Height and reproductive success: is bigger always better?

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Abstract

Height is of great interest to the general public and academics alike. It is an easily observable and easily measurable characteristic, and one which appears to be correlated with a number of salient outcomes, from survival to intelligence to employment and marriage prospects. It is also of interest to evolutionary biologists, as the end product of life history decisions made during the period of growth. Such decisions will depend at least partly on the payoffs to size in adulthood. This chapter surveys the costs and benefits of height during adulthood: what are the consequences of height in terms of mortality rate, mating success and fertility outcomes for each sex, and how much do these differ between environments? It is clear from this survey that relationships between height and fitness correlates show considerable variation between populations, suggesting that the costs and benefits of height depend on environmental conditions. If any tentative conclusion can be drawn it is that while short height is rarely advantageous, particularly for men, tall height is not universally beneficial, particularly for women. We can also conclude that height is clearly still salient for fitness correlates in modern environments, thereby demonstrating that we are yet to leave our biological imperative behind.

1. Introduction

Height is a topic of great interest to academics and the general public alike. It is an easily observable and easily measurable characteristic, perhaps explaining its popularity in both academic research and popular culture. Websites abound on height. You can find out the height of your favourite celebrity¹, discover average heights around the world², calculate the percentage of Americans shorter than you³, predict your child's ultimate height⁴, and find online support if you are particularly short⁵ or particularly tall⁶. Height then is clearly salient to the internet-using general public. Academics are equally fascinated by the subject and their

¹ www.celebheights.com

² http://www.thegreatsleep.com/height.htm

³ http://www.tallpeople.net/wiki/What Percentage of People are Shorter Than Me

⁴ http://www.bbc.co.uk/parenting/your_kids/toddlers_heightcalculator.shtml

⁵ http://www.shortsupport.org/

⁶ http://www.tallclub.co.uk/index.asp

interest appears to be growing: Steckel reported earlier this year that approximately 325 publications on height have been published in the social sciences alone since 1995, and that the rate of publication on the topic had shown a four-fold increase over the previous 20 years (Steckel 2009). This academic research supports the lay view that height is salient for many different outcomes, from intelligence and earnings (Case & Paxson 2008), to suicide rates (Magnusson et al. 2005), sexual orientation (Bogaert 1998) and jealousy (Buunk et al. 2008). Such academic research may be at least partly a matter of convenience, given the ready availability of data, including historical records as well as contemporary data. But to an evolutionary biologist, what does height actually mean?

Adult height is the end product of life history decisions made throughout the period of growth, from conception onwards. Life history theory is the branch of evolutionary biology which aims to understand how energy is allocated over the life course (Roff 1992). It is based on the principle of allocation, which states that energy used for one purpose cannot be used for another purpose. During their lifetimes, organisms continually make decisions about how to optimally allocate energy between functions such as growth, somatic maintenance (including immune function), and reproduction. An individual's final adult height results from the decisions it makes, and also the decisions its mother makes (Wells 2003), about how much energy to allocate to growth compared to maintaining body condition or reproduction. Both the speed and the timing of growth are relatively labile, so that individuals can speed up or slow down growth, or extend or shorten the period of growth to vary final adult height. An important decision in this process is the decision about when to stop growing and start reproducing since humans, like many other species, separate out the periods of growth and reproduction given the costly nature of both. Height, then, is partly determined by the timing of the decision to stop allocating energy to growth and start allocating energy to reproduction instead. Any selection process affecting adult size will therefore act on the period of growth – the timing and speed of growth is the adaptation, rather than final adult size.

Such life history decisions will be affected by the amount of energy available to that individual, so that adult size differs between environments, but these cross-population size differentials are not simply the result of environmental constraints on growth. Individuals who are conceived and grow up in poor environments could grow a little faster during good periods (should they experience them) and/or continue growing a little longer in order to end up as larger adults. Both compensation mechanisms do in fact occur in poorly nourished populations. Children often experience periods of 'catch-up' growth after stalls in growth due to episodes of disease or seasonal food shortages, for example (Martorell et al. 1994). Growth also tends to continue a little longer in poorly nourished populations, with a corresponding later age at reproductive maturity (Teriokhin et al. 2003). Growing fast and growing longer both have costs however. Fast growth appears to have adverse consequences in terms of higher mortality risk in later life (Rollo 2002). Growing longer delays the start to reproduction, which both increases the risk of dying before any offspring have been produced, and means fewer offspring produced overall. Individuals must therefore trade-off any potential benefits of large size against the costs of faster and longer growth. Recent research has begun to explore the potential costs and benefits of growth across populations, in order to understand these life history decisions in more detail. A cross-cultural analysis suggested that where juvenile mortality rates are relatively high, individuals stop growing sooner (and so end up as shorter adults), presumably to reduce the risk of dying before starting to reproduce (Walker et al. 2006). At the extreme end of the continuum, this may be at least part of the explanation for the very short height of pygmy populations in central Africa (Migliano et al. 2007).

The pay-offs to investing in growth versus other functions are also likely to differ between environments because adult height may bring different costs and benefits in different environments. The aim of this chapter is to survey the costs and benefits of height during adulthood: what costs and benefits does height bring in terms of mortality rate, mating success and fertility outcomes for each sex, and how much do these differ between environments? Large size, as a general rule, is frequently considered to be a good thing in fitness terms, bringing both survival and fecundity advantages (Harvey & Clutton-Brock 1985). Larger males tend to be more successful in the competition for mates, and larger females have greater energetic reserves to devote to reproduction. But large size is also energetically costly to maintain (Blanckenhorn 2000). Given the diversity of mating patterns, mortality rates and energy access experienced by our geographically widespread species, it is worth considering exactly how height is related to the various correlates of reproductive success in diverse environments, before any conclusions can be drawn about the fitness benefits of size.

2. A survey of height and correlates of reproductive success in adulthood

2.1 Height and adult mortality

Mortality is one key component of fitness: to ensure any reproductive output, individuals must survive long enough to reproduce and to raise any children produced successfully. Of all the fitness components considered in this paper, the literature on links between height and adult mortality is by far the largest. At a population level, height is clearly related to mortality rates – taller populations have lower mortality, and this holds for both women and men (Gage & Zansky 1995). Here, we are interested in whether this relationship holds at an individual, within-population level. Table 1 presents a summary of studies which have used longitudinal datasets and hazards analysis (the most appropriate statistical technique) to investigate the link between height and all-cause mortality at the individual level (several other studies investigate the height-longevity link using other methods or in particularly biased samples: (Samaras 2007) is an excellent source of for this literature). Most of these studies have been conducted in relatively high income, and therefore low mortality, populations. Most, but not all, find a largely negative relationship between height and risk of death, though this relationship may be weaker at older ages, and for the particularly tall. And two of the studies find a U-shaped, rather than entirely linear relationship for women. Unfortunately there are very few studies on low income, high mortality populations, but the little evidence available suggests that the negative relationship between height and mortality may not hold so strongly here. Of the five relatively high mortality populations studied, in two there is evidence of a negative relationship between height and risk of death (19th century US army veterans and East Belgians), but in both cases the results did not hold across the entire sample. In the other three populations – two in the contemporary developing world and one other historical US population – there is little evidence of any height-mortality relationship, except for Gambian women, in which the relationship is U-shaped.

The explanation for these variable results may lie in the fact that the relationship between height and mortality differs by cause of death. The broadly negative relationship between all-cause mortality and risk of death in high income countries is driven largely by lower risks of cardio-vascular disease in tall individuals; the risk of death from cancer, particularly reproductive cancers, is actually higher among taller individuals (Davey-Smith et al. 2000; Lee et al. 2009; Okasha et al. 2002). The relationships between the main causes of death in

high mortality populations, such as infectious or parasitic disease, are yet to be elucidated, given the lack of data on height and mortality in such populations. But since the main causes of death differ between populations, ages and the sexes, then we would not necessarily expect different populations to show identical relationships between height and mortality. Bearing in mind the caveat that we so far have little data on high mortality populations, some very tentative conclusions can perhaps be drawn from this survey. Firstly, height seems to be more important in high income, low mortality populations, and less so in higher mortality populations, perhaps because of the clear link between height and cardio-vascular disease, a significant cause of death in low mortality populations. Secondly, there are differences in the height-mortality link between men and women. For men, tall height seems to be broadly beneficial, or at least not detrimental, in that height seems to be either negatively related to mortality or not related at all. For women, several populations show a U-shaped relationship, so that tall height may sometimes bring disadvantages, as does short height.

2.2 Height and mating success

Once an individual has survived to reproductive age, the next step on the road to reproductive success is to find a partner. Anyone raised in western culture will be aware of the importance of height in the mating market. In the Anglophone world, women are traditionally supposed to seek 'tall, dark and handsome' men. Academic research backs up these perceptions. Evidence that height matters on the mate market can take one of two forms. We can indirectly test whether height matters by assessing whether individuals state preferences for a particular height, or we can more directly investigate whether height affects the choice of a mate in the real world of marriage. Research on mate preferences suggests that both men and women, at least in western populations, do prefer partners of a particular height. Lab tests of mate preferences and analysis of lonely hearts ads provides support for what social psychologists have described as the 'cardinal rule of dating': both sexes prefer relationships in which the man is taller than the woman (Higgins et al. 2002; Pawlowski 2003; Pierce 1996), though women more so than men (Salska et al. 2008). There is consistent evidence that women do prefer tall men (Shepperd & Strathman 1989), though perhaps not very tall men (Hensley 1994). Men's preferences are sometimes less pronounced, but they do seem to have a preference for short (Shepperd & Strathman 1989) or average height women (Swami et al. 2008).

Studies of mate preferences are problematic, however. Such studies tend to have rather unrepresentative samples: college students and users of lonely hearts ads are not necessarily representative of all men or women. Studies of mate preferences have also been done almost exclusively in western populations. In addition, mate preferences are not necessarily converted into mate choice, which is ultimately what matters for reproductive success. Mate choices will result from mate preferences across a range of criteria, not just physical attractiveness; they will be affected by mate availability and one's own mate value, and perhaps also the preferences of one's parents and family. More convincing evidence that height matters for mating success would be research which found that individuals are actively choosing partners of particular heights as marriage partners.

Assortative mating for height is one indication that height may be salient on the marriage market, and has been examined in many populations. A 1968 review found that a positive correlation between the heights of husbands and wives was relatively common among the 25 populations of European origin included (Spuhler 1968). In a 1977 survey, 26 of 39 (67%) of populations which were European or of European-origin showed evidence of such assortative

mating (Roberts 1977). Studies on non-European populations are less common, but the results are more mixed. The 1968 paper found no evidence for assortative mating in the 2 non-European studies it included, and in the 1977 review, only 2 of 10 (20%) non-European populations showed significant evidence of assortative mating for height. More recent research on non-European populations has found positive assortative mating for height in Bolivian forager-farmers (Godoy et al. 2008), Oaxaca, Mexico (Malina et al. 1983) and Pakistan (Ahmad et al. 1985), but not in Cameroon (Pieper 1981), Gambia (Sear 2006a), Korea (Hur 2003) or Hadza hunter-gatherers (Sear & Marlowe 2009). Overall, then, while positive assortative mating for height appears fairly common among human populations, it is by no means universal, and its frequency may be over-emphasised by the disproportionate number of studies on European populations, where assortative mating for height may be more common.

Assortative mating is the weakest evidence that height matters for mate choice. Alternative explanations are possible, for example, individuals could be assorting on a characteristic which is correlated with height (such as socio-economic status), or it could arise simply because different groups within a population are different in heights. A better measure might be height-specific patterns of mating which are likely to be driven by actual preferences for particular heights. The male-taller norm is one such example. The proportion of marriages in which the female is taller than the male is considerably less than would be expected by random mating in populations in the US (Gillis & Avis 1980), and the UK (Sear et al. 2004). But in both Gambian agriculturalists and Hadza hunter-gatherers the proportion of female-taller marriages is exactly what would be expected by random mating, around 8-9% (Sear et al. 2004; Sear & Marlowe 2009).

A final piece of evidence that height matters would be analyses that showed individuals of particular heights were favoured in terms of the probability or number of marriages (see Table 2). Most, but not all, of these studies find a positive relationship between height and marital success for men. There are fewer studies for women, and the results are a little more mixed: these studies variously show no relationship (Gambia, Hadza), a disadvantage for the shortest women (Bavaria), and a disadvantage for both the shortest and tallest women (UK).

This summary suggests both preferences and choices for height exist in both sexes in at least some populations, but not all. Women seem to choose either tall men, or have no preference at all; a marital advantage for short men is not seen. Men's choices may be somewhat more variable, and they may sometimes avoid shorter women (though such a pattern may also be driven by taller women attempting but failing to achieve their preferred taller partner). Such variability makes sense because what makes a potential mate attractive is likely to vary between populations. Height may confer differential advantages and disadvantages in different ecologies and different subsistence strategies, perhaps growing in importance in agricultural and industrial populations, compared to hunter-gatherers, where large size may actually be a disadvantage in hunting game. As with the mortality research, a very tentative conclusion might be that height matters more to high income, developed country populations, compared to traditional societies, though again the data is far too limited to make this conclusion at all secure.

2.3 Height and fertility outcomes

Life history theory predicts that adult height will be negatively correlated with age at first reproduction, because of the trade-off between growth and reproduction. Height could also

plausibly be related to other fertility outcomes in women, such as reproductive rate, since taller women potentially have access to greater energetic reserves. There is relatively little research on this topic and what there is exists almost exclusively for women, rather than men. Male reproductive success is governed by a different set of factors to female: it is less constrained by the energetic ability to produce children and the time available in which to produce them, and more by the ability to attract mates. For these reasons, and because collecting accurate data on male fertility is more difficult, the study of male fertility is less well-developed than that of female. There is more data for both sexes on relationships between height and total number of children or number of surviving children, but this will be dealt with in the next section.

If there are any patterns between height and components of fitness that hold universally across populations, then one strong candidate is the relationship between height and age at reproductive maturity. The trade-off between growth and reproduction results in a relatively consistent pattern of earlier maturity being correlated with shorter adult height across all types of populations. A number of studies in high or medium income countries suggest that women who have a relatively early age at menarche are shorter as adults, including Brazil (Gigante et al. 2006), two studies in the UK (Nettle 2002b; Ong et al. 2007), Scotland (Okasha et al. 2001), Copenhagen (Helm et al. 1995), Greece (Georgiadis et al. 1997), and a comparative study of 9 European populations (Onland-Moret et al. 2005). This suggests that even in well-nourished populations women experience a trade-off between devoting resources to growth and to reproduction. In natural fertility societies an early menarche is likely also to lead to an earlier first birth, and one study of such a population in rural Gambia found the predicted trade-off between age at first birth and adult height (Allal et al. 2004). In a similar vein, a study using a nationally representative Indian sample found that adult height was negatively related to the number of teenage birth a woman had produced, likely to be correlated with her age at first birth (Brennan et al. 2005). The use of contraception might perhaps be expected to break the link between height and age at first birth, since women in such populations tend to delay births considerably beyond the age at which they could physiologically conceive, but in Finland women who were shorter as adults did have earlier first births, as well as earlier menarche (Helle 2008). These women didn't begin reproducing until their mid-20s on average, but they may have been on a relatively fast life history track, despite the long lag between age at menarche and age at first birth. One partial exception to the earlier maturity-shorter height rule was demonstrated in a Guatemalan study which found that both tall and particularly short women had delayed first births (Pollet & Nettle 2008), suggesting perhaps that no height-reproductive outcome can be considered entirely universal in our species.

Whether height is correlated with reproductive rate, and the ability to conceive, once reproduction is underway is so far little studied. One study of a Gambian population found no relationship between height and the length of birth intervals (Sear et al. 2003). A complication with analysing reproductive rate is that height is known to be correlated with other reproductive outcomes: taller women tend to have easier births (Cnattingius et al. 1998; Liljestrand et al. 1985), higher birthweight babies (Kirchengast et al. 1998), fewer stillbirths (Pollet & Nettle 2008) and frequently higher survival among their children. Higher survival among children will lengthen birth intervals, making a simple analysis of reproductive rate by height complicated. Higher survival amongst one's children is a fitness component itself, however, and may be one of the strongest determinants of fitness for women (Strassmann & Gillespie 2002). The majority of these studies show that tall maternal height brings benefits in terms of better child survival, including populations in the Gambia (Sear et al. 2004),

Guatemala (Pollet & Nettle 2008), Bangladesh (Baqui et al. 1994) and Moazambique (Liljestrand et al. 1985). Despite one study in Peru shorter women have higher child survival (Frisancho et al. 1973), a recent comparative study using Demographic and Health Survey data from 42 developing countries has effectively demonstrated a clear positive relationship between maternal height and child survival that holds across varying levels of development in these countries (Monden & Smits 2008), which is one of the more convincing comparative studies indicating a clear advantage for height, at least for women in high mortality populations.

2.4 Height and reproductive success

The closest proxy for reproductive success in empirical studies is the number of surviving children, or simply number of children in societies with low child mortality. There are a number of studies for both sexes on the relationship between height and overall number of children or surviving children, but these studies are perhaps the hardest of all to compare. The varying ages and control variables, if any, that these studies include in their analysis introduces considerable noise into the data. Analysing only certain ages, for example, may introduce selection effects if height is related to mortality in the population under study. Many of these studies come from populations moving through the epidemiological and fertility transitions, again making not only comparisons difficult, but also an assessment of the effect of height in the population under study, if different cohorts have different fertility, mortality or height.

Table 3 then needs to be interpreted with caution, but it draws together research which has investigated relationships between height and either total number of children (for the low mortality populations) or number of surviving children (for the high mortality populations). These data tend to derive from rather unrepresentative samples so any conclusions must again be tentative, but we can see that for both women and men every possible relationship is seen between height and number of children – positive, negative, non-linear and no relationship. The only conclusion that can be drawn is that the diversity of these results suggests that the relationship between height and reproductive success is heavily dependent on environmental context.

3. Conclusion

This brief survey can only touch the surface of the costs and benefits of height in adulthood, not least because there is relatively little comparable data which can be used to assess the consequences of height across a range of environments. It should also be noted that even where methods and sampling strategies are similar, studies may not be directly comparable because average height varies between populations: a 'tall' Gambian or Guatemalan, for example, will be considerably shorter than a 'tall' westerner. Such empirical analysis investigating relationships between a single fitness outcome and height will also be misleading since there may be interactions between fitness outcomes which may alter the association between height and overall fitness: age at menarche, for example, has been shown to be correlated with both later mortality (Jacobsen et al. 2007) and the birthweight of any children produced (Kirchengast & Hartmann 2000), so that even if an early menarche allows women to get a head-start on reproduction, it may come at a later cost of small babies and higher risk of death. Studies which try to holistically assess the relationship between height and multiple components of reproductive success, including age at first birth, probability of marriage and childlessness, number of children born and child survival within the same

population provide the best means for analysing the height-reproductive success relationship (such as (Nettle 2002b; Pollet & Nettle 2008; Sear et al. 2004), but even these will suffer from selection biases. Theoretical modelling of these relationships is likely to prove the most fruitful strategy for understanding these relationships, as has been done for Ache huntergatherers on the consequences of growth in terms of adult weight (Hill & Hurtado 1996).

If any conclusions can be drawn from this survey then, with appropriate caution, the following trends seem to appear. Firstly, there are no obvious relationships between height and fitness outcomes that hold across all types of population, with the possible exceptions of a trade-off between height and age at reproductive maturity for women, and the higher child survival of tall women in high mortality societies. Instead, the nature of almost all relationships discussed here clearly depend on ecological conditions. A finding that should not perhaps be surprising, given patterns of change in average human heights over our evolutionary history. Over the last few millenia average heights appears to have varied, rather than demonstrating a consistent increase. In fact, estimates suggest extant human populations are somewhat shorter and certainly lighter than ancestral species. Height did increase from australopithecines to *Homo*, but earlier *Homo* species may have been rather taller than modern Homo sapiens (Bogin 2001). Among modern humans, skeletal evidence suggests that human height may have been taller than the average today about 40,000 years ago, but declined over the next few millennia. The advent of agriculture is thought to have shrunk human populations further, after which average heights fluctuated until a steady increase in height began in economically developing countries over the 20th century (Bogin 2001). Such variability suggests variation in the costs and benefits of investing in growth and in the payoffs to size in adulthood throughout our species' history.

Secondly, tall height may bring more benefits in adulthood to men than for women. Short height certainly brings no benefits to men, and tall height rarely seems costly, with the exception of a handful of the studies analysing total number of children. Non-linear relationships seem to be somewhat more common for women and are found across all outcomes: mortality, mating success and fertility. These potentially negative effects of tall height for women may be related to the clear cost of a later start to reproduction, though this is counter-acted in high mortality societies by higher survival amongst the children of tall women.

Finally, it is clear that the importance of height has not diminished in modern western societies. In fact, height may actually matter more in such societies than in more traditional populations, at least for mating success and mortality, if not overall number of children (though, given the low variance in number of children in such low fertility societies, a better measure of reproductive success might be the quality, rather than the quantity of these children, which is beyond the current review). Patterns of growth may therefore still have evolutionary importance today, with both mortality and mating success for men suggesting taller is better in own particular society. Does this mean we may ultimately become a species of Brobdingnagians: if we met our descendants, would they tower over us? This depends on whether this advantage of the tall is genuine, which will require more data. It will also depend on whether all populations will converge on this bigger is better pattern as they develop economically towards the developed world. That the very tall in our societies suffer adverse health and mating consequences, however, suggests that there may be limits to growth. Other factors may also come into play: an economic historian has recently suggested, somewhat controversially, that the obesity epidemic may cause heights to stagnate or even decline in the coming years (Komlos & Baur 2003). A confident prediction of what average heights will be

across the world in a few decades time may be difficult, but I can much more confidently predict that height will still matter, and that we are a long way from leaving our biological imperative behind.

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References

- Ahmad M, Gilbert RI, Naqui AUN (1985): Assortative mating for height in Pakistani arranged marriages. Journal of Biosocial Science 17(2):211-214
- Allal N, Sear R, Prentice AM, Mace R (2004): An evolutionary model of stature, age at first birth and reproductive success in Gambian women. Proceedings of the Royal Society of London, Series B, Biological Sciences 271(1538):465-470
- Allebeck P, Bergh C (1992): Height, body mass index and mortality: do social factors explain the association? Public Health 106(5):375-382
- Alter G, Neven M, Oris M (2004): Height, wealth and longevity in XIXth century east Belgium. Annales de démographie historique 219-37
- Baqui AH, Arifeen SE, Amin S, Black RE (1994): Levels and correlates of maternal nutritional-status in urban Bangladesh. European Journal of Clinical Nutrition 48(5):349-357
- Baten J, Murray JE (1998): Women's stature and marriage markets in preindustrial Bavaria. Journal of Family History 23(2):124-135
- Blanckenhorn WU (2000): The evolution of body size: What keeps organisms small? Quarterly Review of Biology 75(4):385-407
- Bogaert AF (1998): Physical development and sexual orientation in women: Height, weight, and age of puberty comparisons. Personality and Individual Differences 24(1):115-121
- Bogin B (2001): The Growth of Humanity. Wiley-Liss, New York
- Brennan L, McDonald J, Shlomowitz R (2005): Teenage births and final adult height of mothers in India, 1998-1999. Journal of Biosocial Science 37(2):185-191
- Brush G, Boyce AJ, Harrison GA (1983): Associations between anthropometric variables and reproductive performance in a Papua New Guinea highland population. Annals of Human Biology 10(3):223-234
- Buunk AP, Park JH, Zurriaga R, Klavina L, Massar K (2008): Height predicts jealousy differently for men and women. Evolution and Human Behavior 29(2):133-139
- Case A, Paxson C (2008): Stature and status: height, ability, and labor market outcomes. Journal of Political Economy 116(3):499-532
- Cnattingius R, Cnattingius S, Notzon FC (1998): Obstacles to reducing cesarean rates in a low-cesarean setting: The effect of maternal age, height, and weight. Obstetrics and Gynecology 92(4):501-506
- Costa DL (1993): Height, weight, wartime stress, and older age mortality: evidence from the Union Army records. Explorations in Economic History 30(4):424-449
- (2004): The measure of man and older age mortality: evidence from the Gould sample. Journal of Economic History 64(1):1-23

- Davey-Smith G, Hart C, Upton M, Hole D, Gillis C, Watt G, Hawthorne V (2000): Height and risk of death among men and women: aetiological implications of associations with cardiorespiratory disease and cancer mortality. Journal of Epidemiology and Community Health 54(2):97-103
- Devi MR, Kumari JR, Srikumari CR (1985): Fertility and mortality differences in relation to maternal body size. Annals of Human Biology 12(5):479-484
- Engeland A, Bjorge T, Selmer RM, Tverdal A (2003): Height and body mass index in relation to total mortality. Epidemiology 14(3):293-299
- 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? Evolution and Human Behavior 29(6):434-443
- Frisancho AR, Sanchez J, Pallarde.D, Yanez L (1973): Adaptive significance of small body size under poor socioeconomic conditions in Southern Peru. American Journal of Physical Anthropology 39(2):255-261
- Gage TB, Zansky SM (1995): Anthropometric indicators of nutritional status and level of mortality. American Journal of Human Biology 7(6):679-691
- Georgiadis E, Mantzoros CS, Evagelopoulou C, Spentzos D (1997): Adult height and menarcheal age of young women in Greece. Annals of Human Biology 24(1):55-59
- Gigante DP, Horta BL, Lima RC, Barros FC, Victora CG (2006): Early life factors are determinants of female height at age 19 years in a population-based birth cohort (Pelotas, Brazil). J. Nutr. 136(2):473-478
- Gillis JS, Avis WE (1980): The male taller norm in mate selection. Personality and Social Psychology Bulletin 6(3):396-401
- Godoy R, Eisenberg DTA, Reyes-Garcia V, Huanca T, Leonard WR, McDade TW, Tanner S (2008): Assortative mating and offspring well-being: theory and empirical findings from a native Amazonian society in Bolivia. Evolution and Human Behavior 29(3):201-210
- Goldstein MS, Kobyliansky E (1984): Anthropometric traits, balanced selection and fertility. Human Biology 56(1):35-46
- Hacker JD (2008): Economic, demographic, and anthropometric correlates of first marriage in the mid-nineteenth-century United States. Social Science History 32(3):307-345
- Harvey PH, Clutton-Brock TH (1985): Life history variation in primates. Evolution 39(3):559-581
- Helle S (2008): A tradeoff between reproduction and growth in contemporary Finnish women. Evolution and Human Behavior 29(3):189-195
- Helm P, Münster K, Schmidt L (1995): Recalled menarche in relation to infertility and adult weight and height. Acta Obstetricia et Gynecologica Scandinavica 74(9):718 722
- Hensley WE (1994): Height as a basis for interpersonal attraction. Adolescence 29(114):469-474
- Higgins LT, Zheng M, Liu Y, Sun CH (2002): Attitudes to marriage and sexual behaviors: a survey of gender and culture differences in China and United Kingdom. Sex Roles 46(3):75-89
- Hill K, Hurtado AM (1996): Ache Life History: The Ecology and Demography of a Foraging People. Aldine de Gruyter, New York
- Hosegood V, Campbell OMR (2003): Body mass index, height, weight, arm circumference, and mortality in rural Bangladeshi women: a 19-y longitudinal study. American Journal of Clinical Nutrition 77(2):341-347

- Hur Y-M (2003): Assortative mating for personality traits, educational level, religious affiliation, height, weight, and body mass index in parents of a Korean twin sample. Twin Research 6(6):467-470
- Jacobsen BK, Heuch I, Kvale G (2007): Association of low age at menarche with increased all-cause mortality: a 37-year follow-up of 61,319 Norwegian women. Am. J. Epidemiol. 166(12):1431-1437
- Jousilahti P, Tuomilehto J, Vartiainen E, Eriksson J, Puska P (2000): Relation of adult height to cause-specific and total mortality: a prospective follow-up study of 31,199 middle-aged men and women in Finland. American Journal of Epidemiology 151(11):1112-1120
- Kannam JP, Levy D, Larson M, Wilson PWF (1994): Short stature and risk for mortality and cardiovascular disease events: the Framingham heart study. Circulation 90(5):2241-2247
- Kirchengast S (2000): Differential reproductive success and body size in !Kung San people from northern Namibia. Collegium Antropologicum 24(1):121-132
- Kirchengast S, Hartmann B (2000): Association between maternal age at menarche and newborn size. Social Biology 47(1-2):114-126
- Kirchengast S, Hartmann B, Schweppe KW, Husslein P (1998): Impact of maternal body build characteristics on newborn size in two different European populations. Human Biology 70(4):761-774
- Kirchengast S, Winkler EM (1995): Differential reproductive success and body dimensions in Kavango males from urban and rural areas in Northern Namibia. Human Biology 67(2):291-309
- (1996): Differential fertility and body build in !Kung San and Kavango females from northern Namibia. Journal of Biosocial Science 28(2):193-210
- Komlos J, Baur M (2003): From the tallest to (one of) the fattest: the enigmatic fate of the American population in the 20th Century,
- Laara E, Rantakallio P (1996): Body size and mortality in women: A 29 year follow up of 12,000 pregnant women in northern Finland. Journal of Epidemiology and Community Health 50(4):408-414
- Lasker GW, Thomas R (1976): Relationship between reproductive fitness and anthropometric dimensions in a Mexican population. 48 4(775-791):
- Lee CMY, Barzi F, Woodward M, Batty GD, Giles GG, Wong JW, Jamrozik K, Lam TH, Ueshima H, Kim HC, Gu DF, Schooling M, Huxley RR, for The Asia Pacific Cohort Studies C (2009): Adult height and the risks of cardiovascular disease and major causes of death in the Asia-Pacific region: 21 000 deaths in 510 000 men and women. Int. J. Epidemiol. 38(4):1060-1071
- Leon DA, Smith GD, Shipley M, Strachan D (1995): Adult height and mortality in London: early-life, socioeconomic confounding, or shrinkage. Journal of Epidemiology and Community Health 49(1):5-9
- Liao Y, McGee DL, Cao G, Cooper RS (1996): Short stature and risk of mortality and cardiovascular disease: Negative findings from the NHANES I epidemiologic follow-up study. Journal of the American College of Cardiology 27(3):678-682
- Liljestrand J, Bergstrom S, Westman S (1985): Maternal height and perinatal outcome in Mozambique. J Trop Pediatr 31(6):306-310
- Magnusson PKE, Gunnell D, Tynelius P, Davey Smith G, Rasmussen F (2005): Strong inverse association between height and suicide in a large cohort of Swedish men: evidence of early life origins of suicidal behavior? Am J Psychiatry 162(7):1373-1375

- Malina RM, Selby HA, Buschang PH, Aronson WL, Little BB (1983): Assortative mating for phenotypic characteristics in a Zapotec community in Oaxaca, Mexico. Journal of Biosocial Science 15(03):273-280
- Martorell R, Delgado HL, Valverde V, Klein RE (1981): Maternal stature, fertility and infant mortality. Human Biology 53(3):303-312
- Martorell R, Khan LK, Schroeder DG (1994): Reversibility of stunting: epidemiologic findings in children from developing countries. European Journal of Clinical Nutrition 48S45-S57
- McCarron P, Okasha M, McEwen J, Smith GD (2002): Height in young adulthood and risk of death from cardiorespiratory disease: a prospective study of male former students of Glasgow University, Scotland. Am. J. Epidemiol. 155(8):683-687
- Migliano AB, Vinicius L, Lahr MM (2007): Life history trade-offs explain the evolution of human pygmies. Proceedings of the National Academy of Sciences 104(51):20216-20219
- Mitton J (1975): Fertility differentials in modern societies resulting in normalizing selection for height. Human Biology 47(2):189-201
- Monden CWS, Smits J (2008): Maternal height and child mortality in 42 developing countries. American Journal of Human Biology 21(3):305-311
- Mueller U, Mazur A (2001): Evidence of unconstrained directional selection for male tallness. Behavioral Ecology and Sociobiology 50(4):302-311
- Mueller WH (1979): Fertility and physique in a malnourished population. Human Biology 51153-166
- Murray JE (1997): Standards of the present for people of the past: Height, weight, and mortality among men of Amherst College, 1834-1949. Journal of Economic History 57(3):585-606
- (2000): Marital protection and marital selection: Evidence from a historical-prospective sample of American men. Demography 37(4):511-521
- Nettle D (2002a): Height and reproductive success in a cohort of British men. Human Nature 13(4):473-491
- (2002b): Women's height, reproductive success and the evolution of sexual dimorphism in modern humans. Proceedings of the Royal Society of London Series B, Biological Sciences 269(1503):1919-1923
- Okasha M, Gunnell D, Holly J, Smith GD (2002): Childhood growth and adult cancer. Best Practice & Research Clinical Endocrinology & Metabolism 16(2):225-241
- Okasha M, McCarron P, Smith GD, McEwen J (2001): Age at menarche: secular trends and association with adult anthropometric measures. Annals of Human Biology 28(1):68-78
- Ong KK, Northstone K, Wells JCK (2007): Earlier mother's age at menarche predicts rapid infancy growth and childhood obesity. Plos Medicine 4(4):737-742
- Onland-Moret NC, Peeters PHM, van Gils CH, Clavel-Chapelon F, Key T, Tjonneland A, Trichopoulou A, Kaaks R, Manjer J, Panico S, Palli D, Tehard B, Stoikidou M, Bueno-De-Mesquita HB, Boeing H, Overvad K, Lenner P, Quiros JR, Chirlaque MD, Miller AB, Khaw KT, Riboli E (2005): Age at menarche in relation to adult height: the EPIC study. American Journal of Epidemiology 162(7):623-632
- Pawlowski B (2003): Variable preferences for sexual dimorphism in height as a strategy for increasing the pool of potential partners in humans. Proceedings of the Royal Society of London Series B-Biological Sciences 270(1516):709-712
- Pawlowski B, Dunbar RIM, Lipowicz A (2000): Evolutionary fitness: tall men have more reproductive success. Nature 403(6766):156

- Peck AM, Vagero DH (1989): Adult body height, self perceived health and mortality in the Swedish population. J Epidemiol Community Health 43(4):380-384
- Pieper U (1981): Assortative mating in the population of a German and a Cameroon city. Journal of Human Evolution 10(8):643-645
- Pierce CA (1996): Body height and romantic attraction: a meta-analytic test of the male-taller norm. Social Behavior and Personality 24(2):143-149
- Pollet TV, Nettle D (2008): Taller women do better in a stressed environment: Height and reproductive success in rural Guatemalan women. American Journal of Human Biology 20(3):264-269
- Roberts DF (1977): Assortative mating in man: husband/wife correlations in physical characteristics. Bulletin of the Eugenics Society of London Supplement 21-45
- Roff DA (1992): The Evolution of Life Histories. Chapman and Hall, New York
- Rollo CD (2002): Growth negatively impacts the life span of mammals. Evolution & Development 4(1):55-61
- Salska I, Frederick DA, Pawlowski B, Reilly AH, Laird KT, Rudd NA (2008): Conditional mate preferences: Factors influencing preferences for height. Personality and Individual Differences 44(1):203-215
- Samaras TT (2007): Human Body Size and the Laws od Scaling. Nova Science Publishers, New York
- Scott EC, Bajema CJ (1982): Height, weight and fertility among the participants of the 3rd Harvard growth study. Human Biology 54(3):501-516
- Sear R (2006a): Height and reproductive success: how a Gambian population compares to the West. Human Nature 17(4):405-418
- (2006b): Size-dependent reproductive success in Gambian men: does height or weight matter more? Social Biology 53(3-4):172-188
- Sear R, Allal N, Mace R (2004): Height, marriage and reproductive success in Gambian women. Research in Economic Anthropology 23203-224
- Sear R, Mace R, McGregor IA (2003): A life-history approach to fertility rates in rural Gambia: evidence for trade-offs or phenotypic correlations? In Rodgers JL, Kohler HP (eds) The Biodemography of Human Reproduction and Fertility. Kluwer Academic Publishers, Boston
- Sear R, Marlowe FW (2009): How universal are human mate choices? Size does not matter when Hadza foragers are choosing a mate. Biology Letters -
- Shepperd JA, Strathman AJ (1989): Attractiveness and height: the role of stature in dating preference, frequency of dating, and perceptions of attractiveness. Personality and Social Psychology Bulletin 15(4):617-627
- Song Y-M, Sung J (2008): Adult height and the risk of mortality in South Korean women. Am. J. Epidemiol. 168(5):497-505
- Song YM, Smith GD, Sung J (2003): Adult height and cause-specific mortality: a large prospective study of South Korean men. American Journal of Epidemiology 158(5):479-85
- Spuhler JN (1968): Assortative mating with respect to physical characteristics. Eugenics Quarterly 15(2):128-140
- Steckel RH (2009): Heights and human welfare: Recent developments and new directions. Explorations in Economic History 46(1):1-23
- Strandberg MDTE (1997): Inverse relation between height and cardiovascular mortality in men during 30-year follow-up. The American Journal of Cardiology 80(3):349-350
- Strassmann BI, Gillespie B (2002): Life-history theory, fertility and reproductive success in humans. Proceedings of the Royal Society of London Series B-Biological Sciences 269(1491):553-562

- Swami V, Furnham A, Balakumar N, Williams C, Canaway K, Stanistreet D (2008): Factors influencing preferences for height: A replication and extension. Personality and Individual Differences 45(5):395-400
- Teriokhin AT, Thomas F, Budilova EV, Guegan JF (2003): The impact of environmental factors on human life-history evolution: an optimization modelling and data analysis study. Evolutionary Ecology Research 5(8):1199-1221
- Vetta A (1975): Fertility, physique, and intensity of selection. Human Biology 47(3):283-293 Waaler HT (1984): Height, weight and mortality: the Norwegian experience. Acta Medica Scandinavica Suppl. 6791-51
- Walker R, Gurven M, Hill K, Migliano A, Chagnon N, De Souza R, Djurovic G, Hames R, Hurtado AM, Kaplan H, Kramer KL, Oliver WJ, Valeggia CR, Yamauchi T (2006): Growth rates and life histories in 22 small-scale societies. American Journal of Human Biology 18295-311
- Wells JCK (2003): The thrifty phenotype hypothesis: thrifty offspring or thrifty mother. Journal of Theoretical Biology 221143-161

Table 1: summary of studies analysing the relationship between height and all-cause adult mortality (top panel low mortality populations; bottom panel high mortality populations)

Study population	Age	Sex	Height-mortality relationship	Comments	Reference
Norway	20+	Women Men	Negative Negative	Large population-based study; association weaker for tallest men and oldest	(Waaler 1984)
				ages	
Norway	20+	Women	U-shaped	Similar to Waaler 1984	(Engeland et al.
		Men	Negative	but larger sample and longer follow-up	2003)
Sweden	16+	Women	Negative	Random sample of	(Peck & Vagero
		Men	Negative	Swedish adults	1989)
Sweden	18+	Men	Negative	Military conscripts	(Allebeck & Bergh 1992)
Finland	25+	Women	Negative	Population surveys in	(Jousilahti et al.
		Men	Negative	Eastern Finland	2000)
Finland	14+	Women	U-shaped	Fertile women recruited during childbearing years	(Laara & Rantakallio 1996)
Finland	45+	Men	Negative	Helsinki business men	(Strandberg 1997)
England	40+	Men	Negative	Whitehall study of civil servants; strength of association declined with length of follow-up	(Leon et al. 1995)
Scotland	16+	Men	None	Male medical students	(McCarron et al. 2002)
Scotland	45+	Women	Negative	Renfrew/Paisley general	(Davey-Smith et al.
		Men	Negative	population study	2000)
US	< 36	Women	None	Framingham	(Kannam et al. 1994)
		Men	None	· ·	
US	25+	Women	None	NHANES 1	(Liao et al. 1996)
		Men	None		
South Korea	40+	Women	Negative	Civil servants & their	(Song & Sung 2008)
		Men	Negative	dependents	(Song et al. 2003)
Gambia	21+	Women	U-shaped	Rural agriculturalists	(Sear et al. 2004)
		Men	None		(Sear 2006b)
Bangladesh	10+	Women	None	Matlab study	(Hosegood &
					Campbell 2003)
Belgium	50+	Men	Negative	Military conscript data; Birth cohort 1815-28	(Alter et al. 2004)
Belgium	50+	Men	None	Military conscript data; Birth cohort 1829-60	(Alter et al. 2004)
US	55+	Men	Negative	US Union Army records,	(Costa 1993)
	56+		None	19 th C; slightly different	(Costa 2004)
US	20+	Men	None	samples and methods yield different results Amherst College graduates 1834-1949	(Murray 1997)

Table 2: summary of studies analysing the relationship between height and probability or number of marriages (top panel low mortality populations; bottom panel high mortality populations)

Study population	Sex	Dependent variable	Height-mortality relationship	Comments	Reference
UK	Women Men	Probability and number of marriages	N-shaped Positive, except tallest men	Nationally representative sample (NCDS)	(Nettle 2002b)
Poland	Men	Probability of marriage	Positive	Wroclaw	(Pawlowski et al. 2000)
US	Men	Number of wives	Positive	West Point cadets	(Mueller & Mazur 2001)
Gambia	Women Men	Number of marriages	None Positive	Rural agriculturalists	(Sear et al. 2004) (Sear 2006b)
Hadza	Women Men	Number of marriages	None None	Hunter-gatherers	(Sear & Marlowe 2009)
Belgium	Men	Probability of marriage	Positive	Military conscript data; men born 1815-1860	(Alter et al. 2004)
US	Men	Probability of marriage	Positive	US Union Army records, 19 th C	(Hacker 2008)
US	Men	Probability of marriage	Positive	Amherst College graduates 1834-1949	(Murray 2000)
Bavaria	Women	Probability of marriage	Shortest women disadvantaged	Female prisoners, 19 th C	(Baten & Murray 1998)

Table 3: summary of studies demonstrating the relationship between height and number of surviving children (top panel relatively low mortality populations; bottom panel high mortality populations)

Study population	Sex	Height-children relationship	Reference
Poland	Men	Positive	(Pawlowski et al. 2000)
Finland	Women	None	(Helle 2008)
UK	Women	N-shaped	(Nettle 2002b)
	Men	None	(Nettle 2002a)
US	Women	None	(Mitton 1975)
OS .	Men		(Witton 1973)
	IVICII	∩-shaped	
US (West Point cadets)	Men	Positive	(Mueller & Mazur 2001)
US college students 1880-1912	Women	N-shaped	(Vetta 1975)
US college students	Women	None	(Scott & Bajema 1982)
born 1912-1918	Men	None	(2 · · · · · · · · · · · · · · · · · · ·
Mexicans in US	Women	None	(Goldstein & Kobyliansky 1984)
	Men	None	,
Mexicans in US	Women	None	(Lasker & Thomas 1976)
	Men	None	
China	Women	None	(Fielding et al. 2008)
	Men	None	
Namibia hunter-	Women	Negative	(Kirchengast 2000)
gatherers	Men	Positive	
Namibia urban	Men	Negative	(Kirchengast & Winkler 1995)
Namibia horticultural	Women	None	(Kirchengast & Winkler 1996)
pastoralists	Men	Positive	(Kirchengast & Winkler 1995)
Gambia agriculturalists	Women	Positive	(Sear et al. 2004)
	Men	None	(Sear 2006a)
Colombia	Women Men	N-shaped	(Mueller 1979)
		N-shaped	
India	Women	Negative	(Devi et al. 1985)
Guatemala	Women	Positive	(Martorell et al. 1981)
Guatemala	Women	Positive	(Pollet & Nettle 2008)
Papua New Guinea	Women	N-shaped	(Brush et al. 1983)