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Contemporary selection pressures in modern societies? Which factors best explain variance in human reproduction and mating?

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ABSTRACT

Phenotypic traits in humans are under selection pressure and are still evolving, but the relative importance of these traits remains to be investigated. We therefore analyzed jointly phenotypic traits associated with number of children and having ever been married. This provides insights into the relative contribution of each trait and indicates the potential selection pressure induced by a specific trait relative to others. To shed light on potential selection on the genome level, all analyses include a multivariate polygenic risk score of general cognitive ability. We used the data from the Wisconsin Longitudinal Study (WLS), a dataset consisting of 4991 men and 5326 women almost all whites, educated at least at A-level. The focus was on the association between age, education level, wages, religious intensity, fathers' age at child's birth, ratings of facial attractiveness, number of siblings of the respondent, as well as the polygenic risk score of general cognitive ability on the following dependent variables: i) number of children, ii) ever being married, and iii) age at first birth. For each factor we additionally examined the relative contribution to the overall variance explained of the dependent variable. Having been married and, thus, mate selection, is the most important determinant for the number of children for both men and women. Wages explain most of the total variance for "ever married", yet in different directions for men and women, as is also the case for the association between wages and number of children. In both women and men, education explains most of the variance in age at first birth, and the effect is postponing. Furthermore, although the phenotype education is negatively associated with the number of children in both sexes, this holds true for the polygenic risk score for cognitive ability only in men. In addition, in men, the polygenic risk score for cognitive ability also has a positive effect on reproduction due to its positive interaction with wages. Anyhow, with the exception of having ever been married, all other variables explain only a small proportion of the variation in fertility outcomes. Although our results are consistent with the hypothesis that there is selection pressure for rather recently arising traits as education and income, on the basis of our results we are not able to draw any final conclusion on selection.

1. Introduction

In recent years, interest in using evolutionary anthropology to study reproduction in contemporary societies has grown alongside evolutionary explanations for human fertility. Moreover, humans are an especially "good" model for studying evolutionary processes considering the wealth of available data on humans.

According to data on human life-time reproductive success, on multiple phenotypic traits, human genetic variation and its covariation with phenotypic traits, humans are under selection pressure and are still evolving (Stearns, Byars, Govindaraju, & Ewbank, 2010). Phenotypic traits thought to be under selection pressure include, but are not limited to, father's age at child's birth, inter-birth interval, age at menopause, age at death, weight, height, cholesterol level, blood pressure, blood glucose, income, rank, education, occupational status, general wealth (reviewed in Stearns et al., 2010) and political orientation (Fieder & Huber, 2018). Recently, the widespread use of caesarian section has also been shown to induce selection pressure (Fischer & Mittertoecker, 2015; Mitteroecker, 2019).

Proponents of evolutionary psychology have claimed that

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evolutionary approaches to human fertility are of limited importance and that natural selection in contemporary humans plays no or only a very restricted role. This view is not supported by an increasing number of selection studies conducted on contemporary populations (Cheng & Kirkpatrick, 2016; Stulp & Barrett, 2016). On the contrary, there is strong evidence from selection studies on the human genome that evolution and adaptation have not come to an end but have been playing an important role over the past 2000 years (Field, Boyle, Telis, et al., 2016). The common view that behavior in industrial societies is, in part, maladaptive is an unsupported assumption (Stulp, Sear, & Barrett, 2016; Stulp, Sear, Schaffnit, Mills, & Barrett, 2016). An example is status seeking and thus income, for which several recent studies documented that higher income is associated with increased fertility in men (reviewed in Hopcroft, 2019) and, interestingly, also among women of younger cohorts (Kolk, 2018). Conclusions on maladaptiveness in fertility behavior may therefore have been too hasty (Stulp & Barrett, 2016).

Fertility is interesting not only for selection studies, but also on a more proximate level, e.g. in ecology, psychology, evolutionary psychology (Stulp & Barrett, 2016) as well as in demography and the social sciences. Accordingly, measuring fertility and its association with other traits provides an excellent starting point for evolutionary investigations (reviewed in Stulp, Sear, & Barrett, 2016, Stulp, Sear, Schaffnit, et al., 2016), generating greater knowledge on both the evolutionary biology of humans and demographics in modern societies.

Note, however, that claims of selection based solely on phenotypical data, i.e. on differences in reproduction associated with a particular phenotype, remains imperfect. That approach may erroneously conclude that selection acts on a specific trait, thereby neglecting the possibility that another unmeasured trait may actually be responsible for the observed pattern (Courtiol, Tropf, & Mills, 2016). Evidence for selection directly on the genetic level may help avoid this error (Fieder & Huber, 2016; Schaschl et al., 2015). Even the genomic level, however, harbors problems of selection detection. Although genome-wide selection detection algorithms (Field et al., 2016; Sabeti et al., 2007; Szpiech & Hernandez, 2014) successfully detect robust signs of selection within the genome, they often encounter the problem that the phenotypical associations with such "genomic signs of selection" remain unclear and that genomic associations often overlap (Barban, Jansen, De Vlaming, et al., 2016, reviewed in Mills, Barban, & Tropf, 2020). Recently, selection approaches have changed from detecting selection on single candidate genes (Schaschl et al., 2015) to detecting it based on genome-wide association (GWA). An example is the investigation of genome-wide polygenic risk scores and their association with fitness measures (Beauchamp, 2016, Kong et al. 2016). Polygenic risk scores are summary indicators summarizing current estimates of additive genetic influences on a certain phenotype based on GWA studies (Harden & Koellinger, 2020). These scores are then applied to the genome data of the individuals of a target sample, enabling the calculation of the underlying genetic predisposition for a certain phenotype together with the actual phenotypic expression in those individuals. Using such risk scores for education as an indicator of the genomic predisposition for education, Beauchamp (2016) and Kong et al. (2016) report that the genetic predisposition for higher education is associated with having fewer children, indicating selection against education. However, even when using polygenic risk scores, the general problems of selection detection discussed above should be kept in mind. Thus, albeit being promising and innovative, this new approach may still have drawbacks due to the poorly understood relationship between genotype and phenotype (Courtiol et al., 2016). Preferably, selection should therefore be investigated both on the phenotypical and the genome level. Moreover, considering possible interactions both on the phenotypic and genomic level (e.g., genetic correlations) calls for analyzing phenotypes jointly in a multivariate model. Finally, the issue goes beyond whether or not a certain phenotype is significantly associated with differences in reproduction: how much that phenotype contributes among other phenotypes in terms of total variance explained is also important. Although such an approach can never take all possible traits associated with reproduction into consideration, it can still improve our understanding of the contribution of each factor.

Data are typically available for only one generation. Although this hinders drawing conclusions on longer selection scenarios, this approach does highlight potential contemporary selection pressures "acting here and now", including newly arising selection pressures such as education and income. Especially among men, social status has always been a prerequisite for mating and reproduction (Borgerhoff Mulder, 1988; Chagnon, 1988; Hill & Hurtado, 1996). The indicators of social status, however, have varied substantially over time. In modern societies, income may best represent social status: it strongly influences reproduction in both men and women, but in different directions (Barthold, Myrskylä, & Jones, 2012; Fieder et al., 2005; Fieder & Huber, 2007, 2012; Hopcroft, 2006, 2015; Nettle & Pollet, 2008; Weeden, Abrams, Green, & Sabini, 2006). In males, but not in females, personal income is generally positively associated with reproduction (Fieder et al., 2005; Hopcroft, 2006, 2015; Weeden et al., 2006; Fieder & Huber, 2007, 2012; Nettle & Pollet, 2008; Barthold et al., 2012, but see Kolk, 2018). This relationship is primarily caused by a higher number of childless individuals among men of lower status (Fieder & Huber, 2007, 2012; Hopcroft, 2006, 2015; Nettle & Pollet, 2008). Accordingly, female choice seems to be particularly important, a conclusion also highlighted by the finding that women who choose a man with lower income face a higher probability of remaining childless (Fieder & Huber, 2007; Hopcroft, 2015; Huber, Bookstein, & Fieder, 2010). Female preference for male status may indicate sexual selection on relatively new indicators of social status such as income and position in hierarchies (Fieder et al., 2005; Fieder & Huber, 2007, 2012, 2020; Hopcroft, 2006; Hopcroft, 2015). The importance of sexual selection should not be neglected here. This also holds true for culturally evolved traits because some such traits may be attributed to natural selection but for others, sexual selection may provide a faster and more potent selection mechanism within the context of cultural genetic co-evolution (Laland, Odling-Smee, & Feldman, 2000; Laland, Odling-Smee, & Myles, 2010).

We therefore expect that marriage (i.e., finding a mate) is an important predictor of reproduction in both sexes. Moreover, in line with previous findings (Fieder & Huber, 2007; Fieder, Huber, & Bookstein, 2011), social status indicated by income should be a more important predictor of mating in men than in women. Regarding the association between education and reproduction, we further expect a more ambiguous association. Fieder and Huber (2007), for instance, reported a slightly positive association for men and a negative one for women using Swedish data, whereas in the UK and the US, the association was negative for both men and women (Hopcroft, 2006, 2015; Nettle & Pollet, 2008). Education is possibly more a "prerequisite" than an indicator of social status.

Integrating both phenotypic and genomic data in terms of polygenic risk scores of educations may help disentangle the association between education and reproduction (Beauchamp, 2016, Kong et al. 2016). If education is in fact a prerequisite of social status and thus of income, we would predict that particularly in men – notwithstanding the expected negative relationship between the genetic predisposition for education and reproduction (Beauchamp, 2016; Kong et al. 2016) – the effect on reproduction might well be positive due to a proposed positive association between the genetic predisposition for education and income.

How much do other factors apart from education and income contribute to the individual variance in reproduction and thereby exert selection pressure? For instance, religiosity is associated with reproduction in both men and women (Adsera, 2006; Blume, 2009; Brañas-Garza & Neuman, 2007; Iyer & Borooah, 2004; Neuman & Ziderman, 1986; Newman & Hugo, 2006; Schellekens & Van Poppel, 2006). It is apparently a trait of greater importance during the more recent evolution of humankind (Norenzayan et al., 2016). Further factors associated with reproduction include facial attractiveness, which is particularly important for mate choice (Grammer & Thornhill, 1994) but is also related to fertility (Jokela, 2009; Pflüger, Oberzaucher, Katina, Holzleitner, & Grammer, 2012). Paternal age also plays a role. Increasing age of the father is associated with a higher mutation rate in sperm, increasing offspring risk for various diseases as well as lowering the offspring's chances of mating and reproduction (Arslan, Willführ, Frans, et al., 2017; Fieder & Huber, 2015). Age at first birth is another important indicator of overall fertility (Allal, Sear, Prentice, & Mace, 2004; Schmidt et al., 2012), as is the number of siblings (Fernández & Fogli, 2006).

A myriad other factor clearly influences human reproduction in contemporary societies. The available research, however, covers only a limited range of "phenotypes", and only those limited factors can be jointly analyzed to obtain a comprehensive picture of the contribution of each factor and thus to predict current selection pressures. Accordingly, we included variables known to influence reproduction and that are jointly available within one data set (in our case the Wisconsin Longitudinal Study). We analyzed i) which factors are associated with reproduction in terms of number of children, and how much of the variance is explained by each factor, ii) which factors are associated with mate selection in terms of being married, and how much of the variance is explained by each factor, as an indicator of sexual selection, and iii) which factors are associated with age at first birth, and how much of the variance is explained by each factor (based on the fact that reproduction is strongly influenced by age at first birth).

2. Methods

For this analysis, we used data from the Wisconsin Longitudinal Study (WLS). The WLS is a long-term study of a random sample of 4991 men and 5326 women who were born between 1937 and 1940 and graduated from Wisconsin high schools in 1957. Survey data were collected from the original respondents, or their parents, in 1957, 1964, 1975, 1992, 2004, and 2011. In detail, we used the following variables from the WLS: years of education surveyed in 1964, ranging between 12 and 20 years of education after high school graduation (Table 1a); religiosity surveyed as attendance of religious services in 1993 (Table 1b); wages before taxes in yearly sum of US $ earned (in US $1000; men - 25%: 25,000$, 50%: 40,000$, 75%: 56,000$; women - 25%: 2000$, 50%: 14,000$, 75%: 25,000$) surveyed in 1993 by WLS; age of graduate's father at time of graduate's birth calculated as father's birth year minus graduate's birth year; total number of siblings surveyed in 2003 (Table 1c); total number of biological children (Table 1d) surveyed in 1993, when all study participants were older than 50 years of age (thus, all women and almost all men had completed reproduction); whether or not the graduate has at least one child (encoded as 0 = childless, $n = 568$; 1 = one or more children, $n = 6441$); whether or not the graduate was ever married (encoded as 0 = never married, $n = 359$, 1 = married at some point, $n = 8114$); and facial attractiveness calculated based on the raw rating scores of 12 raters (each yearbook photo was rated by six men and six women using a photo-labeled 11-point rating scale ranging from "not at all attractive" (=1) to "extremely attractive" (=11); Cronbach alpha value = 0.83). We traced the reproductive history of WLS participants and summed all births to a count of "number of biological children" for each individual, keeping in mind that men are not to 100% certain of their fatherhood. As we do not have any multigenerational genealogical data (for instance number of grandchildren), we used "number of biological children „as an indicator to estimate current selective pressure (Goodman, Koupil, & Lawson, 2012). There is reason to assume that this measure may also predict long-term fitness because Kaplan et al. (Kaplan, Lancaster, Johnson, & Bock, 1995) demonstrate among men from New Mexico that their number of grandchildren corresponds to their number of children, a monotonic effect that has also been found by (Mueller, 2001) based on five data sets.

To analyze potential genetic associations between the dependent and the explaining variables, we included genetic data in the analysis in terms of the polygenic risk score of educational attainment (i.e., years of education). This score was derived from the Genome Wide Association studies (GWA) published by Lee et al. (2018) based on 1,131,881 individuals, which has already been mapped on the genomic data of the WLS participants. This is the only available polygenic risk score of the WLS suitable for our analysis (the only other available one in the WLS considers depression). Specifically, as recommended by Okbay, Benjamin, and Visscher (2018), we used the "Polygenic score for educational attainment using a multivariate analysis of educational attainment, cognitive performance, self-reported math ability and highest-level math class taken", obtained by MTAG. MTAG is a method that uses GWAS summary statistics for a primary phenotype and for one or more secondary phenotypes to produce an updated set of summary statistics (Turley et al., 2018). MTAG has been mapped on the WLS genomic data and thus represents a broader measure of general cognitive ability. We abbreviated this polygenic score as PolyEduc in all analyses. A more detailed description of the score calculation is available in Okbay et al. (2018). In the WLS sample, PolyEduc explains ~7.7% of the actual variance in educational attainment (adjusted R2 estimated by a linear model of educational attainment regressing on PolyEduc). This is less than in other samples for individuals in a comparable age range (Selzam et al., 2017) as well as less than if polygenic scores are constructed based on Lee et al. (2018) (von Stumm et al., 2020). We attribute this discrepancy to the fact that WLS is not a representative sample because it does not include individuals with an education lower than high school graduation, and thus education does not represent the full possible variance. The WLS data is generally not representative for US society as a whole because it includes mainly middle-class Whites. To control for differences in ancestry of the WLS study participants we included only whites and as recommended Okbay et al. (2018), we added in all further analysis the first 10 principal components (10 PCA) of the covariance matrix of the individuals' genotypic data, to account for the population stratification.

Selection may act in different directions in men and women (Connallon, Cox, & Calsbeek, 2010). We therefore performed all analyses separately by sex. We applied a general linear model (GLM) on a) number of biological children regressing on the year of birth, years of education, attendance at religious services, wages before taxes, father's age at child's birth, number of siblings, rated attractiveness, ever being

Table 1
Descriptive statistics for a) years of education, b) frequency of religious attendance, c) number of siblings, and d) number of biological children.

a) years of education	N	b) Frequency of religious attendance	N	c) number of siblings	N	d) number of children	N
12	4332	Never, or less than once a year	579	0	477	0	568
13	1366	1–2 Times per year	276	1	1446	1	578
14	694	3–5 Times per year	250	2	1566	2	1939
15	577	6–9 Times per year	126	3	1211	3	1973
16	1046	Approximately once a month (10–18 times per year)	324	4	845	4	1144
17	482	Approximately twice a month (19–29 times per year)	338	5	551	5	497
18	249	Approximately three times a month (30–44 times per year)	215	6	371	6	186
19	185	Approximately once a week (45–78 times per year)	2048	7	252	7	68
20	16	twice and more than twice a week (79–128 times per year)	271	8 and more	525	8 and more	56

married as well as PolyEduc and the first 10 PCA based on a Poisson error structure; b) ever being married (0 = never married, 1 = married at some point) regressing on the year of birth, years of education, attendance at religious services, wages before taxes, father's age at child's birth, number of siblings, rated attractiveness as well as PolyEduc and the first 10 PCA based on a binomial error structure; and c) age at first birth regressing on the year of birth, years of education, attendance at religious services, wages before taxes, father's age at child's birth, number of siblings, rated attractiveness as well as PolyEduc and the first 10 PCA based on a Gaussian error structure; we did not include ever being married in the latter analysis because having a least one child is strongly associated with ever being married in the WLS data (~ 3% of the individuals ever married remain childless). For each variable in the model, we further calculated the variance explained by that variable using the function r.squared GLMM implemented in the R library MuMIn (based on variance estimation by Nakagawa and Schielzeth (2013) and beta values (implemented in the function std.coef from the R library MuMIn). As generally polygenic scores are usually not exclusively associated with the phenotype from which they have been derived, but often with a broader range of phenotypes, polygenic scores offer the potential for "cross-trait-predictions" (Mills et al., 2020), hence, to uncover new still unknown associations. This is of particular interest in the case of lifetime reproductive success as interactions between polygenic scores and other explaining variables on number of children may provide hints for potential selective forces (Beauchamp, 2016; Kong et al., 2017; Tropf et al., 2015). To detect such cross-traits predictions, we started the models by including all the two-way interactions of each other explaining variable with PolyEduc, reducing the models stepwise according to the AIC. We further calculated standardized regression coefficients using the R function "std.coef" from the MuMIn library. In addition, as collinearities with PolyEduc may arise, we also run all models excluding PolyEduc (supplement Tables S1-S6).

Additionally, for those who had been married at least once, we calculated the Bateman gradient, i.e. the linear regression of the number of offspring on the number of mates in terms of marriages, based on a Poisson error structure (Walsh & Lynch, 2018).

3. Results

3.1. Number of children

In women, years of education and wages were significantly negatively associated with the number of biological children. Father's age at woman's birth was marginally significantly negatively, whereas the number of siblings, attendance at religious services and ever married were significantly positively associated with number of biological children. In addition, a woman's rated attractiveness was marginally significantly positively associated with number of children (Table 2). No significant association was found for PolyEduc and year of birth. Moreover, none of the interactions with PolyEduc were significant. By far the most of the overall variance of a woman's number of children was explained by ever married (58.6%), followed by wages (6.2%), years of education (4.6%), number of siblings (2%), and religious intensity measured in attendance of church services (1.94%). Although PolyEduc and year of birth were not significantly associated with the number of children, PolyEduc still explained 0.8% and year of birth 0.7% of the overall variance (Table 2). In total the model explains 76.5% of the overall variance of women's number of children.

Among men, years of education were significantly negatively and PolyEduc marginally significantly negatively, whereas rated attractiveness, wages, number of siblings, attendance at religious services and ever married were significantly positively associated with number of biological children. Additionally, number of children regressed significantly positively on the interaction of wages and PolyEduc, indicating a more positive association of wages and number of children in men with a higher genetic predisposition to higher education (Table 3). This finding is also apparent from Fig. 1, displaying the regression of men's number of children on the interaction of PolyEduc and wages: including only individuals with lower PolyEduc (mean PolyEduc – 1 SD), the slope indicates a negative interaction of PolyEduc with increasing wages on the number of children, whereas including only individuals with average or higher PolyEduc (mean + 1SD), the slope indicates a positive interaction of PolyEduc with increasing wages. Accordingly, the number of children increases with increasing wages only among men with mean or higher PolyEduc.

Like in women, ever being married explained the vast majority of the overall variance (~73.8%), followed by religious intensity (1.86%). PolyEduc and the interaction of wages and PolyEduc explained 0.06% and 0.37%, respectively, and all other variables explained between 0.2% und 0.68% of the overall variance (Table 3). In total, the model explains about 78.2% of the variances in men's number of children.

3.2. Ever married

Among women, years of education, father's age at birth and wages were significantly negatively associated with their ever being married; attractiveness was the only parameter that was significantly positively associated with their ever being married. Year of birth, PolyEduc, number of siblings and attendance at religious services showed no statistically significant association (Table 4). Wages explained the highest proportion of the overall variance (~6.5%), albeit in the opposite direction compared to men, followed by attractiveness (~6.3%), level of education (~5.3%), father's age at birth (~4.1%) and PolyEduc (~ 3.1%). All other variables each explained less than 1% of the overall variance (Table 4). Overall the model explains 25.5% of the variance in "ever being married" in women.

Among men, PolyEduc was significantly negatively and years of education marginally significantly negatively associated with their ever

Table 2
Regression of women's number of biological children on year of birth, years of education, rated attractiveness, wages, PolyEduc, number of siblings, ever married, religiousness, and father's age at woman's birth, as well as the first 10 PCAs of population structure (data not shown) based on a Poisson error structure. Standardized estimates (Beta values) and raw estimates are shown.

	Beta	Estimate	Std. Error	z- value	P	% Variance explained
(Intercept)	0.000	−1.929	1.259	−1.532	0.125	
Year of birth	−0.001	−0.002	0.030	−0.070	0.944	0.73%
Years of education	−0.044	−0.038	0.009	−4.431	0.000	4.59%
Father's age at woman's birth	−0.015	−0.004	0.002	−1.716	0.086	0.78%
Attractiveness mean rate	0.016	0.020	0.011	1.854	0.064	0.86%
Wages ($*1000)	−0.057	−0.005	0.001	−4.908	0.000	6.18%
PolyEduc	0.002	0.017	0.090	0.187	0.852	0.84%
Number of siblings	0.039	0.024	0.005	4.461	0.000	2.03%
Attendance at religious services	0.035	0.020	0.005	3.834	0.000	1.94%
Ever married (ref. no)	0.447	3.629	0.447	8.110	0.000	58.57%
Null deviance: 1850.3 on 1888 degrees of freedom						
AIC: 6537.8						

Table 3
Regression of men's number of biological children on year of birth, years of education, rated attractiveness, wages, PolyEduc, number of siblings, ever married, and father's age at man's birth, the significant interaction between wages and PolyEduc, as well as the first 10 PCAs of population structure (data not shown) based on a Poisson error structure. Standardized estimates (Beta values) and raw estimates are shown.

	Beta	Estimate	Std. Error	z	P	% Variance explained
(Intercept)	0.000	−3.021	1.331	−2.270	0.023	
Year of birth	−0.003	−0.008	0.029	−0.260	0.795	0.02%
Years of education	−0.036	−0.023	0.008	−3.061	0.002	0.68%
Father's age at man's birth	−0.012	−0.003	0.002	−1.126	0.260	0.26%
Attractiveness mean rate	0.022	0.027	0.013	2.171	0.030	0.44%
Wages ($*1000)	0.054	0.001	0.000	3.184	0.001	0.11%
PolyEduc	−0.027	−0.256	0.135	−1.905	0.057	0.06%
Number of siblings	0.027	0.016	0.006	2.638	0.008	0.62%
Attendance at religious services	0.061	0.032	0.006	5.772	0.000	1.86%
Ever married (ref. no)	0.587	4.462	0.707	6.308	0.000	73.76%
Wages ($*1000) X PolyEduc	0.051	0.004	0.001	2.668	0.008	0.37%
Null deviance: 1506.1 on 1647 degrees of freedom						
AIC: 5551.1						

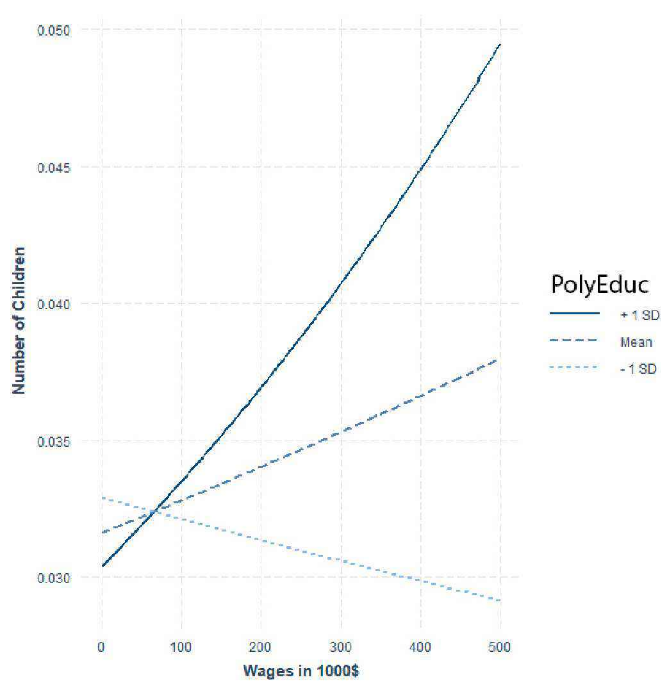

Fig. 1. Interaction plot of men's number of children regressing on the interaction of wages and PolyEduc. Both mean PolyEduc and mean PolyEduc +1 SD are associated with an increase in the number of children, whereas mean PolyEduc – 1 SD is associated with fewer children.

being married, whereas wages were significantly positively and attractiveness marginally significantly positively associated with their ever being married. The other variables, i.e., year of birth, father's age at man's birth, number of siblings and attendance at religious services, showed no significant association with their ever being married (Table 5). Wages explained most of the overall variance of their ever being married (~17.8%%), followed by PolyEduc (~2.5%), father's age at man's birth (~ 2.2%) and attractiveness (~2%). The remaining parameters each explained less than 1% of the overall variance (Table 5). Overall, the model explains 26.5% of the variance in "ever being married".

3.3. *Age at first birth*

In women, year of birth and attractiveness were significantly negatively, number of siblings marginally significantly negatively, and education and father's age at women's birth significantly positively associated with age at first birth (Table 6). Wages and PolyEduc were not significantly associated with age at first birth. Most of variance was explained by years of education (18.2%), followed by PolyEduc (1.24%), all the other variables in the model explaining less than 1% of the overall variance of the model (Table 6). Overall, the model explains 22.5% of the total variance of age at first birth.

In men as in women, year of birth and attractiveness were significantly negatively associated with age at first birth, whereas education, father's age at birth and PolyEduc were significantly positively associated with age at first birth (Table 7). Wages were not significantly associated with age at first birth. Again, as in women, years of education explained most of the overall variance of age at first birth (~5%), albeit the proportion is by far lower, followed again by PolyEduc (1.1%) (Table 7). The overall model explains 8% of the variance of age at first birth (Table 7).

Table 4
Association between women ever being married and year of birth, years of education, PolyEduc, father's age at woman's birth, rated attractiveness, wages, and number of siblings, as well as the first 10 PCAs of population structure (data not shown) based on a binomial error structure. Standardized estimates (Beta values) and raw estimates are shown.

	Beta	Estimate	Std. Error	z- value	P	% Variance explained
(Intercept)	0.0000	9.8577	11.7954	0.8360	0.4033	
Year of birth	−0.0274	−0.0622	0.3022	−0.2060	0.8370	0.00%
Years of education	−0.2737	−0.1682	0.0681	−2.4710	0.0135	5.34%
PolyEduc	−0.1117	−0.7555	0.8261	−0.9150	0.3604	3.13%
Father's age at woman's birth	−0.3378	−0.0518	0.0187	−2.7680	0.0056	4.10%
Attractiveness mean rate	0.4862	0.3865	0.1036	3.7290	0.0002	6.33%
Wages ($*1000)	−0.3842	−0.0195	0.0049	−3.9770	0.0001	6.45%
Number of siblings	0.0126	0.0054	0.0529	0.1030	0.9181	0.00%
Attendance at religious services	0.1397	0.0521	0.0448	1.1640	0.2444	0.14%
Null deviance: 616.95 on 1957 degrees of freedom						
AIC: 581.6						

Table 5
Association between WLS men ever being married with year of birth, years of education, father's age at man's birth, rated attractiveness, wages, PolyEduc and number of siblings, as well as the first 10 PCAs of population structure (data not shown) based on a binomial error structure. Standardized estimates (Beta values) and raw estimates are shown.

	Beta	Estimate	Std. Error	z- value	P	% Variance explained
(Intercept)	0.0000	−8.4074	9.4683	−0.8880	0.3746	
Year of birth	0.1591	0.3157	0.2454	1.2860	0.1983	0.01%
PolyEduc	−0.2943	−2.0396	0.8738	−2.3340	0.0196	2.47%
Years of education	−0.2235	−0.1086	0.0609	−1.7840	0.0744	1.23%
Father's age at man's birth	−0.1236	−0.0187	0.0188	−0.9950	0.3195	2.21%
Attractiveness mean rate	0.2282	0.1899	0.1070	1.7740	0.0761	1.99%
Wages ($*1000)	1.3215	0.0251	0.0055	4.5360	0.0000	17.79%
Number of siblings	−0.1169	−0.0518	0.0522	−0.9930	0.3208	0.11%
Attendance at religious services	0.1940	0.0700	0.0455	1.5380	0.1241	0.66%
Null deviance: 554.27 on 1731 degrees of freedom						
AIC: 537.57						

Table 6
Regression of women's age at first birth on the woman's year of birth, years of education, rated attractiveness, wages, PolyEduc, number of siblings, father's age at women's birth, as well as the first 10 PCAs of population structure (data not shown) based on a Gaussian error structure. Standardized estimates (Beta values) and raw estimates are shown.

	Beta	Estimate	Std. Error	z	P	% Variance Explained
(Intercept)	0.0000	39.7239	6.4174	6.1900	$P < 0.0001$	
Year of birth	−0.0972	−0.7275	0.1644	−4.4260	P < 0.0001	0.481
Years of education	0.4324	0.8138	0.0447	18.2120	P < 0.0001	18.244
Father's age at women's birth	0.0605	0.0300	0.0109	2.7530	0.0060	0.406
Attractiveness mean rate	−0.0915	−0.2401	0.0574	−4.1800	P < 0.0001	0.328
Wages ($*1000)	0.0075	0.0016	0.0047	0.3310	0.7406	0.650
Number of siblings	−0.0402	−0.0540	0.0303	−1.7830	0.0748	0.917
Attendance at religious services	0.0311	0.0385	0.0273	1.4090	0.1589	0.236
PolyEduc	0.0120	0.2534	0.4821	0.5260	0.5992	1.243
Null deviance: 18804 on 1696 degrees of freedom						
AIC: 8524.7						

Table 7
Regression of men's age at first birth on a man's year of birth, years of education, rated attractiveness, wages, PolyEduc, number of siblings, father's age at man's birth, as well as the first 10 PCAs of population structure (data not shown) based on a Gaussian error structure. Standardized estimates (Beta values) and raw estimates are shown.

	Beta	Estimate	Std. Error	z	P	% Variance Explained
(Intercept)	0.0000	34.7585	7.0643	4.9200	P < 0.0001	
Year of birth	−0.0553	−0.3907	0.1827	−2.1390	0.0326	0.128
Years of education	0.2092	0.3374	0.0457	7.3850	P < 0.0001	4.944
Father's age at man's birth	0.0900	0.0474	0.0136	3.4860	0.0005	0.357
Attractiveness mean rate	−0.0947	−0.2834	0.0761	−3.7240	0.0002	0.451
Wages ($*1000)	−0.0389	−0.0025	0.0017	−1.4640	0.1434	0.109
PolyEduc	0.0770	1.8126	0.6299	2.8780	0.0041	1.084
Number of siblings	−0.0143	−0.0213	0.0396	−0.5380	0.5907	0.200
Attendance at religious services	0.0418	0.0546	0.0335	1.6300	0.1033	0.728
Null deviance: 19218 on 1464 degrees of freedom						
AIC: 7851.6						

With the exception of small changes, the results do not change in principle whether or not PolyEduc and 10PCAs are included in the models (cf. Tables 2-7 and supplement Tables S1-S6).

3.4. Univariate associations of PolyEduc with the phenotypes in the models

In both men and women, PolyEduc is significantly positively associated with years of education, explaining about 7.7% of the overall variance in years of education (mean men and women). Also wages, father's age at birth, and attendance of religious services were significantly positively, whereas ever married was significantly negatively associated with PolyEduc (Table 8). PolyEduc explains approximately 5.4% in women and 4.8% in men of the variance of ever being married, 2.8% in women and 3.2% in men of the variance in wages, and 0.9% in women and 0.8% in men of the variance in father's age at birth

Table 8
Univariate associations of PolyEduc with the phenotypes in the models in a) women and b) men.

	Years of education		Father's age at individual's birth		Attractiveness mean rate		Wages ($*1000)		Number of siblings		Attendance at religious services		Ever married (ref. no)	
a) women PolyEduc	2.61***	7.8%	3.67***	0.9%	−0.038NS	0.7%	13.24***	2.8%	0.99NS	4.2%	1.178***	1.8%	−2.09**	5.4%
b) men: PolyEduc	3.48***	7.5%	2.953***	0.8%	−0.199NS	0.5%	21.18**	3.2%	−0.0095NS	3.6%	0.940**	1.7%	−1.789**	4.8%

(Table 8).

3.5. Bateman gradient

The Bateman gradient – the regression of the number of children on the number mates (marriages) for those who had been married at least once – remained non-significant in both men and women (Table 9).

4. Discussion

In both men and women, ever being married is the most important determinant of the number of biological children, explaining ~73% of the variance in men and ~ 59% in women. This finding reflects that, in the context of the WLS data set, marriage was rather obligatory for reproduction (Lundberg & Pollak, 2013) and is thus a good indicator for mate selection. Nonetheless, even though, expectedly, we find a higher Bateman gradient (i.e. the linear regression of an individual's number of children on the number of that individual's mates, which in our case is the number of marriages ranging from 1 to 4) in men than in women, the gradient remained non-significant in both sexes. Hence, no sign of sexual selection was evident in either sex beyond the selection into first marriage. This is in line with other monogamous populations, where the Bateman gradient was also non-significant (Courtiol, Pettay, Jokela, Rotkirch, & Lummaa, 2012). Pettay, Rotkirch, Courtiol, Jokela, and Lummaa (2014) on the other hand, demonstrated based on a preindustrial Finnish population that, in men but not in women, remarriage increased life time reproductive success by lengthening the reproductive period. This was not true, however, for the number of grandchildren (Pettay et al., 2014). We can only speculate why the Bateman gradient remains non-significant in our data. Perhaps, in the case of remarriages, particularly if more than one occurred, not only women but also men might have exceeded their reproductive period.

Our observation that being married explains more of the overall variance in the number of children in men than in women, however, supports theoretical concepts of sexual selection (Bateman, 1948; Trivers, 1972). These concepts suggest that women, the sex with the higher investment in reproduction, are expected to be choosier, thereby increasing the variation in men's reproduction via selection into marriage. Our finding is in line with previous reports on contemporary societies (Buss, 2015, 2016; Fieder et al., 2005; Fieder & Huber, 2007). In men, the historic demographic data also show that mating success is a determinant of reproductive success. The Krummhörn population in Germany (Voland, 1990) or historic Fins (Courtiol et al., 2012) provide examples. To a lesser degree this was also true for women in those cases where the marriage system was strictly monogamous and involved only minimal serial monogamy (Courtiol et al., 2012).

Note that on the basis of our data we are not able to separate individuals who did not marry because they were unsuccessful on the marriage market or actively chose not to marry. Nonetheless, not being married at some point is not only associated with lower number of children but also with a higher chance of remaining childless: among those individuals who did not marry, 96.1% of the men and 92% of the women did remain childless (among married individuals only 3.4% of the men and 3.5% of the women did remain childless). Thus, in the WLS, irrespective whether someone is unsuccessful or unwilling on the marriage market leads in most of the cases to a "drop out" of reproduction.

We further find that wages in both sexes explained most of the variance of their ever being married, and the percentage was again higher in men than in women (~ 17.8% versus ~6.5%). Importantly, the direction was opposite: in men, higher wages predicted a higher proportion of being married, whereas in women higher wages were associated with a lower proportion of being married. The stronger effect of ever being married on reproduction in men, together with the positive association of men's wages and their probability of being selected into marriage, may give a hint to an ongoing sexual selection despite the non-significant Bateman gradient. This view is supported by the finding that women who are married to men of lower income face a pronounced increase in childlessness (Huber et al., 2010). Surprisingly, however, wages explain only little of the overall variance in the number of children in men: this association was moderately positive but explains less than 1% of the overall variance. In women, on the contrary, wages were significantly negatively associated with number of children, explaining 6% of the overall variance. This finding, as well as the negative association between women's wages and their ever being married, clearly point to the well-known difficulties among women in combining career and family obligations.

In addition, albeit in both men and women, education and wages are positively correlated (men: Pearson $r = 0.27^{***}$; women: Pearson $r = 0.25$), only in men, wages and education are differentially associated with number of children: a positive association is found with wages but a negative association is found with education. Although education is to some extent a prerequisite for income, it explains only a small proportion in the variance in income of the WLS participants (men: 7.3% and women 6.3%). Consequently, a negative association between education and number of children is not necessarily concomitant with a negative association with income. Rather, for men, income seems to compensate for the negative effects of education. Furthermore, investigating by a sensitivity analysis (R library sensemakr) whether some unknown confounding variable might cause the different association of income and education with the number of children, we found that in men, such a putative unobserved confounding variable would have to explain at least more than twice of the residual variance explained by education (data not shown). Accordingly, albeit we cannot exclude a confounding variable, it is not very likely. In any case, in both men and women, we should be careful to conclude hastily on causalities particularly in the case of potential multiple associations among variables. Also concerning the positive association of wages and fertility in men, as we measured wages late in life and we do not have complete longitudinal data for income over the life course, we cannot make any final conclusions on causalities: a higher income may lead to more resources and thus to more children; alternatively, someone may be devoted to more work as soon as he has more children. However, childlessness has been shown to contribute largely to the lower offspring count among men of low income (Barthold et al., 2012; Fieder & Huber, 2007; Hopcroft, 2015).

In both sexes, education is negatively associated with reproduction, albeit explaining more of the overall variance in women (~4.6%) than in men (~0.68%). Note that the WLS included only individuals who had finished high school. The sample thus includes only individuals with higher education. The negative impact of higher education on fertility has been frequently documented and can be explained mainly by postponing reproduction (Ní Bhrolcháin & Beaujouan, 2012). Indeed, we find that education explains most of the variance of age at first birth in both sexes, and the postponing effect of education is more pronounced in women. This view is supported by the finding that a woman's higher education may increase her fertility if her postponing having children to pursue education is considered in the analysis (Sanjak, Sidorenko, Robinson, Thornton, & Visscher, 2018). Moreover, Cohen, Kravdal, and Keilman (2011) determined, based on Norwegian data, that childbearing impeded education much more than education impeded childbearing: accordingly, women with advanced degrees had lower

Table 9
Number of children regressing on the number of mates (number of marriages, excluding never married individuals) for a) men and b) women based on a Poisson error structure.

		Estimate	Std. Error	z-value	P
a) men	(Intercept)	1.0082	0.0437	23.069	$P < 0.001$
	number marriages	0.0520	0.0398	1.307	0.191
b) women	(Intercept)	1.1416	0.0402	28.408	P < 0.001
	number marriages	0.0090	0.0367	0.245	0.807

completed fertility on average because those who had one or more children at young ages were more likely to leave educational tracks or leave tracks early (Cohen et al., 2011). This calls for exercising caution when interpreting causalities.

In both sexes, increasing level of education was also associated with a lower probability of ever being married, again with a stronger effect in women. The negative association between level of education and number of children may thus also partly reflect the negative relationship between level of education and ever being married, which, as shown above, in both sexes explained most of the variance in the number of children.

Comparing the effects of the phenotype “education” and its genetic predisposition “PolyEduc” supports the view that, in women, not the genetic predisposition for higher education but education itself seems to interfere with reproduction. PolyEduc is also not significantly associated with ever being married or postponing reproduction in women. This null association contradicts the findings of Beauchamp (2016) and Kong et al. (2016) and may be attributed to including the phenotype education in our models. In contrast to women, in men the effects of both the phenotype education and PolyEduc are at least marginally significant (in the case of number of children) or significant (in the case of ever being married and postponing reproduction). Thus, in men, both education and PolyEduc contribute to postponing reproduction and lower marriage rates and, at least partially as a result of those effects, interfere with reproduction. We only find a marginally significant negative effect of PolyEduc on number of children in men, explaining less than 0.1% of the overall variance. Intriguingly, however, the interaction between wages and PolyEduc and number of children is significant positive, explaining 0.43% of the variance. This finding indicates that, in men, PolyEduc also has a positive effect on reproduction (in addition to its postponing, which decreases the number of children). This is due to its positive “indirect” interaction with wages, because wages, in turn, have a positive effect on the number of children in men via their effect on marriage. PolyEduc is also positively associated with wages in women. In contrast to men, however, they interfere with reproduction. These results hint at the pleiotropic effects of PolyEduc, which is not only associated with education, but also wages, probably as a result of higher cognitive ability and education, and also with the father’s age at birth and religious intensity.

PolyEduc explains only a small proportion of the variance of educational attainment (~ 7.7%), presumably because our sample does not cover the full spectrum of educational attainment but only includes individuals of higher education (at least A level). On basis of the British Twins Early Development Study, which covers the whole educational spectrum, Allegrini et al. (2019) had been able to predict 16% of the variance in educational attainment and 12% of the variance in intelligence by polygenic scores used also from Lee et al. (2018). This is still below the heritability estimates of educational attainment obtained from twin studies (~40% reviewed in Knopik, Neiderhiser, DeFries, & Plomin, 2016), due to the so-called problem of “missing heritability” (Manolio et al., 2009). But even by covering yet only a small proportion of the genetic variance, the Polygenic risk score enables to investigate the underlying genetic architecture of traits (Allegrini et al., 2019; Mills et al., 2020). Thus, if a selection pressure on education exists, it should act to a small but reasonable proportion on the SNPs from which PolyEduc had been derived.

Both education as well as the underlying genetic predisposition indicated by “PolyEduc” explains only a relatively small variance in reproduction. Our results may thus indicate a rather weak negative selection pressure of education on fertility of both men and women compared to the findings of Beauchamp, 2016 and Kong et al. (2017). In addition, in men, the negative effect of education on reproduction does not lead per se to a reduced number of children, but may among other factors lead to higher income and thus higher social status, and so may increase the chances of mating (Fieder et al., 2011) and thus in effect increase reproduction. Also, male income has been found to increase a couple’s number of children for the higher educated and decrease childlessness in female spouses (Huber et al., 2010). For women, however, neither education nor income pays off in terms of reproduction as for women, it is much harder to combine motherhood with a career; education and work also shorten the reproductive period for women. But also for women, education provides enormous non-material and material benefits and allows investing more in each of the fewer offspring, leading to a trade-off between "quantity" and "quality" of offspring (Mace, 2000a, 2000b; Mace, 2007). Accordingly, education is more of utilizing an individual’s intellectual potential for someone’s own benefits and the benefits of the progeny than purely maximizing reproductive output.

Although the genetic architecture of individual income is yet unclear, recently, Hill et al. (2019) found for household income only, that genes linked to differences in income are among genes previously linked with intelligence. Accordingly, female preference for high social status indicated by high income may in part indirectly emerge as a preference for intelligence. In addition, the high prevalence of educational homogamy particularly among academics (Huber & Fieder 2011) indicates that both women and men exhibit to some extent a mate preference for “intelligence”. Hence, both men and women prefer traits indicating social status and intelligence in their mates.

A conclusion on the “resulting selection pressure”, however, is difficult as selection of income and education partly acts in different directions for men and women. In addition, both education and income emerged too recently to represent “selected traits” but are rather a “manifestation” of general traits such as social status, cognitive ability etc. In the case of social status, however, selection may have always been acting on the respective “zeitgeist–traits” indicating social status at that respective time period. Hence overall maybe it will not be possible to find a “strong-proof” for ongoing contemporary selection pressures, but only in retrospect as is currently done successfully on basis of archaeological populations with various methods to detect “signs of past selection in our genomes” (Field et al., 2016; Sabeti et al., 2007).

From our findings, we conclude that a genetic predisposition for increased education and cognitive ability has, at best, a rather weak effect on reproduction, both in women and men. Based on our data we therefore cannot conclude that selection slowly favours lower education. Nonetheless, our data support the view that a “phenotypical approach” has a problem in differentiating between the genetic and environmental influence of a phenotype on the number of children (Courtiol et al., 2016). However, methodological reasons may explain why we come to somewhat different conclusions than Beauchamp: i) our sample does not involve the full range of educational levels, but only those with higher education, and ii) the polygenic risk score calculated for the WLS data is calculated based on a different, more recent GWA study (Lee et al., 2018).

In both sexes, religious intensity measured based on the attendance of religious services is significantly positively associated with reproduction and explained slightly below 2% of the overall variance in reproduction. This finding confirms the frequently observed pro-fertile effects of religiosity (Blume, 2009; Fieder & Huber, 2016). Although it could be speculated that education and religiosity are “selected against” at odds with the secular trend of increasing education and decreasing religiosity (Courtiol et al., 2016) – our data do not support such a claim. The phenotype “education” is marginally significantly positively associated with religious intensity in men (estimate: 0.02294, $P = 0.079$), and not significantly associated in women (estimate: -0.01266; $P = 0.21$). In addition, the genetic predisposition for higher education, PolyEduc, is significantly positively associated with religiosity in both sexes and explains ~1.7% of the variance in the “phenotype religious intensity”. Thus, although PolyEduc predicts both higher education and higher religiosity, these two parameters are oppositely associated with number of children.

Attractiveness has been widely discussed as an important clue in human mate selection and reproduction (Grammer and Thornhill

(1994). Facial attractiveness is clearly positively associated with fertility (Pflüger et al., 2012, Jokela, 2009 based on WLS data). We also find a significant positive association between attractiveness and number of children in men but only a marginally significant positive association between attractiveness and number of children in women, in both cases explaining less than 1% of the overall variation. In women, however, attractiveness explains 6.3% of their overall variance of ever being married. The positive association between attractiveness and marriage is also present in men, but explains only ~2% of the overall variance. These findings indicate that, particularly for women, attractiveness is more important for finding a spouse than for reproduction. Increased marriage rates for more attractive men have also been shown by Prokop and Fedor (2011).

We further included father's age in the analysis and found that, in women, advanced father's age at an individual's birth exerted a marginally significant negative effect on number of children and a significant negative effect on marriage probability, explaining 4.1% of the variance. In men, the association was negative but not statistically significant. Nevertheless, these findings are of particular interest because paternal age directly affects individual genetics: Kong, Frigge, Masson, et al. (2012) conclude that paternal age is generally responsible for the majority of de novo mutations. At the same time, increasing paternal age decreases facial attractiveness (Huber and Fieder 2014; Woodly of Menie, 2017) and increases the odds of mental health disorders (D'Onofrio, Rickert, Frans, et al., 2014). Fieder and Huber (2015) and Arslan et al. (2017) also found that advanced paternal age lowers the chance of ever being married and increases the chance of childlessness. The stronger effect of paternal age in women versus men, particularly on the probability of ever being married, however, is unexpected because sexual selection is typically higher in men (Whitlock & Agrawal, 2009); possibly, women may be somewhat more liable to the detrimental effects of de novo mutations, although this is mere speculation. Interestingly, we also found a significant positive association between PolyEduc and father's age at birth, possibly reflecting the postponing effect of PolyEduc on reproduction already in the parental generation.

Including siblings in the model revealed a significant positive association with number of children in both men and women (explaining ~2% of the overall variance in women, < 1% in men), but no significant association with ever being married. The positive association with the number of offspring may point to social influences on family size, probably by an effect on the desired number of children, as well as to a familial genetic predisposition for fertility (Barban et al., 2016).

5. Summary

In both sexes, ever being married and thus, mate selection, was the most important determinant for fertility in terms of number of children. This effect was greater in men than in women. In men, both the genetic predisposition for education (PolyEduc) and the phenotype education are negatively associated with the number of children. Nonetheless, the positive interaction of PolyEduc and wages in men indicates that higher PolyEduc can indirectly increase fertility via its positive effect on wages, which in turn is the major determinant of ever being married. In women, in contrast, only the effects of the phenotype education but not PolyEduc is significantly negatively associated with number of children. Also the association between wages and number of children is negative in women. Religiousness, paternal age, attractiveness, and number of siblings explain less of the total variance of the number of children compared to ever being married, education and wages.

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WLS: Wisconsin Longitudinal Study (WLS) [graduates, siblings, and spouses]: 1957-2019 Version 13.07. [machine-readable data file] / Hauser, Robert M., William H. Sewell, and Pamela Herd. [principal investigator(s)]. Madison, WI: University of Wisconsin-Madison, WLS. [distributor]; <http://www.ssc.wisc.edu/wlsresearch/documentation/>

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.evolhumbehav.2021.08.001.

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