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ORIGINAL ARTICLE

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Evidence of unconstrained directional selection for male tallness

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Abstract There are many reports on a positive relationship between tallness and socioeconomic success, and between tallness and health in the human male. Accordingly, tallness is an explanatory variable in many studies on health or behavior. Recently, a positive correlation of tallness with fitness has been reported. However, whether this fitness advantage is the effect of the socioeconomic success of tall men (making them good providers) or of body height itself (tallness being directly associated with some genes, i.e., not requiring the father's presence, that are favorable for offspring number or survival) remains unclear. The exact type of selection (against short men, favoring men around some above-average height, favoring only very tall men) also remains unclear. Here, for a cohort of military officers, we show that tallness had a indirect effect on male lifetime fitness, independent of socioeconomic success. The crucial factor was not that tall men had more fecund wives, but that tall men more often had a second family. Selection worked strongly in favor of very tall men, not just against short men. Since there were no hints of any evolutionary check on this selection, these findings suggest unconstrained directional selection for tallness in men.

Keywords *Homo sapiens* · Male · Tallness · Reproduction · Success · Directional selection

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In this paper, in accordance with standard practise in biology, we use the term "fertility" for an individual ability to have children, and the term "fecundity" for the materialization of this ability: number of children born. Note, that the meaning of these two words is exactly reversed in conventional anglophone (but not francophone!) demography.

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Introduction

There are many reports of a positive relationship between tallness and socioeconomic success (Bielicki and Szklarska 1999; Frieze et al. 1990; Gillis 1982; Hensley and Cooper 1987; Jackson 1992; Stogdill 1974; Teasdale et al. 1991) and good health (Kuh and Ben-Shlomo 1997; Kuh and Wadsworth 1993; Macintyre and West 1991; Silventoinen et al. 1999) in men. Accordingly, tallness is an important explanatory variable in many health- or behavior-related studies. At the same time, tallness makes males more desirable mates (reviews in Buss 1994, pp. 38–40; Ellis 1992; Hensley 1994; Jackson 1992; Symons 1979). A recent cross-sectional study relates tallness to fitness (Pawlowski et al. 2000) in the human male, suggesting directional selection against short stature. These findings give rise to two questions:

1. Is the fitness advantage of taller men direct – with women preferring men of higher status (i.e., higher resource potential) and better health – because tall men have a status advantage over shorter men in the labor market, making them better providers for rearing young? Or is the effect indirect – with women preferring tall men because they supply "good" genes (without the father's prolonged presence) favorable for more offspring and better offspring survival? Both direct and indirect effects may, furthermore, be superseded or modified by sexual selection effects: females preferring men with the conspicuous trait tallness which signals direct and indirect benefits to their female mates, in order to get sons with the same market value ("sexy sons").
2. What kind of directional selection is working on male height: a "horse race" competition (biggest prizes go to the fastest horses: the taller, the better), or a "threshold" competition (don't be too short, anything else is OK)? Is there an upper constraint at all (being tall is OK, but being too tall may be harmful)?

A serious limitation of studies to date is that formal education is usually the only measure of status, leading to an inappropriate application of evolutionary reasoning to modern humans. Given that educational homogamy is the most important segregating mechanism in the marriage markets of modern societies (Qian 1998; Ultee and Luijkx 1990), variation in education is equivalent to variation *across* marriage markets rather than variation *within* a marriage market. Such a distinction is not trivial: the formal level of education in many Western societies is or was inversely correlated with number of children, while individual achievement within one marriage market in virtually all populations studied is directly correlated to number of children (Wrong 1956/1980). Therefore, status should be measured by individual achievement within the same formal education category, i.e., within the same marriage market.

Furthermore, only with life course data, but not with cross sectional data – as in in Pawlowski et al. (2000) –can the true selection dynamics be observed.

We have a cohort data set with measures of individual status achievement, well suited to investigate the two questions raised above.

Methods

Of all surviving 539 members from the Class of 1950 of the United States Military Academy at West Point, 437 (81%) participated in a mailed survey in 1991, giving professional and family information. Using public sources, these data were merged with vital data, available measures of academic, athletic, and social performance while at the Academy known to predict career success (Mueller and Mazur 1996), and data on military career after graduation of all men of the class. Thus, we know the date of birth and death (including whether killed in action), height/company, facial dominance score, athletic accomplishments and the General Order of Merit (GOM), which is a measure of academic, athletic and social accomplishments, war college attendance, and final rank for all members of the Class, not only of participants in the survey.

In 1950, the Academy still followed the practice of assigning cadets to companies according to their height so that they would present a uniform appearance on the parade grounds; there were 12 company grades, from shortest to tallest (range 52–60 men). A man's height did not predict which particular service (Air Force or Army) or branch within a service (e.g., Armor, Artillery, Infantry) a man would enter after graduation. Mortality rates in the various branches and services vary both during war and in peacetime. Men were born between 1923 and 1929, with birth year unrelated to height (r=0.040, P=0.420). Height/company at the Academy among the survivors up to 1991 did not predict survey participation (r=0.020, P=0.636). For this study, we selected the 333 respondents (80% of surviving careerists) who had followed military careers for 20 years or more (by which time they could retire with benefits) in order to control for variations in the socioeconomic environment and to apply identical standards of professional success (if not stated otherwise, our findings refer to this sample). These men remained fairly equally distributed over the 12 height groups (range 22–33 men). Height admission requirements at West Point used to be 62–78 inches (157–198 cm), today being 60–80 inches. Exact height, while certainly in the personnel files, is not included in the public sources, and is therefore not accessible. This should not be a problem. Our use of company membership is equivalent to a conversion of the original metric data into "percentile" values, a conversion frequently undertaken in a variety of regression models. In general, betas in such regression models tend to be equal or slightly lower, with P-values equal and slightly higher for categorized variables compared with the original metric ones. Thus, using data transformed by our methodology is more likely to risk underestimate than overestimate the true effect size in such models.

We have no data on the body weight of cadets. Therefore, we cannot test for eventual effects of the body mass index, which may reflect physical appearance features other than mere height, like "physicality" (muscularity, robustness, vigor) which Gangestad and Simpson's (2000) review (see also Mueller 2000) found as predicting an earlier age of first sexual experience and more sexual partners. The athletic minimum performance requirements for admission (today eight correct pull-ups and 54 push-ups in 2 min, among others – see http://www.usma.edu) and the continuing physical training during active service were demanding. Thus, it is difficult to imagine a West Point graduate in active military service from admission to the Academy up to the age 45–50, by which time his professional and reproductive career in most cases was completed, having a BMI outside the "desirable" range as given by the 1959 "Metropolitan Desirable Weight Table", which is still referred to in the "desired weight" column (ranging from a BMI of 27.0 for the shortest and 25.1 for the tallest men) in the currently valid United States Army Maximum Allowable Weight (MAW) Table with MAWs ranging from a BMI of 29.9 for the shortest and 27.9 for the tallest men (Institute of Medicine 1992). Thus, in our study group, the BMI probably would not be useful for differentiating the body appearances of subjects independently of height.

The facial dominance score of these men was measured from their fairly uniform portraits in the class graduation yearbook (method in Mueller and Mazur 1996). Facial dominance – dominant facial looks – is an honest signal of dominance (Mueller and Mazur 1997), is known to predict an earlier age of first sexual experience (Mazur at al. 1994), is helpful in obtaining high rank in the military (Mueller and Mazur 1996, 1997), and in this study population had a weak positive effect on number of children independent of its relation with rank, but was unrelated to height (Mueller and Mazur 1997).

We do not know if there is a difference in mean height between our study group and the general male US population of their age, but we assume that variance in the general male population was greater, so the size of a tallness effect on fitness may be greater in the general population than in our West Point group.

We equated professional success with military rank attained at the time of retirement plus whether or not the respondent graduated from a war college, which is a prerequisite to promotion to the highest ranks. Until 1976, upon graduation, every cadet was given an ordinal number, reflecting his GOM. The GOM is also known to be a powerful career predictor. A four-level category of athletic accomplishments during the Academy (four being the top category; details in Mueller and Mazur 1997) together with facial dominance score were also used as additional career predictors.

Of all graduates, 13% attained the rank of general, making this class one of the most successful in West Point history. Status distribution from major to "full" general (four stars) in our sample matched expectations as derived from the Register of Former Graduates of the West Point Alumni Association.

The West Point Class of 1950 is a sample of the middle-class US population of almost exclusively European origin (two men indicating a non-European ancestry were in the sample). Respondents' fathers had all graduated from high school, and 60% had had at least some college attendance; respondents' mothers had all graduated from high school, and 50% had had at least some college attendance; respondents' first wives had all graduated from high school, and 85% had at least some college; respondents' second wives had all graduated from high school, and 78% had at least some college attendance. Cadets came from a rural background and had a professional soldier as father apparently more often than the average adolescent of their cohorts (with height related to neither of these two variables), but were otherwise without conspicuous selectivities. Since tallness and career chances may also be influenced by the ethnicity of the family of origin, each respondent's

country of origin was coded as East, North, South or West Europe. This variable had a slight effect on height (those with North European origin were tallest, then West, East, South) but none on professional or reproductive success. Catholic respondents with Catholic wives had more children than others, but denomination had no relationship with height or professional success, and, therefore, together with ethnicity was dropped from further analysis.

Reproductive success was measured by marital status, childlessness, number of own children, and parity progression (particularly having an above-average number of children). These were the baby boom years: only 5 respondents never married. The average number of children was 3.16.

Biologists unfamiliar with research in human subjects may raise the objection against survey data on male reproduction that paternity of reported children is not secured without DNA tests and that children respondents had with women other than their wives, may be underreported.

We check the following four possibilities.

A1: nonpaternity of a legal child unknown to respondents

There are some recent estimates of the prevalence of nonpaternity in the general population of developed societies, based on genetic marker analyses. Sasse et al. (1994) estimated the prevalence of nonpaternity in a large unselected Swiss sample at around 0.8%, depending on the method used, with an upper 95% confidence boundary of no more than 1.35%. Sykes and Irven (2000) found in a random sample of British males sharing the same surname "Sykes," a pattern of Y-chromosome microsatellites best compatible with a single surname founder 700 years ago, and an average nonpaternity rate of 1.3% per generation. Creda-Flores et al. (1999), using phenotype data on seven blood groups from a general sample from the Mexican state of Nuevo Leon, estimated the nonpaternity rate there as 11.8%, with a clear social gradient: the higher the status, the lower the rate.

In the middle-class, politically conservative (military personnel are known to be politically somewhat more conservative than the general population) study population with first wives' (median birth year 1935) peak reproductive years before the liberalization of sexual mores in the 1970s, the rate of nonpaternity unknown to legal fathers will be closer to the Swiss and British estimates than the Mexican ones. Creda-Flores et al.'s (1999) finding of a social gradient conforms with the finding that in developed societies also, with increasing social status, men, but not women, have more extramarital sex partners (Pérusse 1993; 1994). Given the universal female preference for marrying a partner with a higher social status than one's own ("hypergyny": Buss 1989, 1994, pp. 25–32; Daly and Wilson 1983, p. 279; Townsend 1998), and the fact that spouse infidelity worldwide is the most important reason for males, but not females, to seek a divorce (Betzig 1989; Mealey 2000, p. 322), the wives of high-status males simply have more to lose by extramarital affairs.

A2: nonpaternity of a legal child known to respondents

Legal fathers who know about their nonpaternity may be less inclined to participate in a survey on marriage and children. This may bias the observed nonpaternity rate downwards. However, the estimates from the Sykes and Irven (2000) data, where this objection cannot be applied, are in the same range as the Swiss estimates: around 1–1.5%. Also, with a response rate as high as in our survey, even if for the sake of the argument we assume that not 1% but 10% of all men among nonresponders had a case of nonpaternity among their children, we would have approximately 2.5%, that is 38 cases of nonpaternity among the approximately 1,250 children of all 400 surviving careerists. Thus, whether or not such men participate in surveys, and whether or not they indicate nonbiological children as their own seemingly has only minimal impact on the estimated prevalence of 1–1.5% nonpaternity also in our study sample.

B1: extramarital children unknown to respondents

In the social microcosmos of the military, the men of our study population were high status and, therefore, attractive mates for long- as well as for short-term relationships (Daly and Wilson 1992, p. 294; Mealey 2000, p. 236). They will, on average, have secured more extra-pair copulations than other men (Pérusse 1993) and, therefore, will have produced more nonpaternity cases than their wives (Pérusse 1994). If mothers of such children were single, they will have had many reasons to find and inform fathers about the fact, even if that took years. If mothers had not done so, the children themselves will have made the attempt, once they were old enough – which generally would have been the case by the time of our survey.

B2: extramarital children known to respondents

Once respondents know, they are unlikely not to have told their wives about eventual illegitimate children, so that respondents had no motivation to conceal the existence of these children per se in the questionnaire. They may, however, have wished not to reveal the illegitimacy of these children. Therefore the questionnaire was carefully designed such that no information regarding the legitimacy versus illegitimacy of children was requested – even at the expense of obtaining other information. We asked for vital data of all of a respondent's children, whether they were "biological", "step", "adopted", or "foster" children, but did not differntiate between "legitimate" versus "illegitimate". We did not ask for the dates of marriage or marriage dissolution, nor did we ask respondents to ascribe listed children to a specific wife.

We have strong evidence that men were unusually open in answering the children-related items: It is generally known from survey research that questions for deceased children are among the most painful and threatening items possible, with an high probability of underreporting. However, of the 1,048 children of our men, 45 were reported to have died by the time of the survey. The incidence of these tragedies is well in the range of the mortality expected for a group of middle-class young adults and adolescents of 15–35 years, and sometimes even younger (in 1983–1987, US mortality up to the 5th year was 1.3%; from 15 to 25 years, 3.2%; from 15 to 45 years 11.4%; see Feachem et al. 1992, p. 45). Because mortality data from the survey seem quite accurate, we have some reason to believe that responses were in general accurate and honest, and accuracy and honesty may therefore also characterize the responses on paternity.

Last but not least: the purpose of this paper is not to produce an accurate estimate of the absolute number of biological children of the study population, but to detect and further analyze eventual statistical relationships between height and relative number of biological children. Only if there is a large systematic error in measuring the number of biological children due to nonpaternity/illegitimacy which at the same time is related to height – such that tall men have more marital children, but that short men at the same time have more (and underreported) extramarital children, or fewer (but incorrectly identified) cases of nonpaternity among their children – would we have reasons to be concerned about the use of survey data on number of children.

Results

Height and health/mortality of respondents

Of the 672 original members of the class, 158 (23.5%: 6% during the 1950s, 1.7% during the 1970s, 6.9% during the1980s, 8.9% in the 1990s) had died by the beginning of 1999. Interestingly, height did not predict mortality – either on the battlefield or elsewhere – throughout the first 40 years after graduation. But from 1989 onwards, when

the last child in this study population had been born, height did predict mortality [exp(B)=1.304 with height z-standardized, χ^2=7.701, P=0.019, n=672]; we chose a semiparametric proportional hazard rate model, because, given the atypical survival function, in this particular population, mortality forces may be present which make questionable the application of the Gompertz-Makeham model or of any other parametric model of mortality].

Serious illness would have been incompatible with active military service. But even if we take an early retirement (5 and more years before mandatory retirement age – 28 years of service for lieutenant colonels and majors, 30 for colonels, and 35 for all generals) as a weak indicator for imperfect health, neither height, number of children, nor childlessness predicted an early retirement. Furthermore, early retiring tall men had as many children and were about as frequently childless than early retiring short men (data not shown). Thus, tall men with imperfect health during their childbearing years seem unlikely to have ended up with a lower fitness than short men with imperfect health.

Height and reproductive success of respondents

Tallness (all height scores z-standardized) was associated with a greater number of marriages [ordinary least squares (OLS) partial regression coefficient r=0.156, P=0.007, n=322; Table 1], greater likelihood of divorce [logistic regression: exp(B)=1.569, partial r=0.163, P=0.003, n=317], greater likelihood of a second marriage [logistic regression: exp(B)=1.564, partial r=0.167, P=0.004, n=317], and a younger second wife, if remarried (OLS partial r=0.280, P=0.069, n=56). Taller men had more children (OLS partial r=0.110, P=0.05, n=322) than shorter men. In particular, the parity progression to a fourth child, decisive for reproductive success in a population with median family size of three, was more frequent among taller men [logistic regression: exp(B)= 1.588, partial r=0.210, P=0.002, n=218]. All results were obtained with career predictors and career parameters statistically controlled.

Status also had a positive effect on fitness, with generals having almost one child more than men of lower rank. But height had no effect on promotions to higher rank, or on staff or war college graduation, or on the timing of these events.

Next, we compared men in the top height quartile (n=75) with the second tallest quartile (n=81). Again, the taller men were more likely to get a divorce [logistic regression: exp(B)=2.105, partial r=0.126, P=0.032, n=154], were more likely to remarry [logistic regression: exp(B)=1.645, partial r=0.108, P=0.127, n=37], were more likely to have a younger (more than 2 years on average) second wife [partial r=0.144, P=0.368, n=35], were less likely to remain childless [logistic regression: exp(B)=8.414, partial r=167, P=0.043, n=156], had more children (OLS partial r=0.145, P=0.079, n=156), and had a fourth child after a third one more often [logistic regression: exp(B)=3.513, partial r=0.280, P=0.006, n=151]. All results were secured with career predictors and career parameters statistically controlled.

While fitness tended to be increase continually with height, the top height quartile stood out in all fitness parameters, while differences among the other three quartiles were not significant (Table 2; for values of childlessness: Fig. 1a; number of own children: Fig. 1b; parity progression to fourth child by height quartile: Fig. 1c).

Men who were in the tallest (of 12) cadet company did not differ in the three fitness measures (average number of children was 3.22, none out of 23 was childless, parity progression to fourth child was 77%) from other men in the top quartile (average number of children was 3.54, 1 of 52 was childless, parity progression to fourth child was 69%).

Table 1 Number of marriages of West Point graduates (Class of 1950) by height quartile

Height quartile	Number of marriages				
	0	1	2	3	Total
Lowest quartile	1	73	7	1	82
Second quartile	1	71	10	2	84
Third quartile	2	60	17	2	81
Top quartile	0	57	16	2	75
Sum	4	261	50	7	322

Were tall men more fecund because their wives were more fertile?

We have only two kinds of health or fertility related data on respondents' wives. (1) No correlation was found be-

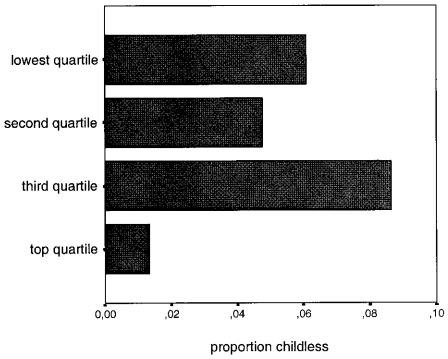
Table 2 Fitness of West Point graduates (Class of 1950; see also Fig.1)

Height quartile	Proportion childless	Mean number of own children	Proportion of fourth children among men with at least three	Mean number of own children per wife	Mean number of own children of one-marriage respondents	Mean number of own children of respondents with two or more marriages
Lowest quartile	0.061	3.06	0.42	2.93	3.11	3.00
Second quartile	0.048	3.17	0.45	2.95	3.18	3.33
Third quartile	0.086	2.99	0.46	2.66	3.02	3.21
Top quartile	0.013	3.44	0.71	2.94	3.25	4.06

Fig. 1a–f Fitness of West Point graduates (Class of 1950) by height quartile. **a** Proportion childless. **b** Mean number of own children per wife. **c** Proportion of fourth children among men with at least three. **d** Mean number of own children. **e** Mean number of own children of one-marriage respondents **f** Mean number of own children of respondents with two and more marriages

a

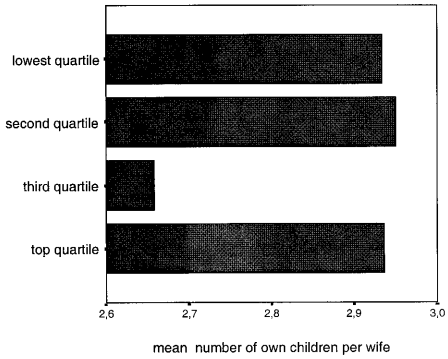
proportion childless, by height quartile



lowest quartile	.061
second quartile	.048
third quartile	.086
top quartile	.013

d

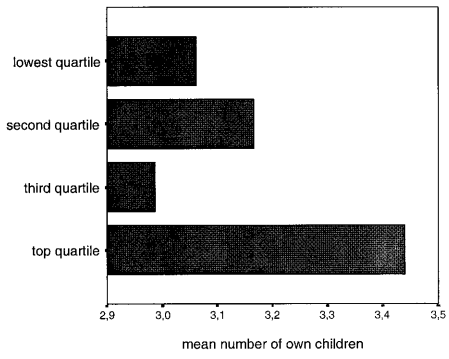
mean number of own children per wife, by height quartile



lowest quartile	2.93
second quartile	2.95
third quartile	2.66
top quartile	2.94

b

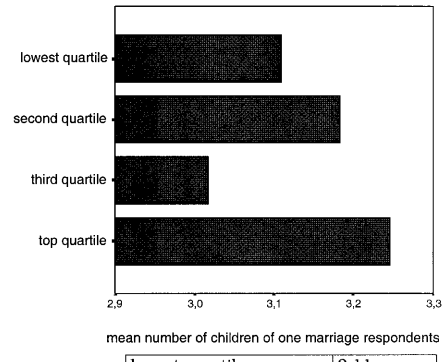
mean number of own children, by height quartile



lowest quartile	3.06
second quartile	3.17
third quartile	2.99
top quartile	3.44

e

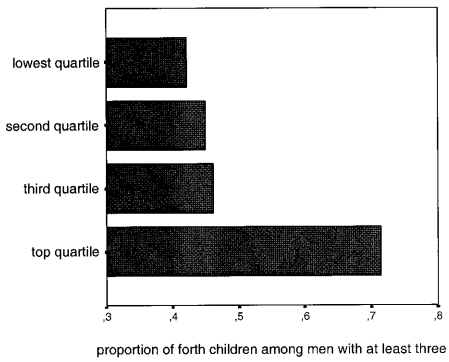
mean number of own children of one marriage respondents, by height quartile



lowest quartile	3.11
second quartile	3.18
third quartile	3.02
top quartile	3.25

c

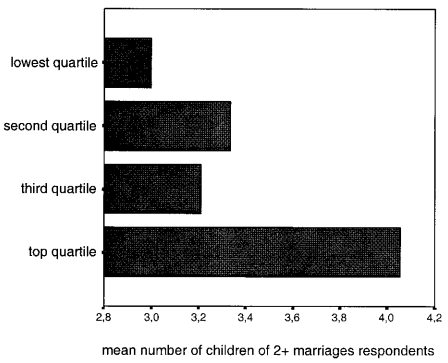
proportion of fourth children among men with at least three, by height quartile



lowest quartile	.42
second quartile	.45
third quartile	.46
top quartile	.71

f

mean number of own children of 2+ marriages respondents, by height quartile



lowest quartile	3.00
second quartile	3.33
third quartile	3.21
top quartile	4.06

tween the death of the first wife, a crude measure of general health, and respondent's height (r=0.004, P=0.931, n=317), which itself was unrelated to a man's birth year. (2) Waiting time before pregnancies is a common measure of fertility in populations (Joffe and Barnes 2000). We do not have the date of marriage, but we know of only four respondents who had impregnated someone before graduation (one first child in 1949, three first children in 1950). But most men did so shortly afterwards (there were 83 first children in 1951, 80 in 1952, 50 in 1953, 49 in 1954: altogether 70% of all first children were born within 4 years after graduation), certainly in most cases within marriage, which only 5 respondents never entered. Neither waiting time for the first child after graduation, which we thus may use as a proxy variable for waiting time for the first child after marriage, nor waiting times before third, fourth and fifth children after the preceding one correlated with height. Waiting time before the second child, however, was directly correlated with the father's height (r=0.127, P=0.018; the necessary significance level here after an α-correction would be 0.010, n=305). We suggest interpreting this isolated result as a random event.

Thus, we have no hint that tall respondents' wives were healthier or more fertile than the wives of other respondents.

In fact, while tall men's wives were no more fecund than other men's wives, taller men did have more wives, and their second wives, if any, were considerably younger than the first wives of these tall men and also considerably younger than the second wives of other men.. The number of biological children per wife was fairly equal for all height quartiles (Table 2; Fig. 1d); even the largest pairwise difference in number of children per wife, i.e., between the second (2.95) and third (2.66) quartile was not significant (t-test P=0.463; OLS partial r=–0.025, P=0.656, n=165; with career predictors and career parameters statistically controlled).

There were no differences in number of children by height quartile for those men who married only once (Table 2, Fig.1e), and again no pairwise difference was significant (OLS partial r=-0.013, P=0.841, n=261). But there were differences in number of children by height quartile for those men who married twice and more (Table 2; Fig. 1f): the tallest quartile on average had almost one child more (t-test top quartile versus the rest (T=1.756; p=0.88; n=57), which is predominantly the effect of the younger second wives of the tallest quartile (OLS partial r=–0.401, P=0.003, n=57), while height itself had no effect any more in this subsample (OLS partial r=–0.059, P=0.651, n=57). In fact, only for the tallest quartile a second marriage came with a greater lifetime reproductive success (T=1.831; p=0.07, n=57).

Thus, we suspect that tall men, as a group, on average were reproductively more successful than other men because they had a greater chance to have a second family with a younger wife.

Survival and reproduction of offspring

From among 1,048 children of our respondents, 45 had died by the time of the survey, tragedies that bore no relation to father's height.

To the degree that tallness is heritable (heritability estimates range from 40% to 91%; Chatterjee et al. 1999), at least sons of tall men may enjoy similar reproductive advantages as their fathers. But what about the reproductive success of the – possibly likewise tall – daughters of tall men? Since we do not know whether these men invested in their children differently by sex, with a concomitant effect on the reproductive success of these children, we looked into the reproductive success of respondents' daughters from daughters-only families. In daughters-only families, there was no correlation between height and number of grandchildren (r=0.040, P=0.798, n=43) or number of grandchildren per child (r=–0.072, P=0.644, n=43). A positive association between father's height and number of grandchildren or number of grandchildren per child in the sons-only families, to be expected because of the positive correlation between father's and sons' height, could also not be observed. Perhaps sons of the respondents, to a higher degree than daughters, had not yet completed their reproductive careers: in the daughters-only families, by the time of the survey, there were 0.94 grandchildren per daughter, while in the sons-only families (n=45), there were only 0.74. grandchildren per son. This, not significant, difference between the two types of families disappears once birth year of first grandchild is statistically controlled. Given the fact that only the oldest daughters of respondents actually may have completed their reproduction by the time of the survey, all that can be inferred from these observations is that there seem to be no costs to daughters and sons of tall men with regard to initiation of a reproductive career.

Discussion

Taller men are fitter

Taller men had more reproductive opportunities (more marriages, younger second wives) and used them to have more children than shorter men. The chances of survival into adulthood of taller men's children were not lower. Tall men's daughters – who on average will also be taller than average – did not display lower fecundity than other men's daughters, thereby eventually neutralizing their fathers' reproductive advantage. Thus, we can conclude that tall men were fitter than others.

The causal mechanisms behind the statistical association

The positive effect of height on reproductive performance was not mediated by men's social status, i.e., their military rank, or by the measures of academic, athletic, and military talent which helped in gaining high status.

In the study population, height was no predictor of socioeconomic success. In this respect, it is not typical for the general US population, but extremely valuable for studying the question as to whether the attractiveness of tall men as mates and their eventual greater reproductive success is the effect of a higher social status or of any other properties of tall men. From our observations, we conclude that in our study population, something other than status made tall men more attractive mates. Since we have no reason to assume that the wives of West Pointers differ profoundly in their mate preference patterns from the general female US population, we may furthermore conclude that in the general population also, status alone does not make taller men more attractive.

The positive effect of height on reproductive performance is not caused by an above-average fertility of taller men, for which no evidence has been published. There is also no association between male fertility disorders and height in otherwise healthy men. All medical conditions for which Raboch and Reisenauer (1976) report an association between tallness and fertility problems (bilateral cryptorchids, unilateral cryptorchids, hypogonadotrophic eunuchoids, Klinefelter's syndrome) would have been incompatible with admission to the Academy and decades of active service in the military. Interestingly, height did not predict mortality throughout the first 40 years after graduation. But from 1989 on, when the last child in this study population had been born, tallness was associated with increased mortality. This result would be in accordance with the finding that, although short men more often commit suicide at a young age (Jiang et al. 1999), a major cause of death among young adults in developed economies, they, in general, live longer lives (Samaras and Storms 1992). On the other hand, the mortality pattern in our study population does not indicate any health problems of taller men with an eventual impact on their reproductive performance. The relationship of male tallness to general health is equivocal, with shorter men more at risk for coronary heart disease (Kee et al. 1999) but less at risk for cancer (Frankel et al. 1998; Giovannucci et al. 1997; Gunnell et al. 1998). These are the two most frequent causes of death in developed societies, indicating health problems at opposite ends of the height distribution. The age distribution of incidences of both types of health problems in our study population, however, will have been such that, again, we cannot assume any noteworthy effect of specific morbidity or mortality on men's fertility, and consequently, fecundity.

Taller men did not achieve their above-average reproduction by being chosen as mates by healthier or more fertile women: mortality of first wives was unaffected by husband's height, and so were waiting times before children. These results are in accordance with published findings. Assortative mating by height is a well-established fact for developed (Gillis and Avis 1980; Ginsburg et al. 1998; McManus and Mascie-Taylor 1984) and traditional (Stark et al. 1990) societies, although the degree of assortment may vary considerably in subgroups of one society (Mueller and Malina 1976). It seems to be the result of initial assortment rather than of selection by death or divorce against couples of large height differences during marriage (Pennock-Roman 1984). Assortative mating by height may even be favored by some evolutionary mechanism because, in a large national sample in Britain, increasing husband-wife height difference came with an increasing probability of having an abnormal pregnancy outcome. Increasing spousal similarity for height is associated with increasing numbers of live-born children even after controlling for parental age, social, and regional differences (Mascie-Taylor and Boldsen 1988). Female preference for taller men does not lead to assortative mating by height, unless some male preference for assortment, too – preference specifically for tall women is not necessary. Indeed, there is some evidence that men may prefer females to be shorter by some fixed relative or absolute amount (Gillis and Avis 1980), but taller women per se seem not to enjoy the mating advantages tall men do (Hensley 1994).

Taken together, we may assume that in our sample also, taller men had taller wives. Taller women, however, are known to be no more fertile than other women. Tall women tend to have menarche somewhat later than shorter women (Helm et al. 1995), but menopause at the same time as other women (van Noord et al. 1997). No abnormal pregnancy outcome risk has been observed to be related to female height (Whitley et al. 1999).

In all stages of mating, women make the choices (Mealey 2000). So the proximate mechanism behind the tall men's advantage in getting reproductive opportunities and turning them into a greater number of children is apparently simple: taller men were, on average, evaluated more favorably by women, chosen more often as mates, and, ultimately, as fathers. There is also ample empirical evidence for female preference for taller men (reviews in Buss 1994, pp. 38–40; Ellis 1992; Hensley 1994; Symons 1979; Gregor 1979 for a traditional society), without any apparent upper limit. Ellis's (1992) speculation about a "central tendency" in women, in that they prefer males with a height near the midpoint of the population distribution, irrespective of their own height, does not find support even in the empirical data (Graziano et al. 1978) he quotes. Hensley's (1994) finding that extremely tall men had slightly fewer dates than other tall men does not show that these men were less desired: perhaps they could afford to engage less in searching activities consistent with taller men having prettier girlfriends anyway (Feingold 1982).

In our sample women did not chose to have more children with tall men; rather, tall men more often found second wives with whom they had a second family – a different mechanism than in Petrie and Williams' (1993) observation of peahens laying more eggs for peacocks with larger trains, or as Cunningham and Russell's (2000) observation of female mallards laying larger eggs for attractive mates.

Second wives have lower fecundity than first wives, whether polygyny is synchronous or serial (Josephson 2001; Low 2000, p. 74 with many references), although at least in some societies, this difference disappears after the first generation (Josephson 1993). Second wives of the tallest quartile in our sample tended to enjoy a better formal education than the second wives of other men (Mann-Whitney test, P=0.037, n=56), which may partly be a cohort effect since tall men had younger second wives, as mentioned. Thus, we may speculate that it may be a special type of women with nonmainstream biographies who actually select those tall men with children as the fathers of their, in most cases, small families. At the same time, these women make those tall men reproductively more successful than other men.

These women possibly made their choice because tallness is a highly heritable trait, and a reliable indicator of male offsprings' potential for high status, even if the mate himself does not have high status. For a woman of any height, a mate's tallness will give her taller daughters (not harmful) and taller sons (possibly useful). In many social settings, height confers high status on men, and seemingly in no social setting does it confer low status. Thus, as the motivation to produce high-status children should be all the more pressing, the smaller the planned or expected family size at the onset of reproduction, so should be the motivation to produce tall children.

Everyday experience suggests that, on average, taller men are heavier (hence the use of the body mass index instead of the body weight alone as a measure of obesity) and physically stronger than shorter men (thus, in disciplines like boxing, wrestling, and all budo sports – but not in e.g., fencing, tennis, or badminton – there are weight classes in order to keep these sports attractive to shorter and lighter athletes). All else being equal, tall men are more likely to win in a physical confrontation, and therefore may be more intimidating and more likely to gain a dominant position in many social encounters and structures. In extreme situations, an increment of social status can decide between life and death: Survivor rates for adult males on board the RMS Titanic were 30.3% in the first class, 9.1% in the second, 12.7% in the third (own calculations based on the published passenger lists). Of the 91,000 German, Hungarian, Italian, and Romanian soldiers taken captive by the victorious Soviet troops after the fall of Stalingrad, the turning point of the Second World War in Eastern Europe, 6,000 survived to come home after the war. Of the 24 generals among those captured, 23 made it (Calvocoressi et al. 1989; Piekalkiewics 1977). Adult male status also matters for those who depend on it economically: survivor rates for adult women and minors of both sexes on board the RMS Titanic were 94.5 % in the first class, 87.8 % in the second, 46.5 % in the third.

We may speculate that an advantageous second-best strategy for women who cannot or do not want to have as many children as their age peers is to select such tall men, who, because they are older and with financial obligations towards their first families, will have to compromise in mate selection, too.

The shape of the selection function

Tall men appear to have a particular fitness advantage rather than the shortest men suffering a special deficit. Although extremely tall and short men are excluded from our sample, we have a considerable range of heights, with tallness varying independently of socioeconomic advantage.

Furthermore, even the tallest 8% of men (the top category of 12) did not suffer any fitness setback compared with other tall men. If stature is to be an evolutionarily stable signal for some fitness-enhancing quality, there has to be some adverse selection against tall men who are low on this quality (Grafen 1990; Zahavi 1977). In the study population, however, there was no additional fitness disadvantage for tall men low on any quality known to be predictive of fitness like status, academic, athletic and military performance while on the Academy, facial dominance, ability to make friends, or social activities (Mueller and Mazur 1996, 1997, 1998). One could imagine that height would be associated with more physical conflicts, and that only individuals of high quality would be able to carry that cost. However, the casualities the class took on the battlefield were equally distributed over height categories.

Besides these, we know of no other potential constraints upon height as a determinant of fitness, so long as the man is not too big to manage coitus or does not command a disproportionate share of family resources which might otherwise sustain his wife and children, both unlikely in the study population.

Thus, selection seemingly follows most closely a "horse race" model, with a few winners taking most of the prize, measured in fitness differentials. Discerning no fitness disadvantage to tallness, we are left with the possibility of unconstrained directional sexual selection in favor of ever increasing male height within the observed phenotype range. Our findings may contribute to the mounting evidence for a substantial role of such selection in human evolution (Civetta and Singh 1999; Gavrilets 2000; Wykhoff et al. 2000).

Sexual selection effects

It is difficult, on the other hand, to assess, the extent to which sexual selection of males for the conspicuous trait tallness is superseding or modifying the selection of tall men for the real direct (not in our study population) and indirect benefits tallness confers on the females making the choice, in particular because our data, even if controlling for social status, are still nonexperimental (Sheldon 2000), and because the theory of sexual selection in the life course perspective needed here is still insufficient (Andersson 1994, pp. 433–443; Ryan 1998;

Møller and Thornhill 1998; Sheldon 2000). In any case, we found no evidence for tall stature being an evolutionarily stable signal for some other fitness-enhancing quality, which leaves open the question whether women overselected men for their tallness.

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