HEIGHT, MARRIAGE AND REPRODUCTIVE SUCCESS IN GAMBIAN WOMEN

Rebecca Sear, Nadine Allal, Ian A. McGregor
and Ruth Mace

ABSTRACT

We examine the relationship between height and reproductive success (RS) in women from a natural fertility population in the Gambia. We observe the predicted trade-off between adult height and age at first birth: women who are tall in adulthood have later first births than short women do. However, tall women have reproductive advantages during the rest of their reproductive careers, primarily in the lower mortality rates of their children. This ultimately leads to higher fitness for taller women, despite their delayed start to reproduction. The higher RS of tall women appears to be entirely due to the physiological benefits of being tall. There is no evidence that female height is related to patterns of marriage or divorce in this population.

INTRODUCTION

Life history theory is concerned with the optimal allocation of energy between functions such as reproduction, somatic maintenance and growth (Roff, 1992; Stearns, 1992). Since energy is usually a limited resource, trade-offs are predicted

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between these functions. Energy allocated to reproduction, for example, is expected to be traded-off against energy allocated to growth. Here, we investigate the relationships between growth, body size, and reproduction in a food-limited population by analysing the relationship between adult height and reproductive success in women.

Previously, evolutionary ecologists have investigated the trade-off between growth and reproduction in human females by using weight as a measure of growth (Hill & Hurtado, 1996). Height and weight are highly correlated, but height may be a better measure of growth because growth in height is irreversible, whereas weight is far more labile. Weight is affected both by the ability to acquire energy in adulthood (after the period of growth has ended), and by reproductive events themselves (Winkvist et al., 2003).

Though there is a genetic component to height, in a marginally nourished community where infectious disease is widespread and untreated, there will also be a strong environmental component influencing the final adult height individuals achieve (Roberts et al., 1978). Nutrition clearly plays a role in determining how much energy is available for growth, so that access to food resources during childhood will affect adult height (Gunnell et al., 2000; Rivera et al., 1995; Silventoinen, 2003). Adult height is also at least partly determined by life history trade-offs occurring during childhood. Growth clearly requires considerable energy, but immune defence is also energetically expensive (Read & Allen, 2000). Children who are devoting much energy to fighting off pathogens will have few reserves left over to expend on growth (Crompton & Nesheim, 2002; Silventoinen, 2003). The growth-immune defence trade-off can clearly be seen in this Gambian population: a higher incidence of diarrhoeal episodes is associated with slower growth rates (Rowland et al., 1977).

Trade-offs between growth and immune defence must be made throughout childhood, but at puberty, women face another trade-off: when to stop investing in growth and start investing in reproduction. Because both functions are so energetically expensive, once women have begun to reproduce they rarely grow any further. Switching at a young age from growth to reproduction may confer fitness benefits, by increasing the amount of time women have available for reproduction (Käär & Jokela, 1998). But delaying reproduction and investing more energy in growing to a large size may also be reproductively advantageous. In many species, size is positively correlated with survival rates, as large size provides protection against environmental stresses and predation (Roff, 1992). So growing tall may increase the probability that women will survive throughout their reproductive years (Elo & Preston, 1992; Jousilahti et al., 2000). Though, for our species at least, the relationship between height and mortality may be more complicated than a simple inverse correlation (see Engeland et al., 2003; Samaras et al., 2003).

Size is also positively related to fecundity (Roff, 1992). This relationship may be partly mediated through the greater energy reserves that large females can devote to reproduction (Hill & Hurtado, 1996), but there may also be reproductive advantages of size which are independent of body weight. For example, childbirth is unusually dangerous for human females because of the difficulty of getting a large-brained baby through a pelvis designed for bipedal locomotion (Rosenberg, 1992). Tall women have wider pelves than shorter women, which allow them to have easier births and higher birthweight babies, both factors which reduce infant and maternal mortality (Kirchengast et al., 1998; Martorell et al., 1981; Rey et al., 1995; Sokal et al., 1991).

So far, we have considered the physiological trade-offs that may affect the relationship between height and reproductive success (RS). A recent study which directly correlated female height with RS suggested that height may be negatively correlated with RS in women, not because of their delayed start to reproduction or any other physiological factors, but because they are less successful at attracting mates than shorter women (Nettle, 2002). This is rather surprising from an evolutionary point of view, since received wisdom in evolutionary biology is that it is physiology that primarily determines mammalian female RS, as females invest so much energy in gestation and lactation. Variation in attracting mates is usually considered to have more of an impact on male RS. However, Nettle's study used data from a Western society. Western populations have unusual demographic patterns compared to the majority of human societies: mortality and fertility are extremely low, and rates of non-marriage relatively high.

In the West, men appear to place high importance on physical attractiveness when choosing mates. A large literature in evolutionary psychology has been devoted to identifying which physical characteristics men find most attractive. This research is based on the hypothesis that the features which men find most attractive are those which indicate high reproductive value (Symons, 1992). The list of attractive features includes narrow waists, symmetrical features and large breasts (Furnham et al., 1998, 1997; Hume & Montgomerie, 2001; Perrett et al., 1999; Singh, 1993; Singh & Young, 1995; Streeter & McBurney, 2003). Tall height is not included in this list because it (supposedly) does not correlate with reproductive potential (Nettle, 2002). Western men do clearly show preferences for shorter women, or at least women who are shorter than they are. In laboratory studies of mate preferences, men tend to rate shorter women as more attractive than taller ones (Shepperd & Strathman, 1989), and rate relationships in which the female partner is shorter than the male as more desirable than the reverse (Pawlowski, 2003). Lonely hearts advertisements get fewer responses from men if the advertising woman describes herself as tall (Pawlowski & Koziel, 2002). These idealised preferences translate into behaviour: in a study of 720

American couples, in only one case was the wife taller than the husband (Gillis & Avis, 1980).

A central tenet of evolutionary psychology is that our mental architecture evolved in the "environment of evolutionary adaptedness" (EEA), when humans were hunter-gatherers, and there has been no further evolution since then (e.g. Symons, 1992). This means our mating preferences will be universal across all cultures. A major problem with this research is that the hypothesis that mating preferences are constant across cultures is rarely tested. The vast majority of the mate preference research by evolutionary psychologists has been done on Western populations. The little research done on the mating preferences of non-Western populations suggests that there are cultural differences. Waist-hip ratio, an apparently important trait when Western males are choosing partners, appears to be ignored by Tanzanian and Amazonian hunter-gatherers in favour of absolute weight (Wetsman & Marlowe, 1999; Yu & Shepard, 1998). It seems much more plausible to us, as evolutionary ecologists, that men adjust their mate preferences according to their particular social and ecological conditions. Though the underlying premise that men prefer women who display signs of high reproductive value may well be universal, the details of mate choice may differ cross-culturally. In societies with different levels of resources, different physical characteristics may be better markers of reproductive potential. Men in the West, where resources are plentiful and obesity is linked with less successful reproduction (Sebire et al., 2001), tend to find relatively slim women attractive (Tovee et al., 1999). In societies where resources are scarce, heavier women are thought to be attractive (Furnham & Baguma, 1994).

In this study, we will firstly determine whether there are any relationships between female height and reproductive outcomes. Is there a trade-off between height and age at first birth? Are there any advantages to growing tall in terms of faster reproductive rate or higher child survival rates? What is the overall relationship between height and RS? We also examine whether women in this population gain a survival advantage themselves by growing tall. Finally, we will look at marriage patterns by female height, in order to investigate whether there is any evidence that Gambian men use height as a cue when choosing a marriage partner.

DATA AND METHODS

The data were collected from four villages (Keneba, Manduar, Kanton Kunda, and Jali) in rural Gambia. Demographic data have been collected continuously from these villages since 1950 (McGregor, 1991). Ian McGregor, under the auspices of the U.K. Medical Research Council, conducted anthropometric surveys on all available villagers at least annually between 1950 and 1980, collecting information on heights and weights. He also collected supplemental information on marriages, migration and the health of these villagers. Between 1950 and 1974, the villagers had very little access to medical care. As a result, both fertility and mortality were high. Women gave birth to around seven children on average, but 43% of these children died before the age of 5 years. In 1975, a permanent medical clinic was set up in one of the villages. The availability of medical care led to a rapid reduction in mortality rates. Fertility also declined, but this decline only became evident by the late 1980s. Unless otherwise stated, the analyses that follow use only data collected between 1950 and 1974, when this was a natural fertility, natural mortality environment.

This population was largely Mandinka, though in the early 1960s around a quarter of the inhabitants of the largest village (Keneba) could be identified as descendants of slaves to the Mandinka. Slaves were predominantly of the Jola ethnic group, but these families had integrated into the dominant Mandinka culture, adopting their traditions and customs (Thompson, 1965). This was a highly polygynous society where all women married, married young and spent very little time during their adult lives outside a marital union (even post-reproductive women contracted “nominal” marriages, as only married women could attain Paradise when they died). Traditionally, women were betrothed before puberty and the marriage process began at menarche (Thompson, 1965). This was a patrilocal society, but women usually did not transfer to live in their husbands’ compounds until after the birth of a child or two. There was a large disparity in the ages of husbands and wives, as men tended to marry at considerably later ages than women (mean age at first birth for women was 18 years, for men 31 years). The fathers of the couple arranged first marriages for both men and women. Men arranged their subsequent marriages themselves. Fathers still arranged subsequent marriages for women, but with the woman’s consent. Divorce and remarriage were common for both sexes: 46% of all marriages in Keneba ended in divorce (Thompson, 1965). Divorce could be used by both men and women to end unsatisfactory marriages, though the divorce process was much easier for men than for women.

During this period the population was largely a subsistence agriculture community, with rice, sorghum and millet the staple crops. The population was mainly vegetarian, including meat and fish only occasionally in their diets (McGregor, 1991). Food shortages occurred annually during the rainy season, which coincided with the period of heaviest agricultural labour and when infectious disease, particularly malaria, was widespread. Individuals generally lost weight during this season, but gained weight again during the dry season when food was more abundant and infectious disease less common. These Gambian individuals were relatively short and thin compared to their Western counterparts. The average height of women in the database was 157.75 cm ($n = 1164$), of men 168.32 cm ($n = 931$). Women averaged a body mass index (BMI) of 20.67, and only a small proportion (4%) achieved a BMI of over 25, considered a marker for overweight. Children grew relatively well in terms of Western standards for the first few months of life, but growth faltering occurred during the latter half of the first year. After the first few months (when babies were exclusively breast-fed), growth was strongly affected by season, with children growing rapidly during the dry season but slowly or not at all during the rainy season (McGregor et al., 1968).

Reproduction

Age at First Birth

We first analysed the relationship between final adult height and age at first birth. The sample included all women who had a first birth between 1950 and 1974, who were 25 years or younger at their first birth and who were at least 25 years old in 1975. Because of the extremely young age at which women married, any first births reported after the age of 25 were likely to be due to either inaccurate reporting or fertility problems. The latter problems are likely to affect relatively few women, at least before their first births. In her study of marriage and childbirth in Keneba during the early 1960s, Thompson reports that first births after the age of 25 are rare (Thompson, 1965), and less than 4% of women in this village remained childless (Billewicz & McGregor, 1981). By including only women who were at least 25 in 1975 we avoid biasing our sample towards women who had their first birth at a young age. We ran a linear regression model using adult height as the dependent variable and age at first birth as the independent variable. The woman's year of birth was included as a control variable. As each individual's height was measured at all anthropometric surveys, the height variable we included in our models was calculated as the mean of all height measurements taken after the woman reached 21 years.

Length of Birth Intervals and Child Mortality

We then analysed the effects of female height on birth interval length and child mortality. Again, we used only data collected between 1950 and 1974. For both analyses, we used event history analysis. This is a technique which models the probability of an event happening over time, in this case either a birth or a death (Allison, 1984). Multi-level discrete-time event-history models were fitted, using MLwiN 1.1 software (Rasbash et al., 2000). Discrete-time event-history models are essentially logistic regression models where the dependent variable is the probability of the event occurring, and which include a function of time as a covariate. Because of the longitudinal nature of the dataset, a number of records from the same woman (either birth intervals or children) were included in each analysis. Multi-level models are able to control for this non-independence of data points, with the inclusion of a mother-level random effect (see Sear et al., 2002, 2003, for further details of this technique applied to this dataset).

Maternal age was controlled for in both models. In the birth interval analysis, a variable for whether the child at the start of the interval was still alive was also included in the model, as this was highly correlated with length of birth intervals. For this analysis, time since last birth was modelled as a quadratic function, as this most accurately captured the relationship between time and probability of giving birth. For the child mortality analysis, time (in this case the age of the child) was modelled as a series of dummy variables, since the probability of child mortality varied considerably over the first 5 years of a child's life. These models assume proportional hazards, i.e. that the relationship between the probability of the event and time is identical for all values of the covariate. Interactions between time and all variables were included in preliminary models to test this assumption. Only significant interactions were retained in the final models.

Reproductive Success

Linear regression was used to determine the effect of height on completed fertility, using only data on parous women who had completed their reproductive careers before 1975 (i.e. had reached the age of 50 by 1975). We ran two models using different measures of completed fertility as our independent variable: total number of children born and number of children surviving to 14 years. The latter we use as a proxy for reproductive success. Many of the women in this sample would have begun reproducing before 1950. Retrospective information was collected on births that occurred before 1950 but this information is likely to be less accurate than that collected after 1950. A variable for year of birth was included in these models to control for this under-reporting of births before 1950. We also controlled for the mean age at which the height measurements were taken. Some of these women were likely to be relatively old when their heights were measured, and height is known to decrease with age.

Survival

We conducted a discrete-time event history analysis on the probability of death for adult women to determine whether height was correlated with adult mortality.

To exclude the effects of the medical clinic on mortality we again only used data collected between 1950 and 1974. Women were entered into the analysis at the age of 21 years, or the age they were in 1950 if they were older than 21 in 1950. All women still alive in 1975 were censored in 1975 and dropped from the analysis. We have again controlled for year of birth and the mean age at which the height measurements were taken.

Marriage

For the analysis of marriage, we used data from two of the four villages in the database (Keneba and Manduar). Ian McGregor constructed genealogical trees for these two villages that listed all marriages between 1950 and 1980. We do not have information on *when* these marriages occurred, so we cannot censor the marriage data in 1975, as we did for the child mortality and birth interval analyses. However, we have little reason to believe that the establishment of the permanent medical clinic dramatically changed marriage patterns in this village, so feel confident that by using data collected up until 1980 we are not biasing our dataset.

In the analyses that follow, we have included all marriages in our database. It is possible that the relative fluidity of marriage in this population will bias the results: those individuals with multiple marriages will be included several times in the same analysis. In an attempt to overcome this problem, we ran all the analyses described below on a sample including only women's first marriages. In no case did these results differ from those obtained using the full sample, so we have only included the results of the full sample analyses here. Because of the universal nature of marriage for women, and the lack of information on age at marriage, we are unable to investigate the impact of height on the probability of marriage or age at marriage. Instead, we have looked for any evidence that height is used as a cue to a desirable marriage partner by investigating whether there is a male-taller norm in this population and whether there is any evidence for assortative mating. We have also examined the effects of female height on the probability of divorce.

To determine whether there is any evidence of a male-taller norm, we calculated the proportion of marriages where the wife was taller then the husband. We then randomly paired up each of these husbands with a wife from this dataset to determine the proportion of wife-taller marriages that would have occurred if these individuals had married a random member of this population. We conducted a chi-square test to determine whether the observed proportion of wife-taller pairings was significantly different from the proportion expected under random pairing. For comparison, we conducted the same analysis on the dataset used to demonstrate that taller women have lower RS in the West (Nettle, 2002). These data came from the U.K. National Child Development Survey (NCDS), a survey of all children born in the U.K. during one week of 1958.[1] The heights of both parents of these children were recorded in 1969, and we have used this parental height data to look for a male-taller norm. To examine the evidence for assortative mating for height in the Gambian population, we conducted a bivariate correlation of the heights of husbands and wives.

Finally, we conducted logistic regression on the probability of divorce. Strictly speaking, the probability of divorce should be analysed using event history analysis, to avoid censoring problems. We are unable to do this because we have no data on the timing of marriage. Using ordinary logistic regression may introduce biases because marriages that occurred relatively soon before 1980 may have eventually ended in divorce, but only after our marriage records end. To overcome this problem, we restricted our analysis to those marriages in which the wife was at least 50 in 1980, where the marriage presumably took place considerably earlier than 1980 (in practice, these results were no different from those obtained using the whole sample). We investigated both whether the absolute height of the woman was correlated with divorce, and whether marriages in which the wife was taller than the husband were more likely to end in divorce. In both models, we controlled for whether any children had been born to the marriage, as this is the strongest correlate of divorce in this dataset.

RESULTS

Reproduction

Table 1 shows the results of the linear regression correlating adult height with age at first birth. There is a significant positive association between age at first birth and adult height, indicating that women who had an early first birth are

Table 1. Linear Regression Model Showing Effect of Age at First Birth on Adult Height ($N = 329$).

Variable	Estimate	SE
Constant	63.096	97.890
Age at first birth	0.410**	0.123
Year of birth	0.110*	0.050

*$p < 0.05$.
**$p < 0.01$.

Table 2. Results of the Event History Model Analysing the Effect of Female Height on Length of Birth Intervals ($N = 2532$ Birth Intervals of Which 1708 Were Closed).

Variable	Estimate	SE
Constant	-15.470^{**}	1.207
Height	0.010	0.007
Time (months since birth)	0.476^{**}	0.019
Time squared	-0.005^{**}	0.0003
Maternal age	0.219^{**}	0.033
Maternal age squared	-0.005^{**}	0.001
Child death	7.652^{**}	0.391
Child death × time	-0.344^{**}	0.023
Child death × time squared	0.004^{**}	0.0003
Between woman variance[a]	0.332^{**}	0.041

[a] The significant between woman variance indicates that there is a correlation between the lengths of the birth intervals of any one woman.

$^{**}p < 0.01$.

shorter in adulthood than those who began reproducing later. Our analysis of the effects of height on the probability of birth demonstrates that there is a positive relationship between height and reproductive rate, but that this is not statistically significant (Table 2). There is, however, a significant negative relationship between maternal height and the probability of child death (Table 3). Figure 1 suggests that this protective effect of maternal height is linear and quite considerable, representing a drop in child mortality of around 2% for each cm of height. It should be noted that this effect of height is independent of the effect of female weight on child mortality. When maternal weight is included in the event history model, the negative relationship between height and child mortality is still highly significant ($\beta = -0.022$, $SE = 0.007$, $p = 0.0014$).

Overall, this leads to higher reproductive success for tall women (Table 4 and Fig. 2). There are significant positive relationships between height and both total number of children born and number of children surviving to adulthood. That tall women have a greater number of births than shorter women suggests the cumulative effect of the faster reproductive rate of tall women may be significant over the whole life course. Alternatively, it may be that total fertility is underestimated for this (relatively old) sample of women. The majority of these women would have started reproducing before 1950, and they may not have reported all the children they had who died before 1950. In either case, the number of children surviving

Table 3. Results of the Event History Model Analysing the Effects of Female Height on Child Mortality ($N = 2495$ Children of Whom 881 Died).

Variable	Estimate	SE
Constant	2.627**	1.227
Maternal height	−0.026**	0.007
Maternal age	−0.044	0.032
Maternal age squared	0.001	0.001
Child's age (months)		
1	(reference group)	
2–4	−0.975**	0.166
5–7	−0.624**	0.151
8–10	−0.163	0.134
11–13	−0.284*	0.142
14–16	−0.730**	0.168
17–19	−0.716**	0.170
20–22	−0.658**	0.171
23–25	−0.785**	0.182
26–28	−0.584**	0.173
29–31	−0.918**	0.202
32–34	−0.784**	0.195
35–37	−1.051**	0.220
38–40	−1.392**	0.260
41–43	−1.286**	0.253
44–46	−1.304**	0.260
47–49	−1.619**	0.303
50–52	−1.415**	0.283
53–55	−2.235**	0.419
56–58	−1.926**	0.366
59–60	−1.780**	0.347
Between mother variance[a]	0.116*	0.046

[a] The significant between mother variance indicates that the children of the same mother have correlated probabilities of dying.

$^{*}p < 0.05$.

$^{**}p < 0.01$.

to 14 years is likely to be more accurately recorded for these women, and this variable is clearly positively related to female height.

Survival

Table 5 shows the results of the event history analysis on the probability of adult death. Height is significantly related to adult mortality for women, though the

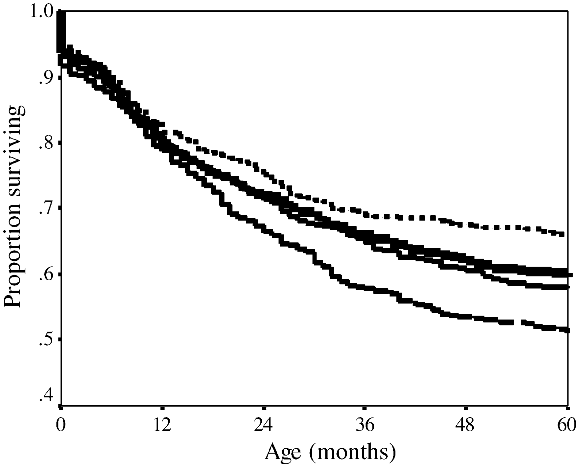


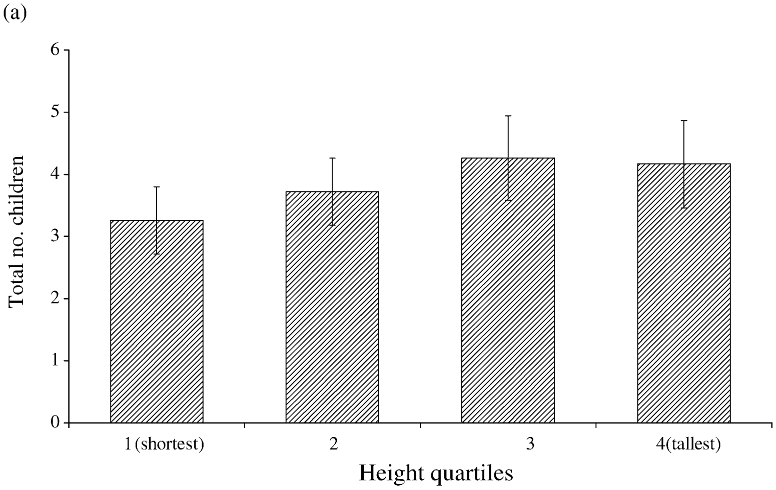
Fig. 1. Kaplan-Meier Plot Showing Effect of Maternal Height on Child Survival Over First 5 Years of Life. *Note:* Maternal height is divided into quartiles and shown in the following order: first (shortest) quartile represented by bottom line, then second quartile, third quartile, and fourth (tallest) represented by the top line.

relationship is not linear. The best fit for this model is a quadratic function of height, so both height and height squared are included in the final model. Figure 3 indicates that women at both ends of the height continuum suffer higher mortality rates than women of average height.

Table 4. Results of Linear Regression Models Analysing the Effect of Height on Completed Fertility ($N = 216$).

Variable	Model 1		Model 2	
	Dependent Variable: Total Number of Births		Dependent Variable: Number of Children Surviving to 14 Years	
	Estimate	SE	Estimate	SE
Height	0.061*	0.026	0.050*	0.021
Mean age at which measurements were taken	0.108*	0.031	−0.048	0.025
Year of birth	−0.032	0.026	−0.045*	0.021

$^{*}p < 0.05$.



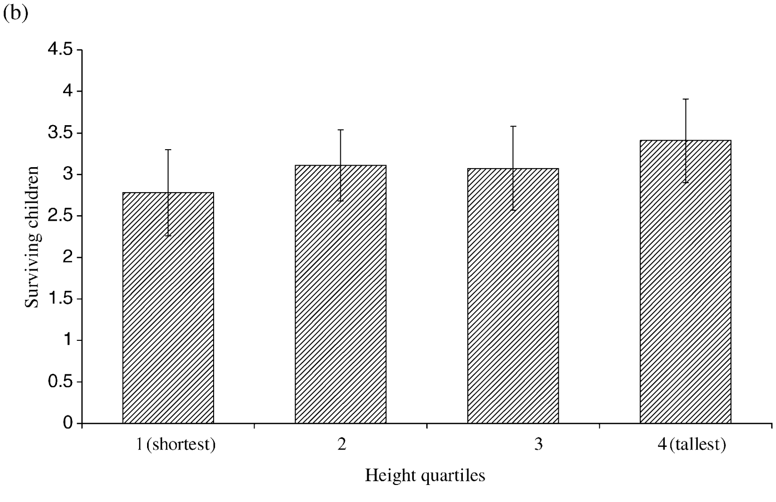


Fig. 2. Mean Number of Children (±95% Confidence Intervals) by Height Quartile of Woman. (a) Total Number of Children. (b) Number of Children Surviving to Age 14.

Table 5. Results of the Event History Model on the Probability of Adult Death ($N = 588$ Women of Whom 156 Died).

Variable	Estimate	SE
Constant	559.0**	54.136
Height	−1.757*	0.480
Height squared	0.006*	0.001
Woman's age	0.090**	0.015
Mean age at which height measurements were taken	−0.277**	0.019
Year of birth	−0.218**	0.019

*$p < 0.05$.
**$p < 0.01$.

Marriage

Individuals in the Gambian database were shorter than their U.K. counterparts were, and sexual dimorphism in height was slightly greater in the U.K. than the Gambia. Mean heights ± standard deviations (cm) for married individuals in each sample were as follows: Gambian women 157.82 ± 5.66 ($n = 684$) and men 168.19 ± 6.48 ($n = 500$); U.K. women 162.03 ± 6.52 ($n = 12{,}989$) and men 174.50 ± 7.48 ($n = 12{,}989$). Gambian women achieved 93.83% of male height, U.K. women 92.85% of male height. In the Gambian database, of 889 marriages where

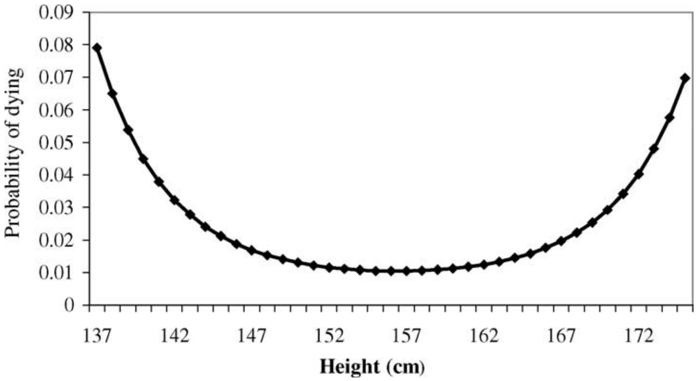


Fig. 3. Model Predictions of the Relationship Between Height and Adult Mortality. *Note:* Predictions are calculated from the model presented in Table 5, and plotted across the range of heights observed for women in this sample (137–175 cm). Mean values are used for control variables (age, year of birth and mean age at measurement).

the heights of both husband and wife were known, 86 (9.7%) were marriages where the wife was taller than the husband was. Pairing these husbands and wives randomly resulted in 101 (11.4%) pairings where the woman was taller than the man. A chi-square test indicates that the actual proportion of wife-taller marriages did not differ significantly from that which occurred under random pairing ($\chi^2 = 2.51$, $p = 0.113$). In the U.K. National Child Development Survey (NCDS), in only 484 (3.7%) of 12,989 marriages was the wife taller than the husband was. If these couples were paired randomly, we would expect 1111 (8.6%) wives to be taller than their husbands are. This figure is significantly different from the observed proportion ($\chi^2 = 386.95$, $p < 0.001$).

There is no evidence that assortative mating for height occurred in this Gambian population. The Pearson correlation coefficient between the heights of husbands and wives is 0.051 ($p = 0.130$, $N = 889$), confirming the results of previous research on this study population using a slightly smaller sample (Roberts et al., 1978). In contrast, Mascie-Taylor reports a correlation of 0.277 ($p < 0.001$) between husbands' and wives' heights in the U.K. NCDS (Mascie-Taylor, 1987).

Finally, we found no evidence that female height is linked to the probability of divorce. Controlling for whether any children had been born to the marriage, there is no significant correlation between the wife's height and the probability of divorce, nor are marriages in which the wife was taller than the husband was more likely to break up (Table 6).

Table 6. Results of Logistic Regression Models on the Probability of Divorce Showing the Effects of (a) Absolute Height of the Wife and (b) Relative Height of the Wife.

	Estimate	SE
(a) Absolute Height of Wife ($N = 306$)		
Variable		
Constant	2.887	3.454
Wife's height	−0.016	0.022
Childless	−1.217**	0.249
(b) Relative Height of Wife ($N = 270$)		
Independent variable		
Constant	−0.225	0.519
Wife taller than husband	0.489	0.503
Childless	−1.232***	0.270

**$p < 0.01$.
***$p < 0.001$.

DISCUSSION

We have found that female height is positively correlated with reproductive success in this Gambian population. We find the predicted trade-off between final adult height and age at first birth, so that women who begin reproducing early end up as relatively short adults (see also Allal et al., 2004). But the advantages to growing tall of higher child survival and perhaps faster reproductive rate outweigh the disadvantage of starting reproduction late so that, overall, tall women have higher RS than shorter women. Growing tall does not appear to bring any great survival advantage to the woman herself. Though expending enough time and energy to grow to around average height appears to be beneficial in terms of lower mortality rate, growing taller than average has survival costs. Large size may increase the energy requirements for maintaining body condition (somatic maintenance), so that growing too tall may be disadvantageous during periods of food shortage.

This analysis suggests that the greater RS of tall women is entirely due to the physiological advantages of being tall, as we find no evidence that height is related to marriage patterns in this community. This relationship could be mediated by a number of factors. Height is highly correlated with weight, so the relationship between height and successful reproduction could simply be a function of the greater energetic reserves that large women can devote to gestation and lactation. However, we also find evidence of a link between height and successful reproductive outcomes that is independent of body weight. The relationship between maternal height and child mortality is still highly significant even after controlling for maternal weight, suggesting that there are advantages to tall height that are unrelated to energetic status. These may include the lower probability of complicated birth and higher birthweights of the babies of taller women.

This analysis of maternal height and child mortality may also be affected by environmental and genetic correlations between mothers and their children. In human populations, large size is likely to reflect greater *access* to resources, as well as the ability to store greater energy reserves. Height is known to be correlated with socio-economic status: tall individuals are those who received relatively good nutrition in childhood (Bielicki & Szklarska, 1999; Floud et al., 1990; Lasker & Mascie-Taylor, 1989). In this population, if we assume that women who were brought up in resource-rich households also marry into resource-rich households, a correlation between height and child mortality may be seen because tall women have access to relatively plentiful resources. In addition to shared environment, shared genetic factors may also cause a correlation between maternal height and child mortality. Tall women are likely to be those who were not only well nourished in childhood, but also were able to fight off disease successfully. If there is a genetic component to this ability to resist disease (as is highly plausible in this West African environment, e.g. Hill et al., 1991), then these women may have passed on their resistant genes to their offspring, who will thus have relatively high survival probabilities. In support of these hypothesised correlations, the relationship between maternal height and child mortality is seen throughout the first 5 years of the child's life (Fig. 1), beyond the period when difficult labour or low birthweight might be predicted to affect survival adversely.

Our analysis does not allow us to distinguish between these (not necessarily mutually exclusive) hypotheses for the link between maternal height and child mortality, but whatever the proximate mechanisms that bring about this correlation, evidence is accumulating that child mortality may be of vital importance in determining women's RS (Pennington, 1992; Strassmann & Gillespie, 2002). There is clearly variation between women in their ability to raise children successfully to adulthood (Curtis & Steele, 1996; Ronsmans, 1995), as confirmed by the significant correlation between the mortality risks of siblings reported here (Table 3). This variation may be caused by differences in genetic makeup, differences in environment and access to resources and/or differences in ability to care for children. In high mortality environments, an ability to keep children alive may be equally as or even more important to RS than the ability to give birth to many children. This suggests that in the EEA, as well as throughout the majority of human history, height may have been positively correlated with RS for women.

This casts doubt on the hypothesis that men have universal preferences for short women (partly) because height is not an indicator of reproductive potential in women (Nettle, 2002). As evolutionary ecologists, we do not subscribe to the view held by evolutionary psychologists that the human species has not had time to adapt to the novel environments encountered since the subsistence switch to agriculture. A hallmark of the human species is behavioural flexibility, and we would expect mating preferences to be different in societies living under different social and ecological conditions. It may be that height confers few reproductive advantages to women in Western societies because child mortality rates are very low, in which case Western men would have no reason to find tall women attractive. In the West, men may be more concerned with social norms that require husbands to be taller than their wives (though this begs the question of why this social norm exists). In the Gambia, this male-taller norm does not appear to be present, as the proportion of marriages in which the wife is taller than the husband is not different from that expected by chance, and is considerably higher than that reported for Western societies. There is also no demonstrable effect of female height on the probability of marriage breakdown. This suggests that Gambian men have little aversion to tall women, or women who are taller than they are.

Although we find no evidence of a preference for short women in the Gambia, neither have we any evidence that Gambian men actively prefer tall women. Given the positive correlation between height and RS, we might expect this if men do base their mate choice decisions on the expected reproductive value of women. Instead, the results of our marriage analyses suggest that height is simply irrelevant to mate choice in the Gambia. Assortative mating for height is common in Western societies (Susanne & Lepage, 1988), as well as some non-Western ones (Ahmad et al., 1985), suggesting that men and women actively choose partners of a similar height to themselves. In our Gambian database there is no correlation between the heights of husbands and wives. This is a highly polygynous society, with the majority of men having more than one wife during their lifetimes. It may be that the polygynous nature of the society affects male mating strategies. Since men have the potential to increase dramatically their RS by taking another wife, men may focus on obtaining quantity rather than quality of wives.

It is important to note that we are not directly testing the preferences of Gambian men in this study. We are analysing behavioural patterns and inferring mating preferences from our observations of which women Gambian men actually marry (and stay married to). It may be that the Gambian men do have preferences for tall (or short) women, but that they have less freedom to implement their preferences than men in the West do. Marriages, in particular first marriages, are usually arranged by the fathers of the couple in this traditional society (Thompson, 1965). Parents may be more concerned with factors such as social status and political ties than with the physical attractiveness of potential mates (although even individuals themselves make little mention of physical characteristics when asked what would make a “good husband” or a “good wife.” In focus group discussions conducted by one of us (NA) on this subject, social and economic considerations appeared paramount, as much was made of characteristics such as honesty, good behaviour, hard work, respect, being Muslim and having resources). Gambian men may also have more constraints on their choice of mates because individuals in a rural agricultural community are likely to have a much smaller pool of potential partners than members of modern Western society do. Particularly as this Gambian society is polygynous, where women are much in demand, marry very young and spend very little time during their reproductive years outside of a marital union. Western men are not only likely to encounter more available women than rural Gambians, they are also exposed to a much wider variety of women though images in the media. This wider pool of mates in the West, along with greater freedom to choose their own mates, may result in quite different mating patterns compared to the Gambia, even if men’s underlying preferences are identical.

In conclusion, we are not able to determine whether there genuinely are differences in mate preferences between Western and Gambian men, or whether mate preferences are similar in both societies but not expressed in the same way. We have shown that the relationship between height and marriage patterns clearly does differ, suggesting that mate preferences should be examined more thoroughly outside Western environments before claims of universality can be confidently made. We believe that a much more satisfactory approach to the study of human behaviour is to consider social and ecological conditions, and to test evolutionary hypotheses across a variety of different cultures. Given the remarkable diversity of social systems and subsistence strategies that human groups have developed, and the remarkably wide range of ecological conditions that humans are able to live in, we think that human variation is, in any case, far more interesting to research than are human universals.

NOTE

1. City University Social Statistics Research Unit, National Child Development Study Composite File Including Selected Perinatal Data and Sweeps One to Five, 1958–1991 [computer file]. 2nd ed. National Birthday Trust Fund, National Children's Bureau, City University Social Statistics Research Unit [original data producers]. Colchester, Essex: U.K. Data Archive [distributor], 25 July 2000. SN: 3148.

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