

Height, Age at First Birth, and Lifetime Reproductive Success: A Prospective Cohort Study of Finnish Male and Female Twins

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The associations between height and reproductive success in humans have attracted long-time scientific interest, but in addition to rather mixed previous results, little is still known about the background mechanisms of these associations. We analyzed the association of adult height with age at first birth and lifetime reproductive success using a twin study design that is able to optimally take into account family background and estimate the contributions of genetic and environmental factors. Information on live births as of June 2009 for 7,830 Finnish twins born 1950–1957 was extracted from the national population register. We found evidence for non-linear associations in men, as men in the third sex-specific height quintile had the highest probability of having one to two children, or three or more children at individual level analyses, and also to have any children when analyzing twin pairs discordant for height. Furthermore, the probability of having a spouse was highest in the third height category in men. Short stature was associated with earlier age at first birth in females, explained by correlated genetic factors, but not with lifetime number of children or having a spouse. Our results suggest that average stature may give some advantage for reproduction in males. In females, genetic factors explained the association between short stature and young age at first birth, which may suggest the role of hormonal factors.

■ **Keywords:** height, timing of reproduction, humans, reproductive success

The association between height at adulthood and lifetime reproductive success in humans has attracted long-time scientific interest. It has been suggested that women show a preference for taller than average men when seeking sexual partners (Courtiol et al., 2010), and taller men also have a higher probability of getting married (Nettle, 2002a). Since tallness is associated with better health and socioeconomic position (Batty et al., 2009), favoring tall men may offer long-term benefits for the offspring of women, thus increasing their evolutionary fitness. In females, tall stature may reflect better physical health and thus increased capability of having children, especially in the presence of environmental stress (Pollet & Nettle, 2008). There is evidence that tall stature is associated with better reproductive health in women, such as reduced need for emergency cesarean section (Stulp et al., 2012b). However, in addition to the tentative advantage of taller stature on reproductive success, it may also have disadvantages. Growth is an energy-consuming process, and thus reaching tall stature

consumes energy and time that could otherwise be used for reproduction. Thus, allocating energy to growth versus early reproduction may reflect different adaptive strategies (Walker et al., 2006). These strategies probably offer different costs and benefits in different environments and may contribute to the large variation in height both between and within human populations (Eveleth & Tanner, 2003).

Previous studies in Western countries have shown that tall stature is associated with later timing of menarche (McIntyre & Kacerosky, 2011; Onland-Moret et al., 2005),

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and a previous Finnish study also reported that tall stature is associated with older age at first birth (AFB) in women (Helle, 2008). This may be, however, a special feature of developed societies as in agrarian societies tall stature has been found to predict earlier rather than later menarche (McIntyre & Kacerosky, 2011). When studying lifetime reproductive success in males, tallness was associated with a higher number of children in a study of US cadets (Mueller & Mazur, 2001) and in the Polish population (Pawlowski et al., 2000), but no association was found in a study of US college students (Scott & Bajema, 1982), in Mexicans living in the United States (Goldstein & Kobyliansky, 1984), in the United Kingdom (Nettle, 2002a), in China (Fielding et al., 2008), or in Gambia (Sear, 2006). In another cohort of US college students (Vetta, 1975) and high-school graduates (Stulp et al., 2012a), average stature was associated with the highest number of children. When studying childlessness, the results are more consistent: short stature in men was associated with higher probability of childlessness in the United Kingdom (Nettle, 2002a) and Poland (Pawlowski et al., 2000). In females, a positive association between stature and lifetime reproductive success was found in Gambia (Sear, 2006) and Guatemala (Pollet & Nettle, 2008), whereas in the United Kingdom the association was curvilinear and women who were shorter than average had higher reproductive success than the shortest and taller than average women (Nettle, 2002b); no association was found in US college students (Scott & Bajema, 1982), in Mexicans living in the United States (Goldstein & Kobyliansky, 1984), in China (Fielding et al., 2008), or in Finland (Helle, 2008).

A shortcoming in these previous studies on the association between height and reproduction is, however, that they have not properly adjusted for socioeconomic or other environmental covariates which could contribute to this association. Childhood socioeconomic background is especially important to consider as growth takes place during childhood and adolescence, and childhood environment can affect adult life in multiple ways. As height is associated with childhood socioeconomic background (Silventoinen, 2003) and high social position is found to be associated with higher fertility in males and lower fertility in females (Kravdal & Rindfuss, 2008; Nettle & Pollet, 2008), these factors rather than height itself may explain this association. Adjusting the results for measured socioeconomic factors offers only a partial solution, as no study can fully observe all relevant social factors. In this study, we analyze this question utilizing a twin study design. Using twin pairs raised in the same family who differ in the number of children they have as adults allows an analysis of the role of height on reproductive success when family background can be regarded as standardized. Furthermore, the twin study design offers the opportunity to quantify the role of genetic and environmental factors behind the variation of different traits and covariation of their mutual associations. We used a large and nationally representative Finnish twin data set

that allows participants to be followed up to 51–59 years of age, and thus we have been able to analyze the lifetime number of children also in men.

Data and Methods

The data were derived from the older cohort of the Finnish Twin Cohort Study (Kaprio & Koskenvuo, 2002). Questionnaires were mailed in 1975 and 1981 to all same-sex Finnish twin pairs born before 1958 and with both co-twins alive in 1975. The response rates to these questionnaires were 89% and 84%, respectively. Height, marital history, and education, classified into eight classes described elsewhere (Silventoinen et al., 2000), were sent identical questionnaires at both times. Those respondents still studying when reporting their level of education were assumed to have reached the next possible category given in the questionnaire. For height and education, we used the questionnaire responses in 1981, and if these were not available then the data from the questionnaire in 1975 were used. Marital history was classified as currently living or previously lived with a spouse (married, co-habiting, divorced, and widowed) in 1981 or in 1975. Self-reported height showed high correlations with measured height in a subsample of 100 men and 127 women in this same cohort (Pearson $r = .98$ in men and $.96$ in women), showing good reliability of self-reported height (Silventoinen et al., 2000).

Information on live births is available for participants born after 1950 in the Finnish population register. This register was updated until June 2009 and linked to the cohorts born between 1950 and 1957 in our study sample, using unique personal identification numbers assigned to all Finnish citizens. The participants alive in 2009 were 51–59 years of age at the time of the end of the follow-up and therefore effectively post-reproductive. From 9,006 twin individuals who answered the questionnaires in 1975 or 1981, we removed 1,168 twin individuals who were living with their co-twin in 1981. This is because a large proportion of these twins remained childless and therefore this group may not be representative to the general population in terms of reproduction. However, we replicated the analyses in the whole data set to confirm whether this restriction affected the results. Furthermore, individuals from triplet or quadruplet births were excluded from the data ($N = 8$). In the final study sample, we had 3,595 male and 4,235 female twin individuals, including 1,076 monozygotic (MZ) and 2,445 dizygotic (DZ) complete twin pairs, and 787 twin individuals without information on their co-twin. The study was approved by the ethical committee of the Department of Public Health, University of Helsinki. Informed consent was obtained from all respondents.

We analyzed the association between height and lifetime number of children among twin individuals using both Poisson regression and multinomial logistic regression models producing odds ratios (OR). Poisson regression

was used to make the results comparable with previous studies. However, we also conducted multinomial logistic regression models because the association between height and number of children may not be similar at different levels of fertility. For example, it is possible that different factors may affect the transition to first, second, third, and further parities; for example, mate choice is probably most crucial in having any children. For this reason, height was classified into sex-specific quintiles and the number of children into three categories (no children, 1–2 children, and 3 children or more) in the multinomial logistic regression models. We then adjusted the results for education used as a categorized covariate because of possible non-linearity and after that additionally for marital history. As the twins were sampled as pairs, there is a lack of statistical independence between twins in a pair. Therefore, within-pair correlations were taken into account in the estimation of the standard errors using a survey cluster option (Williams, 2000). The analyses were continued by studying pairwise associations in twin pairs discordant for height, that is, belonging to a different quintile of height, and having any children using a conditional logistic regression model. Since twins reared together share their childhood family environment, and MZ twins also share their gene sequence, any within-pair associations would indicate that the association between height and reproduction is not because of familial factors. After these analyses, we conducted similar analyses for marital history to get more insight into the role of this factor in the formation of the association between height and reproduction. These analyses were carried out using the Stata/SE statistical software, version 11.2 (StataCorp, College Station, Texas, USA).

We continued the analysis by studying the association of height with lifetime number of children and AFB by applying genetic twin models if a linear association in regression models was found between them. This was done in order to disentangle the effects of genetic and environmental factors. The classical twin analysis is based on the comparison of similarity of MZ twins, who are genetically identical at gene sequence level, to DZ twins who share, on average, 50% of their segregating genes. The variation within traits and covariation between two traits were decomposed to additive genetic factors (*A*), which is the sum of the effects of all alleles affecting the trait; common environmental factors (*C*), including the effect of environment shared by co-twins; and specific environmental factors (*E*), including environmental effects unique to each twin individual as well as all measurement errors. This was done by using bivariate Cholesky decomposition. The assumptions of twin modeling, that is, equal means and variances for MZ and DZ twins, were tested by comparing the genetic models with saturated models, which do not make these assumptions. The comparisons in model fit between the nested models were based on the change of χ^2 -goodness-of-fit statistics and degrees of freedom ($\Delta\chi^2_{\text{degrees of freedom}}$). The genetic

TABLE 1
Age at First Birth and Lifetime Number of Children in Height Quintiles

| | N | Height | | Age at first birth | | Number of children (%) | | |
|-------------------|-------|--------|------|--------------------|------|------------------------|-----|----|
| | | Mean | SD | Mean | SD | 0 | 1–2 | 3+ |
| Men | | | | | | | | |
| Shortest quintile | 810 | 169 | 3.48 | 27.2 | 5.59 | 26 | 49 | 25 |
| 2nd quintile | 698 | 174 | 0.81 | 27.0 | 5.20 | 23 | 51 | 26 |
| 3rd quintile | 670 | 177 | 0.89 | 27.3 | 5.26 | 19 | 55 | 26 |
| 4th quintile | 779 | 180 | 1.06 | 27.0 | 4.91 | 24 | 49 | 27 |
| Tallest quintile | 643 | 186 | 2.98 | 27.3 | 4.98 | 22 | 49 | 29 |
| All | 3,600 | 177 | 6.26 | 27.2 | 5.20 | 23 | 50 | 27 |
| Women | | | | | | | | |
| Shortest quintile | 935 | 156 | 2.79 | 25.1 | 5.24 | 18 | 54 | 28 |
| 2nd quintile | 871 | 161 | 0.89 | 25.1 | 5.02 | 18 | 60 | 22 |
| 3rd quintile | 953 | 164 | 0.82 | 25.3 | 5.06 | 17 | 59 | 24 |
| 4th quintile | 703 | 167 | 0.79 | 25.4 | 4.83 | 20 | 54 | 26 |
| Tallest quintile | 776 | 172 | 2.04 | 26.4 | 5.21 | 21 | 54 | 25 |
| All | 4,236 | 164 | 5.62 | 25.4 | 5.10 | 19 | 56 | 25 |

modeling was carried out with the Mx statistical package, version 1.7.03, using the raw data analysis option (Neale, 2003). As the distribution of AFB was somewhat skewed, we normalized it by using logarithmic transformation and used this in the statistical modeling.

Results

Table 1 presents descriptive statistics for height, AFB, and number of children. In childlessness and other categories of number of children, no linearity was seen over the height quintiles in men or women. An increasing trend in AFB over height quintiles was seen in women but not in men. In men, the regression coefficient of height was not statistically significant (β for 10 cm = 0.004; 95% CI = -0.008, 0.016) when predicting log AFB. In women, a clear negative association was found (β for 10 cm = -0.699; 95% CI = -1.229, -0.169). However, there was also some leveling off in this association in the tallest women, and a weak but statistically significant positive regression coefficient for the square of height was seen (β for 10 cm = 0.022; 95% CI = 0.006, 0.038).

Figure 1 presents the mean number of children by height. Some non-linearity was seen in both men and women, but the confidence intervals were wide. When we modeled the number of children using Poisson regression, we found a weak positive but statistically non-significant trend in men (β for 10 cm = 0.006; 95% CI = -0.002, 0.010) whereas in women the association virtually did not exist (β for 10 cm = -0.01; 95% CI = -0.05, 0.03).

We then conducted a multinomial logistic regression model for height quintiles when predicting the transitions in the categories of the number of children born (Table 2). The third quintile and having no children were used as the reference categories in the models (OR = 1.00). In males, the highest probability of having one to two children was in the third quintile.

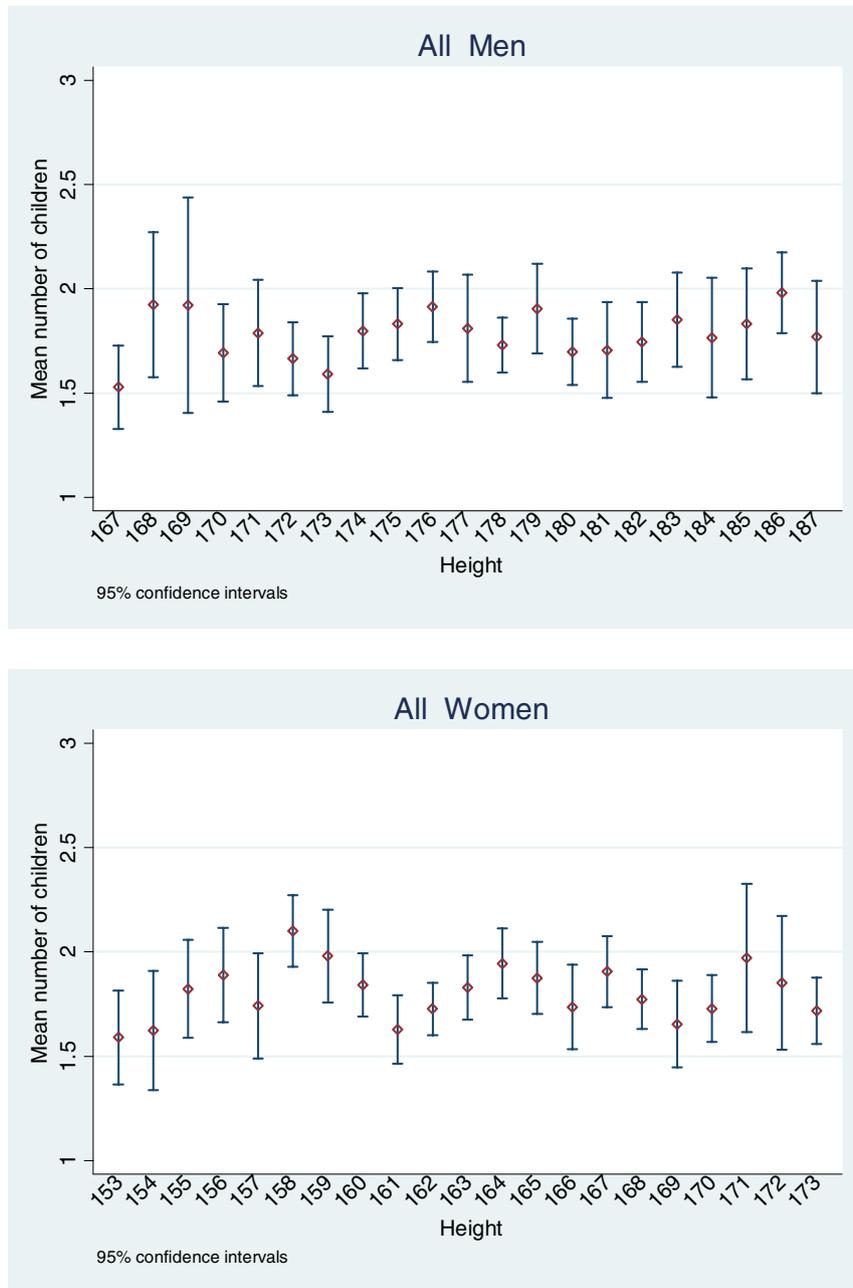


FIGURE 1
(Colour online) Mean number of children with 95% confidence intervals by height in men and women.

When adjusted for education and marital history, the difference in other categories decreased slightly. When analyzing the probability of having three or more children, the tallest and third quintiles showed the highest probabilities, but these associations were not statistically significant when education and marital history were adjusted for. When we replicated the results in the whole data set, the differences were slightly smaller, but the similar pattern was seen (Table S1 of the Supplementary Material). In women, no statistically significant associations were found between height and number of children.

We then continued the analyses by studying the probability of having any children within twin pairs discordant for height quintile using the conditional logistic regression model (Table 3). Number of children was used in these analyses as a dichotomized variable as only discordant pairs are informative, and thus this analysis has less power than when using all twins as individuals. The probability of having any children was highest in the third quintile in males, and this association decreased slightly when education and marital history were adjusted for. In the whole data set, the differences were again somewhat smaller, but still the

TABLE 2
Odds Ratios of Height Quintiles for 1–2 and 3 Children or More Compared to Childlessness in the Multinomial Logistic Regression Model

| | Model 1 | | Model 2 | | Model 3 | |
|----------------------|---------|-----------|---------|-----------|---------|-----------|
| | OR | 95% CI | OR | 95% CI | OR | 95% CI |
| Men | | | | | | |
| 1–2 children | | | | | | |
| Shortest quintile | 0.67 | 0.51–0.88 | 0.68 | 0.52–0.90 | 0.74 | 0.55–1.00 |
| 2nd quintile | 0.78 | 0.59–1.03 | 0.78 | 0.59–1.04 | 0.81 | 0.59–1.10 |
| 3rd quintile | 1.00 | | 1.00 | | 1.00 | |
| 4th quintile | 0.71 | 0.54–0.94 | 0.72 | 0.55–0.95 | 0.71 | 0.53–0.96 |
| Tallest quintile | 0.81 | 0.61–1.08 | 0.79 | 0.59–1.05 | 0.76 | 0.55–1.05 |
| p value of the trend | 0.30 | | 0.48 | | 0.88 | |
| 3 children or more | | | | | | |
| Shortest quintile | 0.70 | 0.51–0.96 | 0.73 | 0.53–1.00 | 0.81 | 0.57–1.14 |
| 2nd quintile | 0.85 | 0.62–1.17 | 0.86 | 0.62–1.18 | 0.89 | 0.63–1.27 |
| 3rd quintile | 1.00 | | 1.00 | | 1.00 | |
| 4th quintile | 0.81 | 0.59–1.10 | 0.80 | 0.58–1.09 | 0.80 | 0.56–1.12 |
| Tallest quintile | 1.01 | 0.73–1.41 | 0.97 | 0.70–1.35 | 0.95 | 0.66–1.37 |
| p value of the trend | 0.06 | | 0.17 | | 0.58 | |
| Women | | | | | | |
| 1–2 children | | | | | | |
| Shortest quintile | 0.86 | 0.67–1.10 | 0.82 | 0.64–1.06 | 0.85 | 0.65–1.11 |
| 2nd quintile | 0.92 | 0.71–1.19 | 0.92 | 0.71–1.19 | 0.92 | 0.70–1.21 |
| 3rd quintile | 1.00 | | 1.00 | | 1.00 | |
| 4th quintile | 0.76 | 0.59–0.99 | 0.78 | 0.59–1.01 | 0.76 | 0.57–1.02 |
| Tallest quintile | 0.76 | 0.59–0.98 | 0.80 | 0.62–1.02 | 0.77 | 0.58–1.01 |
| p value of the trend | 0.17 | | 0.46 | | 0.27 | |
| 3 children or more | | | | | | |
| Shortest quintile | 1.05 | 0.79–1.41 | 1.01 | 0.76–1.36 | 1.05 | 0.78–1.44 |
| 2nd quintile | 0.81 | 0.60–1.10 | 0.82 | 0.60–1.12 | 0.82 | 0.59–1.13 |
| 3rd quintile | 1.00 | | 1.00 | | 1.00 | |
| 4th quintile | 0.87 | 0.64–1.18 | 0.89 | 0.66–1.21 | 0.87 | 0.62–1.21 |
| Tallest quintile | 0.82 | 0.61–1.10 | 0.86 | 0.64–1.17 | 0.82 | 0.59–1.14 |
| p value of the trend | 0.20 | | 0.42 | | 0.25 | |

Note: Model 1 = adjusted for birth year and zygosity; model 2 = additionally adjusted for education; model 3 = additionally adjusted for marital history.

TABLE 3
Pairwise Odds Ratios of Height Quintiles in Pairs Discordant for Height for Having Any Children in the Conditional Logistic Regression Model

| | Model 1 | | Model 2 | | Model 3 | |
|----------------------|---------|-----------|---------|-----------|---------|-----------|
| | OR | 95% CI | OR | 95% CI | OR | 95% CI |
| Men | | | | | | |
| Shortest quintile | 0.51 | 0.31–0.84 | 0.50 | 0.30–0.83 | 0.52 | 0.27–1.01 |
| 2nd quintile | 0.61 | 0.38–0.96 | 0.61 | 0.38–0.97 | 0.66 | 0.36–1.24 |
| 3rd quintile | 1.00 | | 1.00 | | 1.00 | |
| 4th quintile | 0.68 | 0.43–1.06 | 0.69 | 0.43–1.09 | 0.89 | 0.49–1.59 |
| Tallest quintile | 0.62 | 0.37–1.04 | 0.57 | 0.33–0.97 | 0.60 | 0.30–1.21 |
| p value of the trend | 0.36 | | 0.47 | | 0.42 | |
| Women | | | | | | |
| Shortest quintile | 0.92 | 0.57–1.47 | 0.89 | 0.55–1.43 | 0.97 | 0.54–1.73 |
| 2nd quintile | 0.96 | 0.64–1.45 | 0.93 | 0.61–1.41 | 1.11 | 0.66–1.85 |
| 3rd quintile | 1.00 | | 1.00 | | 1.00 | |
| 4th quintile | 0.78 | 0.50–1.19 | 0.77 | 0.50–1.19 | 0.83 | 0.49–1.41 |
| Tallest quintile | 0.71 | 0.43–1.17 | 0.70 | 0.42–1.16 | 0.79 | 0.42–1.46 |
| p value of the trend | 0.29 | | 0.36 | | 0.42 | |

Note: Model 1 = adjusted for birth year and zygosity; model 2 = additionally adjusted for education; model 3 = additionally adjusted for marital history.

similar pattern was seen (Table S2). In women, no association was found.

We also conducted similar analyses for marital history (Table 4). In males, the highest probability of having a spouse was in the third category and lowest in the shortest category. The pattern was similar in the analyses using twins as individuals and for discordant twin pairs, but the

differences were larger in the latter analysis. When using the whole data set, the results were largely similar (Table S3). In females, no differences were found.

Finally, we analyzed the genetics of height, log AFB, number of children, and their mutual correlations by using genetic twin modeling. Compared with the saturated models, the fit of univariate models was good in men

TABLE 4
Odds Ratios in the Logistic Regression Model and Pairwise Odds Ratios in Pairs Discordant for Height in the Conditional Logistic Regression Model of Height Quintiles for Partnership History

| | All study cohort | | | | Pairwise associations | | | |
|-----------------------------|------------------|-----------|---------|-----------|-----------------------|-----------|---------|-----------|
| | Model 1 | | Model 2 | | Model 1 | | Model 2 | |
| | OR | 95% CI | OR | 95% CI | OR | 95% CI | OR | 95% CI |
| Men | | | | | | | | |
| Shortest quintile | 0.75 | 0.60–0.94 | 0.76 | 0.60–0.95 | 0.67 | 0.44–1.02 | 0.67 | 0.44–1.03 |
| 2nd quintile | 0.87 | 0.69–1.09 | 0.87 | 0.69–1.10 | 0.83 | 0.56–1.23 | 0.83 | 0.56–1.23 |
| 3rd quintile | 1.00 | | 1.00 | | 1.00 | | 1.00 | |
| 4th quintile | 0.85 | 0.68–1.06 | 0.89 | 0.71–1.11 | 0.96 | 0.65–1.42 | 0.97 | 0.66–1.44 |
| Tallest quintile | 0.95 | 0.75–1.20 | 0.97 | 0.77–1.23 | 0.89 | 0.57–1.38 | 0.88 | 0.56–1.37 |
| <i>p</i> value of the trend | 0.07 | | 0.04 | | 0.18 | | 0.19 | |
| Women | | | | | | | | |
| Shortest quintile | 0.95 | 0.76–1.16 | 0.92 | 0.74–1.13 | 0.93 | 0.64–1.36 | 0.94 | 0.64–1.37 |
| 2nd quintile | 0.92 | 0.75–1.14 | 0.94 | 0.76–1.16 | 1.04 | 0.70–1.57 | 1.02 | 0.68–1.55 |
| 3rd quintile | 1.00 | | 1.00 | | 1.00 | | 1.00 | |
| 4th quintile | 0.94 | 0.75–1.17 | 0.96 | 0.77–1.20 | 1.03 | 0.66–1.60 | 1.01 | 0.64–1.57 |
| Tallest quintile | 0.91 | 0.73–1.14 | 0.98 | 0.78–1.22 | 1.05 | 0.65–1.70 | 1.03 | 0.64–1.68 |
| <i>p</i> value of the trend | 0.89 | | 0.55 | | 0.75 | | 0.83 | |

Note: Model 1 = adjusted for birth year and zygosity; model 2 = additionally adjusted for education.

($\Delta\chi^2_6 = 4.6, p = .59$ for height and $\Delta\chi^2_6 = 8.7, p = .19$ for log AFB) and women ($\Delta\chi^2_6 = 11.9, p = .06$ for height, $\Delta\chi^2_6 = 5.5, p = .48$ for log AFB and $\Delta\chi^2_6 = 2.6, p = .86$ for number of children), suggesting that the assumptions of twin modeling were not violated. Only for the number of children in men the fit was non-optimal ($\Delta\chi^2_6 = 21.5, p = .002$), but was still close to the Bonferroni-corrected *p* value of six tests ($p = .008$). To find the best-fitting model, we removed common environmental effect for log AFB ($\Delta\chi^2_1 = 2.6, p = .11$ in men and $\Delta\chi^2_1 = 1.8, p = .18$ in women) and for the number of children ($\Delta\chi^2_1 = 0, p = 1.00$ and $\Delta\chi^2_1 = 0.79, p = .37$, respectively). For height, this effect was statistically significant ($\Delta\chi^2_1 = 5.3, p = .02$ and $\Delta\chi^2_1 = 6.7, p = .01$, respectively), showing that the common environmental component is needed in the model. For females, we also conducted Cholesky decomposition to analyze the correlation between height and log AFB. We were able to drop a specific environmental correlation between log AFB and height ($\Delta\chi^2_1 = 0.2, p = .63$). In men, no association between height and log AFB was found, and thus we were not able to make similar analysis. Furthermore, because in men there was evidence for non-linear association between height and the number of children and in women no association was found, it was not possible to conduct similar genetic modeling for this association.

Table 5 shows the results for the best-fitting genetic models. Genetic factors were important for height and they explained 78% of the variation in men and 80% of the variation in women. For AFB and the number of children, the specific environmental factors were more important, but still a substantial proportion of the variation of AFB (30% in men and 42% in women) and number of children (42% and 48%, respectively) was explained by genetic factors. In women, the genetic correlation between height and AFB was 0.18, suggesting that 3% of the genetic variation of these two traits is shared.

TABLE 5
Additive Genetic (a^2), Common Environmental (c^2), and Specific Environmental (e^2) Standardized Variance Components for Height, Age at First Birth, and Number of Children and Additive Genetic Correlation (r_A) Between Height and Age at First Birth

| | Men | | Women | |
|--|----------|-----------|----------|-----------|
| | Estimate | 95% CI | Estimate | 95% CI |
| Height | | | | |
| a^2 | 0.78 | 0.69–0.87 | 0.80 | 0.72–0.88 |
| c^2 | 0.11 | 0.01–0.20 | 0.11 | 0.03–0.18 |
| e^2 | 0.11 | 0.10–0.13 | 0.10 | 0.09–0.11 |
| Age at first birth^a | | | | |
| a^2 | 0.30 | 0.21–0.38 | 0.42 | 0.35–0.49 |
| e^2 | 0.70 | 0.62–0.79 | 0.58 | 0.51–0.65 |
| Number of children | | | | |
| a^2 | 0.37 | 0.31–0.44 | 0.38 | 0.33–0.44 |
| e^2 | 0.63 | 0.56–0.69 | 0.62 | 0.56–0.67 |
| Correlation between height and age at first birth, r_A | – | | 0.18 | 0.11–0.25 |

Note: ^aLogarithmic transformation was used.

Discussion

Our results do not support the hypothesis that tallness is linearly associated with reproductive success in males. In contrast, lifetime reproductive success was highest in men with average stature. This result remained when adjusting for education as a measure of adulthood socioeconomic status and marital history. Importantly, we also found a similar association when analyzing twin pairs discordant for height. Since twin pairs are the same age and were raised in the same family, this is strong evidence that this association is not affected by childhood family background. Many studies conducted in Western developed countries (Goldstein & Kobylansky, 1984; Nettle, 2002a; Scott & Bajema, 1982), in China (Fielding et al., 2008), and in a traditional Gambian population (Sear, 2006) have not found a linear association between adult height and lifetime reproductive success in males. Thus, our findings are consistent with

previous empirical evidence suggesting that the association between tallness and men's reproductive success is at best weak. The long-lasting hypothesis of the better reproductive success of tall men is thus probably based more on theoretical considerations than on solid empirical evidence. Sexual selection for physical traits is very common in the animal kingdom (Andersson, 1994), and a correlation between reproductive success and large body size is found in many higher primates (Kappeler & van Schaik, 2004). Thus, it is tempting to seek a similar association also in humans. However, while sexual selection on body size has led to large sexual dimorphism in many higher primates (Plavcan, 2001), in humans the difference in height between men and women is generally relatively small (Gray & Wolfe, 1980). Therefore, it may not be surprising that tallness in males is not strongly associated with reproductive success in humans.

We found in this study that males with average stature had the best reproductive success. The same result has been found for the number of children in an early study of US males who were college students between 1880 and 1912 (Vetta, 1975) and US high-school students who graduated in 1957 (Stulp et al., 2012a). Furthermore, Stulp and colleagues found that in eight of the ten previous studies reporting no association between height and reproductive success in males, there was evidence for the curvilinear association (Stulp et al., 2012a). These studies and our results together suggest that sexual selection may balance average height in the population rather than favor tall or short stature. A possible explanation for this result may be assortative mating for height, which is well known in humans (Spuhler, 1982). Thus, females are not seeking a partner who is very tall, but modify their preferences according to their own height. A Finnish twin study showed that approximately half of the spousal correlation in height is because of same socioeconomic background — that is, social homogamy — and half because of phenotypic assortment (Silventoinen et al., 2003). Even when this tendency is not fixed and especially short and tall persons can modify their mate preferences to maximize the number of potential partners (Pawlowski, 2003), very short and tall men may still have problems with finding a suitable partner. We found some evidence for this, because the probability of having a spouse was also highest in the men with average stature. However, differences in the reproductive success remained, even when marital history was adjusted for.

In common with a previous Finnish study (Helle, 2008), we found that short stature in females was associated with earlier AFB. This finding can be associated with the timing of puberty as short stature has been reported to be associated with earlier age at menarche in several European populations (Onland-Moret et al., 2005). However, the reason for this association is not clear. It has been suggested that the association between height and AFB could be because of a trade-off between allocating energy to continuing growth

or to beginning reproduction (Allal et al., 2004). However, in our study cohort, only 1% of women had the first birth under 18 years of age, and even in the shortest quartile of women AFB was 25 years. Since growth virtually ceases in girls before 17 years of age (Thodberg et al., 2012), it is likely that only a few women had their first birth while still growing. Furthermore, a recent review suggested that the positive association between female stature and age at puberty is specific to highly developed societies, whereas in agrarian societies the association is reversed (McIntyre & Kacerosky, 2011); these results do not support the hypothesis that the energy trade-off would be contributing to this association. In our study cohorts, contraception was also generally used, and at least the large majority of the pregnancies were planned. This may suggest that this association is rather because short stature is associated with a decision to begin reproduction early than because of any causal association. Utilizing genetic twin modeling, we found in this study that the association between height and AFB was because of common genetic factors. The trait correlation between these two traits was, however, only modest, and thus only 3% of the genetic variation was shared between height and AFB. Because all causal associations between these traits would be modeled as part of specific environment, the hypothesis of the energy trade-off between growth and reproduction is not supported by our study (Walker et al., 2006). One explanation would be that the same hormonal factors, which are strongly genetically regulated, contribute to early puberty, leading to shorter adult stature, and also contribute to stronger childbearing motivation at an early age.

It is noteworthy that not all persons wishing to have children can do so because of biological reasons. The 12-month prevalence of infertility was estimated to be 9% in a large international study, with little difference between developed and less developed countries (Boivin et al., 2007). Thus, the proportion of persons with no children is a mix of those desiring them but unable to have them because of social or biological reasons, and those deciding not to have children. Given that better-off persons have more access to health care and are generally taller, this may be a partial confounder despite adjustment for education in our models. Infertility may be due to acquired factors, such as infections of the reproductive organs, or idiopathic biological factors. At the extremes of biological factors are chromosomal abnormalities such as Klinefelters syndrome, who are tall and infertile men, and Turner syndrome, who are short and infertile women (Frühmesser & Kotzot, 2011). The influence of hormonal factors can be inherited, such as congenital adrenal hyperplasia, or can be external as the result of hormonal treatments to induce growth or reduce growth in childhood (Chiavaroli et al., 2010; Hendriks et al., 2011).

While these specific conditions are rare, genetic variation in the genes underlying the chromosomal abnormalities is common in the population. As some 200 genes are now known to be associated with height in the populations

(Lango Allen et al., 2010) and copy-number variants particularly associated with short stature have also been identified (Dauber et al., 2010), it is possible that some of these also affect fertility, given the complex relationships between growth, puberty, and sexual maturation. However, in our data, stature in males was associated in a similar way with having any children than with further parities, and in females no association was found. Potentially different biological and social pathways between height and reproduction emphasize that it should not be expected a priori that height is associated with all parities in a similar way. Alternatively, the number of children could be considered as a categorical variable, allowing that the association between height and probability of having any further children is not independent of pre-existing parity, such as we have done in this study. We found some evidence for this because the association between height and reproduction was more visible when using the number of children as categorized variable than when using the total number of children. This suggests that in higher parities other factors than height become more dominant and thus can confound the association.

Our study has strengths as well as limitations. A major strength of our study is that we had information on a large number of twins that allowed us to optimally take into account the family background and also to analyze the role of genetic and environmental factors behind the association between height and AFB. Furthermore, the study participants were 51–59 years of age at the end of the follow-up, and thus we can safely say that we have information on virtually all participants for the lifetime number of children also in males. Also, the information on children is register based and thus is not prone to reporting bias. A limitation is that twins may not be fully representative to the general population. We found some evidence for this, because a part of twins were living with their co-twin, and in these twins childlessness was more common than in the general population. We removed these pairs from the analyses as they may not be representative of the whole Finnish population. After this exclusion, the fertility rate in our data is very close to the general Finnish population in these cohorts, suggesting that our data of twins are representative (Miettinen, 2010). When we replicated the analysis in the whole data set, we found that the associations were slightly weaker than in the restricted data. This suggests that other mechanisms may affect the number of children in those twins living with their co-twin.

To conclude, our results do not support the hypothesis that tall stature is associated with higher reproductive success. Instead, we showed that among men average stature may give some advantage for reproduction. Among women, short stature was associated with an early age at reproduction, and this association was because of shared genetic factors. Height is thus associated with reproduction, but these associations and their background may be more complex than previously assumed.

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Supplementary Material

To view supplementary material for this article, please visit <http://dx.doi.org/10.1017/thg.2012.150>.

References

- Allal, N., Sear, R., Prentice, A. M., & Mace, R. (2004). An evolutionary model of stature, age at first birth and reproductive success in Gambian women. *Proceedings of the Royal Society B: Biological Sciences*, 271, 465–470.
- Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.
- Batty, G. D., Shipley, M. J., Gunnell, D., Huxley, R., Kivimäki, M., Woodward, M., . . . Smith, G. D. (2009). Height, wealth, and health: An overview with new data from three longitudinal studies. *Economics & Human Biology*, 7, 137–152.
- Boivin, J., Bunting, L., Collins, J. A., & Nygren, K. G. (2007). International estimates of infertility prevalence and treatment-seeking: Potential need and demand for infertility medical care. *Human Reproduction*, 22, 1506–1512.
- Chiavaroli, V., Liberati, M., D’Antonio, F., Masuccio, F., Capanna, R., Verrotti, A., . . . Mohn, A. (2010). GnRH analog therapy in girls with early puberty is associated with the achievement of predicted final height but also with increased risk of polycystic ovary syndrome. *European Journal of Endocrinology*, 163, 55–62.
- Courtiol, A., Raymond, M., Godelle, B., & Ferdy, J. B. (2010). Mate choice and human stature: Homogamy as a unified framework for understanding mating preferences. *Evolution*, 64, 2189–2203.
- Dauber, A., Yu, Y., Turchin, M. C., Chiang, C. W., Meng, Y. A., Demerath, E. W., . . . Hirschhorn, J. N. (2010). Genome-wide association of copy-number variation reveals an association between short stature and the presence of low-frequency genomic deletions. *Nature*, 467, 832–838.
- Eveleth, P. B., & Tanner, J. M. (2003). *Worldwide variation in human growth* (2nd ed.). Cambridge: Cambridge University Press.
- Fielding, R., Schooling, M., Adab, P., Cheng, K. K., Lao, X. Q., Jiang, C. Q., & Lam, T. H. (2008). Are longer legs associated with enhanced fertility in Chinese women? *Evolution and Human Behavior*, 29, 434–443.
- Frühmesser, A., & Kotzot, D. (2011). Chromosomal variants in Klinefelter syndrome. *Sexual Development*, 5, 123.
- Goldstein, M. S., & Kobyliansky, E. (1984). Anthropometric traits, balanced selection and fertility. *Human Biology*, 56, 35–46.
- Gray, J. P., & Wolfe, L. D. (1980). Height and sexual dimorphism of stature among human societies. *American Journal of Physical Anthropology*, 53, 441–456.

- Helle, S. (2008). A tradeoff between reproduction and growth in contemporary Finnish women. *Evolution and Human Behavior*, 29, 189–195.
- Hendriks, A. E., Laven, J. S., Valkenburg, O., Fong, S. L., Fauser, B. C., de Ridder, M. A., . . . Drop, S. L. (2011). Fertility and ovarian function in high-dose estrogen-treated tall women. *Journal of Clinical Endocrinology and Metabolism*, 96, 1098–1105.
- Kappeler, P. M., & van Schaik, C. P. (2004). Sexual selection in primates: Review and selective preview. In M. Kappeler & C. P. van Schaik (Eds.), *Sexual selection in primates: New and comparative perspective* (pp. 3–23). Cambridge: Cambridge University Press.
- Kaprio, J., & Koskenvuo, M. (2002). Genetic and environmental factors in complex diseases: The older Finnish twin cohort. *Twin Research*, 5, 358–365.
- Kravdal, Ø., & Rindfuss, R. R. (2008). Changing relationships between education and fertility: A study of women and men born 1940–1964. *American Sociological Review*, 73, 854–873.
- Lango Allen, H., Estrada, K., Lettre, G., Berndt, S. I., Weedon, M. N., Rivadeneira, F., . . . Hirschhorn, J. N. (2010). Hundreds of variants clustered in genomic loci and biological pathways affect human height. *Nature*, 467, 832–838.
- McIntyre, M. H., & Kacerosky, P. M. (2011). Age and size at maturity in women: A norm of reaction? *American Journal of Human Biology*, 23, 305–312.
- Miettinen, A. (2010). Voluntary or involuntary childlessness? Socio-demographic factors and childlessness intentions among childless Finnish men and women. *Finnish Yearbook of Population Research*, 45, 5–45.
- Mueller, U., & Mazur, A. (2001). Evidence of unconstrained directional selection for male tallness. *Behavioral Ecology and Sociobiology*, 50, 302–311.
- Neale, M. C. (2003). *Mx: Statistical modeling*. Richmond, VA: Department of Psychiatry, Virginia Commonwealth University.
- Nettle, D. (2002a). Height and reproductive success in a cohort of British men. *Human Nature*, 13, 473–491.
- Nettle, D. (2002b). Women's height, reproductive success and the evolution of sexual dimorphism in modern humans. *Proceedings of the Royal Society B: Biological Sciences*, 269, 1919–1923.
- Nettle, D., & Pollet, T. V. (2008). Natural selection on male wealth in humans. *American Naturalist*, 172, 658–666.
- Onland-Moret, N. C., Peeters, P. H., van Gils, C. H., Clavel-Chapelon, F., Key, T., Tjonneland, A., . . . Riboli, E. (2005). Age at menarche in relation to adult height: The EPIC study. *American Journal of Epidemiology*, 162, 623–632.
- Pawlowski, B. (2003). Variable preferences for sexual dimorphism in height as a strategy for increasing the pool of potential partners in humans. *Proceedings of the Royal Society B: Biological Sciences*, 270, 709–712.
- Pawlowski, B., Dunbar, R. I., & Lipowicz, A. (2000). Tall men have more reproductive success. *Nature*, 403, 156.
- Plavcan, J. M. (2001). Sexual dimorphism in primate evolution. *Yearbook of Physical Anthropology*, 44, 25–53.
- Pollet, T. V., & Nettle, D. (2008). Taller women do better in a stressed environment: Height and reproductive success in rural Guatemalan women. *American Journal of Human Biology*, 20, 264–269.
- Scott, E. C., & Bajema, C. J. (1982). Height, weight and fertility among the participants of the Third Harvard Growth Study. *Human Biology*, 54, 501–516.
- Sear, R. (2006). Height and reproductive success: How a Gambian population compares with the West. *Human Nature*, 17, 405–418.
- Silventoinen, K. (2003). Determinants of variation in adult body height. *Journal of Biological Science*, 35, 263–285.
- Silventoinen, K., Kaprio, J., & Lahelma, E. (2000). Genetic and environmental contributions to the association between body height and educational attainment: A study of adult Finnish twins. *Behavior Genetics*, 30, 477–485.
- Silventoinen, K., Kaprio, J., Lahelma, E., & Koskenvuo, M. (2000). Relative effect of genetic and environmental factors on body height: Differences across birth cohorts among Finnish men and women. *American Journal of Public Health*, 90, 627–630.
- Silventoinen, K., Kaprio, J., Lahelma, E., Viken, R. J., & Rose, R. J. (2003). Assortative mating by body height and BMI: Finnish twins and their spouses. *American Journal of Human Biology*, 15, 620–627.
- Spuhler, J. N. (1982). Assortative mating with respect to physical characteristics. *Journal of Social Biology*, 29, 53–66.
- Stulp, G., Pollet, T. V., Verhulst, S., & Buunk, A. P. (2012a). A curvilinear effects of height on reproductive success in human males. *Behavioral Ecology and Sociobiology*, 66, 375–384.
- Stulp, G., Verhulst, S., Pollet, T. V., Nettle, D., & Buunk, A. P. (2012b). Parental height differences predict the need for an emergency caesarean section. *PLoS One*, 6, e20497.
- Thodberg, H. H., Juul, J., Lomholt, J., Martin, D. D., Jenni, O. G., Caflisch, J., . . . Kreiborg, S. (2012). Adult height prediction models. In V. R. Preedy (Ed.), *Handbook of growth and growth monitoring in health and disease* (pp. 27–57). New York: Springer.
- Vetta, A. (1975). Fertility, physique, and intensity of selection. *Human Biology*, 47, 283–293.
- Walker, R., Gurven, M., Hill, K., Migliano, A., Chagnon, N., De Souza, R., . . . Yamauchi, T. (2006). Growth rates and life histories in twenty-two small-scale societies. *American Journal of Human Biology*, 18, 295–311.
- Williams, R. (2000). A note on robust variance estimation for cluster-correlated data. *Biometrics*, 56, 645–646.