital for attracting mates and investing in future offspring, for example, in 20th-century Kenya (Borgerhoff Mulder 1990), and 18th- and 19th-century Finland (Moring 1996) and Germany (Volland and Dunbar 1997). They also considered marital fertility only, that is, number of children of a married person, but chance of marrying as the other determinant of lifetime fertility among all men (married and unmarried) was not given due attention (see Preston et al. (2001) on fertility decomposition). Consequently, it can be misleading to conclude that fertility differential has disappeared or reversed just based on marital fertility data, a problem with Vining (1986).

The above gaps were partly filled by some evolutionary analyses designed to investigate whether socioeconomic status indeed failed to bring any benefit to reproduction in contemporary societies. Here, men were treated independently of women and male chance of marrying received special attention. A low status brought a high risk of having no marriage partners among Swedish men aged 45–55 years in 2000 (Fieder and Huber 2007). A similar result was found in other contemporary populations/countries (Brazil, Mexico, Panama, South Africa, United Kingdom, United States of America, and Venezuela) (Nettle and Pollet 2008; Fieder et al. 2011): men with lower status remained more likely never married. The positive effect from high socioeconomic status on chance of marrying found in these contemporary societies was also reported for historical populations in the process of fertility transition, for example, 19th-century Sweden at the beginning of fertility decline (Low 1994) and the US population in 1910 (Pollet and Nettle 2008). Thus, high-status men might still have higher lifetime fertility in transitional or posttransitional societies, because they tend to have a lower chance of childlessness due to their higher chance of marrying (Fieder and Huber 2007; Nettle and Pollet 2008).

These evolutionary analyses generally focused on a time cross-section in each studied population rather than on whole course of the fertility transition. Consequently, we lack an investigation of the cross-time dynamics of status-related differential in male chance of marrying. In light of results from the mentioned analyses covering either transitional or posttransitional stages and those covering a pretransitional stage (e.g., Kinoshita 1990), the differential in male mating success seems to have been invariant with time or independent of fertility transition in a specific population. We also lack an investigation of variation in status-related differential in age at marriage of both ever-married men and their wives during the fertility transition and consequently, lack an investigation of the linkage between the variation and the dynamics of differential in male chance of marrying. Clarifying the linkage would play an important role in understanding why status-related differential in lifetime fertility was not observed among married or reproducing men in posttransitional societies such as contemporary Sweden (Fieder and Huber 2007) and United Kingdom (Nettle and Pollet 2008). Currently, the variation that a positive differential (early marriage promoted by high status) in age at marriage changed firstly into a neutral one and then remains neutral or turns negative can only be inferred from synthesizing previous analyses focusing on populations at different stages of the fertility transition. Specifically, some analyses on pretransitional societies indicated a benefit of high status for early marriage (e.g., Kinoshita 1990; Røskaft et al. 1992; Moring 1996; Pettay et al. 2007), whereas others showed

that this advantage disappeared or reversed in transitional or post-transitional societies (e.g., Notestein 1931; Glick and Landau 1950; Kaplan et al. 2002; Booth 2010).

This study investigates the dynamics of socioeconomic status-related differentials in male lifetime fertility and its determinants—chance of marrying, age at marriage, and so on—in response to socioeconomic changes and how these dynamics were linked with each other over the fertility transition. Here, life fertility refers to lifetime number of children born. To achieve the aim, we conduct a case study on male mating and reproductive patterns across the whole course of the Finnish fertility transition, by taking advantage of individual-based, multigenerational life-history records of men entering marriage market during the transition (1890s–1960s) and using data before the transition (1810s–1880s) as a control.

MATERIALS AND METHODS

Life-history data

The Evangelical Lutheran Church of Finland kept church registers in each parish across the whole country from 1749 onward. These registers included by law the information on birth and death, marriage and reproduction (if any), and immigrations and emigrations (if any). Currently, the registers are accessible to the public: for persons living before 1900, see <http://hiski.genealogia.fi/historia/indexe.htm>; for those living in the 20th century, see published genealogies (e.g., Lumia 2010). Survival and reproduction details of a sample of men once living in 3 parishes were reconstructed from such registers; including geographically distinct parish areas into the study helped to reduce the likelihood that any arising results could be typical of 1 region. Two parishes (Hiittinen and Kustavi) are located at the southwestern archipelago and the third one (Ikaalinen) is in Mainland Finland (Lummaa 2001).

Based on their occupation, the primary measure of socioeconomic status in European countries (e.g., Braveman et al. 2005; Goodman et al. 2012), these men were classified into 3 socioeconomic groups: upper class, middle class, and lower class. Our data set does not contain records of income, but period-specific relative wealth level of each occupation was taken into account in the classification (see Karskela (1997) for occupational prestige and its positive association with wealth ownership or accumulation ability in 19th-century Finland and Alestalo and Uusitalo (1980) for that in 20th-century Finland). Education—another determinant of status in contemporary societies—was not considered because education levels were too low for nearly all men in these rural parishes during most of our study period to provide any meaningful comparison. According to the above classification methodology, the composition of each class was simple in the first half of the 19th century: the upper class consisted of parish clerks and farmers owning their own land, the middle class consisted of crofters and small occupation holders such as shoemakers and fishermen, and the lower class consisted of hired farm laborers. Since the second half of the 19th century, class elements have become more and more diverse. For example, besides occupations just mentioned, upper class would also include businessmen and engineers, middle class would also include pilots and postmasters, and lower class would also include other industry laborers like stokers and sailors. [Supplementary Table S1](#) shows occupational composition of each class in selected decades.

Fertility declined in Finland from about the 1890s to 1960s (Coale 1986; Lutz 1987; Pitkänen 2003). We used the men estimated to marry before the Finnish fertility transition (i.e., 1810s–1880s) as

a control to those estimated to marry during the transition (i.e., 1890s–1960s), to study whether and how mating and reproduction patterns shifted in the latter period and whether and how any shift changed the fertility heterogeneity among men from different socio-economic classes. Here, regardless of whether a man ultimately succeeded in marrying or not, the year when he turned 30 and was estimated to enter the “mating market” (Kaplan et al. 2002) was called his estimated marriage year (note: ever-married men married on average at age 28.3 over these 160 years). For example, estimated marriage year of a man born in 1856 would be 1886.

This study considered men surviving to age 50 for the following reason. Adulthood mortality declined drastically during the 160 years: about 26% of men alive at age 15 and estimated to marry in the 1810s did not survive to age 50 (note: majority of unmarried men died before age 50), but this figure declined to around 5% in the 1960s. Evidently, survival can be one of the major determinants of mating and reproductive success before the fertility transition, whereas this possibility was reduced greatly in the transition. Therefore, to make the pretransitional period a meaningful control, we focused on men surviving to age 50 in both periods; this choice is also expected to shed light on mating and reproduction patterns in contemporary societies, where adulthood mortality is negligible (Human Mortality Database 2013).

The sampling process is summarized as follows. First, we selected, in an initial sample, all men completely tracked from birth to death, estimated to marry between the 1810s and 1960s, and alive at age 50. For these men, records of marital status and lifetime number of children were complete. However, some of them lacked records of occupation and we cannot evaluate whether the absence was random, that is, whether lack of a record was biased toward certain occupations. From the initial sample, we then selected those men for statistical computations who had a record of occupation, that is, socioeconomic status. Some of the married men in this final sample lacked records of their own and/or their wives’ age at marriage; we used contingency table analysis to indicate that absence of such records was independent of socioeconomic status in both pretransitional and transitional periods (see Supplementary Table S2).

Statistical methods

Regarding status-related differentials, we investigated associations between socioeconomic status and 1) chance of marrying among all men (i.e., both married and unmarried men were included), 2) age at marriage among married men and their first wives, 3) lifetime fertility among married men (i.e., marital fertility), and 4) lifetime fertility among all men (note: in our data set about 1% of unmarried men were registered as once fathering any children; we have no other reference data on prevalence of children born outside marriage). The first 3 analyses focused on determinants of lifetime fertility among all men and the last one focused on lifetime fertility itself. All these associations were analyzed along time to study the dynamics of status-related differentials in male mating or reproduction.

Regarding links between dynamics of differentials in different traits, we investigated 1) the linkage between age at first marriage and occupation shift (i.e., having an occupation different from father’s), which was used to reflect achieving a middle or upper status through own effort rather than inheritance; 2) the linkage between the differential in a man’s age at first marriage and that in his first wife’s age at marriage with him; 3) the linkage between the differential in wife’s age at marriage and that in lifetime fertility (i.e., marital fertility); 4) the linkage between the differential in

marital status (used to model chance of marrying; see below) and that in lifetime fertility among all men. The first 3 linkages were analyzed for married men only.

We used generalized linear mixed models (GLMMs) to investigate dynamics of status-related differentials in fertility determinants or fertility itself (response variables), by including male socioeconomic status and a time variable as fixed effects and residential parish as a random effect. Here, estimated marriage decade, instead of estimated marriage year, was used as the time variable to net out fluctuations in fertility or its determinants (e.g., Grier and Tullock 1989), because we did not know the mechanistic functional forms (linear, quadratic, etc.) of trends in these response variables. To investigate the 4 linkages just outlined, we included 3 fixed effects in GLMMs (with interactions considered): male socioeconomic status, estimated marriage decade, and the third one regarding the specific linkage in question. For example, in the analysis of the linkage between differential in marital status and that in lifetime fertility among all men, lifetime fertility was the response variable and marital status was the third fixed effect. We then used path analysis to look at how much of the status-related differential in lifetime fertility was via the path that socioeconomic status influenced marital status (i.e., the differential in mating success), which then influenced fertility. For each GLMM, we used likelihood ratio test to simplify maximum model to minimum adequate model, with Akaike information criterion value as a complementary criterion in model comparison (Crawley 2002; Gillespie et al. 2008; Liu et al. 2012). These 2 criteria generally gave the same significance result; when there was any conflict, the simpler model suggested by either criterion was adopted. In models where effect of socioeconomic status was significant, combining upper class with middle class to make a simplified contrast termed high status (upper or middle classes) versus low status (lower class) did not cause significant loss in explanatory power in terms of likelihood; thus, only the results of the simplified contrast are shown.

In the logistic regression analysis of chance of marrying, marital status was modeled as a binary variable and assigned 1 or 0 according to whether a man succeeded in marrying at least once or not. For an ever-married man, his age at first marriage and his first wife’s age at marriage with him were modeled as normally distributed variables after a reciprocal transformation. Lifetime fertility, that is, lifetime number of children, was modeled as a normally distributed variable after a logarithm transformation, rather than as a variable with Poisson distribution in light of over-dispersion. Both transformations were suggested by Box–Cox plot (Crawley 2002). Note that back-transformed estimations from models were not equal to arithmetic means calculated from the raw data; however, the significance tests and trends predicted by the models were consistent with patterns shown in the raw data (Figure 1). For accuracy and consistency, all means, standard errors, and figures were based on the raw data.

We conducted all analyses in R 2.11.1 (R Development Core Team 2010), using the statistical packages “lme4” (Bates and Maechler 2009) for GLMMs and “languageR” (Baayen 2010) for indicating significance levels from GLMMs (“lme4” itself does not give significance levels of *t* values). Given that sibling competition could influence male mating and reproductive success (e.g., Gibson and Gurmu 2011; Nitsch et al. 2013), we also ran models including number of siblings and birth order as covariates. These models produced similar results, especially for the transitional period, but they included substantially fewer observations because many subjects lacked records of these 2 variables. Thus, we only present

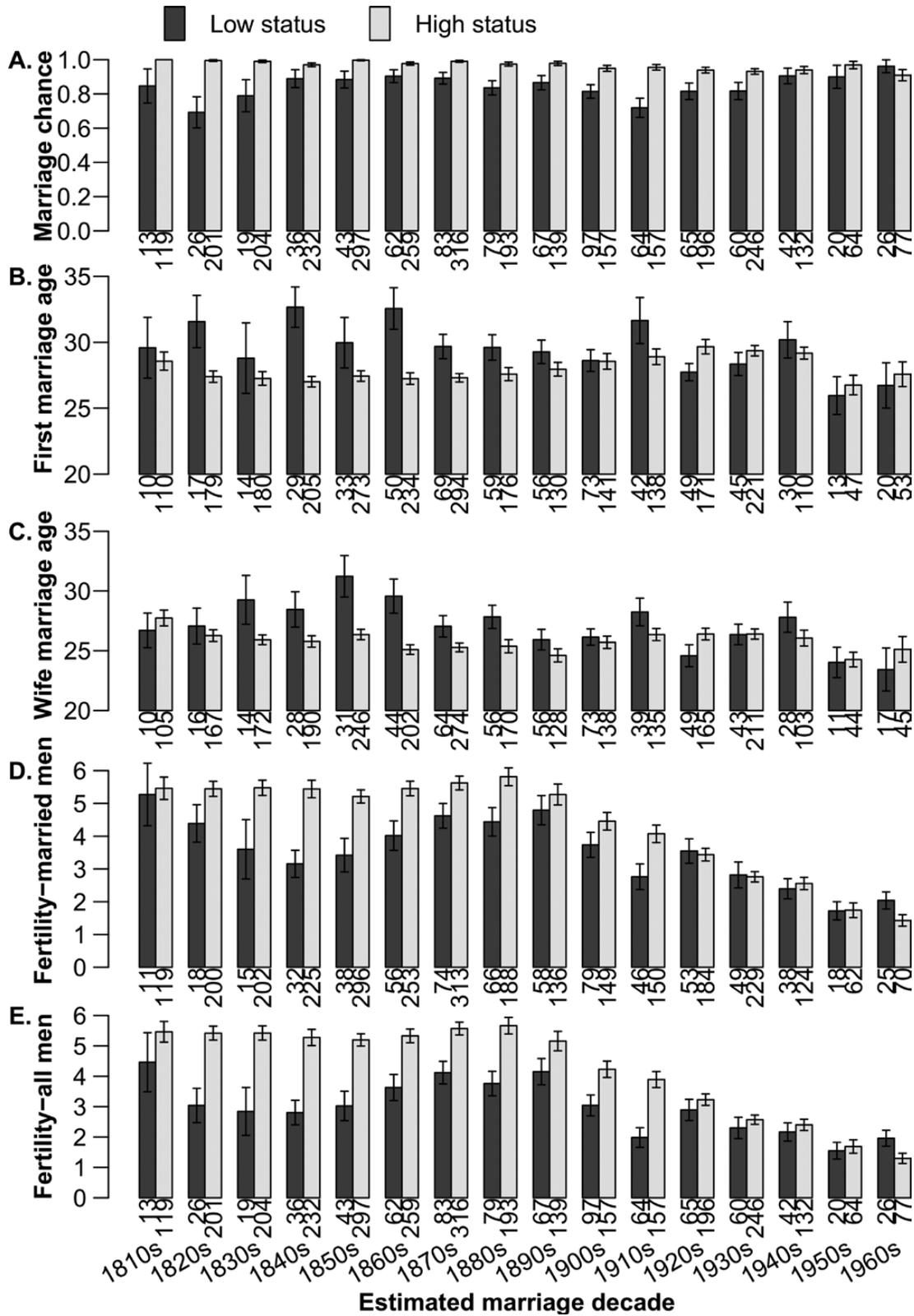


Figure 1

Dynamics of (A) chance of marrying, (B) male age at first marriage, (C) first wife’s age at marriage, (D) lifetime fertility among ever-married men, and (E) lifetime fertility among all men along marriage decades (*x* axis). The *x* axis is the same for all 5 panels (A–E) although only the one for panel (E) is plotted; marriage decade, ranging from the 1810s to 1960s, refers to an estimated rather than real marriage decade (see Life-history data for details). In (A and E), regardless of whether he remained single throughout his lifetime or not, any man surviving to age 50 is included; in (B–D), only ever-married men are included. In each decade, there are 2 bars: the dark gray bar for low-status men is next to the light gray bar for high-status men; bars for different decades are separated with space; the figure legend is the same for all panels although only the one for panel (A) is plotted. Error bar refers to standard error and number at the bottom of each bar refers to sample size.

below the results from models without controlling for sibling number and birth order and include outputs from models controlling for them in [Supplementary Table S3](#).

RESULTS

Differential in chance of marrying

Before the fertility transition (1810s–1880s), high-status men who survived to age 50 had a 98.6% chance to marry; in contrast ($z = 9.97$, $P < 0.001$), low-status men had only an 85.9% chance to marry ([Figure 1A](#)). This advantage for high-status men persisted over the 80 years: in contrast to the 1810s (the reference decade), the change in the effect of socioeconomic status on chance of marrying in any later decade was not significant (all P values > 0.05). Chance of marrying kept constant across the period ($\chi^2_7 = 7.52$, $P = 0.38$).

During the transition (1890s–1960s), high-status men still had a higher chance of marrying than low-status men (94.5% vs. 83.0%; $z = 6.95$, $P < 0.001$) ([Figure 1A](#)). This advantage for high-status men was again invariant with time, as shown by the nonsignificant interaction between socioeconomic status and marriage decade ($\chi^2_7 = 11.76$, $P = 0.11$). Chance of marrying did not change significantly with time ($\chi^2_7 = 7.52$, $P = 0.38$).

Differential in timing of first marriage

Before the fertility transition (1810s–1880s), age at first marriage among ever-married high-status men was 27.4 (± 0.2) years, significantly earlier than that (30.6 ± 0.5 years) of low-status men ($t = 6.52$, $P < 0.001$) ([Figure 1B](#)). The differential in age at first marriage did not change significantly along time (interaction effect socioeconomic status \times marriage decade: $\chi^2_7 = 13.22$, $P = 0.07$) and male age at first marriage did not change significantly with time ($\chi^2_7 = 6.04$, $P = 0.54$).

Throughout the fertility transition (1890s–1960s) (socioeconomic status \times marriage decade: $\chi^2_7 = 8.39$, $P = 0.30$), high-status men had a similar age at first marriage as low-status men (28.8 ± 0.2 vs. 28.9 ± 0.4 years; $\chi^2_1 = 0.03$, $P = 0.85$). Male age at first marriage changed with time ($\chi^2_7 = 25.07$, $P < 0.001$): men married at a younger age during the 1950s and 1960s ([Figure 1B](#)).

The disappearance (from the onset of the fertility transition; see [Figure 1B](#)) of differential in age at first marriage between low- and high-status men was caused by differentiated shifts in timing of marriage. From the 1880s to 1920s, age at first marriage among low-status men did not change significantly with time (Pearson's coefficient of the correlation between age at first marriage and estimated marriage year: $r = -0.037$, $t_{277} = -0.62$, $P = 0.54$), whereas first marriage was postponed steadily among high-status men ($r = 0.12$, $t_{754} = 4.43$, $P < 0.001$) ([Figure 1B](#)). Underlying the postponement was the fact that among high-status men, proportion of men inheriting occupation and thus high status of father declined from 63.6% in the 1880s to 27.8% in the 1920s (note: among those who did not inherit a high status, i.e., low-status men and those high-status men whose occupation was different from that of their father, proportion of men managing to get a high status increased from 52.1% to 71.6% during the period). In other words, more and more men achieved their high status not through inheritance. However, men achieving a high status through an occupation different from father's married on average 1.36 years later than those achieving a high status through inheritance ($t = -3.16$, $P < 0.01$) ([Figure 2](#)). Once occupation shift was controlled for, the effect of

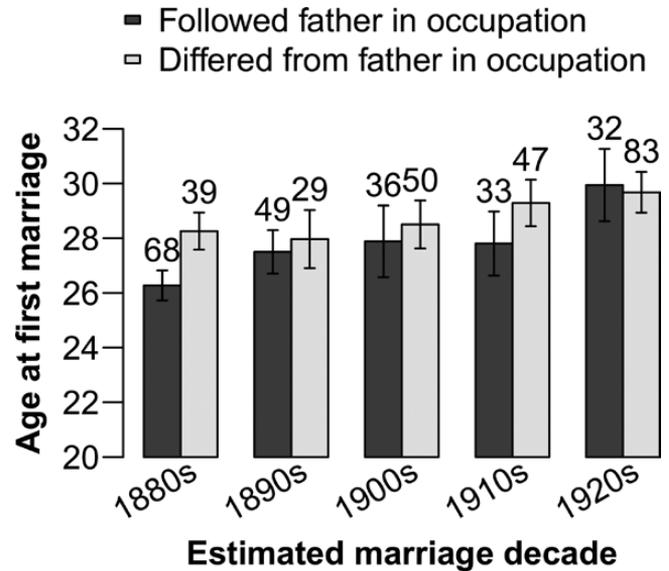


Figure 2

Male age at first marriage in response to occupation inheritance pattern from the 1880s to 1920s (estimated marriage decade). Only ever-married men in middle or upper classes are included. Dark gray bars represent men having the same occupation as their fathers and light gray bars represent men different from their fathers in occupation. Error bar refers to standard error and number above each error bar refers to sample size.

estimated marriage decade on age at first marriage was not significant among high-status men ($\chi^2_4 = 8.13$, $P = 0.09$); otherwise, the effect was significant ($\chi^2_4 = 12.11$, $P < 0.05$), consistent with correlation analysis.

Differential in age at marriage of the first wife

Before the fertility transition (1810s–1880s), high-status men married for the first time younger wives than low-status men (25.8 ± 0.2 years vs. 28.4 ± 0.5 years; $t = 5.85$, $P < 0.001$) ([Figure 1C](#)). The differential in wife's age at marriage did not change significantly with time (socioeconomic status \times marriage decade: $\chi^2_7 = 5.31$, $P = 0.62$) although wife's age at marriage itself shifted (declining in general) along time ($\chi^2_7 = 21.02$, $P < 0.01$).

During the fertility transition (1890s–1960s), wife's age at marriage (with the men under question) among high-status men was on average 25.9 (± 0.2) years, similar to that (26.1 ± 0.4 years) among low-status men ($\chi^2_1 = 0.17$, $P = 0.68$) ([Figure 1C](#)). The similarity largely persisted across the fertility transition (socioeconomic status \times marriage decade: $\chi^2_7 = 14.34$, $P = 0.05$; borderline significance was caused by significant interaction in a single decade, i.e., the 1920s). As the case with male age at first marriage, wife's age at marriage changed significantly along time ($\chi^2_7 = 24.35$, $P < 0.001$), being younger in the 1950s and 1960s ([Figure 1C](#)).

The disappearance of differential in wife's age at marriage during the fertility transition was driven by the fact that in contrast to the pretransition days, low-status men married younger wives since the beginning of the transition ([Figure 1C](#)), which, in turn, was partly driven by the assortative mating by age in the context of earlier marriage among low-status men from the 1870s ([Figure 1B](#)). The coefficient of correlation between men's age at first marriage and their wife's age at marriage was 0.42 ($t_{1787} = 19.31$, $P < 0.001$) in the pretransition period and 0.57 ($t_{1283} = 25.02$, $P < 0.001$) in the fertility transition, respectively. Path analysis indicated that before

the transition, 37.1% of the effect of male socioeconomic status on wife's age at marriage (i.e., the differential in wife's age at marriage) was via the path that male status affected male age at first marriage (i.e., the differential in male age at first marriage), which then affected wife's age at marriage.

This analysis included those men who married at least once and 8.44% of those married men married at least twice, but the results did not change qualitatively when the analysis focused on those men who married only once during their lifetime.

Differential in lifetime fertility among married men, that is, differential in marital fertility

Before the fertility transition (1810s–1880s), ever-married high-status men consistently had more children than low-status men (socioeconomic status \times marriage decade: $\chi^2_7 = 4.68$, $P = 0.70$). Specifically, high-status men had 5.48 ± 0.08 children in their lifetime (decade effect: $\chi^2_7 = 8.82$, $P = 0.27$), whereas low-status men had only 4.14 ± 0.18 children (contrast: $t = 5.70$, $P < 0.001$). Wife's age at marriage was negatively associated with male fertility (coefficient of correlation: $r = -0.50$, $t_{1787} = -24.24$, $P < 0.001$). Path analysis indicated that among ever-married men, 42.5% of the effect of socioeconomic status on lifetime fertility (i.e., the differential in male marital fertility) was via the path that male status affected wife's age at marriage (i.e., the differential in wife's age at marriage), which then affected male lifetime fertility.

During the fertility transition (1890s–1960s), ever-married high-status men had similar numbers of children in their lifetime as low-status men (3.42 ± 0.09 vs. 3.27 ± 0.15 children; $\chi^2_1 = 2.27$, $P = 0.13$) (Figure 1D). This similarity was stable over the 8 decades (socioeconomic status \times marriage decade: $\chi^2_7 = 9.73$, $P = 0.20$). Marital fertility declined significantly along time ($\chi^2_7 = 189.31$, $P < 0.001$; Figure 1D). In these parishes, ever-married low-status men had a similar chance (around 83%) of having at least 1 child as high-status men during the fertility transition, so status-related similarity in marital fertility meant similarity in fertility among reproducing men, because average of the latter fertility is the quotient of dividing average marital fertility by chance of having children among ever-married men. Indeed, there was no differential in fertility when childless men were excluded ($\chi^2_1 = 1.76$, $P = 0.18$).

Differential in lifetime fertility among all men (married and unmarried)

Before the fertility transition (1810s–1880s), high-status men surviving to age 50 had on average $5.41 (\pm 0.08)$ children in their lifetime, significantly more than that (3.56 ± 0.17 children) among low-status men ($t = 9.02$, $P < 0.001$) (Figure 1E). Such an advantage for high-status men persisted over these 8 decades (socioeconomic status \times marriage decade: $\chi^2_7 = 5.64$, $P = 0.58$) and additionally, lifetime number of children did not change significantly over this period ($\chi^2_7 = 7.61$, $P = 0.37$). Path analysis indicated that among all men, 40.3% of the effect of socioeconomic status on lifetime fertility (i.e., the differential in lifetime fertility) was via the path that socioeconomic status affected male marital status (i.e., the differential in male chance of marrying), which then affected lifetime fertility.

The differential in lifetime fertility between high- and low-status men was also significant from the 1890s to 1910s (all P values < 0.05), but from the 1920s, the difference was nonsignificant (all P values > 0.05) (Figure 1E). Thus, the differential in lifetime fertility changed with time, as indicated by the significant interaction between socioeconomic status and marriage decade ($\chi^2_7 = 20.37$, $P < 0.01$).

DISCUSSION

Based on analyzing life-history records of individuals living in historical Finnish parishes, we conduct one of the first studies on dynamics of differentials in mating and reproductive traits between high- and low-status men and how these dynamics were linked with each other over the fertility transition. Our study indicates that the status-related differential in male chance of marrying remained invariant during the Finnish fertility transition. The finding adds to previous studies focusing only on a time cross-section and is consistent with Chang et al. (2011) on Chinese women (1986–2011), one of the few studies on dynamics in female preference for mates in a shifting socioeconomic context. Mechanisms underlying status-related differential in male mating success could include female choice of wealthy men (Borgerhoff Mulder 1990; Buss 1998), male–male competition (Buss 1998), and arranged marriage (Borgerhoff Mulder 1990). Current evidence points to the first factor. Arranged marriage withered in Finland from the 1860s onward and if a man (suitor) wanted to marry a woman, he had to get her consent first (Talve 1979), indicating the presence of female choice. Given that occupation-based status rank corresponded to wealth rank (see Life-history data for details), it can be inferred females favored men with a middle or upper status in these historical parishes probably because such a status can bring benefits to themselves and their future offspring.

The invariant status-related differential in male mating success had far-reaching effects on other mating and reproductive traits of men in the Finnish fertility transition. First, around the onset of the transition, most of the men who did not inherit a high status struggled for such a status. This struggle induced delayed marriage among those eventually achieving a high status, which was 1 of 2 reasons underlying the disappearance of differential in male age at first marriage in the fertility transition. At that time, the local population was expanding (Moring 1996) and economy of Finland had shifted from a traditional agricultural system to one with more diverse methods of subsistence, for example, ship construction, business, and public service (Alestalo 1986). Consequently, achieving a middle or upper status was increasingly through an occupation different from father's (see also Goodman et al. (2012) on 1915–1929 Sweden, where parental occupation only had a small [albeit significant] effect on offspring income; for status or wealth transmission in small-scale societies, e.g., an agricultural society, see Mace (1998) and Borgerhoff Mulder et al. (2009)). Men getting a high status through inheriting father's occupation could inherit occupationally specific possessions and tools and more importantly, gain competence from an early age onward because they may have helped their father since a young age, which explained early marriage opportunity for them. In contrast, those getting a high status not in this manner needed time to firstly accumulate competence in new occupations (see also Glick and Landau (1950) on 20th-century United States); before achieving professional competence, they would have only a low marriage chance typical for low-status men, which explained delayed marriage among them. The other reason for the disappearance of differential in male age at first marriage was earlier first marriage among low-status men from the 1870s onward: economic constraints on low-status men were eased somewhat in the latter half of the 19th century and they could afford to establish a new household at an earlier age than before (Moring 1996).

Kaplan et al. (2002) once noticed that parents delayed their marriage and reproduction in response to expansion of skill-based labor market to increase future investment in offspring. However, they did not consider how men responded to the market expansion-induced

change in status inheritance system to achieve mating success, the first checkpoint for an adult on the road toward reproductive success. Evidently, shift of status or wealth inheritance system would induce multiple responses in individual mating and reproduction. For example, besides triggering delayed marriage among high-status men, it could also alter the pattern of sibling competition: family size or birth order affected individual mating or reproduction only in the pretransition period when a high status was generally achieved through inheritance (Supplementary Table S3). This observation is consistent with the finding by Gibson and Gurm (2011) on rural Ethiopia.

Assortative mating has been observed in human populations along many dimensions like age, stature, and intelligence (Harris 1912). In these parish communities, as a result of the assortative mating by age, around 37% of differential in wife's age at marriage (i.e., high-status men married younger wives) arose for the reason that high-status men themselves married at a younger age in the pretransition period. This linkage partly explained why once the differential in marriage age between high- and low-status men disappeared during the fertility transition, the differential in wife's age at marriage also disappeared; this, in turn, gave a clue to the disappearance of status-related differential in male marital fertility because more than 40% of differential in the fertility was explained by that in wife's age at marriage. As indicated, nondifferential fertility among ever-married men implied nondifferential fertility among reproducing men during the fertility transition. Thus, the finding from this study sheds light on why differential fertility was not observed among reproducing men in contemporary Sweden and United Kingdom (Fieder and Huber 2007; Nettle and Pollet 2008).

Clarifying differentials in determinants of lifetime fertility among all men (married and unmarried) helps to understand the change of differential in lifetime fertility itself between high- and low-status men along time. Among all men, average lifetime fertility was the product between chance of marrying and average marital fertility; then, the differential in lifetime fertility declined with the decline in marital fertility (Figure 1D) during the fertility transition, when the differential in chance of marrying remained constant, but there was no differential in marital fertility. The analysis explains why a significant differential in lifetime fertility is not found among all men in later decades when there were only moderate samples; presumably, if sample sizes in these decades were sufficiently large, we might still detect some significant differential.

If individual fitness is measured in terms of lifetime fertility, our result shows that among all men, status-related differential in absolute fitness declined over the fertility transition, but this does not mean phenotypic selection—which depends on the relative, not the absolute, fitness (Futuyma 1998; Courtiol et al. 2012)—on male socioeconomic status also declined with time. According to the differentials in mating success and marital fertility, it can be shown that coefficient of selection on status remained somewhat constant at $1 - 0.83/0.945 = 12.2\%$ over the transition, a figure on a par with gradients of selection on male income in various industrial societies (for a review, see Nettle and Pollet (2008)). The significant selection on male status throughout the transition is also indicated by using relative fertility (i.e., dividing lifetime fertility of a man estimated to marry in a given decade by mean lifetime fertility in that decade) as a response variable in modeling status–fertility relationship among all men (result not presented here).

To summarize, this study indicates invariant status-related differential in male mating success and invariant assortative mating by

age between ever-married men and their spouses. These invariant factors underlay the transitions of status-related differentials in age at marriage of ever-married men and their spouses, in marital fertility, and finally, in lifetime fertility among all men in a time when the system of achieving a high status shifted from inheritance to self-effort with the spread of competence/skill-based labor market of new occupations. By such findings, this study contributes to an evolutionary understanding of the change of status–fertility relationship in human fertility transition and, consequently, helps to understand the link between status and fertility in contemporary societies, where self-effort through education is an increasingly important pathway to a high status (Kaplan et al. 2002). Meanwhile, our study confirms continuing phenotypic selection on male status or wealth in modern societies. However, the conclusion from this study is warranted to be tested using data from other sources, given the possible bias with our sample (e.g., those men not having a status record were excluded).

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

FUNDING

J.L. received financial support from Kone Foundation, Max Planck Society, and The University of Sheffield (7777ORSAS; 77772007). V.L. was supported by grants from Kone Foundation, The European Research Council (204116), and The Royal Society (516002.K5760).

We thank L. Iso-Iivari, K. Pokkinen, A. Siitonen, and T. Verho for collecting data needed for the research. We thank Y.-H. Chen, A. Courtiol, M. Lahdenperä, A. Maklakov, J. Pettay, and anonymous reviewers for comments on early versions of the manuscript, and *Behavioral Ecology* production team for copy-editing work.

Handling editor: Alexei Maklakov

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