

*Original Research Article***The Effect of Female Height on Reproductive Success Is Negative in Western Populations, But More Variable in Non-Western Populations**GERT STULP,^{1,2*} SIMON VERHULST,² THOMAS V. POLLET,¹ AND ABRAHAM P. BUUNK^{1,3}¹*Department of Psychology, University of Groningen, Groningen, The Netherlands*²*Department of Behavioral Biology, University of Groningen, Groningen, The Netherlands*³*Royal Netherlands Academy of Arts and Sciences, The Netherlands*

Objective: In this article we examine the association between female height and reproductive success in a US sample and present a review of previous studies on this association. We also outline possible biological explanations for our findings.

Methods: We used data from a long-term study of 5,326 female Wisconsin high school graduates to examine the association between female height and reproductive success. Twenty-one samples on this association were covered by our literature review.

Results: Shorter women had more children surviving to age 18 than taller women, despite increased child mortality in shorter women. Taller women had a higher age at first birth and age at first marriage and reached a higher social status, but the negative effect of height on reproductive success persisted after controlling for these variables. However, while these effects were quite consistent in Western populations, they were not consistently present in non-Western populations. Our review also indicated that child mortality was almost universally higher among shorter women.

Conclusions: We conclude that shorter women have a higher number of live births but that final reproductive success depends on the positive effect of height on child survival. *Am. J. Hum. Biol.* 24:486–494, 2012. © 2012 Wiley Periodicals, Inc.

Female height may in various ways be associated with reproductive success. First, shorter women may have more reproductive success than taller women because of the trade-off between investing energy in somatic growth or reproduction (Stearns, 1992). This trade-off is evidenced by the fact that women who have menarche at an earlier age typically reach a shorter adult height than women who have menarche at a later age (McIntyre and Kacerosky, 2011; Okasha et al., 2001). Similarly, women who have their first child at an earlier age are shorter than women who give birth at a later age (Helle, 2008). Thus, taller women seem to become fertile at a later age than shorter women and women who invest energy in reproduction at an early age (e.g., early menarche or child birth) reach a shorter adult height, which may result in a negative relationship between female height and reproductive success.

In addition, the positive relationship between height and social status could translate into decreased reproductive success for taller women, and thus into more reproductive success for shorter women. In Western societies, education and income reflect social status and height is positively correlated with education (Cavelaars et al., 2000; Silventoinen et al., 1999), as well as with income (Judge and Cable, 2004). Both education and income are negatively associated with female reproductive success: relatively highly educated women and women with high incomes have less offspring (reviewed in Hopcroft, 2006; Nettle and Pollet, 2008).

The higher potential reproductive success among shorter women, however, may be counteracted by the negative relationship between maternal height and child morbidity and mortality. Shorter women are at a higher risk for complications during pregnancy, such as stillbirths (Bresler, 1962), failure to progress in labor (Sheiner et al., 2005), and the need for Caesarean sections (Kirch-

engast and Hartmann, 2007; Stulp et al., 2011). The adverse effect of short height is not limited to complications during pregnancy, but extends to the health of the newborn baby as shorter women are more likely to give birth to infants with a relatively low birth weight (Camilleri, 1981) and with relatively low Apgar scores (a health assessment score directly after delivery; Camilleri, 1981; Casey et al., 2001). Both measures are predictors of child morbidity and mortality (Casey et al., 2001; McIntire et al., 1999). Although little is known about the relationship between height and child mortality in developed countries (although see Bresler, 1962), maternal height is almost universally negatively related to child mortality in developing countries (Monden and Smits, 2009) and in low- to middle-income countries (Özaltın et al., 2010).

To complicate matters further, the increased ability to attract mates by average height women compared to shorter and taller women may translate into decreased reproductive success for both shorter and taller women. Indeed, a recent review of the attractiveness of female height suggests that men prefer partners shorter than themselves, but do not have a general preference for shortness (Courtiol et al., 2010). These preferences result

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*Correspondence to: Gert Stulp, Grote Kruisstraat 2/1, 9712 TS Groningen, The Netherlands. E-mail: gertstulp@gmail.com

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in women of average height being considered more attractive than either short or tall women. Consistent with this pattern is the curvilinear association between height and jealousy, with average height women being least jealous of attractive rivals (Buunk et al., 2008), and least competitive toward other women (Buunk et al., 2009). Therefore, short as well as tall women may have more difficulty in attracting a partner.

In the present article, we aimed to disentangle the association between female height and reproductive success by taking into account the various factors that might underlie this association. We did so, first, by examining the relationship between height and reproductive success in a broad sample of a Wisconsin (US) population. As a proxy for reproductive success, the number of children ever born and surviving to reproductive age was used. To disentangle whether an observed relationship between height and reproductive success could be explained by the trade-off between reproduction and growth, social status, child survival, or the ability to attract a partner, we examined the relationship between height and these factors, and how these factors affected reproductive success. For the trade-off between reproduction and growth we examined the association between height and age at the birth of the first child as well as the association between height and reproductive success in women who already had reached their final stature. We used both education and income as measures for social status. As a measure of child survival, we used the proportion of children surviving to 18 years. As proxies for the ability to attract mates, we examined whether a woman was ever married and the age when she married. Second, we provide a review of all studies on the relationship between female height and reproductive success that we could locate and against this background we evaluated to what extent our findings from a US population can be generalized. In this way we aim to contribute to the understanding of the selection pressures shaping the evolution of female height.

MATERIAL AND METHODS

Wisconsin longitudinal study

We used the Wisconsin longitudinal study (WLS), a long-term study of a random sample of 10,317 men and women, born primarily in 1939, who graduated from Wisconsin high schools in 1957 (Wollmering, 2006; <http://www.ssc.wisc.edu/wlsresearch/>). Survey data on a wide variety of topics were collected at several time points (1957, 1964, 1975, 1992, and 2004), covering almost 50 years of the participants' lives. The WLS sample is broadly representative of White, non-Hispanic American men and women who have completed at least a high-school education. Respondents are mainly of German, English, Irish, Scandinavian, Polish, or Czech ancestry. Approximately 66 percent of Americans aged 50–54 in 1990 and 1991 were non-Hispanic White persons who completed at least 12 years of schooling. As about 75 percent of Wisconsin youth graduated from high school in the late 1950s (Wollmering, 2006), our sample was biased toward well-educated people.

The key variables for this study were height, education, income, number of children ever born, number of children surviving to reproductive age (18 years), age at the birth of the first child, whether the respondent was ever being married and age at first marriage. Only biological children

were included in the offspring counts. We combined the data from separate time points to maximize sample size. Thus, when data for a certain variable were missing at one time point, we used data from a different time point for that variable, combining the data into one new variable. For height, education, the number of children ever born and surviving to reproductive age, age at the birth of the first child, and ever being married we used data from 1992 and 2004. In 1992, all women were at least 52-years old, and were thus unlikely to conceive more children. Education was measured as 'how many years of education does the graduate have based on his or her highest degree?' (ranging from high school degree = 12 years of education to postdoctoral education = 21 years of education). We combined data from 1975 and 1992 for age at first marriage. For income we used the 1974 data only (total earnings in US\$ last year), because inflation and career development make income more difficult to compare across decades.

Statistical analyses were performed using SPSS 16. To examine the associations between height, education and income, we used Pearson correlations. For the effects of height on different measures of reproductive success (number of children ever born, number of children surviving to 18 years, proportion of children surviving until reproductive age, age at the birth of the first child, ever being married, and age at first marriage) we used generalized linear models with the appropriate error distribution (normal, Poisson, or binomial). To test for possible curvilinear effects of height, we included a squared term of height in all models. All tests were two-tailed and the significance level was set to $\alpha = 0.05$.

Previous research on the relationship between female height and reproductive success

We searched for studies on the relationship between female height and reproductive success using specific search terms (female, height, stature, reproductive success, and number of children) in electronic databases (PubMed and Web of Science) and by checking references of relevant papers. Only studies in which the number of live born children or the number of surviving children was used as a measure of reproductive success were used. Ideally, we would have carried out a meta-analysis but unfortunately too few studies reported the required estimates of effect size necessary to conduct such an analysis.

For each study, we determined the power to detect the effect of height on number of children, based on the N of the study, a P level of 0.05, and a given effect size using G*Power 3, version 3.1.2 (Faul et al., 2007). G*Power is a flexible statistical power analyses program for statistical tests commonly used in social and behavioral research. The effect size used in the power analysis was determined by performing a linear regression on our data regressing number of children on height. Linear regression was used to determine the effect size rather than the Poisson regression applied in the present study, to facilitate comparison with the few studies that performed a regression analysis.

RESULTS

Wisconsin longitudinal study

For 4,059 out of 5,326 women, height was available. The descriptive statistics for these women and the sample size

TABLE 1. Characteristics of the women from the Wisconsin Longitudinal Study for whom height was available

	Mean \pm SD	Minimum	Maximum	N
Height (cm)	164.18 \pm 6.26	139.70	198.12	4,059
Education (years)	13.26 \pm 1.97	12	21	4,059
Annual income in '74 (\$)	17,037 \pm 18,457	0	300,000	3,873
Number of children ever born	2.78 \pm 1.65	0	10	4,059
Number of children surviving to 18	2.72 \pm 1.63	0	10	4,059
Age at first marriage	21.70 \pm 3.62	16	54	3,878
Age at first birth	23.17 \pm 3.61	17	47	3,232

TABLE 2. Poisson regression parameter estimates (\pm S.E.) of the effects of height (cm), education (years), and income in 1974 (US \$) on number of children ever born and number of children surviving to 18 years

	Number of children ever born		Number of children surviving to 18 years	
Intercept	2.40 ($\pm 2.48 \times 10^{-1}$)	2.77 ($\pm 2.60 \times 10^{-1}$)	2.30 ($\pm 2.50 \times 10^{-1}$)	2.65 ($\pm 2.62 \times 10^{-1}$)
Height	-8.39×10^{-3} ($\pm 1.51 \times 10^{-3}$)	-5.30×10^{-3} ($\pm 1.56 \times 10^{-3}$)	-7.92×10^{-3} ($\pm 1.52 \times 10^{-3}$)	-4.75×10^{-3} ($\pm 1.57 \times 10^{-3}$)*
Education		-5.65×10^{-2} ($\pm 5.42 \times 10^{-3}$)		-5.58×10^{-2} ($\pm 5.47 \times 10^{-3}$)
Income		-5.29×10^{-5} ($\pm 2.90 \times 10^{-6}$)		-5.26×10^{-5} ($\pm 2.93 \times 10^{-6}$)
N	4,059	3,873	4,059	3,873

All estimates significant at the $P < 0.001$ level, except * $P = 0.0025$.

available for all variables (and hence analyses) are summarized in Table 1. Poisson regression revealed that height had a negative effect on number of children ever born (Table 2; Fig. 1a). Thus, shorter women had more live births than taller women. In contrast, logistic regressions revealed that there was a positive linear effect of maternal height (in cm) on the proportion of children surviving until 18 years [intercept = -0.0751 (± 1.80), $P = 0.967$; $B = 0.0244$ (± 0.0110); $P = 0.027$; $N = 3,613$]. To illustrate this finding we calculated that women one standard deviation below average (157.92 cm) had 97.8% surviving offspring whereas for women of average height (164.18 cm) this was 98.1%. Thus, the relationships between height and child survival and height and number of ever born children are opposite, with the effect of height being positive for child survival but negative for children ever born.

The effect of female height on child survival was small and hence the effect of height on number of children surviving to reproductive age (18 years) was still negative (Table 2; Fig. 1a). Yet, as expected because of the positive association between height and child survival the effect of height on number of surviving children was smaller in magnitude than the effect of height on number of children ever born (Fig. 1a). In industrialized societies, infant and child mortalities are low. In this study, 192 out of 3,613 (5.3%) mothers reported that at least one child had deceased before the age of 18. Hence, there was a strong correlation between number of children ever born and number of children surviving to the age of eighteen years old ($r = 0.98$, $N = 3,613$, $P < 0.0001$).

Height correlated positively with the age of the mother at the birth of her first child (log-transformed for normality; $r = 0.09$; $P < 0.0001$; $N = 3,232$), indicating that taller women had their first child at a later age. As women rarely grow in stature after the birth of their first child (Allal et al., 2004), shorter women are perhaps shorter because they have their first child at a younger age, and the negative association between height and reproductive success might be a result of this trade-off between growth and reproduction. Therefore, we reanalyzed the above

relationships between height and number of (surviving) children for women who had their first child at an age of 21 and older, when final stature has been reached. These results were very similar [Poisson regression parameter estimate (\pm S.E.) for height; ever born children: $B = -0.00678$ (± 0.00189); $P < 0.001$; $N = 2,479$; surviving children: $B = -0.00625$ (± 0.00191); $P = 0.001$; $N = 2,479$].

We also investigated the association between height and the ability to attract attract mates, namely being married and age at first marriage. There was a trend that women who never married (4%, 165 out of 4,053) were slightly taller than ever married women (t test: $t_{4051} = 1.68$, $P = 0.09$; Cohen's $D = 0.13$). In line with this trend, we found that among married women age at first marriage (log-transformed for normality) increased with height ($r = 0.06$; $P < 0.001$; $N = 3,878$). The negative relationship between height and reproductive success in married women with at least one child, although attenuated, was still significant after controlling for age at first marriage and age at first birth [both log-transformed; Poisson regression parameter estimate (\pm S.E.) for height; ever born children: $B = -0.00374$ (± 0.00161); $P = 0.020$; $N = 3,216$; surviving children: $B = -0.00335$ (± 0.00162); $P = 0.039$; $N = 3,216$].

We repeated the above analyses while including the variables education and income. Height was significantly correlated with both education (Fig. 1b; $r = 0.08$, $N = 4,059$, $P < 0.0001$) and income (Fig. 1c; $r = 0.05$, $N = 3,873$, $P < 0.001$), but accounted for $< 1\%$ of the variation in both variables. Although education and income both had a negative effect on the number of children ever born and the number of children surviving to reproductive age, the negative effect of height remained significant (Table 2). To compare the effects of height, education and income, we calculated the decrease in number of children when increasing the trait with one standard deviation. Increasing one standard deviation in height reduced the number of ever born children by 3.3%, for education this was 10.7% and for income 20.2%. Thus, the effect of height was approximately three times weaker than the effect of education and about six times weaker than the effect of

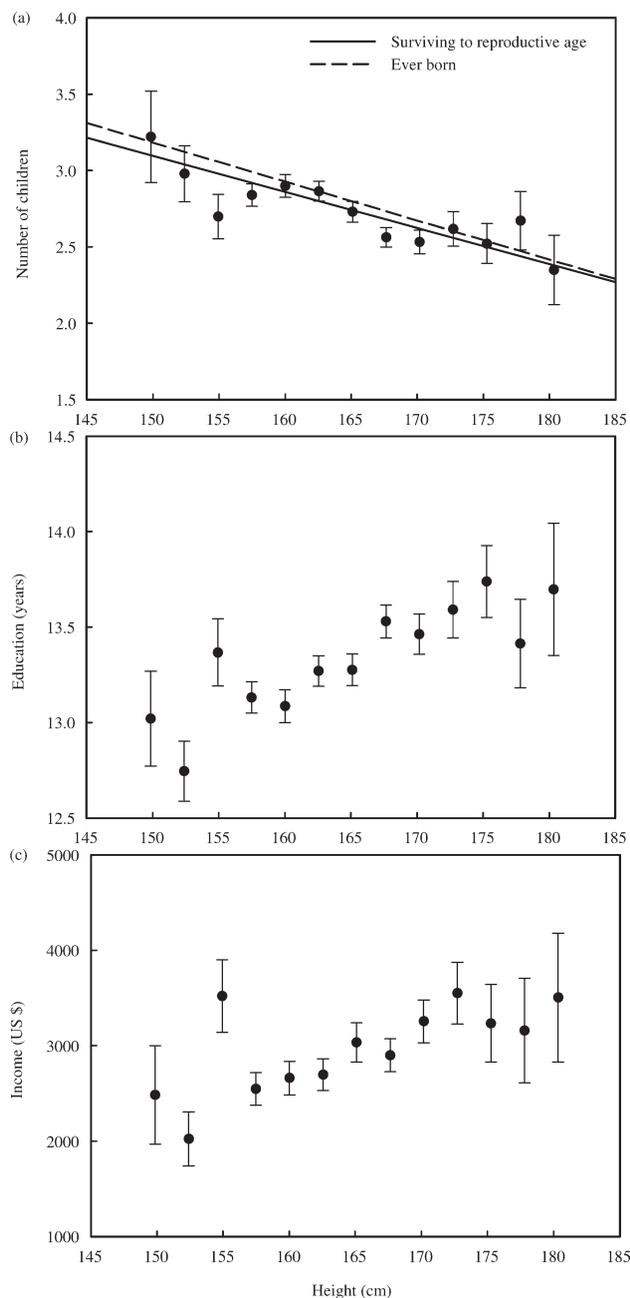


Fig. 1. The effect of height on (a) the number of children surviving to 18 (with Poisson regression lines), (b) the number of years of education, and (c) annual income (US \$) in 1974 binned by inch of height (mean \pm S.E.). Given that height was measured in inches, we binned data using this unit of measurement (which was converted into cm). Bins below 59 in. and above 71 in. were collapsed.

income. Similarly, for the number of children surviving to the age of 18; increasing one standard deviation in height reduced the number of surviving children by 2.9%, for education this was 10.6% and for income 20.1%. Thus, again the effect of height was approximately three times weaker than the effect of education and about seven times weaker than the effect of income. No significant interactions between height, education and income were found

(see Supporting Information S-Tables 1 and 2 for parameter estimates in low income, high income, low education, and high education mothers).

The effect of height on the proportion of surviving children, age at first marriage, and age at the birth of the first child remained significant when controlling for education and income. Furthermore, no significant quadratic effects were found (see Supporting Information S-Tables 3–7 for parameter estimates of the effects of height, height², education, and income on all dependent variables).

Previous research on the relationship between female height and reproductive success

We identified 20 scientific publications reporting the relationship between height and reproductive success measured as number of live born or living children, of which one article included data on two different populations (Kirchengast and Winkler, 1996). Including the present study this brings the total to 22 studies (Table 3). A variety of effects of female height on reproductive success were reported, including positive ($N = 3$), negative ($N = 10$; including the present study), null ($N = 7$), and curvilinear effects ($N = 2$).

In part, this variation in results may be due to methodological factors, such as differences in sampling procedure (for instance including only parous women or including women who have not yet reached the end of their reproductive careers), differences in sample size (and hence statistical power), or differences in the number of predictor variables considered in the statistical analysis (which also affects statistical power). To examine the effect of differences in sample size, we determined for each study the power to detect the effect of height on reproductive success, based on the N of the study, a P level of 0.05, and an effect size of $r = 0.09$ (Table 3). The latter was taken from a linear regression of number of ever born children on height using the data from the present study. We used ever born children as outcome measure as more studies in our review used this measure rather than the number of surviving children (linear regression of number of surviving children on height resulted in an r of -0.08). The choice of this effect size, at least for Western populations seems justified, as one of the few studies that reports an effect size of height on lifetime reproductive success was very similar to ours ($r = -0.083$; Byars et al., 2010). Given these parameters, an N of 966 was needed to obtain a power of 0.80. The fact that the required sample size is so large is mainly due to the low effect size of the relationship we study (low, but not uncommon; Kingsolver et al., 2001). The seven studies that did not find any relationship all had a power smaller than 0.6 to detect $r = 0.09$. The power decreases even further when samples use wide age ranges (e.g., Mueller et al., 1981), only parous women (e.g., Nenko and Jasienska, 2009) or different ethnicities (e.g., Scott and Bajema, 1982). We will not consider these null findings any further.

Results from Western samples were very similar to each other: every study that found a significant effect, reported a negative association between height and reproductive success ($N = 5$). More variation was found among the non-Western samples; positive ($N = 3$), curvilinear ($N = 2$) as well as negative ($N = 5$) effects were reported. Brush et al. (1983) found a curvilinear effect of height on the number of children. However, the peak of the curvilinear effect

TABLE 3. Studies on the association between female height and reproductive success

Study	Sample	N	Age	Control factors	Height effect on repr. success	Height effect on child mort.	Power
<i>Non-Western populations</i>							
Mueller (1979)	Families (at least one child) from a Malnourished population in Colombia	349	<29–65+	Age ² SES SES ²	No ^{1,a}	-	0.39
Shami and Tahir (1979)	Pakistani women (at least one child)	827	?		Curvilinear ^{1,II,b}	-	0.74
Lasker and Thomas (1976)	Mexican women who have lived in US	147	>25	Age	No ¹	-	0.19
Mueller et al. (1981)	Mexican women in Mexico or US	121	16–85	Age ²	No ¹	-	0.17
Martorell et al. (1981)	Malnourished Guatemalan Indian women (at least one child)	380	15–47	Residence Age	Positive ^{1,II,c}	Negative ^d	0.42
Brush et al. (1983)	Papua New Guinean Women	152	21–44	Age	Curvilinear ^{1,II}	-	0.20
Devi et al. (1985)	Undernourished population of Jalaris, India	291	23–55	Age Number of conceptions	Negative ^{1,II}	Positive ^e	0.34
Kirchengast and Winkler (1996)	Kung san women from Namibia	93	18–65	Age	Negative ^{1,II}	Negative ^f	0.14
Kirchengast and Winkler (1996)	Kavango women from Namibia	85	18–60	Age	Negative ^{1,II,g}	Negative ^f	0.13
Kirchengast (2000)	Kung san women from Namibia	65	25–40	Age	Negative ^{1,II}	Negative ^h	0.11
Sear et al. (2004)	Farming community in rural Gambia (at least one child)	216	>50	Age	Positive ^{1,II}	Negative ⁱ	0.26
Pollet and Nettle (2008)	Women from stressed environment in rural Guatemala	2571	18–35	Age Age ²	Positive ^{1,j}	Negative ^k	>0.99
Fielding et al. (2008)	Chinese women	6709	>50	Ethnicity Education Age Education Parental possessions	Negative ^{1,l}	- ^m	>0.99
<i>Western populations</i>							
Clark and Spuhler (1959)	Women from European descent from Michigan, US	324	20–70		No ^{1,n}	-	0.37
Bailey and Garm (1979)	White females from 10 different states in US	~1,261	45–65	Income	Negative ^{1,o}	- ^p	0.89
Scott and Bajema (1982)	Females who attended public schools in Boston, US	600	±50–55	Income	No ^{1,q}	-	0.60
Nettle (2002)	Children born in UK in a certain week in 1958	3,554	42	Occupational class	Negative ^{1,r}	-	>0.99
Deady and Law Smith (2006)	White women from UK, US, Canada, and Australia	315	>45	Social class father Age	Negative ^{1,II}	-	0.36
Helle (2008)	Finnish women	271	>55	Parental income Education Birth cohort Area	No ¹	-	0.32
Byars et al. (2009)	Participants from the Framingham Heart study	2,227	Postmenopausal	Height ² Education Whether native born	Negative ^{1,II}	-	0.99
Lenko and Jasienska (2009)	Rural women from Poland (at least one child)	328	21–85	Whether smoker Medicine use Age	No ^{1,III}	-	0.37

TABLE 3. (Continued)

Study	Sample	N	Age	Control factors	Height effect on reprod. success	Height effect on child mort.	Power
This study	White women from Wisconsin	4,059	>63	Education Income	Negative ^{1,II}	Negative	>0.99

N indicates sample size. The power is the probability of detecting the effect size estimated by our analyses ($r = 0.09$) at a significance level of $\alpha = 0.05$ given the sample size *N* (see text for further explanation).

^IDependent variable: number of surviving children.

^{II}Unknown whether surviving or ever born children were used as dependent variable.

^{III}Instead of height, these authors used a composite measure of many bone measurements. Height was not a strong determinant of this composite measure.

^{IV}The authors divided height into several height classes and found that the number of children (both surviving and ever born) was significantly higher in the average height classes (combined) compared to the other height classes.

^VThe authors report a negative relationship between height and ever born children, although this relationship was not significant.

^{VI}As dependent variables, both number of deceased children and child mortality were used.

^{VII}The dependent variable was number of post-natal deaths.

^{VIII}The authors found a negative correlation between height and number of deceased children.

^{IX}The negative relationship between height and number of live births was significant, the relationship with number of surviving children only marginally significant.

^XA comparison between heights of mother with 0, 1–3, or 4 or more dead children was not significant. However, a clear graph of the negative correlation between height and number of deceased children was provided.

^{XI}Child mortality was the dependent variable.

^{XII}The optimum of the curvilinear effect reported by Pollet and Nettle (2008) reported was nearly two standard deviations above average. Thus, for the normal range of ± 2 standard deviations, the relationship between height and reproductive success was positive.

^{XIII}Proportion of surviving children was used as dependent variable. Similar as above, the optimum was nearly two standard deviation above average.

^{XIV}The effect disappeared after controlling for education and parental possessions.

^{XV}Shorter women had a higher risk for miscarriage.

^{XVI}Mitton (1975) reanalyzed this sample only incorporating women older than 40. No effects of height were found.

^{XVII}Taller women had fewer children than shorter women (*t* test comparison between short and tall height group).

^{XVIII}Short women (<15th percentile) had more stillborn children than tall women (>85th percentile), although this difference was not statistically significant.

^{XIX}Childless women were shorter. However, ethnicity was not controlled for.

^{XX}Nettle (2002) reported a curvilinear effect. However, the optimum was nearly two standard deviations below average. Thus, for the normal range of ± 2 standard deviations, the relationship between height and reproductive success was negative.

could not be established as appropriate estimates or graphs were not given. This peak could thus have been either to the left or the right of the height distribution, which would substantially alter the interpretation of the results.

Given the variety in results found in non-Western samples, and the fact that these effects were found using substantially smaller samples, for such samples the use of our low effect size and power calculations based on this estimate ($r = 0.09$) may not be fully justified. Therefore, we determined the effect size of one of the non-Western studies that was most comparable to our study (using postreproductive women; Sear et al., 2004), and for which appropriate information was available. We found an effect size of $r = 0.16$ for the relationship between height and the number of ever born children, which was substantially higher than our effect size and in the opposite direction. Given these parameters, an *N* of 304 was needed to obtain a power of 0.80. Two of the three non-Western studies that did not find an effect had a power lower than 0.5 to detect this effect size.

DISCUSSION

We found a negative relationship between female height and reproductive success, measured as the number of children ever born. A better measure of reproductive success also incorporates child survival to reproductive age. Although a positive relationship between height and child survival was found, this effect was not very strong and shorter women still had more children that survived to age 18 than taller women. Thus, the increased number of children ever born translated into higher reproductive success for shorter women despite the decreased child survival these shorter women experienced.

Given that height is related to education (Cavelaars et al., 2000; Silventoinen et al., 1999), and that our sample consisted of female high-school graduates, the observed relationship between height and reproductive success may have been biased. Our review of studies on the relationship between female height and reproductive success, however (Table 3), confirmed our finding that across Western populations female height is negatively associated with reproductive success, as five out of nine studies documented a similar negative effect. The four remaining studies in Western populations found no effect of height, which was likely due to small sample size and hence low statistical power to detect an effect of the magnitude we found in our study.

In non-Western populations the relationship between height and reproductive success was more variable. There can be different causes for this variation. One possibility is that there is true variation in selection pressures between populations and over time, which in itself is not unusual (Siepielski et al., 2009). Alternatively, but not mutually exclusive, conclusions across studies may differ for methodological reasons, such as low statistical power (see above) or differences in sampling procedure (e.g., including young women who have likely not ended their reproductive careers). The variation in the non-Western populations can also partly be explained by the relationship between female height and child survival. In line with previous findings on the relationship between female stature and child mortality (42 developing countries: Monden and Smits, 2009; 54 low- to middle-income countries:

Özaltın et al., 2010; but see Devi et al., 1985), we found that female height is consistently negatively related to child mortality in non-Western populations (with one exception: Devi et al., 1985). Even in our Western sample, female height was negatively associated with child mortality. In an environment with few resources height might be a reflection of health, nutritional status, and greater access to resources (Sear et al., 2004; Silventoinen, 2003), all of which have a positive influence on the survival of children. If child mortality is high, the positive relationship between female height and child survival will result in more surviving offspring, and potentially in more reproductive success for taller women. Indeed, in all studies that found a positive association between height and the number of surviving children, maternal height was positively associated with child survival. Thus, we conclude that the positive association between height and reproductive success in non-Western populations can be explained by the increased survival probability of offspring from taller women (Martorell et al., 1981).

Although the number of live births is a potentially biased measure, because of potential underreporting of deceased children (Sear et al., 2004) and not incorporating abortions in early prenatal development (Frisancho et al., 1973), most studies in which such data are available show that shorter women have more live births (this study, Devi et al., 1985; Martorell et al., 1981; but see Sear et al., 2004). The increased number of live births by shorter women might be a strategy to compensate for future or past child loss (e.g., a quantity–quality trade-off; Borgerhoff Mulder, 2000).

A possible mechanism through which the negative relationship between height and reproductive success in Western populations can arise, is the positive relationship between height and social status. In line with previous research, we found that education and income, both measures of social status, had a negative effect on female reproductive success (reviewed by Hopcroft, 2006; Nettle and Pollet, 2008). Moreover, the effects of education and income were substantially larger than the effect of height (about three and six times larger, respectively). While we found that height was positively associated to both education and income (in line with Cavelaars et al., 2000; Judge and Cable 2004; Silventoinen et al., 1999), the relationship between height and reproductive success was independent of these measures. Thus, the negative relationship between height and reproductive success among women from Western societies cannot be explained by the relationship between height and social status. This finding was in agreement with most studies from Western populations that included measures of social status, and still found a negative effect of height on reproductive success. As previously discussed, social status (or greater access to resources) could be positively associated with reproductive success in environments with few resources, and the association between height and social status in these populations could then translate into higher reproductive success for taller women. Unfortunately, only a minority of studies (3 out of 13 studies in non-Western populations) report on measures of social status, making it difficult to systematically review how the relationship between social status and height affects reproductive success crossculturally.

Another possible explanation for why taller women have fewer children is the trade-off women face between

investing energy in growth or reproduction (Stearns, 1992). Taller women become fertile at a later age than shorter women (Okasha et al., 2001) and women who invest energy in reproduction at an early age (e.g., early menarche or child birth) reach a shorter adult height (Helle, 2008). We also found that taller women had their first child at a later age, which is in line with previous research (Allal et al., 2004; Pollet and Nettle, 2008; Sear et al., 2004). However, in our Wisconsin sample, the relationship between female height and reproductive success persisted after controlling for the age at the birth of the first child. Additionally, we found that height negatively predicted the number of children in women who already reached their final adult height. Hence, there must be additional mechanisms causing the pattern between height and reproductive success.

The positive association between height and age at menarche is in line with life-history theory, but seems restricted to Western populations (McIntyre and Kacerosky, 2011). A recent meta-analysis showed that the association was reversed in small-scale societies; taller women had menarche at an earlier age (McIntyre and Kacerosky, 2011). The rationale for this association is that women grow toward an appropriate skeletal status before reproduction can be initiated (Ellison, 1982). This finding may also partly explain the difference in findings on the association between height and reproductive success between Western and non-Western societies. Whereas in Western societies shorter women can reproduce at an earlier age than taller women, in non-Western societies the reverse is true. Thus, the positive association between height and reproductive success observed in non-Western populations may be explained by the earlier sexual maturity of taller women in these populations.

The ability to attract mates is another possible mechanism through which the increased reproductive success of shorter women can arise, if shorter women would have an advantage in finding a partner. Consistent with the finding that taller women receive fewer responses from men on newspaper advertisements (Pawlowski and Koziel, 2002), we found that non-married women tended to be taller than ever married women and that shorter women married at a younger age, suggesting that shorter women are indeed better able to attract mates. Women who were married and women who married at an earlier age had higher reproductive success, thus partly explaining the observed negative relationship between height and reproductive success. The reason why shorter women seem to be favored in our sample is not entirely clear, although a potential functional explanation is that shorter women are sexually mature at an earlier age and actually achieve more live births than taller women (Nettle, 2002). Our result that height is negatively related to the ability to attract mates is different from findings on mate preference studies, which indicate that average height women are considered most attractive (reviewed in Courtiol et al., 2010). This discrepancy may be explained by the fact that lab-based preferences may not necessarily reflect actual mate choice (Riebel et al., 2010; Todd et al., 2007). For instance, other, potentially far more important characteristics (such as kindness, personality or ethnicity) play a role in choosing a mate, obscuring the preferences for height. Similarly, mutual mate choice may result in ending up with a less than preferred partner. A second reason for the discrepancy is the interpretation of marriage

patterns to reflect the ability to attract mates. The younger age at marriage of shorter women may equally well mean that these women are less critical in accepting a partner.

Regardless of the mechanism causing the higher reproductive success of shorter women, our findings suggest that in particular in Western populations there is a selection pressure on women favoring lower height. Moreover, the contrast with non-Western populations suggests that this may be a relatively recent development. Whether this will lead to shorter height in the future is uncertain however (but see Byars et al., 2010 for a quantitative prediction for a specific population). First, in addition to the selection pressure on female height within cohorts, as we identified here, there is a secular trend that height increases (Silventoinen, 2003). Second, because offspring height is determined by the genes they inherit from both their parents (Silventoinen, 2003), the selection pressure on height in males also plays a role. We recently showed that average height men obtained higher reproductive success than either taller or shorter men (Stulp et al., in press). Thus, predictions on how height will evolve in the future should be based on the integration of the selection pressures acting on height in both sexes, and these predictions likely differ from predictions based on either sex in isolation.

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LITERATURE CITED

- Allal N, Sear R, Prentice AM, Mace R. 2004. An evolutionary model of stature, age at first birth and reproductive success in Gambian women. *Proc Biol Sci* 271:465–470.
- Bailey SM, Garn SM. 1979. Socioeconomic interactions with physique and fertility. *Hum Biol* 51:317–333.
- Borgerhoff Mulder V. 2000. Optimizing offspring: the quantity-quality tradeoff in agropastoral Kipsigis. *Evol Hum Behav* 21:391–410.
- Bresler JB. 1962. Maternal height and the prevalence of stillbirths. *Am J Phys Anthropol* 20:515–517.
- Brush G, Boyce AJ, Harrison GA. 1983. Associations between anthropometric variables and reproductive performance in a Papua New Guinea highland population. *Ann Hum Biol* 10:223–234.
- Buunk AP, Park JH, Zurriaga R, Klavina L, Massar K. 2008. Height predicts jealousy differently for men and women. *Evol Hum Behav* 29:133–139.
- Buunk AP, Pollet TV, Klavina L, Figueredo AJ, Dijkstra P. 2009. Height among women is curvilinearly related to life history strategy. *Evol Psych* 7:545–559.
- Byars SG, Ewbank D, Govindaraju DR, Stearns SC. 2010. Evolution in health and medicine Sackler colloquium: natural selection in a contemporary human population. *Proc Natl Acad Sci USA* 107:1787–1792.
- Camilleri AP. 1981. The obstetric significance of short stature. *Eur J Obstet Gyn R B* 12:347–356.
- Casey BM, McIntire DD, Leveno KJ. 2001. The continuing value of the APGAR score for the assessment of newborn infants. *N Engl J Med* 344:467–471.
- Cavelaars AEJM, Kunst AE, Geurts JJM, Crialesi R, Grötvedt L, Helmer U, Lahelma E, Lundberg O, Mielck A, Rasmussen NK, Regidor E, Spuhler T, Mackenbach JP. 2000. Persistent variations in average height between countries and between socio-economic groups: an overview of 10 European countries. *Ann Hum Biol* 27:407–421.
- Clark PJ, Spuhler JN. 1959. Differential fertility in relation to body dimensions. *Hum Nat Int Bios* 31:121–137.
- Courtioi A, Raymond M, Godelle B, Ferdy J. 2010. Mate choice and human stature: homogamy as a unified framework for understanding mating preferences. *Evolution* 64:2189–2203.
- Deady DK, Law Smith MJ. 2006. Height in women predicts maternal tendencies and career orientation. *Per Indiv Differ* 40:17–25.
- Devi MR, Kumari JR, Srikumari CR. 1985. Fertility and mortality differences in relation to maternal body size. *Ann Hum Biol* 12:479–484.
- Ellison PT. 1982. Skeletal growth, fatness, and menarcheal age: a comparison of two hypotheses. *Hum Biol* 54:269–281.
- Faul F, Erdfelder E, Lang A-G, Buchner A. 2007. G*Power 3: a flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behav Res Meth* 39:175–191.
- Fielding R, Schooling CM, Adab P, Cheng KK, Lao XQ, Jiang CQ, Lam TH. 2008. Are longer legs associated with enhanced fertility in Chinese women? *Evol Hum Behav* 29:434–443.
- Frisancho AR, Sanchez J, Pallardel D, Yanez L. 1973. Adaptive significance of small body size under poor socio-economic conditions in southern peru. *Am J Phys Anthropol* 39:255–261.
- Hopcroft RL. 2006. Sex, status, and reproductive success in the contemporary united states. *Evol Hum Behav* 27:104–120.
- Judge TA, Cable DM. 2004. The effect of physical height on workplace success and income: preliminary test of a theoretical model. *J Appl Psychol* 89:428–441.
- Kingsolver JG, Hoekstra HE, Hoekstra JM, Berrigan D, Vignieri SN, Hill CE, Hoang A, Gibert P, Beerli P. 2001. The strength of phenotypic selection in natural populations. *Am Nat* 157:245–261.
- Kirchengast S. 2000. Differential reproductive success and body size in Kung San people from northern Namibia. *Coll Antropol* 24:121–132.
- Kirchengast S, Hartmann B. 2007. Short stature is associated with an increased risk of cesarean deliveries in low risk population. *Acta Med Lit* 14:1–6.
- Kirchengast S, Winkler EM. 1996. Differential fertility and body build in Kung San and Kavango females from northern Namibia. *J Biosoc Sci* 28:193–210.
- Lasker GW, Thomas R. 1976. Relationship between reproductive fitness and anthropometric dimensions in a Mexican population. *Hum Biol* 48:775–791.
- Martorell R, Delgado HL, Valverde V, Klein RE. 1981. Maternal stature, fertility and infant mortality. *Hum Biol* 53:303–312.
- McIntire DD, Bloom SL, Casey BM, Leveno KJ. 1999. Birth weight in relation to morbidity and mortality among newborn infants. *N Engl J Med* 340:1234–1238.
- McIntyre MH, Kacerovsky PM. 2011. Age and size at maturity in women: a norm of reaction? *Am J Hum Biol* 23:305–312.
- Mitton JB. 1975. Fertility differentials in modern societies resulting in normalizing selection for height. *Hum Biol* 47:189–200.
- Monden CWS, Smits J. 2009. Maternal height and child mortality in 42 developing countries. *Am J Hum Biol* 21:305–311.
- Mueller WH. 1979. Fertility and physique in a malnourished population. *Hum Biol* 51:153–166.
- Mueller WH, Lasker GW, Evans FG. 1981. Anthropometric measurements and Darwinian fitness. *J Biosoc Sci* 13:309–316.
- Nenko I, Jasienska G. 2009. Fertility, body size, and shape: an empirical test of the covert maternal depletion hypothesis. *Am J Hum Biol* 21:520–523.
- Nettle D. 2002. Women's height, reproductive success and the evolution of sexual dimorphism in modern humans. *Proc Biol Sci* 269:1919–1923.
- Nettle D, Pollet TV. 2008. Natural selection on male wealth in humans. *Am Nat* 172:658–666.
- Okasha M, McCarron P, Davey Smith G, McEwen J. 2001. Age at menarche: secular trends and association with adult anthropometric measures. *Ann Hum Biol* 28:68–78.
- Özaltın E, Hill K, Subramanian SV. 2010. Association of maternal stature with offspring mortality, underweight, and stunting in low- to middle-income countries. *JAMA* 303:1507–1516.
- Pawlowski B, Koziol S. 2002. The impact of traits offered in personal advertisements on response rates. *Evol Hum Behav* 23:139–149.
- Pollet TV, Nettle D. 2008. Taller women do better in a stressed environment: height and reproductive success in rural Guatemalan women. *Am J Hum Biol* 20:264–269.
- Riebel K, Halveck M-J, Verhulst S, Fawcett TW. 2010. Are high-quality mates always attractive? State-dependent mate preferences in birds and humans. *Commun Integr Biol* 3:271–273.
- Scott EC, Bajema CJ. 1982. Height, weight and fertility among the participants of the third Harvard growth study. *Hum Biol* 54: 501–516.
- Sear R, Allal N, Mace R. 2004. Height, marriage and reproductive success in Gambian women. *Res Econ Anthropol* 23:203–224.
- Shami SA, Tahir AM. 1979. Operation of natural selection on human height. *Pakistan J Zool* 11:75–83.

- Sheiner E, Levy A, Katz M, Mazor M. 2005. Short stature—an independent risk factor for cesarean delivery. *Eur J Obstet Gyn R B* 120:175–178.
- Siepielski AM, DiBattista JD, Carlson SM. 2009. It's about time: the temporal dynamics of phenotypic selection in the wild. *Ecol Lett* 12:1261–1276.
- Silventoinen K. 2003. Determinants of variation in adult body height. *J Biosoc Sci* 35:263–285.
- Silventoinen K, Lahelma E, Rahkonen O. 1999. Social background, adult body-height and health. *Int J Epidemiol* 28:911–918.
- Stearns SC. 1992. *The evolution of life histories*. Oxford: Oxford University Press.
- Stulp G, Verhulst S, Pollet TV, Nettle D, Buunk AP. 2011. Parental height differences predict the need for an emergency Cesarean section. *PLoS ONE* 6:e20497.
- Stulp G, Pollet TV, Verhulst S, Buunk AP. A curvilinear effect of height on reproductive success in human males. *Behav Ecol Sociobiol* doi: 10.1007/s00265-011-1283-2.
- Todd PM, Penke L, Fasolo B, Lenton AP. 2007. Different cognitive processes underlie human mate choices and mate preferences. *Proc Natl Acad Sci USA* 104:15011–15016.
- Wollmering E, editor. 2006. *Wisconsin longitudinal study handbook*. Madison: Wisconsin Longitudinal Study.