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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.

The association between height at adulthood and lifetime consumes energy and time that could otherwise be used for reproductive success in humans has attracted long-time scientific interest. It has been suggested that women show preference for taller than average men when seeking sexual partners (Courtiol et al., 2010), and taller men also have 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

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), which 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

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and a previous Finnish study also reported that tall stature that allows participants to be followed up to 51–59 years is associated with older age at first birth (AFB) in women of age, and thus we have been able to analyze the lifetime (Helle, 2008). This may be, however, a special feature of number of children also in men.

developed societies as in agrarian societies tall stature has been found to predict earlier rather than later menarche

(McIntyre & Kacerosky, 2011). When studying lifetime re- **Data and Methods**

productive success in males, tallness was associated with The data were derived from the older cohort of the Finnish higher number of children in a study of US cadets (Mueller Twin Cohort Study (Kaprio & Koskenvuo, 2002). Question- & Mazur, 2001) and in the Polish population (Pawlowski naire were mailed in 1975 and 1981 to all same-sex Finnish et al., 2000), but no association was found in a study of twin pairs born before 1958 and with both co-twins alive US college students (Scott & Bajema, 1982), in Mexican in 1975. The response rates to these questionnaires were living in the United States (Goldstein & Kobylansky, 1984), 89% and 84%, respectively. Height, marital history, and in the United Kingdom (Nettle, 2002a), in China (Fielding education, classified into eight classes described elsewhere et al., 2008), or in Gambia (Sear, 2006). In another co- (Silventoinen et al., 2000), were sent identical question- hort of US college students (Vetta, 1975) and high-school naire at both times. Those respondents still studying when graduates (Stulp et al., 2012a), average stature was associated reporting their level of education were assumed to have ated with the highest number of children. When studying reached the next possible category given in the question- childlessness, the results are more consistent: short stature naire. For height and education, we used the questionnaire in men was associated with higher probability of childless-responses in 1981, and if these were not available then the ness in the United Kingdom (Nettle, 2002a) and Poland data from the questionnaire in 1975 were used. Marital his- (Pawlowski et al., 2000). In females, a positive association was classified as currently living or previously lived with between stature and lifetime reproductive success was found spouse (married, co-habiting, divorced, and widowed) in in Gambia (Sear, 2006) and Guatemala (Pollet & Nettle, 1981 or in 1975. Self-reported height showed high correla- 2008), whereas in the United Kingdom the association was with measured height in a subsample of 100 men and curvilinear and women who were shorter than average had 27 women in this same cohort (Pearson .98 in men higher reproductive success than the shortest and taller than and .96 in women), showing good reliability of self-reported average women (Nettle, 2002b); no association was found height (Silventoinen et al., 2000).

in US college students (Scott & Bajema, 1982), in Mexicans Information on live births is available for participants living in the United States (Goldstein & Kobylansky, 1984), born after 1950 in the Finnish population register. This in China (Fielding et al., 2008), or in Finland (Helle, 2008). register was updated until June 2009 and linked to the

A shortcoming in these previous studies on the association between height and reproduction is, however, that ple, using unique personal identification numbers assigned they have not properly adjusted for socioeconomic or other to all Finnish citizens. The participants alive in 2009 were environmental covariates which could contribute to this 51–59 years of age at the time of the end of the follow- association. Childhood socioeconomic background is esup and therefore effectively post-reproductive. From 9,006 pecially important to consider as growth takes place during twin individuals who answered the questionnaires in 1975 childhood and adolescence, and childhood environment or 1981, we removed 1,168 twin individuals who were living can affect adult life in multiple ways. As height is associated with their co-twin in 1981. This is because a large propor- with childhood socioeconomic background (Silventoinen, tion of these twins remained childless and therefore this 2003) and high social position is found to be associated group may not be representative to the general population with higher fertility in males and lower fertility in females in terms of reproduction. However, we replicated the analy- (Kravdal & Rindfuss, 2008; Nettle & Pollet, 2008), these facces in the whole data set to confrm whether this restriction tors rather than height itself may explain this association. affected the results. Furthermore, individuals from triplet or Adjusting the results for measured socioeconomic factors, quadruplet births were excluded from the data (N = 8). In offers only a partial solution, as no study can fully observe the final study sample, we had 3,595 male and 4,235 female all relevant social factors. In this study, we analyze this ques- twin individuals, including 1,076 monozygotic (MZ) and tion utilizing a twin study design. Using twin pairs raised 2,445 dizygotic (DZ) complete twin pairs, and 787 twin in- in the same family who differ in the number of children dividuals without information on their co-twin. The study they have as adults allows an analysis of the role of height was approved by the ethical committee of the Department on reproductive success when family background can be of Public Health, University of Helsinki. Informed consent regarded as standardized. Furthermore, the twin study dewas obtained from all respondents.

sign offers the opportunity to quantify the role of genetic We analyzed the association between height and life- and environmental factors behind the variation of different time number of children among twin individuals using traits and covariation of their mutual associations. We used both Poisson regression and multinomial logistic regres- a large and nationally representative Finnish twin data set sion 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 statistical software, version 11.2 (StataCorp, College Station, Texas, USA).

We continued the analysis by studying the association between height with lifetime number of children and AFB by applying a linear association in regression models if a linear association was found (for 10 cm = -0.699; 95% CI = -1.229, -0.169). However, there was also some level of non-linearity in this association in the tallest women, and a weak but statistically significant positive regression coefficient for the square of height was seen (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 non-significant trend in men (for 10 cm = 0.006; 95% CI = -0.002, 0.010) whereas in women the association virtually did not exist (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 between 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 ($\Theta = 1.00$). In males, the highest probability of having one to two children was in the third quintile.

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

		Height			Age at 1st birth		Number of children (%)		
		N	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 the formation of the association between height and reproduction. These analyses were carried out using the Stata statistical software, version 11.2 (StataCorp, College Station, Texas, USA).

In men, the regression coefficient of height was not statistically significant (for 10 cm = 0.004; 95% CI = -0.008, 0.016) when predicting log AFB. In women, a clear negative association was found (for 10 cm = -0.699; 95% CI = -1.229, -0.169). However, there was also some level of non-linearity in this association in the tallest women, and a weak but statistically significant positive regression coefficient for the square of height was seen (for 10 cm = 0.022; 95% CI = 0.006, 0.038).

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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 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 were informative, and thus this analysis has less power than 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.

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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						
1D2 children						
Shortest quintile	0.67	0.51D0.88	0.68	0.52D0.90	0.74	0.55D1.00
2nd quintile	0.78	0.59D1.03	0.78	0.59D1.04	0.81	0.59D1.10
3rd quintile	1.00		1.00		1.00	
4th quintile	0.71	0.54D0.94	0.72	0.55D0.95	0.71	0.53D0.96
Tallest quintile	0.81	0.61D1.08	0.79	0.59D1.05	0.76	0.55D1.05
p value of the trend	0.30		0.48		0.88	
3 children or more						
Shortest quintile	0.70	0.51D0.96	0.73	0.53D1.00	0.81	0.57D1.14
2nd quintile	0.85	0.62D1.17	0.86	0.62D1.18	0.89	0.63D1.27
3rd quintile	1.00		1.00		1.00	
4th quintile	0.81	0.59D1.10	0.80	0.58D1.09	0.80	0.56D1.12
Tallest quintile	1.01	0.73D1.41	0.97	0.70D1.35	0.95	0.66D1.37
p value of the trend	0.06		0.17		0.58	
Women						
1D2 children						
Shortest quintile	0.86	0.67D1.10	0.82	0.64D1.06	0.85	0.65D1.11
2nd quintile	0.92	0.71D1.19	0.92	0.71D1.19	0.92	0.70D1.21
3rd quintile	1.00		1.00		1.00	
4th quintile	0.76	0.59D0.98	0.78	0.59D1.01	0.76	0.57D1.02
Tallest quintile	0.76	0.59D0.98	0.80	0.62D1.02	0.77	0.58D1.01
p value of the trend	0.17		0.46		0.27	
3 children or more						
Shortest quintile	1.05	0.79D1.41	1.01	0.76D1.36	1.05	0.78D1.44
2nd quintile	0.81	0.60D1.10	0.82	0.60D1.12	0.82	0.59D1.13
3rd quintile	1.00		1.00		1.00	
4th quintile	0.87	0.64D1.18	0.89	0.66D1.21	0.87	0.62D1.21
Tallest quintile	0.82	0.61D1.10	0.86	0.64D1.17	0.82	0.59D1.14
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	0.31D0.84	0.50	0.30D0.83	0.52	0.27D1.01
2nd quintile	0.61	0.38D0.96	0.61	0.38D0.97	0.66	0.36D1.24
3rd quintile	1.00		1.00		1.00	
4th quintile	0.68	0.43D1.06	0.69	0.43D1.09	0.89	0.49D1.59
Tallest quintile	0.62	0.37D1.04	0.57	0.33D0.97	0.60	0.30D1.21
p value of the trend	0.36		0.47		0.42	
Women						
Shortest quintile	0.92	0.57D1.47	0.89	0.55D1.43	0.97	0.54D1.73
2nd quintile	0.96	0.64D1.45	0.93	0.61D1.41	1.11	0.66D1.85
3rd quintile	1.00		1.00		1.00	
4th quintile	0.78	0.50D1.19	0.77	0.50D1.19	0.83	0.49D1.41
Tallest quintile	0.71	0.43D1.17	0.70	0.42D1.16	0.79	0.42D1.46
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. In the whole data set, the results were largely similar (Table S3).

We also conducted similar analyses for marital history. In females, no differences were found. (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 genetic twin modeling. Compared with the saturated twins as individuals and for discordant twin pairs, but the models, the fit of univariate models was good in men

previous empirical evidence suggesting that the association to beginning reproduction (Allal et al., 2004). However, the association between tallness and men's reproductive success is 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 been linked 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 1910 (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 and half because of phenotypic assortment (Silventoinen et al., 2003). Even when this tendency is controlled for, 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 that 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 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

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