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Period of Marriage and Genetic Similarity in Height between Spouses in the United States over the 20th Century

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Abstract

Social norms regarding who marries whom have changed dramatically in the United States across the 20th century. These changes may influence the level of genetic similarity between spouses. This study investigates whether genetic similarity in height between husband and wife was influenced by a historical transition in spouse selection criteria, the transition from the companionate marriage to the individualized marriage, a great transition occurred in the 1960s. In the companionate marriage, husband and wife chose each other as companions, and the emphasis was on playing marital roles well: husbands being good breadwinners and wives being good homemakers. In the individualized marriage, the emphasis switched to individual feelings. As a result, when choosing their partners people tended to pay less attention to height, suggesting a smaller genetic correlation for height between spouses. Using data from the Health and Retirement Study, we find that the genetic correlation for height declined substantially in the individualized marriage. We conduct a number of analyses to test for the confounding effects of cohort and age, and to address population stratification, selection issues, and genetic relatedness between spouses. Evidence suggests that the effect of this transition is robust.

It has been well-documented that individuals tend to marry those who are similar to themselves on a wide range of phenotypes including height, weight, age, race and ethnicity, education, religion, psychiatric conditions, and disease risks (e.g., Kalmijn 1991b; Mare 1991; Merikangas 1982; Qian 1997; Rosenfeld 2008; Schwartz and Mare 2005; Speakman et al. 2007; Spuhler 1982; Stulp et al. 2017; Vandenberg 1972). Particularly, the degree to which spouses resemble each other genetically has important consequences (Fisher 1919; Wright 1921). Spousal genetic similarity influences disparity between families and intergenerational transmission of phenotypes and genetic traits (Epstein and Guttman 1984). For example, when spouses both have genetic variants for a disease (i.e. genetically similar in the variants), their children inherit these variants and are more likely to have the disease than children of parents who are genetically less similar in the variants. Moreover, genetic similarity between spouses can influence genetic composition in the population, such as the level of genetic variance by redistributing genes (Lewontin, Kirk and Crow 1968).

Recently, researchers from disciplines across the social and biological sciences investigate genetic similarity between spouses using genome-wide data (Conley et al. 2016; Guo et al. 2014; Robinson et al. 2017; Yengo et al. 2018; Zou et al. 2015). These studies find that spouses are more similar to each other across the whole genome than are random pairs of individuals (see Abdellaoui, Verweij and Zietsch 2014; Domingue et al. 2014 for a debate). They also assess spousal similarity at trait-associated genetic loci. These studies report a correlation of height-associated loci between husband and wife, but mixed findings for body mass index (BMI)-associated loci (Conley et al. 2016; Robinson et al. 2017; Yengo et al. 2018).

These studies rely on an implicit assumption that spouse selection criteria stay the same across time and culture. Based on this assumption, researchers combine data from different

historical periods and from various cultures and societies to estimate genetic similarity between husband and wife (e.g., Robinson et al. 2017; Yengo et al. 2018). However, spouse selection criteria do change throughout human history. For example, the past century is a period in American history that redefines who marries whom due to a number of events including the rise of individualism, changing marriage and divorce laws, economic development, and secularization (Cherlin 2004). As one example, anti-miscegenation laws, which made it illegal for individuals to marry someone of another race, were ruled unconstitutional by the Supreme Court in 1967. Thereafter, the number of interracial marriages increased significantly (Qian 1997; Rosenfeld and Kim 2005). The assumption that individuals would always choose the same type of person to marry does not seem to be valid, at least in the United States in the past century.

In this study, we investigate the extent to which genetic similarity between spouses was influenced by a great historical change in spouse selection criteria in the United States over the past century—the transition from the companionate marriage to the individualized marriage. Changes in spouse selection criteria may alter the spousal correlation of heritable phenotypes and, by extension, alter the degree of spousal genetic similarity over time. As a result, there can be important implications including changes in 1) the genetic variance in the population, 2) the correlation between relatives, and 3) the average homozygosity (Bulmer 1980; Crow and Kimura 1970). We find that the transition altered the degree of genetic similarity in height between husband and wife. We conduct a number of analyses to address selection issues and to test for confounding factors such as age and cohort. Evidence shows that the effect of the transition on genetic assortative mating is robust.

Background

Historical Transition from the Companionate Marriage to the Individualized Marriage

The transition from the companionate marriage to the individualized marriage is a major and profound change in spouse selection criteria in the history of American marriage (Cherlin 2004, 2010). The companionate marriage arose during the late 19th and early 20th centuries and became the prevailing type of marriage by the 1950s. The notion that the husband was the head of the family and provided for his wife and children was an essential element of the companionate marriage (Burgess and Locke 1945). Being good breadwinners and homemakers provided satisfaction to husband and wife. Romantic attachment and love were another essential element of the companionate marriage. In the companionate marriage, husband and wife were each other's companions, friends, and lovers. In contrast, before the companionate marriage, people did not typically view spouses as friends and lovers. Romantic love was considered unnecessary in marriage by many people. Rather, spouses were supposed to be mutual supporters as there were no welfare programs or Social Security benefits (Cherlin 2010). People cared more about the practical side of marriage such as the ability to manage a farm, earn money, or run a household.

Starting in the 1960s, when choosing a marriage partner, people began to place emphasis on individual choice and “the development of their own sense of self and the expression of their feelings” (Cherlin 2004 p. 852), rather than on traits such as height. Individual feelings became increasingly important in the decision of marriage. Satisfaction from fulfilling the role of husband or wife and raising the children was no longer enough. This transition—from role to self—is reflected in a study of popular magazines published in the 1960s and 1970s. This study

finds a steady increase in the number of articles advocating individualism and communication between spouses for a successful marriage (Cancian 1987). As people thought more about their own feelings, the companionate marriage was gradually supplanted by the individualized marriage. Unlike the companionate marriage in which the husband was the breadwinner and the wife was the homemaker, the individualized marriage encouraged the wife to take paying jobs outside the home, indicating a more equal relationship.

The rise of the individualized marriage occurred during a period of social and political upheaval. The 1960s and 1970s saw the civil rights movement, the feminist movement, the sexual revolution, changes in laws regarding marriage and divorce, and growing female participation in the labor force—all of which promoted individualism in marriage in some way (Cherlin 2010). The individualized marriage can also be understood from the perspective of modernization. Modernization is an umbrella term for the rise of individualism, economic development, urbanization, geographic mobility, and secularization. Modernization means that mate selection becomes increasingly independent of parents, families, communities, the church, and other third parties (Schwartz 2013).

Many other aspects of marriage also started to change greatly in the 1960s, in part due to the individualization of family life. After 1960 the number of interracial marriages and same-sex unions rose sharply (Rosenfeld and Kim 2005). The rise of these nontraditional unions could be attributable to the increasing independence among American youth. As young adults moved away from their parents to begin their educations or careers, parental control over the children weakened substantially. Residential autonomy for young people allowed for freer individual choice about marriage. Rosenfeld and Kim show that in the post-1960 area, the percentage of children living with their parents declined, and nontraditional couples were more likely to move

away from the state of their births (a proxy for residential independence from parents and communities of origin).

Genetic Similarity between Spouses

A growing number of studies investigate genetic similarity between husband and wife. By examining overall similarity across the whole genome, two studies find that spouses are more genetically similar than randomly generated pairs (Domingue et al. 2014; Guo et al. 2014). However, as Guo and colleagues (2014) point out, it is necessary to further examine assortment on trait-associated genes because direct allelic comparison between homologous genes overlooks genetic assortment on different genes for the same phenotype. For example, spouses may assort by body weight, but the body weight of the husband depends on genes A, B, and C, while the body weight of the wife depends on genes D, E, and F. Using the Health and Retirement Study (HRS) data, Conley and colleagues (2016) examine spousal genetic associations for height, BMI, depression, and education. The authors find that spouses are similar in the polygenetic scores for height and education, but not for BMI or depression. However, using the HRS data together with other data sources, Robinson and colleagues (2017) find statistically significant correlations for height- and BMI-associated loci between husband and wife.

We decide not to consider BMI. When information on BMI at the time of marriage is not available, it is impossible to determine whether spousal similarity in BMI many years after marriage correctly reflects preferences for BMI at the time of marriage. Suppose that individuals with similar weights marry each other (a positive correlation of BMI), but many years later husbands have gained much weight while their wives have not. This leads to a weaker correlation of BMI than the correlation of BMI at the time of marriage. Hence, estimates of

preferences for BMI can be misleading if the data do not have any information about BMI at the time of marriage. Interpreting genetic correlation between spouses for BMI is also difficult for the same reason. The HRS data do not collect information about weight at the time of marriage. Therefore, we do not consider genetic correlation for BMI. Height, by contrast, tends to remain the same in adulthood, although it might decrease with age due to kyphosis. There is little reason to believe that spousal similarity in height years after marriage is significantly different from similarity in height at the time of marriage.

Robinson and colleagues' (2017) analysis includes six different sources of data from the United Kingdom, the United States, and the website 23andme, resulting in a highly heterogeneous sample of over 24,000 spousal pairs in terms of historical period, culture, and social setting. Using a similar highly heterogeneous sample, Yengo and colleagues (2018) report evidence of genetic assortative mating for height and education. Combining data from different historical periods and diverse cultural settings yields large samples, which are considered desirable for detecting genetic assortment (Robinson et al. 2017; Yengo et al. 2018). Large samples are useful in estimating the *average* level of genetic assortative mating across historical periods and societies, but highly heterogeneous samples may not be useful in identifying the consequences of changes in mate selection criteria over time in a particular society.

Further, previous studies (Robinson et al. 2017; Yengo et al. 2018) do not distinguish first marriages from remarriages. Yet, research has shown that first marriages and remarriages can differ in assortative mating patterns (Kalmijn 1994; Qian 1997; Schwartz and Mare 2005). Therefore, understanding of trends on assortative mating can be improved if we distinguish first marriages from remarriages.

Lastly, to date research on genetic similarity between spouses has not taken into consideration changes in spouse selection criteria over time and the potential impact of the changes on genetic similarity between spouses. Conley and colleagues (2016) test the idea that genetic similarity between spouses changes over time. They state that there is no evidence to support that idea. In their model, the dependent variable is the person's polygenic score for a trait, and the independent variables are his or her spouse's polygenic score for the trait, birth year of the spouse, and the interaction between the polygenic score and birth year. By treating birth year as a continuous variable, the authors presume that changes in genetic similarity over time are a linear cohort effect. However, as reviewed above, historical transitions in spouse selection criteria do not appear to be a linear cohort effect in the United States in the past century.

Assortative Mating for Height

Height, a highly heritable and polygenic trait (Fisher 1919; Yang et al. 2010), is a long-studied trait in research on assortative mating (Pearson 1899; Spuhler 1982; Stulp et al. 2017). Moreover, height is correlated with evolutionary fitness such as reproductive success (Pawłowski, Dunbar and Lipowicz 2000) and health (Paajanen et al. 2010). In addition, a study finds that the polygenic score for height is associated with coronary artery disease (Nelson et al. 2015). Our study focuses on assortment on polygenic score for height (i.e., genetic similarity in height).

Hypothesis

We hypothesize that spousal genetic similarity in height would begin to decrease starting in the 1960s when the individualized marriage started to overtake the companionate marriage in the

United States. Height would not be as important in the individualized marriage because the spouse selection criteria would lean towards individual needs and choice. In the individualized marriage, the decision to marry would be more heavily influenced by how the two individuals felt about each other. Height might be less of an issue as the result of the increasing importance of expressive individualism in marriage. Previous research has shown that sorting on ascribed characteristics decreased (e.g., Kalmijn 1991a; Kalmijn 1991b; Rosenfeld and Thomas 2012). Therefore, we expect a decline in the number of marriages in which tall individuals choose tall individuals and short individuals choose short individuals. Although height would still be a spouse selection criterion (e.g., Courtiol et al. 2010), after the 1960s more and more individuals would choose partners based on characteristics other than height. Consequently, the phenotypic and genetic correlations between spouses for height would be smaller in the individualized marriage than in the companionate marriage.

Materials and Methods

Data

We used data from the Health and Retirement Study (HRS), a large-scale, longitudinal survey of a representative sample of Americans over the age of 50. The HRS, launched in 1992, surveyed more than 22,000 individuals. It collected rich information on marriage history, health, and work every two years. Year of marriage for respondents in the HRS ranged from the 1940s to the 1990s, covering the period when the transition from companionate marriage to individualized marriage occurred. The HRS began to collect salivary DNA in 2006. Genotyping was conducted using the Illumina HumanOmni2.5-4v1 array. More than 12,000 individuals were genotyped and the genotype data passed CIDR's quality control process. We used imputed genotype data

extracted from data contained in the database accessed through the dbGaP system (http://hrsonline.isr.umich.edu/sitedocs/genetics/HRS_1000G_IMPUTE2_REPORT_AUG2012.pdf).

Measures

As discussed above, the rise of the individualized marriage started in the 1960s. We categorized marriages based on whether they occurred in 1960 or before (the companionate marriage) or after 1960 (the individualized marriage). We tried other cut-off years such as 1961 and 1962 and results were similar (Table S1).

To measure spousal genetic similarity in height, we calculated a polygenic score for height using results from two genome-wide association studies (GWASs) of height in individuals of European ancestry (Allen et al. 2010; Wood et al. 2014). The GWASs examined the association between genetic variants and height, and identified genetic variants that pass the genome-wide significance level, 5×10^{-8} . Based on the GWAS results, risk alleles (i.e., the alleles associated with a height increase) were multiplied by the effect sizes (i.e., the GWAS coefficients). Next, we summed the products. This sum was divided by the absolute value of the sum of GWAS coefficients and then multiplied by the total number of SNPs. Doing so made it easier to interpret the polygenic score—one unit of the score corresponded to two risk alleles. This approach was similar to the method of calculating polygenic scores in previous studies (Qi et al. 2012; Speliotes et al. 2010). Finally, we summed the score to obtain the polygenic score for height. The polygenic score was standardized within men and within women (the mean is 0 and standard deviation is 1). We calculated the polygenic score using the “top hits” SNPs, that is, SNPs that pass the genome-wide significance level.

To validate the polygenic score for height, we examined the association of height with the polygenic score in the HRS data. Note that neither of the two GWASs (Allen et al. 2010; Wood et al. 2014) used the HRS data. We used ordinary least squares (OLS) regression. The association of height with the polygenic score was replicated. Table 1 shows that one unit increase in the polygenic score (equivalent to two risk alleles) was associated with a height increase of 0.05 inches (t-test; $P < 0.001$). Approximately 6% of the phenotypic variation of height was explained. We tried controlling for 10 principal components (PCs) to address population stratification (we will discuss population stratification below) and obtained similar results.

Analytical Sample

We restricted analysis to non-Hispanic whites, because the polygenic score for height was based on the two GWASs that analyzed individuals of European ancestry. In the HRS data, there were 2,695 non-Hispanic white spousal pairs. After excluding pairs with missing data in the phenotype and genotype data, 2,663 pairs remained. We then excluded pairs with missing data in key variables—year of marriage and how many times the respondent married, resulting in 2,124 pairs. Of these pairs, 1,429 are first marriages, 272 were marriages in which one person married once and the other person married twice, and the remaining 423 were marriages in which both spouses married twice.

We focused on the 1,429 first marriages and excluded the 695 remarriages, because assortative mating patterns could differ between first marriages and remarriages (Kalmijn 1994; Qian 1997; Schwartz and Mare 2005). The final analytical sample consisted of 1,429 non-Hispanic white spousal pairs. Table 2 presents sample characteristics by period of marriage.

Analytical Strategy

To assess genetic similarity in height between husband and wife, we used a random-effects model to calculate the intraclass correlation coefficient (ICC). Equation (1) describes the random-effects model.

$$\text{GeneticHeight}_{ij} = \beta_{0j} + \beta_{ij}\text{PrincipalComponents}_{ij} + e_{ij} \quad (1)$$
$$\beta_{0j} = \beta_0 + e_j$$

where $\text{GeneticHeight}_{ij}$ was the polygenic score for height of individual i in couple j . In the model, we controlled for 10 Principal Components (PCs) to address population stratification.

The ICC represents the genetic correlation between spouses for height, after taking into consideration population stratification. The greater the ICC is, the more genetically similar the couple is. The ICC was estimated from Equation (1) as follows:

$$\text{ICC} = \sigma_{\alpha}^2 / (\sigma_{\alpha}^2 + \sigma_{\varepsilon}^2)$$

where σ_{α}^2 represents between-couple variance and σ_{ε}^2 represents within-couple variance.

When we assessed phenotypic similarity in height between spouses, the dependent variable in Equation (1) was replaced by the height of individual i in couple j , and the ICC represents the correlation between spouses for height.

We assessed the effect of the historical transition from the companionate marriage to the individualized marriage on genetic assortative mating by comparing the ICC for pre-1960 marriages (the companionate marriage) and the ICC for post-1960 marriages (the individualized marriage). If the ICC for post-1960 marriages was smaller, then our hypothesis that genetic similarity declines in the individualized marriage was supported. We took the following steps.

First, we used a bootstrapping procedure to generate 1,000 samples. Second, using these 1,000 samples we estimated 1,000 ICCs for pre-1960 marriages and 1,000 ICCs for post-1960 marriages. Third, we conducted the Kolmogorov-Smirnov test to compare the empirical distributions of the two sets of ICCs. We also tried bootstrapping 1,000 samples from pre-1960 marriages and 1,000 samples from post-1960 marriages, and results were similar.

Addressing Population Stratification

Population stratification, systematic differences in allele frequencies between populations, is a potential confounder in genetic studies (Belsky and Israel 2014; Cardon and Palmer 2003; Martin et al. 2017). The issue of population stratification occurs when individuals from different populations have different allele frequencies due to diversity in background ancestry, which are unrelated to outcome. Population stratification can cause a spurious relationship between the alleles and the outcome. A well-known example is “the chopstick gene” (Hamer and Sirota 2000). A genetic variant is found to be associated with the use of chopsticks, but this variant has nothing to do with chopstick use. This genetic variant has different allele frequencies in Asians and Caucasians. The spurious relationship between this variant and chopstick use is caused by the different allele frequencies in Asians and Caucasians, rather than biological reasons.

We restricted the sample to non-Hispanic whites, but there were further race/ethnicity divisions. If population stratification was not addressed, the genetic correlation between husband and wife was confounded by spousal genetic similarity within race/ethnicity divisions.

To address population stratification, we followed a well-established method, Principal Components Analysis (Price et al. 2010). This method uses PCs as covariates to correct for population stratification. PCs were estimated from genome-wide SNP data. Our random-effects

model allowed for addressing population stratification by including the first 10 largest PCs in Equation (1) as individual-level independent variables. PCs were based on 67,385 SNPs in the HRS data using Eigensoft (Price et al. 2006)

Results

We found evidence that the degrees of phenotypic and genotypic correlations for height between husband and wife depended on the historical period when the couple married. Table 3 shows that the correlation of height between spouses was 0.191 for the companionate marriage (i.e., pre-1960 marriages) and it dropped to 0.169 in the individualized marriage (i.e., post-1960 marriages). The difference was statistically significant. The genetic correlation for height also decreased substantially in post-1960 marriages. Panel A in Figure 1 shows that the correlation in the companionate marriage was 0.062, almost twice that of the individualized marriage at 0.032. The difference was statistically significant. Evidence suggests that spouses were less similar in the polygenic score for height in the individualized marriage.

However, it is important to consider alternative explanations before we may conclude that the individualized marriage led to a decline in genetic similarity between spouses.

Addressing Confounding Effects of Age at Marriage and Cohort

Essentially, we considered the effect of the transition as a period effect by examining the differences between pre-1960 marriages and post-1960 marriages. However, period effects are often confounded with age and cohort effects (Hobcraft, Menken and Preston 1982).

In more recent decades, individuals tended to delay marriage. Thus, in the post-1960 era it is possible that the effect of individualized marriage was confounded by the delayed age at

marriage. Table 2 shows that before 1960 men and women, on average, married at 22 and 20, respectively, whereas after 1960 the mean ages at marriage were 24 and 22, respectively. It is possible that when individuals married at older ages, height was not as important a factor in choosing partners. Hence, an alternative explanation for our findings is that the genetic correlation for height between spouses declined when individuals delayed marriages.

Another possible confounder is cohort. If individuals born in recent cohorts tended to pay less attention to height when choosing partners than those born in earlier cohorts, the effect of the individualized marriage was spurious. Therefore, what we found might be only a cohort effect, but not a period effect.

To address the confounding effects of age at marriage and cohort, we used two methods. The first method added two variables to Equation (1)—age at marriage, and birth year representing cohort—to control for the confounding effects of these two factors. Equation (2) describes the model.

$$\text{GeneticHeight}_{ij} = \beta_{0j} + \beta_{ij}\text{PrincipalComponents}_{ij} + \beta'_{ij}\text{AgeAtMarriage}_{ij} + \beta''_{ij}\text{BirthYear}_{ij} + e_{ij}$$

$$\beta_{0j} = \beta_0 + e_j \quad (2)$$

We calculated the ICC based on Equation (2). Results are plotted in Panel A in Figure 1. The effect of the individualized marriage remained after controlling for age at marriage and birth year. Table 3 shows that the genetic correlation for height was 0.029 in the individualized marriage, smaller than the 0.062 found in the companionate marriage. The difference was statistically significant.

The second method restricted the sample to a group of individuals who married on average at the same age or individuals born in the same cohort. In other words, we compared the companionate marriage and the individualized marriage when the two types of marriages had the

same mean age at marriage or came from the same cohort. If the difference between pre-1960 marriages and post-1960 marriages persisted, then it suggests that age at marriage and cohort did not threaten our findings.

In Panel B of Figure 1, we addressed age at marriage. We compared the genetic correlation for height among individuals who married, on average, at the same age. The first group consisted of pre-1960 marriages in which the mean age at marriage was 21 for wives. The second group consisted of post-1960 marriages in which the mean age at marriage was also 21 for wives. We obtained the two groups by randomly excluding a subset of younger wives in pre-1960 marriages and randomly excluding a subset of older wives in post-1960 marriages. We called it the marriage-age-comparable sample for wives. We employed the same method to obtain a marriage-age-comparable sample for husbands, in which the mean age at marriage was 23 for both pre- and post-1960 marriages. The pattern remained. The correlation was greater in the companionate marriage than that in the individualized marriage. For example, the correlation was 0.085 and 0.038 in the companionate marriage and the individualized marriage, respectively, in the marriage-age-comparable sample for wives (Table S2).

In Panel C, we restricted the sample to those couples who married at ages 18-28. This is another way to address the confounding effect of age at marriage. We first examined marriages in which wives married at ages 18-28. Next, we looked at marriages in which husbands married at ages 18-28. We then examined marriages in which both spouses married at ages 18-28. Panel C shows a pattern similar to the one found in Panel A. For example, the genetic correlation for height was 0.087 in the companionate marriage and 0.035 in the individualized marriage for pairs in which both spouses married at ages 18-28 (Table S2).

In Panel D, we addressed the cohort issue by restricting the sample to individuals born in the same cohort. We selected individuals born in 1933-1945 so that approximately half of this cohort married before 1960 and the other half after 1960. For example, among pairs in which wives were born in 1935-1945, 353 pairs married in 1960 or before, and 313 pairs married after 1960. Because Table 2 shows that age at marriage for men was about two years older than for women, it made sense to adjust for this two-year, gendered difference in age at marriage. We selected wives born in 1935-1945 and husbands born in 1933-1943. When we combined them, the whole cohort was born in the years 1933 through 1945. Results were consistent with findings in panels A through C. For example, the genetic correlation for height was 0.063 in the companionate marriage and 0.000 in the individualized marriage for the cohort in which both spouses were born in 1933-1945 (Table S2).

Addressing Selections

Selection due to mortality might bias our results. The HRS started in 1992 when respondents were at least 50 years old. The genotyping started in 2006. In other words, respondents had to survive to 2006 to be included in the HRS genotype data. This means that we only included respondents who lived longer. The comparison of pre- and post-1960 marriages was therefore subject to bias from mortality selection as pre-1960 couples (born as early as in 1920) were more likely to die before the DNA collection in 2006 than post-1960 couples (born as late as in 1964). In addition, given that height and the polygenic score for height are associated with health outcomes (Nelson et al. 2015; Paajanen et al. 2010), mortality selection might further bias our findings.

We addressed this selection issue in Panel D in Figure 1. If it is reasonable to assume that individuals born in 1933-1945 had a similar likelihood of being included in the HRS DNA sample, then Panel D suggests that selection did not seriously undermine the effect of the individualized marriage. The reason is that the genetic correlation for height was still statistically smaller in the individualized marriage than in the companionate marriage for this cohort.

Selection due to marital dissolution and remarriage should be addressed because assortative mating patterns could be different for first marriages and remarriages (Kalmijn 1994; Qian 1997; Schwartz and Mare 2005). In the post-1960 period, the divorce rate increased a great deal (Rosenfeld 2006), resulting in more remarriages. In our final analytical sample, only 40 pre-1960 marriages were remarriages, while more than 600 post-1960 marriages were remarriages. As mentioned above, to address this issue we excluded remarriages in our analysis and focus on first marriages only.

Genetic Relatedness between Spouses

Another alternative explanation for the greater genetic correlation for height in the companionate marriage is that spouses were more closely related to each other in the companionate marriage period. For example, consanguineous marriages were more prevalent in the early 20th century (Lebel and Opitz 1983; Slatis, Reis and Hoene 1958). Closer genetic relatedness between spouses in the companionate marriage could result in a higher genetic correlation for height. If this is the case, the explanation for our findings is simply that spouses were less closely related in post-1960 marriages.

To test this possibility, we compared genome-wide genetic relatedness between husband and wife in the companionate marriage and the individualized marriage. On the basis of

2,443,179 SNPs in the HRS imputed genotype data, we constructed a measure of genome-wide relatedness between husband and wife using the GCTA method (Yang et al. 2011). The GCTA method estimated genome-wide relatedness between individuals. We standardized relatedness estimated from the GCTA method by calculating the correlation between individuals x_i and x_j using the formula

$$\frac{\text{covariance}(x_i, x_j)}{\sqrt{\text{variance}(x_i)\text{variance}(x_j)}}$$

This standardization made the interpretation straightforward. For example, ego with ego genome-wide relatedness was 1 (i.e., the correlation between x_i and x_i , the same individual i).

Before using this measure for the HRS data, we first verified its validity in an independent, separate dataset, the Framingham Heart Study (FHS) (see Appendix for data description). Specifically, we examined genome-wide genetic correlations between parents and offspring in the FHS. Because a child receives half of the genome from one parent, the expected genome-wide genetic relatedness is 0.5. A total of 287,525 SNPs were used to construct the measure in the FHS genotype data. The mean genome-wide genetic relatedness between parent and offspring was 0.50, which was consistent with the expected value of the parent-offspring genetic relationship. The evidence suggests that this was a valid measure of genome-wide relatedness.

As this measure had been verified in the FHS, we then compared genome-wide relatedness between husband and wife in pre- and post-1960 marriages in the HRS. Figure 2 shows the results. The solid line represents the empirical cumulative distribution of genome-wide relatedness between spouses for pre-1960 marriages. The dashed line represents the distribution for post-1960 marriages. The two distributions overlap well. In addition, the mean genome-wide relatedness was 0.0175 for pre-1960 marriages and 0.0178 for post-1960 marriages. The

difference was not statistically significant (t-test, $p = 0.30$). This evidence suggests that couples in the companionate marriage were no more related than couples in the individualized marriage. Thus, we are more confident in our findings.

It should be noted that the FHS did not collect information on year of marriage. However, year of marriage was essential to distinguish the companionate marriage from the individualized marriage. As a result, we were unable to use the FHS data for our analysis.

Discussion

Our work suggests that the magnitude of genetic similarity between husband and wife was affected by a significant historical change in mate choice criteria in the United States over the 20th century. Starting in the 1960s, the companionate marriage lost ground, and the individualized marriage rose to prominence. As a result, height became much less important than individual needs and feelings when choosing partners. We focus on first marriages and find that this transition has an impact on spouse correlations of height and the polygenic score for height. Both correlations become smaller in the individualized marriage. Evidence shows that this pattern is robust. The effect of the individualized marriage remains after we control for population stratification, age at marriage, and cohort in different ways. The effect of the individualized marriage would be spurious if spouses were more related in the companionate marriage than in the individualized marriage. However, we find no evidence to support this idea. Additionally, our analysis shows that mortality selection does not seriously affect our findings.

Our findings that sorting on height decreases are in line with the modernization theory regarding assortative mating (Schwartz 2013). The modernization theory argues that in modern societies, ascribed characteristics become less important than achieved characteristics, and the

influence of parents and third parties on mate selection declines. Drawing on the theory, assortative mating researchers show that sorting on ascribed characteristics decreases and sorting on achieved characteristics increases (e.g., Kalmijn 1991a; Kalmijn 1991b; Rosenfeld and Thomas 2012). The individualization of marriage is an important aspect of the modernization theory.

As consistently pointed out by prior research on the American family in the past century, the post-1960 era bore witness to dramatic changes such as the postponement of first marriage, the rise of cohabitation and divorce, increasing interracial marriage, greater acceptance for childbearing outside of marriage, and same-sex unions (e.g., Bumpass 1990; Cherlin 2004; Rosenfeld 2006; Smith 1999). The era also saw significant changes in other social and political domains: female labor force participation, family law, the feminist movement, the sexual revolution, and the civil rights movement (Cherlin 2010). The individualistic view of marriage can be seen as the product of these interrelated influences. The power of social norms to regulate family life declined. Individuals had more freedom to choose their partners. Our findings align with these changes. We find that sorting on height and polygenic score for height decreased in the post-1960 era, although a preference for tallness still existed in mate selection (Courtiol et al. 2010).

The following limitations should be noted. The HRS data is unique in that it covers the time period when the transition to individualized marriage occurred in the United States, and it contains detailed information about marriage history. However, the unique nature of the HRS data means that few datasets can be used to enlarge our sample or serve as a replication sample. Nevertheless, with more large-scale surveys that collect genomic data, it is possible that researchers will obtain larger samples and conduct replication analyses to better understand the

processes and consequences of genetic assortative mating in different periods and societies. In addition, polygenic scores do not capture complete genetic influences on height. About 6% of variation in height is explained by the polygenic score in our analysis. As the understanding of the genetics of height advances, future research might have better measures with which to examine genetic assortative mating on height and other traits.

In human society, mate choice is continuously shaped by social norms regarding who marries whom. Patterns of assortative mating are diverse across time and culture. By focusing on a meaningful historical transition from the companionate marriage to the individualized marriage, this study highlights the importance of considering a previously overlooked dimension of genetic similarity between spouses—the dynamic nature of mate choice criteria. Greater social forces might cause shifts in mate choice criteria and leave marks on human evolution at the genetic level. Our findings that spousal genetic similarity in height, an important trait associated with evolutionary fitness (Pawłowski et al. 2000), declines in last century in the United States might have profound evolutionary implications. When appropriate data become available in the future, it would be interesting to examine the impact of this decline on human evolution.

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Table 1. Association of Polygenic Score for Height with Height, Ordinary Least Squares

Estimates

Independent variable	Coefficient
Polygenic score for height	0.05***
Adjusted R ²	0.06
N of individuals	9,708

*** $p < 0.001$, ** $p < 0.01$, and * $p < 0.05$

Table 2. Sample Characteristics by Period of Marriage

	Period of marriage	
	1960 and before (companionate marriage)	After 1960 (individualized marriage)
Year of marriage (%)		
1940-50	20.63	--
1951-60	79.37	--
1961-70	--	65.43
1971-80	--	29.89
1981-90	--	4.27
1991-2000	--	0.41
Age at marriage, wife		
Mean	20.10	22.06
SD	2.76	4.09
Age at marriage, husband		
Mean	22.42	24.54
SD	2.83	4.43
Birth year, wife (%)		
1920-30	25.17	0.56
1931-40	66.14	9.93
1941-50	8.67	64.05
1951-60	--	24.80
1961-70	--	0.70
Birth year, husband (%)		
1920-30	39.27	0.84
1931-40	59.59	26.32
1941-50	1.13	54.84
1951-60	--	18.04
Genome-wide relatedness between spouses		
Mean	0.0175	0.0178
SD	0.00477	0.00680
N of pairs	703	726

Table 3. Phenotypic and Genetic Correlation between Spouses for Height, by Period of Marriage

Period of marriage	Phenotypic correlation	Genetic correlation		N of pairs
		Controlled for PCs	Controlled for PCs, age at marriage and birth year	
1960 and before (companionate marriage)	0.191	0.062	0.062	703
After 1960 (individualized marriage)	0.169	0.032	0.029	726
<i>p</i> value for difference*	<0.001	<0.001	<0.001	

* the Kolmogorov-Smirnov test

Supplementary Table S1. Using Different Cut-Off Years to Define Marriages: Genetic Correlation between Spouses for Height, by Period of Marriage

	Period of marriage		<i>p</i> value for difference*
	Companionate marriage	Individualized marriage	
	1960 and before	After 1960	
Genetic correlation	0.062	0.032	<0.001
<i>N</i> of pairs	703	726	
	1961 and before	After 1961	
Genetic correlation	0.053	0.039	<0.001
<i>N</i> of pairs	761	668	
	1962 and before	After 1962	
Genetic correlation	0.056	0.039	<0.001
<i>N</i> of pairs	821	608	

* the Kolmogorov-Smirnov test

Supplementary Table S2. Robustness Checks: Genetic Correlation between Spouses for Height, by Period of Marriage

	Period of marriage		<i>p</i> value for difference*
	1960 and before (companionate marriage)	After 1960 (individualized marriage)	
Wives, marriage-age-comparable sample	0.085	0.038	<0.001
<i>N</i> of pairs	603	606	
Husbands, marriage-age-comparable sample	0.088	0.011	<0.001
<i>N</i> of pairs	623	596	
Wives married between ages 18 and 28	0.085	0.053	<0.001
<i>N</i> of pairs	586	632	
Husbands married between ages 18 and 28	0.074	0.003	<0.001
<i>N</i> of pairs	676	615	

Both spouses married between ages 18 and 28	0.087	0.035	<0.001
<i>N</i> of pairs	571	560	
Wives born between 1935 and 1945	0.074	0.013	<0.001
<i>N</i> of pairs	353	313	
Husbands born between 1933 and 1943	0.068	0.000	<0.001
<i>N</i> of pairs	309	359	
Both spouses born between 1933 and 1945	0.063	0.000	<0.001
<i>N</i> of pairs	300	302	

* the Kolmogorov-Smirnov test

Figure Captions

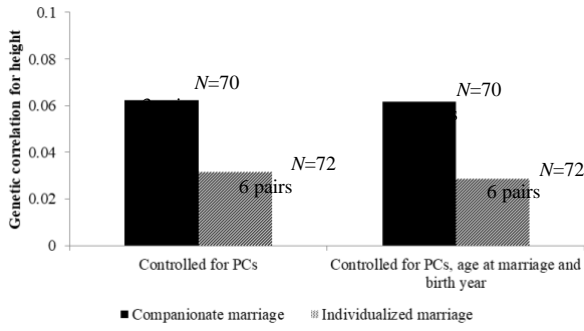
Figure 1. Transition from the companionate marriage to the individualized marriage and genetic correlation between spouses for height, addressing population stratification, confounding effects of age at marriage and cohort. **Panel A.** Addressing population stratification, and confounding effects of age at marriage, and cohort. Principal components (PCs) are controlled for in Equation (1) to address population stratification (left). In addition to PCs, age at marriage and birth year are controlled for in Equation (1) to address the confounding effects of age and cohort (right). **Panel B.** Using marriage-age-comparable samples to address confounding effect of age at marriage. Marriage-age-comparable samples were generated by randomly excluding a subset of younger couples who married before 1960 and a subset of older couples who married after 1960. In the marriage-age-comparable sample for wives, the mean ages at marriage are both 21 for pre- and post-1960 marriages; in the age-comparable sample for husbands, the mean ages at marriage are both 23 for pre- and post-1960 marriages. **Panel C.** Using the sample in which spouses married between the same range to address the confounding effect of age at marriage. The sample only includes marriages in which the range of age at marriage is 18 to 28. **Panel D.** Using the sample in which spouses come from the same cohort to address the confounding effect of cohort. The sample only includes couples born in 1933-1945. Mean age at marriage for husbands is two years older than that of wives. To compensate for this difference, the husband cohort is two years older than the wife cohort.

Figure 2. Examining whether spouses were more related to each other in the companionate marriage than the individualized marriage: comparing the empirical cumulative distribution of genome-wide relatedness between husband and wife. The difference in the mean of genome-

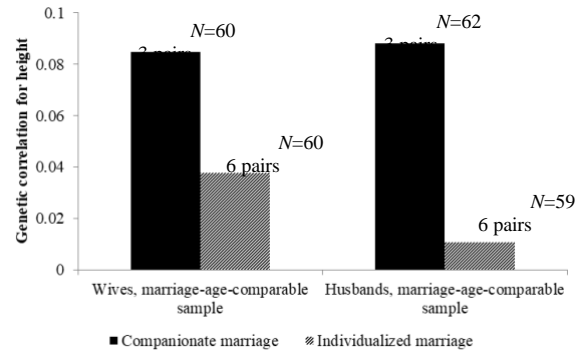
wide genetic relationship between spouses married before 1960 and after 1960 is -0.000320
($p=0.30$).

Figure 1.

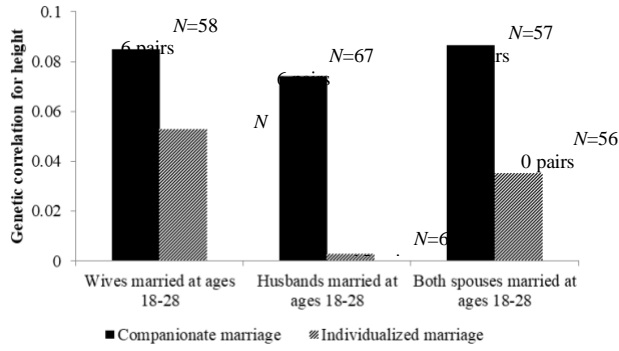
Panel A



Panel B



Panel C



Panel D

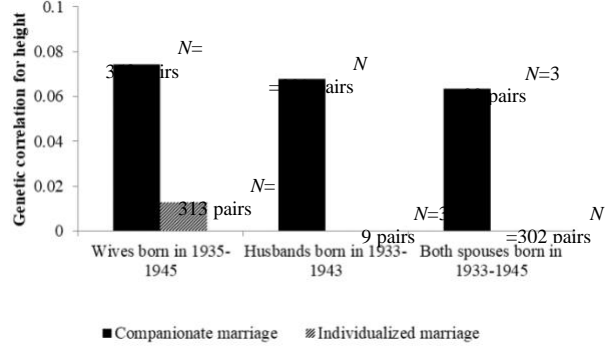
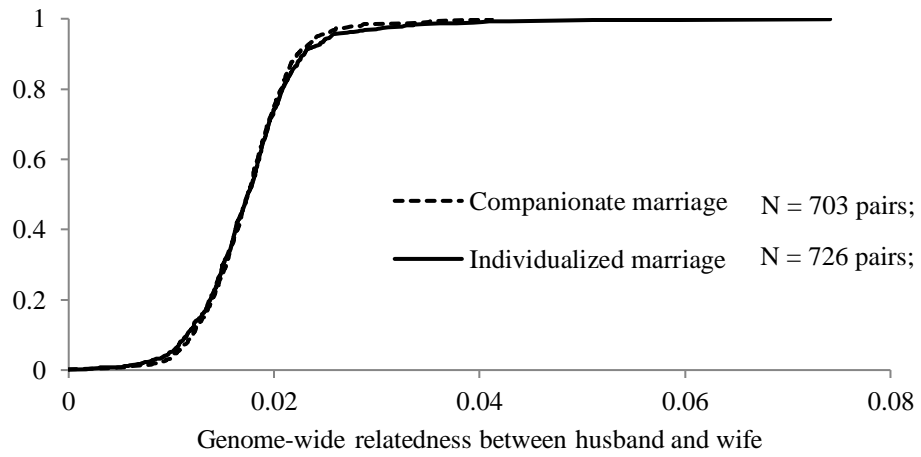


Figure 2.



Appendix

Genetically determined height was measured by a polygenic score. We calculated the score using two sets of published genome-wide association studies (GWAS) results. The first set of GWAS results identified 180 genetic loci (Allen et al. 2010) that passed the genome-wide significance level and the second identified 697 SNPs (Wood et al. 2014) that passed the genome-wide significance level. In the HRS imputed genotype data, 159 out of 180 SNPs are available and 584 out of 697 SNPs are available. A total of 60 SNPs out of 159 SNPs overlap 584 SNPs. For the 60 SNPs we used the first set of GWAS results. The first set in our data consists of 159 SNPs and the second consists of 524 SNPs ($= 584 - 60$).

Of all 3,214 spousal pairs we identified (including non-Hispanic white pairs and other race/ethnicity pairs), 249 pairs reported different years of marriage. A total of 163 pairs reported a difference of five years or less in year of marriage. The reason might be that a spouse does not recall the date correctly. Given that the difference was relatively small, we randomly selected one of the years reported by the two spouses as the year of marriage for the pair. The remaining 86 pairs reported a difference of six years or more in year of marriage. In most of the 86 pairs, at least one spouse married more than once. It is possible that individuals confused the year of current marriage with the date of a previous marriage. We decided to exclude these 86 pairs. When there were missing data in a person's year of marriage, we imputed it with his or her spouse's reported year of marriage.

The Framingham Heart Study (FHS) is a community-based, prospective, longitudinal study. The FHS followed three generations of participants: (i) the Original Cohort enrolled in 1948 ($N = 5,209$); (ii) the Offspring Cohort consist of the children of the Original Cohort and their spouses, who were enrolled in 1971 ($N = 5,124$); and (iii) the Generation Three Cohort

consists of the grandchildren of the Original Cohort, who were enrolled in 2002 (N = 4,095) (<https://www.framinghamheartstudy.org/>). Genotyping for FHS participants was performed by Affymetrix (Santa Clara, CA, USA) using the Affymetrix 500K GeneChip array. The standard quality control filter is applied. Individuals with 5% or more missing genotype data are excluded from analysis. X chromosome SNPs, SNPs with a call rate of 99% or a minor allele frequency of 0.01 are also eliminated from analysis. The application of the quality control filter leaves 8,738 individuals with 287,525 SNPs from the 500K genotype data.