Sex, stature and status

Stulp, Gert

SEX
STATURE
STATUS

Natural selection on
height in contemporary
human populations

Gert Stulp

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Prof. dr. M.C. Mills

Prof. dr. M. van Vugt

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CHAPTER 1

SEX
STATURE
STATUS

Natural selection on height in contemporary human populations

A synthesis

Gert Stulp

The shortest person ever to have lived, Chandra Bahadur Dangi, reached an adult height[1] of only 55 centimeters. He was, therefore, about the same size as one of Robert Pershing Wadlow's feet, who was the tallest man ever recorded, with a height of 2 meters and 72 centimeters[2]. Although these examples form the extremes of the height continuum, anyone who has travelled can confirm that height varies quite substantially across different populations: while the shortest people on earth, the Efe hunter-gatherers from Congo, barely reach 150 centimeters on average, the tallest people, the Dutch, reach a whopping 185 centimeters[3]. Even within a population, substantial variation exists: the 5% shortest and 5% tallest Dutch people differ in height by approximately 30 cm (McEvoy & Visscher, 2009). We cannot help but notice these differences in stature; we register almost instantly who is taller and shorter than we are. Indeed, as an upright walking animal, height may well be our most conspicuous feature.

As with all biological traits, height is a product of the interaction between environmental and genetic factors. Although, strictly speaking, the influence of the two cannot be separated, it is possible to identify both the genetic underpinnings and the specific environmental factors that influence height. Indeed, two of the most consistent findings with respect to height variation within populations - socioeconomic gradients in height and the fact that grown-up children tend to be taller than their parents - are most likely explained by environmental factors. In what follows, I explore these environmental effects in more detail, before going on to discuss the genetic basis for height in human populations.

ENVIRONMENTAL INFLUENCES ON HEIGHT

Growth, and therefore stature, is very much dependent on nutrition (Silventoinen 2003). More specifically, a person's height at any particular age partly reflects that person's history of *net* nutrition (Deaton, 2007; Steckel, 2002a): that is, the difference between the energy gained through food intake minus the loss of energy due to factors like disease and physical activity. Indeed, repeated bouts of biological stress - whether from food deprivation, physically

1 The Merriam-Webster dictionary defines height as "The distance from the bottom to the top of something standing upright" and the Oxford English Dictionary defines it as "The measurement of someone or something from head to foot or from base to top". The Dutch word for height is 'hoogte', which is used to describe the height of nearly everything, except human beings, for which 'lengte' (i.e., length) is used.

2 Guinness Book of Records; Wadlow wore a US size 37, which translates into 49.6 cm.

3 This value refers to average male height; given that they are the tallest people in the world, it is ironic to note that the Dutch live in the *Nether*lands, or as they are sometimes called, the *low*lands.

strenuous work, or illness (Batty et al., 2009; Nyström Peck & Lundberg, 1995; Silventoinen, 2003; Steckel, 1995) often lead to the stunting of growth and reduced adult height.

Lack of nutrition, particularly protein deficiency, is recognized as one of the main contributors to reduced infant growth in developing countries, and supplementary food programs have been shown to produce clear improvements in growth rates (Beaton & Ghassemi, 1982; Edozien et al., 1976; Silventoinen, 2003). Due to the strong association between growth and nutrition, both UNICEF and the World Health Organization collect growth data as a means to assess the success of its supplementary food programs and to establish indicators of malnutrition (Onis et al., 1993; Steckel, 1995). The positive effects of supplemental feeding are obviously not restricted to developing nations, however; experiments conducted as long ago as 1928 showed that the provision of extra milk increased the growth of schoolchildren in the UK (Leighton & Clark, 1929; Orr, 1928).

In addition to, and intertwined with, the effects of malnutrition, childhood disease is known to adversely affect growth. Mounting an immune response to fight infection increases metabolic requirements and can thus affect net nutrition. In addition, disease frequently prevents food intake, impairs nutrient absorption, and causes nutrient loss (Silventoinen, 2003). Accordingly, recurrent infection is associated with a lower height-for-age (Dowd et al., 2009). In one study, children that experienced four or more bouts of pneumonia or bronchitis were, on average, 2.5 cm shorter than children without such a history of infection (Tanner, 1969).

Adverse economic and social conditions in childhood, such as psychosocial stress, housing conditions and physically strenuous work, also lead to short stature in adulthood, (Cavelaars et al., 2000; Mascie-Taylor, 1991; Nyström Peck & Lundberg, 1995). Family size can also be a risk factor (Lawson & Mace, 2008; Rona et al., 1978): the presence of (many) siblings in childhood, for instance, significantly reduces an individual's height (presumably because finite resources have to be distributed across all children, which leads to both reduced nutrient intake and increased psychosocial stress). Even in a wealthy, well-nourished population like the UK (Lawson & Mace, 2008), those raised with four siblings are, on average, 3 cm shorter than those born without siblings.

It is clear, therefore, that childhood environment affects adult height, and that these environmental effects on stature are often substantial. Perhaps the best illustration of the often dramatic nature of these effects comes from studies comparing the offspring of those who emigrated to more affluent populations with those remaining in their less affluent native population (Bogin et al., 2002; Kim, 1982). Maya children born in the US, for instance, are 12 cm taller than Maya children born in Guatemala (Bogin et al., 2002). Indeed, environmental differences during childhood probably account for the social gradients in height observed throughout the world, where those of higher socioeconomic status tend to be taller on average than those of lower socioeconomic status.

Social gradients in height

In a study examining ten different European countries, Cavelaars et al (2000) found that, without exception, more highly educated individuals were taller than less educated individuals, with height differences ranging from 1.2 to 3 cm. Similarly, a meta-analysis by Judge and Cable (2004) found that height was consistently positively related to income and other measures of professional success. In addition, variation in height across social classes is known to be greater in poorer countries (Deaton, 2007; Silventoinen, 2003), whereas an improved standard of living reduces the extent of such differences (Garcia & Quintana-Domeque, 2007; Teasdale et al., 1989).

These social gradients in height are argued to be a consistent feature of human societies, both cross-culturally and historically; something that is captured by the common use of the term "big man" in many societies to denote an individual of both authority and importance (Van Vugt et al., 2008). According to Ellis (1992) this phrase is "*a conflation of physical size and social rank and ... 'big men' are consistently big men, tall in stature*" (p. 279); as such, it is clearly based on the notion that 'big men' really do gain more access to resources.[4]

One of the aims of my thesis was to further test this hypothesis, and I[5] present several lines of evidence to suggest that height is, indeed, linked to social sta-

4 An illustrative example of the phrase "a 'big' man" is Charlemagne (or: Charles the Great). Based on bone measurements (Rühli et al., 2010), the 'Father of Europe', born in 742, was estimated to be 1.84 meters tall, putting him in the 99th percentile for his time and place. Translated to present day, Charlemange would still have been 5 cm shorter than the author.

5 A thesis is a collection of scientific work by one person, the author, even though most, if not all, of the scientific work presented here has been conducted in collaboration. Thus, when I say 'I', I actually mean 'we', which is to say 'My co-authors and I'. For the sake of readability, I will use 'I', but rest assured that all my co-authors were of major importance in the work performed, and I fully acknowledge their contribution.

tus. These include the findings that both female and male height are related to both education and income in a sample of US high-school graduates (**Chapters 9** and **10; Figures 9.1b, c and 10.1b, c**); that only 7 out of 43 US presidents have been below average height and that, on average, presidents have been approximately 7 cm taller than the average population height (**Chapter 3; Figure 3.3**); and that professional football referees are taller than their assistants suggesting that the increased social rank of taller individuals can be found even in very homogenous settings (**Chapter 2; Figure 2.1**).

Although childhood living conditions undoubtedly contribute to the positive relationship between height and social status, it is also possible that social gradients reflect the greater social mobility of taller individuals (Bielicki & Charzewski, 1983; Bielicki & Szklarska, 2000). That is, taller individuals (regardless of social class) may compete more successfully against those who are shorter, and so attain higher status. A second aim of my thesis, therefore, was to investigate whether taller individuals showed increased dominance over shorter individuals, in ways that potentially could translate into various kinds of social advantage, and so contribute to their increased social status (**Chapter 4**; discussed below).

The secular trend in height

The finding that grown-up children are, on average, taller than their parents across all social classes, referred to as the secular trend in height, is also attributed to increased economic prosperity. This trend of increasing height is found across the globe, and has been observed in both developed and developing countries, although the onset of the trend may vary.

An increased standard of living as an explanation for the secular trend in height is well supported by the strong correlation between increases in height and increases in national gross product (Floud et al., 2011), child survival (Bozzoli et al., 2009), and life expectancy (Steckel, 1995, 2002b) within a population. This in turn reflects several important changes in public health, including the understanding of the germ theory of disease, increased personal hygiene, better health care for children including vaccinations, and improved diet (Steckel, 1995). The secular trend in height is so reliable in this respect that increases in height are widely used by historians and economists as a proxy for a nation's development and welfare levels (Floud et al., 2011; although this approach should be used with caution (Deaton, 2007; Steckel, 1995), and it does not seem to apply to all African height trends).

Environmental variation and between-population variation in height

There is marked variation in average height among countries, as shown clearly by the example of the Efe people of the Congo and the people of the Netherlands. The Republic of Congo and the Netherlands are, obviously, separated by many thousands of kilometers, and differ markedly in terms of their ecology, yet differences in stature can also be seen at a finer scale, between neighbouring populations. The Nzimé from Cameroon, for instance, are 12 centimeters taller than the neighbouring Baka tribe (Becker et al., 2012). Similarly, the Belgians and the Dutch share a language but are divided by height: Belgians are, on average, 5 centimeters shorter than their Dutch neighbors (Komlos & Lauderdale, 2007). How can we explain these between-population differences in stature?

It is apparent that much of this variation in height between populations results from differences in the standard of living, as described above. Accordingly, more developed nations tend to be taller than less developed nations. Furthermore, many developing nations are also now experiencing a secular trend of increasing height, as reflecting improved economic conditions, with some almost catching up to the average height of more developed nations (Garcia & Quintana-Domeque, 2007). Although economic prosperity is undoubtedly an important factor in explaining major differences between populations from different regions, it cannot account for the major height differences that exist between populations of equivalent wealth. The people of the Netherlands provide a particularly noteworthy example in this respect. In 1860, the average height for Dutch (military) men[6] was 165 centimeters, which was lower than many other Western populations. For instance, men from the US ranked number one in terms of average height from the 18th to the early 20th century (Komlos & Baur, 2004), towering over the Dutch by around 5-8 cm. One hundred and fifty years later, Dutch men now rank as the tallest in the world[7], with an average height of 185 centimeters[8]; an increase of 20 cm. This increase

6 Much of the historical data on stature is based on heights from conscripts (i.e., individuals in the military), which are often exclusively male. Female height data are therefore not readily available, and the reader will have to forgive me for presenting data on male heights alone in many comparisons.

7 Although people living in the Dinaric Alps (a mountain chain crossing several countries in Southern Europe) are the tallest in the world with men averaging 185.6 cm in stature (Pineau et al., 2005). The studied regions in Croatia and Bosnia and Herzegovina constitute only a small part of these countries, however, and average heights across these nations as a whole is still lower than that of the Dutch. Basketball players from the former Republic of Yugoslavia (through which these Alps run) have always been noted for their height (Pineau et al., 2005).

8 http://dined.io.tudelft.nl/en,1,dined2004,301#tabledata: The TU Delft DINED anthropometric database. With a height of 2.00 meters, the author is partly responsible for this high average.

in stature has been continuous and regular, with the exception of the periods covered by the two World Wars (Liestøl & Rosenberg, 1995; Silventoinen, 2003). In contrast, the heights of US males have increased by only 6 cm during this same period. Economic prosperity is not sufficient to explain the height discrepancy between the Dutch and the North-Americans because Americans actually have a higher per capita income, invest more in health care, and have a similar caloric intake compared to the Dutch (Steckel, 2002b). Part of the difference in average height can, however, be attributed to differences in social equality: despite its higher per capita income, social inequality is much higher in the US than in the Netherlands, and the health care system is not equally accessible to everyone. Greater equality in access to resources increases the average height of a population because the increase in height by the poor is stronger than the stagnation or decrease in the height of the wealthy. Interestingly, North Americans achieved near modern heights by the 1700s (Steckel, 1995, 2002a) when, somewhat ironically perhaps, income and wealth were probably more equally distributed than they are today and inequality was much reduced in the US compared to Europe.

Equivalent differences also exist for countries that lie in much closer proximity, not separated by an ocean. Although in most North-European countries, the secular trend in height has been slowed or stopped (Garcia & Quintana-Domeque, 2007), the Dutch, apparently not yet tall enough, keep growing taller (Fredriks et al., 2000). The reasons for the Dutch superiority in height have all been related to subtle variations in nutrition and health care. Social welfare, the medical system and universal health care are all of a very high standard in the Netherlands, and Dutch mothers are also known to make good use of the health care system (de Beer, 2004), all of which are likely to have substantial consequences for average stature. It has also been suggested that the type and quality of food eaten by the Dutch may give them an anthropometric advantage (Fredriks et al., 2000), as the Dutch consume a high proportion of dairy products, particularly milk (Fredriks et al., 2000; de Beer, 2012), which have a substantial influence on stature[9]. Thus, subtle variations in health care and nutrition between countries, which are not easily caught under the umbrella of economic prosperity, probably account for much of the variation in height that exists between populations. It is clear, then, that environmental factors exert a powerful influence on height, and can account for much of the individual variation in height seen between individuals and between populations. There is, however, another source of variation with potentially even

9 Drinking three glasses of milk from age ten to adulthood increases height by 2.3 cm, compared to drinking less than one glass per day (de Beer, 2012).

greater explanatory influence on an individual's height: genes.

GENETICS OF HEIGHT

It is clear that no genetics textbook can do without a discussion of human height any more than it can do without fruit flies. This is because human height is a classic example of a quantitative trait under genetic influence, and the study of stature was essential to the emergence of fundamental concepts in inheritance and genetics. Over a hundred years ago, in the late 19th century, Francis Galton, a cousin of Charles Darwin, was the first to address the genetic transmission of height. Galton (1886) clearly laid out why height was such an ideal subject of study: "*The advantages of stature as a subject in which the simple laws of heredity may be studied will now be understood. It is a nearly constant value that is frequently measured and recorded, and its discussion is little entangled with considerations of nurture, of the survival of the fittest, or of marriage selection*" (p. 251). Indeed, height can be readily and accurately measured, and the distribution of heights in a population lends itself perfectly to mathematical and statistical calculation (something which was acknowledged by Galton: "*The statistical variations of stature are extremely regular*", p. 251). Yet, Galton was wrong about the other 'advantages' of using stature as a subject of study. In contrast to Galton's confident assessment, height *is* related to 'nurture', the 'survival of the fittest' (**Chapters 8-11**), and 'marriage selection' (**Chapters 4-6**). These errors aside, it is nevertheless true that Galton was the first to show a relationship statistically between the heights of parents and the heights of their children, leaving the reader "*beyond doubt [of] the existence of a simple and far-reaching law that governs the hereditary transmission*" (p. 246).

Although Galton's research was suggestive in showing that stature is at least partly under genetic control, common environmental factors may equally well have caused the positive relationship between the heights of parents and offspring that he observed. The development of so-called "twin studies" would partially resolve this problem[10]. For several decades now, twin studies have been used to estimate genetic and environmental influences on complex trait variation. Such studies have contributed to an increased awareness that genetic variation exerts an influence on almost every conceivable facet of human life, including such trivial pursuits as watching television and Internet use (van Dongen et al., 2012). One of the most crucial pieces of information provided by twin studies is an estimate of a trait's 'heritability' (h^2 or H^2). Heritability de-

10 Note that this same Galton recognized the importance of twins for studying inheritance in 1875.

scribes the proportion of observable differences in a trait between individuals in a population that is due to genetic differences between these individuals (Visscher et al., 2008; van Dongen et al., 2012). In the classical twin design, heritability is based on a comparison of resemblance between monozygotic and dizygotic (or ‘fraternal’) twins (van Dongen et al., 2012). Monozygotic twins are formed from the splitting of a single fertilized egg cell and are therefore genetically identical. Dizygotic twins, in contrast, are a product of simultaneous but separate fertilisations of two individual eggs, and share on average 50% of their genome. Such twins are therefore no different than ordinary siblings, genetically speaking, yet their environments, both pre- and postnatal, are much more similar. The correlation of a certain phenotypic trait between monozygotic twins is then compared to the correlation of that trait in dizygotic twin to estimate its heritability.

Twin-studies have consistently shown that the heritability of height is around 0.80 (Perola et al., 2007; Silventoinen, 2003; Visscher et al., 2006, 2007), i.e., that 80% of the variation in height between individuals in a population is due to genetic differences. An example: from the 29 cm difference between the 5% shortest and 5% tallest in a typical European, 26 cm can be attributed to genetic underpinnings (McEvoy & Visscher, 2009; Visscher, 2008). In addition to twin studies, a recent innovative study used the genetic similarity between ordinary siblings to calculate the heritability of height. Ordinary siblings share 50% of their genes, on average, but their genetic similarity can vary with a standard deviation of 4% around this overall value (Visscher et al., 2006, 2008). Using variation in genetic similarity and the variation in height differences between pairs of sibs, a heritability of 0.80 was estimated (Visscher et al., 2006). The heritability estimate of 0.80 for height therefore seems to be exceptionally reliable: it has been observed repeatedly across different populations and using different methodologies, although it should be noted that its high value seems restricted to more affluent populations. Heritabilities in developing countries are slightly lower. For instance, the heritability in a Nigerian sample was 0.62 (Luke et al., 2001), in a Chinese sample 0.65 (Li et al., 2004), and in a Jamaican sample 0.74 (Luke et al., 2001). Similarly, with an increased standard of living, heritability also increases over time within a population (Silventoinen et al., 2000). A potential explanation for these findings is that in poor environments, differences in factors like food abundance exert a greater influence on adult height than an individual’s genetic make-up. In contrast, in richer environments differences in food abundance are less severe and, as a consequence, their effects on growth will be diminished compared to genetic effects (Charmantier & Garant, 2005).

The high heritability of stature does not mean that height is a result of genes that exert large effects, as scientists working on Genome Wide Association (GWA) studies have (somewhat reluctantly) discovered. Since the completion of the Human Genome Project in 2003, scientists have been able to identify genetic variants associated with certain traits and diseases by comparing individual genomes. As early as 1918, the geneticist and statistician Sir Ronald Fisher proposed that a 'polygenic' model could explain variation in height, implying that many genes, each with a small effect, had an influence on stature (Fisher, 1918). He was right. Whereas GWA-studies have shown that 83% of the variation in size between breeds of horses (which can differ by as much as one meter) can be explained by just four loci (Makvandi-Nejad et al., 2012), its success in explaining human body size has been less convincing[11]. In 2008, three consortia of research groups using GWA-techniques, examining over 63,000 individuals, at an estimated cost of 30 million US dollars, identified a total of 54 loci affecting variation in height (Visscher, 2008), which explained about 5% of observed variation. Height truly is a polygenic trait, as suggested by Fisher's analyses, with nearly 1% of all human genes contributing to height variation in some way (Lango Allen et al., 2010). Aulchenko and colleagues (2009) note that the 'Victorian method' of measuring parental heights to establish the height of offspring (as developed by Galton) will long stay unsurpassed in terms of both accuracy (about 40%) and cost. Although it is surely true that measuring parental heights is cheaper than fully genotyping individuals, recent progress in genotyping allows us to explain 45% of the variance in height when considering all genetic variants simultaneously (Yang et al., 2010).

Understanding more about genetic influences on height therefore helps to reinforce the fact (perhaps ironically) that the secular trend in height primarily reflects environmental influences, and is unlikely to be the consequence of any significant genetic change; height would not be expected to increase so rapidly over such a short period if this were the case (Deaton, 2007; McEvoy & Visscher, 2009). To be more precise, if the Dutch increase in height were solely genetic, this would mean that, in every generation, the 30% shortest individuals in the population had failed to reproduce at all (assuming a generation time of 25 years and a heritability of 0.8)[12]; a selection pressure high enough to be considered implausible (Kingsolver et al., 2001). It is worth noting, how-

11 Sex-chromosome abnormalities (e.g., having an additional X or Y chromosome) and certain kinds of mutations can profoundly affect height, yet they are too rare to explain any significant degree of variation in the population, and I will not discuss them further.

12 I thank Ido Pen for assisting with this calculation.

ever, that while genetic underpinnings are unlikely to have a major role in the secular trend in height seen around the world, their effects cannot be ruled out entirely. Furthermore, because height has such a high heritability, any selection on height is likely to be followed by a genetic response, resulting in succeeding generations being genetically shorter or taller. The question then becomes: why would selection act on height in the first place?

DARWIN'S LEGACY

Natural selection - the struggle for life

In 1859, Charles Darwin published '*On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*'; a monumental title for a monumental work of 540 pages, which took him almost two decades to write, and yet, at its heart, lies an idea so elegant, simple and clear that Thomas Huxley, Darwin's great friend, was moved to comment "*how extremely stupid not to have thought of that*" (Huxley, 1900, p. 189)[13]. As scientific theories go, it is entirely true that the theory of natural selection is one that is intuitively easy to grasp, being based on just three straightforward premises and their logical conclusion: (i) all organisms show variation in their morphology, behaviour or physiology ('The principle of variation'); (ii) organisms resemble their parents more than any other individuals in the population, i.e., part of the variation between individuals is heritable ('The principle of inheritance'); (iii) there is competition among organisms for scarce and finite resources, and some individuals compete better than others because of the way they vary from others of their kind. This competition occurs because organisms produce more offspring than can ever survive and give rise to breeding individuals ('The principle of adaptation'; or, alternatively, we can call this 'The principle of selection'). From this, it follows that some individuals will leave more offspring than others because the particular traits they possess allow them to survive and reproduce more effectively. The offspring of such individuals will inherit these advantageous traits, and 'natural selection' will have taken place. The gradual process by which the inherited characteristics of animals change over many generations is referred to as evolution.

Enormous progress has been made in evolutionary biology since Darwin, par-

13 Although French Nobel Prize winner Jacques Monod adds: "*Another curious aspect of the theory of evolution is that everybody thinks he understands it. I mean philosophers, social scientists, and so on. While in fact very few people understand it, actually, as it stands, even as it stood when Darwin expressed it, and even less as we now may be able to understand it in biology*." http://bioinfo.med.utoronto.ca/Evolution_by_Accident/Modern_Synthesis.html

ticularly with respect to the mechanisms of inheritance. These developments have led to the realization that, strictly speaking, organisms are not the focus of evolution, but rather genes inside the bodies of those organisms (Dawkins, 1976). A more appropriate definition of natural selection, therefore, is the differential survival of alternative alleles through their effects on replication success (Davies et al., 2012). Although genes supply the raw material of evolution, it is the body in which those genes reside in that gets 'selected' in its environment. Thus, the most successful genes are usually those that are most effective in enhancing the survival and reproductive success of the bodies in which they are found (or the relatives of that body).

Life history theory

An important concept related to natural selection is life history theory (Stearns, 1992). Life history theory aims at understanding how energy is allocated over the life course and rests on the simple principle that energy can be invested only once, such that energy used for one purpose cannot be used for any other. Thus, the concept that energy is 'traded-off' in various ways is key to an understanding of life history evolution. Perhaps the most important choice that every individual has to make is whether to invest in current or future reproduction. At the heart of this choice lies the trade-off between growth, somatic maintenance, and reproduction.

Life history strategies depend on the interaction between intrinsic and extrinsic factors. Intrinsic factors relate to how traits are connected to each other, and the resulting constraints on how these traits can vary. Extrinsic factors are ecological influences on survival and reproduction. Using these concepts of trade-offs, intrinsic and extrinsic factors, life history theory has proved to be very fruitful in explaining differences between species. Rates of mortality are, for instance, closely tied to age and size at maturity and longevity (Stearns, 2000). High extrinsic mortality usually leads to a fast life history, such that individuals grow and mature fast, reproduce at an early age, have large litters, and a shorter lifespan. These patterns can similarly be applied to cross-population differences in humans. The average lifespan of a population predicts the average age at first birth: in countries where adults are not likely to grow very old, women have their first child at an earlier age on average (Nettle, 2011). This pattern is also evident at even finer scales: differences in longevity between neighbourhoods in a UK city correlate with differences in age at first birth in line with the predictions of life history theory (Nettle, 2011; Nettle et al., 2010).

As a result of the trade-off between growth, somatic maintenance, and reproduction, an individual's body size, or height, can to an extent be viewed as the outcome of life history decisions. Indeed, different life-history strategies are likely to underlie variation in height between populations (Walker et al., 2006), and differences in ecological factors may help determine the optimal body size for a particular environment. One such factor is nutrition. When resources are limited, bigger bodies are likely to be disadvantageous because they have higher energy demands than smaller bodies (Blanckenhorn, 2000; Migliano et al., 2007). As a result, average height is predicted to be lower under such conditions. An additional extrinsic factor affecting optimal height in a population is the rate of mortality (both juvenile and adult; Walker et al., 2006). When individuals face high mortality risk, energy should be dedicated to reproduction rather than growth, so that individuals are able to reproduce at an early age, well before mortality is likely to kick in. Another example of an ecological factor influencing optimal height is temperature. Stress from heat or cold may be alleviated by increasing or decreasing respectively the ratio of surface area to body mass (Katzmarzyk & Leonard, 1998; Ruff, 2002). Following the pattern observed in other species, humans that inhabit colder regions are both heavier and have shorter relative limb length, thus reducing their surface area to body mass ratio (Katzmarzyk & Leonard, 1998). These thermoregulatory stressors affect weight and breadth more than height, as populations living in the tropics vary greatly in stature, but show little variation in body breadth (or width). In contrast, populations living in colder climates have absolutely wider bodies, and thus lower surface area/body mass, regardless of their stature (Ruff, 2002).

Life history trade-offs have also been suggested to explain the short stature of Pygmies, with all of the above ecological factors considered as possible explanations: the low average height of Pygmies has been hypothesized to reflect adaptations to a hot and humid climate, food scarcity, and high adult mortality (Becker et al., 2012; Migliano et al., 2007; Perry & Dominy, 2009). A more directly ecological hypothesis put forward to explain pygmies' reduced stature is the high density of forest cover, and the difficulty of maneuvering through such terrain with larger bodies (Perry & Dominy, 2009). Pygmy stature thus provides an excellent case study of the manner in which ecology can influence optimal body size.

Given both the predictions of life history theory and observed variation in ecology between populations, it seems highly unlikely that, for any trait, there exists a single optimal value that holds true for all populations (Marlowe &

Wetsman, 2001; Sear, 2010). Rather, we should recognise that optimal trait value will be contingent on those ecological factors specific to a given population. The benefits gained by attaining a certain height, for instance, will be entirely dependent on the unique properties of a given population in relation to its ecology, with the result that selection pressures on height are likely to vary widely across populations. In this thesis, I focus mainly on the relationship between height and natural selection in modern Western populations, whose ecology is characterized by low mortality and plentiful resources.

Natural selection and human height

Mortality is a key component determining an individual's ability to contribute offspring to the next generation, and there is strong selection on organisms to stay healthy and survive until they are mature enough to reproduce. It therefore seems reasonable to suppose that natural selection will act on human height, to the extent that this trait is related to health and survival.

There is some evidence to suggest that human height is related to health in Western populations. In a large sample of Finns, Silventoinen et al. (1999) found that taller men had a lower risk for long-standing illnesses and also perceived themselves as healthier than average height and shorter men. Shorter men, by contrast, were at greater risk for cardio-vascular diseases. These patterns were different for women, with shorter and taller individuals most at risk for having a long-standing illness, particularly a musculo-skeletal disease, compared to those of average height. Short women furthermore perceived themselves to be least healthy.

These patterns of health and disease are partially reflected in the link between height and all-cause mortality. A review by Sear (2010) indicated that, in Western populations, taller men have lower mortality than shorter men. Taller women also had lower mortality compared to shorter women in most studies, although some reported a curvilinear effect, such that average height women had highest survival[14] .The negative relationship between height and risk of death is mostly a consequence of the increased risk for cardio-vascular dis-

14 A review by Samaras (2009) concluded something strikingly different, namely that taller individuals have a shorter lifespan. Whereas Sear (2010) reviewed only those studies that employed longitudinal datasets and conducted a hazard analysis, Samaras' (2009) review focused exclusively on studies that used cross-sectional data and presented cross-population comparisons. As longitudinal data are obviously favoured over cross-sectional or cross-population data, I currently favour the conclusions drawn by Sear (2010). Nevertheless, the stark contrast in the inferences drawn by these reviews raises some doubt about the validity of either conclusion, and future research is perhaps needed to settle this issue.

eases in shorter individuals, although there is an increased risk of death by cancer for those of taller stature. Thus, short men and women tend to be at a disadvantage in terms of health and survival in Western populations. Too few studies have addressed these issues in non-Western populations to draw any meaningful conclusions (Sear, 2010).

Natural selection may also act on the ability to successfully raise children to adulthood, and shorter women seem at a disadvantage here, as child morbidity and mortality are negatively related to maternal height. Shorter women are also at a higher risk for complications during pregnancy and delivery, such as stillbirth (Bresler, 1962), failure to progress in labor (Sheiner et al., 2005), and the need for Caesarean sections (Kirchengast and Hartmann, 2007). In **Chapter 8**, I show that these effects can be quite substantial: shorter women have a 10% higher risk of an emergency Caesarean section compared to taller women when giving birth to their first child (**Figure 8.2a**). For women below 150 cm, this risk increases to over 50%. In addition to maternal height, I also show that the difference in height between parents is also related to the risk of complications at birth. Specifically, the likelihood of an emergency Caesarean section is higher when the father is much taller than the mother (particularly when the baby is heavy; **Figure 8.2c, d**).

In addition to the adverse effects of short stature during pregnancy, maternal height is related to the health of newborns. Shorter women are more likely to give birth to infants with relatively low birth weights (Camilleri, 1981), and with relatively low Apgar scores (a health assessment administered directly after delivery; Camilleri, 1981; Casey et al., 2001), both of which are predictors of child morbidity and mortality (Casey et al., 2001; McIntire et al., 1999). Moreover, maternal height is also negatively related to child mortality in developing (Monden and Smits, 2009) and low- to middle-income countries (Özaltin et al., 2010). As detailed in **Chapter 9**, most of the literature on this issue shows very clearly that taller women have increased child survivorship in non-Western populations (**Table 9.3**), and I was able to show that this relationship extended to a Western, low mortality population (**Figure 9.1a**).

Taken together, the above evidence suggests that natural selection is very likely to act on human height, and that it may do so differentially between the sexes. Shorter men and women are at a disadvantage in terms of health and survival in Western populations, which may affect their chances to reproduce. It is also apparent that taller women may suffer some penalty from their decreased health status. In addition, shorter women have both an increased risk of child mortality and of complications during delivery, which natural selection potentially disfavours. There is another potential evolutionary force acting on height that I have yet to consider, however, one that may be relatively important in low mortality environments: the ability to obtain a mate.

Sexual Selection - competing for mates by force or charm

Darwin (1859) recognized that, in some species, where male and females possessed the same general habits, striking differences nevertheless existed between the sexes. Thinking purely in terms of natural selection this seemed odd: surely, if a trait were beneficial to survival, then both sexes should possess it? Even more puzzling is that some of these sexually dimorphic traits seemed detrimental to the survival of their possessors. Darwin solved this conundrum by suggesting that the existence of such traits could be easily explained by "*what I have called Sexual Selection*" (p. 87). He continues: "*This form of selection depends, not on a struggle for existence in relation to other organic beings or to external conditions, but on a struggle between the individuals of one sex, generally the males, for the possession of the other sex. The result is not death to the unsuccessful competitor, but few or no offspring*."

Twelve years later he expanded on the issue in his book '*The Descent of Man and Selection in Relation to Sex*', in which he distinguished two forms of sexual selection (Darwin, 1871): "*The sexual struggle is of two kinds; in the one it is between individuals of the same sex, generally the males, in order to drive away or kill their rivals, the females remaining passive; whilst in the other, the struggle is likewise between the individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the more agreeable partners*" (p. 398). Sexual selection[15], then, refers to the competition for mates either by force (intra-sexual competition) or charm (inter-sexual selection). Is there any evidence that human height is related to sexual selection?

HUMAN HEIGHT AND INTRA-SEXUAL COMPETITION

In '*The Descent of Man*', Darwin suggested that males were larger than females in most mammals because males compete more strenuously for ac-

15 I have defined natural selection as the differential survival of alternative alleles through their effects on replication success. Sexual selection is a determinant of replication success, and as such falls under the umbrella of 'natural selection'. 'Natural selection' as used in the title of this thesis therefore also refers to sexual selection.

cess to mates, and large size is advantageous in such contests (Darwin, 1871; p. 260). Among mammals, larger males are indeed more likely to win fights against smaller males (Archer, 1988), and so occupy higher social ranks and show increased social dominance (Andersson, 1994; Ellis, 1994). Thus, the increased *physical dominance* associated with body size may enhance access both to resources and females (Andersson, 1994; Blanckenhorn, 2000).

For humans, there is some evidence to suggest that height is related to physical dominance, mirroring these findings from other mammals (Ellis, 1994): taller men are physically stronger (Carrier, 2011; Puts, 2010; Sell et al., 2009), more aggressive (John Archer & Thanzami, 2007), and have better fighting ability (Archer & Thanzami, 2007; Sell et al., 2009; von Rueden et al., 2008). The physical superiority of taller men is thought to contribute significantly to their achieving greater access to resources, both historically and cross-culturally (Ellis, 1992).

Physical strength and fighting ability are unlikely to be major determinants of social status in modern Western societies, however, given that individuals are prohibited by law from using force against another individual. Yet, in addition to the clear social gradient in height seen among contemporary Western populations, overwhelming evidence suggests that human height is also positively related to leadership, income and professional achievement, all of which are proxies for access to resources (Judge & Cable, 2004; **Chapters 2, 3, 9 and 10; Figures 2.1, 3.3, 9.1b, c, 10.1a,b**). Several hypotheses have been put forward to explain the relationship between stature and status for those societies in which physical force cannot be used with impunity. These include the relationship between height and parental resources (Persico et al, 2004); the decreased health of shorter men and women (Silventoinen et al., 1999); and the increased cognitive ability associated with height (explained by factors such as genes and/or nutrition; Silventoinen et al, 2004). Intriguingly, Persico et al. (2004) observed that taller individuals remained at an advantage with respect to achieving high status, even after controlling for all of the above variables, suggesting that other factors also contribute to this relationship. In my thesis, rather than interpreting the correlation between height and social status in contemporary populations as an indirect consequence of the relationship between height and those factors *causing* height, I consider the possibility that height *directly* influences the likelihood of obtaining high social status. More specifically, I test the hypothesis that height is related to *interpersonal dominance* in non-physical confrontations. Dominance in the animal kingdom is defined as 'an attribute of the pattern of repeated, agonistic interactions between two individuals, characterized by a consistent outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation' (Drews, 1993, p. 283). Although dominance as such is a relational measure (based on repeated interactions), and not an absolute property of an individual, for present purposes I will refer to interpersonal dominance as the likelihood that an individual will win a dyadic confrontation, and I test the hypothesis that the probability of winning is proportional to the height of individuals in relation to their opponents. The nature of such confrontations can be as diverse as society itself, and although the advantage of winning a single contest may be small, the accumulation of many small advantages may well be instrumental to achieving high social status.

In **Chapter 2**, I show that referees in the 2010 World Cup and the French Ligue 1, are on average over 4 cm taller than their assistants, suggesting that height matters in achieving the highest position within the officiating team (**Figure 2.1**). Additionally, I show that taller referees assign fewer fouls during a match, compared to shorter referees (**Figure 2.2a**). This suggests that taller referees, because of their increased dominance, are better able to keep control of the match, resulting in players committing fewer fouls. This, in turn, suggests that, because taller referees are better able to keep control, they are more often assigned to adjudicate more prestigious and/or important matches between high-ranking teams compared to shorter officials (**Figure 2.2b**).

Although the above results are suggestive of a relationship between height and dominance, data on direct confrontations and dominance are needed to provide a more convincing and conclusive test. In **Chapter 3**, therefore, I test whether stature has any influence on individuals competing for one of the most important positions in the world: the US presidency. As predicted, the height of the candidates was found to influence significantly the outcome of presidential elections: 15% of the variation in the proportion of popular votes received was predicted by the ratio of the height of the candidates (**Figure 3.1**). That is, the taller a candidate was compared to his opponent, the higher proportion of popular votes he received. Moreover, Presidents that were reelected were taller than those denied a second term (**Figure 3.2**). Moreover, these effects were found in a sample already biased towards tall men: on average, presidential candidates were 7 cm taller than the average US male (**Figure 3.3**). Height is a surprisingly important determinant of contest outcome for one of the most influential and important political positions in the world.

The effect of height on the outcome of a confrontation was also apparent in a behavioural experiment I performed, in which male and female participants interacted in a same-sex dyadic negotiating game (**Chapter 4**). Participants were first asked to individually rank twelve items (e.g., extra clothing, a pistol, a compass) on importance for survival (the "Arctic survival task"). Subsequently, participants were assigned to same-sex pairs at random, and were instructed to rank the items again, but this time as a team. As a measure of interpersonal dominance, I examined the extent to which the joint ranking diverged from the subject's initial rankings. I found that relatively taller individuals had a larger influence on the joint rankings, but only when the difference between initial rankings was large (**Figure 4.5**).

Having established an effect of height on interpersonal dominance using an experimental approach, I then conducted a series of observational studies (**Chapter 4)** in order to assess whether such effects could also be detected in more ecologically valid settings; more specifically, I investigated the effect of height on the outcome of brief, natural encounters between unrelated individuals in the absence of verbal interaction. This is important because patterns that emerge in a controlled laboratory setting may be quantitatively unimportant in the real world. In the first observational study, customers were observed entering and leaving a supermarket, the entrance to which involved passing through a passageway that was too narrow for two individuals to walk through simultaneously. Thus, when one individual entered the supermarket at the same time as someone else was trying to exit, one individual had to give way to the other, which I considered a confrontation. The results showed that men and women who gave way to others were, on average, 4 cm shorter than the individual they let pass (**Figure 4.2**).

In a follow-up study (**Chapter 4**), confederates of varying height walked in a straight line through a busy shopping street against the flow of pedestrian traffic, while others recorded who gave way (or did not) to the confederate. People were significantly more likely to give way to a taller confederate than to a shorter one (**Figure 4.3a, b**). Furthermore, pedestrians were less likely to bump into a taller compared to a shorter individual (**Figure 4.3c, d**). In a third observational study (**Chapter 4**), confederates were positioned such that they partially blocked a busy pathway. When confronted by a same-sex individual blocking the pathway, taller pedestrians were more likely to maintain their direction and heading, thereby passing in closer proximity to the blocking individual than shorter pedestrians (**Figure 4.4**). In contrast, when the blocking individual was of the opposite sex, shorter individuals were more likely to maintain their path. Thus, multiple studies, using a diverse array of methodologies, support the notion that human height is positively related to interpersonal dominance.

This raises the question of *how* human height directly relates to dominance in non-physical confrontations. Possible explanations include the fact that, first, even though using force against other individuals is prohibited by law, the increased physical strength (Sell et al., 2009) and fighting ability (von Rueden et al., 2008) of taller individuals may be perceived by others as more threatening, even if the contest is non-physical. Taller people are also perceived as more competent, authoritative, and dominant (Cinnirella & Winter, 2009; Judge & Cable, 2004; Marsh et al., 2009; Young & French, 1996; Blaker et al., in press), and taller US presidents were similarly perceived to be "greater" as President, and possessing more leadership qualities (**Chapter 3; Figure 3.4**). These height-dependent perceptions by others can contribute to increased dominance of taller individuals, if others perceive such individuals as more competent, authoritative, and dominant than themselves. Height may also affect how we regard and behave ourselves (which, in part, reflects how other people perceive us). For instance, taller people, particularly men, tend to have higher self-esteem than shorter people (Judge & Cable, 2004), which may result in taller individuals behaving with greater self-confidence in various kinds of social interaction. To some extent, then, the greater dominance of taller men may be the result of an expectancy effect or 'self-fulfilling prophecy".

HUMAN HEIGHT AND INTER-SEXUAL SELECTION

Studies of sexual selection in humans have focused primarily on the traits that make an individual attractive to the opposite sex (Puts, 2010); that is, intersexual selection[16]. A central premise of this form of sexual selection is that traits that signal high reproductive potential should be preferred (Marlowe & Wetsman, 2001). More specifically, men seem to prefer cues that signal fertility and health in women, whereas women apparently look for cues of genetic quality and resources in men. These differences in preferred traits are thought to arise from differences in parental investment between the sexes (Trivers, 1972). Parental investment is usually higher in females, who are initially biased towards higher investment levels by the fact that the size of the female egg cells are bigger than the sperms cells of males. Because of this imbalance in investment, male reproductive success is more constrained by the number

16 Sometimes referred to as 'mate choice'. This term however implies that 'choice' is the only relevant aspect of this domain of sexual selection. **Chapter 6** should make clear that this is not the case.

of matings gained, whereas female reproductive success is more constrained by the quality of the resources available, which are often provided by males. As a result, females often have more to lose from poor mate choice decisions than males, which explains why females are usually the choosier sex. Human offspring are very costly to raise, because of their long period of dependence before reaching adulthood. Thus, humans have to invest heavily in order to produce offspring that will be able to reproduce themselves. Even though a human male possesses sufficient sperm cells to repopulate the earth if needed, the resources provided by a male are often limited, and hence males cannot easily raise large numbers of offspring[17]. Because of these limitations, men also show some degree of choosiness. Male choosiness is even higher when a monogamous mating structure exists, and the choice of a female partner largely determines the reproductive success of a male, as in the case of contemporary Western human populations.

Human height is potentially under sexual selection because stature may operate as a cue that signals greater potential to contribute to the reproductive success of the opposite sex. As discussed above, shorter women are at a disadvantage when it comes to health, mortality, obstetric problems, and offspring survival. A preference for average height or taller women, therefore, can be considered adaptive from this perspective. However, taller women are fertile at a later age than shorter women, which may also factor into male mate preferences.

When male height can be used as a cue in inter-sexual selection, women are predicted to favour tall men. Taller men are healthier, have lower mortality, and greater access to resources (see above; **Chapters 2**, **3**, and **10**). There may, however, be a limit to the women's height preferences. Women who are partnered to men much taller than themselves experience an increased risk for emergency Caesarean section (**Chapter 8; Figure 8.2c**). Thus, women potentially face a trade-off between the benefits associated with increased partner height and the costs of an increased risk of obstetric complications. Given the complexity of the potential selection pressures operating on humans, and the limits on both male as well as female abilities to invest in young, predicting exactly what each sex will favour with respect to height is equally complex,

17 Although historically there have been some extremely reproductively successful men: Genghis Khan (~1162-1227) is perhaps the most extreme example with 1 in 200 men in the entire world believed to be direct descendants of the founder of the Mongolian empire (Zerjal et al., 2003). Similarly, Ismael the Bloodthirsty (~1634-1727) is said to have fathered 867 children. In comparison, the largest number of children born to a woman is 69. However, these children were born in 'only' 27 births.

and not always obvious. In the next section, then, I present an initial exploration of how height influences mating preferences, choice and pairing decisions.

Preferences and pairing in relation to height

Human height is a partner characteristic that is valued by both men and women, and preferences for partner height have been well studied (reviewed in Courtiol et al., 2010b). In general, average height women and above-average height to taller men are considered most attractive by the opposite-sex. Non-random mating patterns with respect to height have also been observed in several populations, suggesting that these lab-based preferences play out in the real world, at least to some degree. Below, I consider these preferences for partner height in more detail, and consider the extent to which these preferences are realized among actual couples. In addition to reviewing previous research (mostly based on an extensive review by Courtiol et al., 2010b), I also present data from my own studies of a large sample of Dutch students (**Chapter 5**), US speed-daters (**Chapter 6**), and UK parents (**Chapter 7**).

Assortative mating

In both men and women, questionnaire-based data suggests that, as the height of an individual increases, so does the preferred height of their partner, indicating preferences for assortative mating (Courtiol et al., 2010b). Similar patterns have been found in responses to both online advertisements (Pawlowski & Koziel, 2002) and at speed dating events (Kurzban & Weeden, 2005). These assortative preferences are also apparent in my studies of a student sample (**Chapter 5; Figure 5.1**) and a sample of speed-daters (**Chapter 6; Figure 6.1**).

Assortative mating for height also exists among actual couples (Gillis & Avis, 1980; Mcmanus & Mascie-Taylor, 1984; Oreffice & Quintana-Domeque, 2010; Silventoinen, Kaprio, Lahelma, Viken, & Rose, 2003; Spuhler, 1982). Spuhler (1982), for instance, reviewed assortative mating with respect to physical height in 28 populations from across the world and found an average between-partner height correlation of .2. Similarly, in both the student sample (**Chapter 5**) and British sample of parents (**Chapter 7**; **Figure 7.1)**, I show that partner heights are positively correlated. The strength of assortative mating observed in these couples is lower, however, than the strength of the preferences for assortment with respect to height apparent from preference studies

(**Chapter 5**; Courtiol et al., 2010b). This implies that an assortative preference for height is only weakly realized in actual couples.

Male-taller norm (female-shorter norm)

In general, women prefer men who are taller than themselves and, conversely, men prefer women who are shorter than themselves (Courtiol et al., 2010b; Fink, Neave, Brewer, & Pawlowski, 2007; Pawlowski, 2003; Salska et al., 2008). In **Chapters 5** and **6**, I extend these findings by showing that this male-taller preference is particularly pronounced in women (**Figures 5.1** and **6.1**). That is, when asked what height would be minimally acceptable in a partner, women reported that they wanted a partner that was at least 4 cm taller than themselves, on average (**Chapters 5** and **6**), whereas men did not necessarily prefer to be taller than their partner. This male-taller norm is again found in actual couples: Gillis and Avis (1980) report that, in only 1 out of 720 US/UK couples, was the woman taller than her partner. If couple formation occurred at random with respect to height, the number of couples in which the female was taller than the male would be approximately 2 out of 100, because women are, on average, shorter than men. This low value is, however, still 14 times higher than the observed 1 / 720 (see Sear (2006) for a more recent study replicating this finding in a Western population), suggesting a strongly expressed male-taller norm in this population.

To establish whether this same male-taller norm existed in the sample of British couples (**Chapter 7**), I compared the distribution of height differences of actual couples to simulations of random mating with respect to height. More specifically, I generated 10,000 samples in which men and women from the sample were randomly paired, after which the distribution of height differences resulting from these generated samples were compared to the observed height differences in the population. Clear evidence was found for a male-taller norm, as men were more frequently taller than their partner than would be expected by chance (**Figure 7.2b**). I extended this finding by showing that couples in which the man was much shorter than the woman were relatively less likely to occur than couples in which the man was only slightly shorter than the woman. Thus, when the male-taller norm is violated, there is only a very slight deviation. Although the male-taller norm was present in this population, the magnitude of it was low: when mating was at random with respect to height in simulated samples, the male-taller norm was violated in 10.2% of the couples, whereas in the actual population this norm was violated in 7.5% of the couples; a 26.3% reduction.

Male-not-too-tall norm (female-not-too-short norm)

Not only do both men and women prefer the man to be taller than the woman in a romantic couple, they also prefer that the man should not be too tall relative to the woman: the 'male-not-too-tall norm' (Courtiol et al., 2010b; Fink et al., 2007; Pawlowski, 2003; Salska et al., 2008). In a sample of British undergraduates who stated their height preferences, the largest acceptable height difference reported for both sexes was that the man should be no more than 26 cm taller than the woman (Fink et al., 2007). Men and women also stated their maximal accepted partner height in the two samples studied for this thesis. In the student sample, both men and women reported an average maximum acceptable height difference of 25 cm between the man and the woman. Similarly among speed-daters (**Chapter 6**), men tolerated a height difference of 25 cm, but women were more tolerant of, and more willing to accept, on average, a height difference of 28 cm. A conflict in height preferences between the sexes was also observed: on average, women preferred larger partner height differences than men (Courtiol et al., 2010b; **Chapters 5** and **6**).

The extent to which the male-not-too-tall norm is expressed in actual couples has not been studied previously. Again, comparing the distribution of height differences in actual couples to simulations of random mating with respect to height in British parents, I was able to show that the male-not-too-tall norm also exists in actual pairs (**Chapter 7; Figure 7.2**). Couples in which the male was more than 25 cm taller than the female partner occurred at a significantly lower frequency than expected by chance. As with the male-taller norm, when the male-not-too-tall norm was violated, the deviation was slight (e.g., a partner height difference of 30 cm was relatively more likely to occur than a partner height difference of 35 cm, but both were less likely to occur than expected by chance). Again, the size of this effect was not large: while 15.7% of the couples were predicted to violate the male-not-too-tall norm under random mating in simulated populations (with the assumption that the norm lies at a height difference of 25 cm), in the actual population this norm was violated by 13.9% of the couples; a reduction of 11.7%.

Preferred partner height differences are dependent on one's own height

According to Pawlowski (2003), preferred partner height differences are dependent on an individual's own height: both shorter men and taller women prefer smaller partner height differences than do taller men and shorter women. In both the student and the speed-dating samples that I analysed, this same pattern of preference was observed (**Chapters 5** and **6; Figures 5.1** and **6.1)**. In addition, partner height differences were dependent on an individual's own height in the sample of actual British couples used in a different set of analyses (**Chapter 7**). Notably, however, realized differences with respect to height between actual partners were different from those reported in preference studies (**Chapter 5**; Courtiol et al., 2010b). In conclusion, although all known preference rules for height were qualitatively realised in actual couples, these effects were generally modest and much lower than those inferred from explicitly stated preferences.

From preferences to choice to pairing

Many factors can prevent an individual from realizing its preferences when it comes to making an actual choice of partner. A low availability of mates that possess the preferred traits(s) will obviously constrain and limit choice (Widemo & Sæther, 1999), but even under conditions when numerous potential mates are available, assessing each individual may require such a prohibitive amount of time and resources, that a compromise is inevitable (Fawcett & Johstone, 2003; Reynolds & Gross, 1990; Widemo & Sæther, 1999). Even when preferred potential mates are both located and selected, there is still no guarantee that an individual will be able to exert its choice due to competition from same-sex rivals (Wong & Candolin, 2005).

It is also the case that a wide variety of traits are factored into the process of mate choice, and it is highly unlikely that a potential mate will possess all the traits that a given individual prefers (Buss et al., 1990; Fawcett & Johstone, 2003). In addition, for some preferred traits, there is a likely to be a trade-off: there is evidence to suggest, for instance, that cues of attractiveness trade-off against parental investment (Magrath & Komdeur, 2003). Thus, there is no reason to expect that mate preferences can and will be realized in actual choice.

Finally, even once a mate has been selected, there is no guarantee that this choice will inevitably lead to successful pair formation. It is entirely possible that mate choice will not be reciprocated (Baldauf et al., 2009; Johnstone et al., 1996) and, after a pair is formed, there is always the risk that the partner is then taken by more attractive alternatives (Rusbult & Buunk, 1993). Mating preferences alone therefore provide little predictive power with respect to establishing the actual mating patterns of a population (Courtiol et al., 2010a); a point of great pertinence to studies of human mate choice, which have placed a disproportionate emphasis on mate preferences alone.

As part of an attempt to remedy this situation, in **Chapter 6**, I explore the relationship between preferences, choice and pairing in relation to height in a speed-dating setting. Human speed-dating provides an excellent 'model system' in which to investigate the association between these processes. In essence, speed-dating events allow single people to meet a large number of number of individuals over the course of an evening, and potentially find a suitable "match". All individuals meet and converse with each other over the course of a 3-minute 'date', and then indicate whether they would be willing to engage in further contact (by responding "Yes" or 'No" on a designated score sheet). If two individuals respond positively to each other on the score sheet, they make a "match", and the speed-dating agency provides each party with the other's contact details so they can arrange to meet again, in a more conventional setting (For more details see **Chapter 6**; Finkel & Eastwick, 2008; Kurzban & Weeden, 2005, 2007; Lenton & Francesconi, 2011).

From preferences to choice to pairing: the case of height

The increased attractiveness of taller men and average height women as revealed by preference studies (discussed above; see also **Figure 6.2**), was very much in line with the association between height and popularity observed during speed-dating. Average height women were chosen more frequently (i.e., received a 'Yes' response) than either shorter or taller women (**Figure 6.4b**). Similarly, taller men had a higher chance of receiving a 'Yes' response than shorter men. Given these similarities between the average population preference for height and the average choices for height made during speed-dating (**Figure 6.4b**), there is the temptation to conclude that preferences do, in fact, map directly onto choices. A more detailed examination of whether an individual's height preferences translated into actual choice (**Figure 6.3**), however, revealed that non-preferred potential partners retained a high (albeit reduced) probability of being chosen (42.8% and 25.4% for men and women respectively).

In addition, as argued above, even when a preferred mate is chosen, there is no guarantee that such choices lead to successful pair formation when the choice is not reciprocated. Indeed, I found that, on average, men favoured quite small height differences (7 cm) when making their choices, whereas women favoured significantly larger height differences (on average 25 cm; **Figure 6.5**)[18]. The highest likelihood of pair formation was therefore at a height

18 Dudley Moore, British actor and comedian (1 meter 58) summarizes it best: "I'm attracted to tall women, but I have no choice..."

difference of 19 cm, which lay between the most frequent choices of men and women. Thus, the conflict in choice between the sexes that arises through mutual mate choice (and which is also apparent in their stated preferences: **Chapters 5 and 6**), ultimately results in sub-optimal pair formation for each sex.

Given that preferences for partner height are only partially realized in actual choice, it seems likely (and indeed obvious) that individuals take into account a variety of other characteristics besides height when choosing a mate. Given that non-preferred partners were still very likely to be chosen, it would seem that height, while highly salient and clearly of significance in choice and pairing processes, is not so important that it prevents individuals from going against their stated preferences. It is also clear that individuals' choice of partners often goes unreciprocated, as one would expect given a process of mutual mate choice, and that this, in turn, gives rise to sub-optimal pair formation with respect to height for both sexes. Overall, it is apparent from these findings that the pathway from mate preferences to pairing is long, convoluted and somewhat unpredictable.

Height is valued more by women and is more important for men's satisfaction with their own height

One consistent feature of mate preferences in relation to height across all my studies was that women place more on importance on height in their (potential) partner than men. First, in both my samples in which preferences were measured (**Chapters 5** and **6**), I found less variation in all measures of preferences across women than men, suggesting that women agree more on what constitutes preferred partner height. Because of this, the difference between the least preferred and most preferred height is much higher in women than in men. This was evident from both stated preferences (**Figure 6.2**), and also from the chances of receiving a 'Yes' response during speed-dating (**Figure 6.4b**). Second, women reported a narrower preferred height range than men and they also displayed a narrower range of chosen heights during actual speed-dating. Thus, not only did women possess both a narrower preferred and chosen height range than men, but they were also less likely to respond positively to an individual falling outside of their preferred range (**Figure 6.3**). Third, male but not female height was related significantly to the chance of obtaining a match (**Figure 6.4c**).

The finding that women place more importance on partner height than men is also apparent when examining how satisfied men and women are with their partner's height in the student sample (**Chapter 5**). Female partner height had no influence on men's satisfaction with respect to height (**Figure 5.2d**), whereas women were most satisfied with their partner's height when he was tall rather than short (**Figure 5.2c**). Partner height differences were also more important in explaining partner satisfaction in women than in men: women were most satisfied with their partner's height when he was 23 cm taller than they were, whereas men were most satisfied with their partner's height when they were only 8 cm taller than their partner (**Figure 5.3**). These optima are remarkably similar to those obtained when examining the highest likelihood of choice with respect to partner height difference made during speed-dating (25 cm and 7 cm respectively). Thus, women not only state that they prefer larger partner height differences, but they also choose larger partner height differences, and they are also more satisfied with larger partner height differences than men.

Given the importance that women place on partner height compared to men, it is not surprising that satisfaction with one's own height is more important for men than for women. Using data from the student sample and a sample of 58,823 men and women collected via the internet by Lever et al. (2007), I was able to show that height is a much more important factor in explaining satisfaction with one's own height for men (student sample: 32% and internet sample: 32%) than it is for women (student sample: 7% and internet sample: 14%). Unsurprisingly, given the role of male height in aspects of mate choice, men who are taller than average report the highest level of satisfaction with their own height, whereas shorter men report least satisfaction (**Figure 5.2a**). For women, in contrast, those who are only slightly above average height report greater satisfaction with their own height than do shorter and taller women (**Figure 5.2b**).

SELECTION PRESSURES ON HUMAN HEIGHT

So far, I have established that height is related to a number of proxies of both natural and sexual selection in human populations, dealing with both the ability to obtain a mate and intra-sexual competition in some depth. The logical next step is to ask whether any of these height-related factors significantly influence reproductive success. In **Chapters 9** and **10** of my thesis, I therefore present analyses on the relationship between height and reproductive success using data from the Wisconsin Longitudinal Study, a long-term study of a random sample of 10,317 men and women who graduated from Wisconsin high schools in 1957 (for a more elaborate description of the sample see the Material and Methods of **Chapters 9-11**).

Is human height related to reproductive success in the Wisconsin Longitudinal Study?

Female height

Among Wisconsin high-school graduates, a negative relationship between female height and reproductive success was observed, such that shorter women had the highest number of children (**Chapter 9; Figure 9.1a**). Short women (two standard deviations below average height) were predicted to give birth to 0.6 (18.9%) more children than tall women (two standard deviations above average height).

Previous studies have noted a positive relationship between female stature and child survivorship (Monden & Smits, 2009; Özaltin et al., 2010), possibly because of the increased obstetric problems associated with lower maternal height and the consequences thereof (**Chapter 8**). In our sample, female body size was also positively related to child survival to the age of eighteen (**Figure 9.1a)**. As child mortality was low in this sample (~5%), however, the increased number of ever-born children translated into higher reproductive success for shorter women, despite the decreased child survival these shorter women experienced.

Given that women of average height are considered most attractive in both preference studies and speed-dating studies (Courtiol et al., 2010b; **Chapter 6**), one might expect that average height women either would marry at a younger age or be more likely to be married than either shorter and taller women. Instead, married women tended to be shorter than non-married women, and among married women, those who married youngest were the shortest (**Chapter 9**). The negative effect of height on reproductive success was attenuated when controlling for age at marriage, indicating that shorter women partly achieved their higher reproductive success by marrying at an earlier age.

Education and income, both known to have a negative association with female reproductive success (Hopcroft, 2006; Nettle & Pollet, 2008), and these findings were replicated in this sample. The finding that shorter women are more reproductively successful could therefore be mediated by the fact that taller women are having fewer children because they are more likely to be educated and wealthier. Controlling for these measures of social status (which indeed were negatively associated with reproductive success; **Figure 9.1b, c**) did not, however, affect the negative relationship between female height and reproductive success. Overall, then, these results show that shorter women had the highest reproductive success, partly because they were more likely to get married and to do so at a younger age (**Chapter 9**).

Male height

The relationship between male height and reproductive success in the Wisconsin sample was substantially different to that observed in women (**Chapter 10**). Average height men attain higher reproductive success (i.e., produce more children in their lifetime) than both shorter and taller men (**Figure 10.1a**). More specifically, the highest reproductive success (predicted to be 2.6 children) was obtained by men slightly (but non-significantly) below average height. Men who were two standard deviations (12.9 cm) shorter or taller than the optimum produced 0.24 fewer children (a reduction of 9.3%).

Although height was not related to either being married or to the total number of marriages, average height men did marry at an earlier age than shorter and taller men. Controlling for age at marriage attenuated the relationship between height and reproductive success, suggesting that average height men produced more children by marrying at a younger age. If we consider age at marriage as a proxy for mate value, then it would seem reasonable to suggest that average height men were considered most attractive in this sample. If this were the case, however, the finding that taller men married at a later age is at odds with the previously described positive association between height and mate preferences (**Chapter 5**) and success during speed-dating (**Chapter 6**).

Previous research has shown that income has a positive effect while education has a negative effect on male reproductive success (Hopcroft, 2006; Nettle & Pollet, 2008), and these findings were replicated in this sample. As height is positively related to education and income cross-culturally, the relationship between height and reproductive success may be determined by these measures, as least in part. Although height was positively related to both education and income in this sample (**Figure 10.1b, c**), controlling for these measures of social status did not affect the curvilinear relationship between height and reproductive success. Taken together, then, these results suggest that, in this sample, average height men have highest reproductive success partly because they marry at a younger age than both shorter and taller men, but not because they are more educated or have higher incomes. What is most notable about these findings, however, is the stark contrast between the selection pressures acting on female height and those acting on males.

Intralocus sexual conflict

Sexually antagonistic selection pressures - that is, differential selection on a trait for males and females - can lead to intralocus sexual conflict. This conflict occurs when the genetic expression of a trait is determined similarly in each sex (i.e., there is a strong intersexual genetic correlation; Bonduriansky & Chenoweth, 2009), but the trait undergoes contrasting selection; as a result, the selection pressures on one sex constrain the other from achieving its sex-specific fitness optimum. Consider the example of human hip width: wide hips are necessary for childbirth, but they impair efficient locomotion. Thus, selection pressures will 'push' women to having wider hips, whereas selection on men will 'push' them toward a narrower optimum hip width. A problem thus arises when hip width is heritable, and is similarly expressed by the sexes: women with wider hips will produce daughters with beneficial wider hips, but their sons will also possess wider hips that are less beneficial for males (and vice versa for mothers with narrow hips). Thus, whether the expression of hip width is beneficial depends on the sex of the individual in which the trait is expressed. The sexes are competing, as it were, for the optimal genes in their body. It is this process that characterizes intralocus sexual conflict.

Something similar may occur with respect to height, because average height men enjoy the highest reproductive success, whereas the greatest reproductive success in women is associated with below-average height. Given that height is highly heritable, intralocus sexual conflict is likely, particularly because the sex-specific expression of height is very limited (Silventoinen, 2003; Silventoinen et al., 2001): tall parents get tall sons *and* tall daughters and short parents get short sons *and* short daughters. It should also be noted, however, that intralocus sexual conflict need not always occur; parents may, for instance, bias their sex ratio to resolve the conflict. In brown anoles (lizards) large body size is beneficial for male reproductive success, but detrimental to that of the female. When female anoles mate with large males, they produce more sons than daughters, whereas they produce more daughters than sons when they mate with small males (Cox & Calsbeek, 2010). In addition, maternal and paternal effects can resolve intralocus sexual conflict. That is, investing resources differentially in offspring may overcome an offspring's initially weak starting position, genetically speaking (Foerster et al., 2007). Given these possibilities, I therefore investigated whether intralocus sexual conflict occurs over human height.

To this end, I extended the above analyses from the Wisconsin Longitudinal Study to include data from the siblings of the respondents (**Chapter 11**). This provided data on 3,522 sibling pairs with full information on height and the number of ever-born children. This analysis revealed clear evidence for intralocus sexual conflict (**Figure 11.1**): in short sibling pairs, greater reproductive success accrued to the female sibling compared to the male sibling, whereas in average height sibling pairs greater reproductive success accrued to the male sibling compared to the female sibling. To put this in concrete terms: should you be born into a short family, you would be more likely to have nieces and nephews via your sister than your brother. In contrast, should your family be of average height, your brother would be more likely to make you an aunt or uncle. In contrast to the clear evidence for intralocus sexual conflict, there was no evidence of any relationship between height and offspring sex-ratio (in line with Denny (2008), using a much larger sample), indicating that, at least with respect to height, humans do not attempt to bias their sex-ratio to reduce intralocus sexual conflict.

Intralocus sexual conflict has previously been argued to underlie variation in reproductive success (and its components) in humans, and is one of the drivers of genetic variation in fitness in a population. Male homosexuality, for instance, is hypothesized to be a consequence of alleles that increase female fecundity but are detrimental to male fecundity (Camperio-Ciani et al., 2004). Variation in sibling attractiveness has also been attributed to intralocus sexual conflict (Garver-Apgar et al., 2011): physically and hormonally masculine men and women rated their brothers as more attractive than their sisters. I therefore extended these existing studies by showing that sexually antagonistic selection acts on a heritable, sexually dimorphic physical characteristic (human height), and that it results in intralocus sexual conflict in ways that influence Darwinian fitness as measured by number of children (**Chapter 11**).

Do short women and average height men show greater reproductive success in general?

To assess the generalizability of the relationship between height and reproductive success in the Wisconsin Longitudinal Study (i.e., the increased reproductive success of short women and men of average height), I reviewed all previous work that considered this question (**Chapters 9** and **10**). Methodological issues, such as differences in sampling procedures, variation in sample size (and hence statistical power), and the selection of variables considered in a statistical analysis, can lead to marked differences in the nature of the selection pressures identified, and these are extensively discussed in **Chapters 9** and **10**.[19]

Between-population variation in selection pressures on female height

Since my review on the relationship between female height and reproductive success (**Chapter 9**; **Table 9.3**), one additional study has been published (namely Sorokowski et al., 2012[20]). To investigate patterns of variability, I divided studies into those conducted on Western and non-Western populations. In non-Western populations, there was a high degree of variability in the association between female height and reproductive success: taller woman had the greatest number of children in three populations, average height women were the most reproductively successful in two populations, and shorter women had the highest reproductive success in five populations. In contrast, all five Western populations studies to date (and in which a significant effect was found) reported a negative association between height and reproductive success.

Between-population variation in selection pressures on male height

Two additional studies (Sorokowski et al., 2012; Stearns et al., 2012[21]) have been published on the relationship between male height and reproductive success, since my review on this topic (**Chapter 10**; **Table 10.1**). As with the results for women, there was more consistency in the relationship between height and reproductive success for men in Western compared to non-Western populations. In non-Western populations, taller men had the most children in one population, shorter men did so in two populations, and average height men were also found to have greater reproductive success in two populations. In Western populations, male height was positively related to the number of

19 Many studies reported a null finding between height and reproductive success (**Tables 9.3** and **10.1**), which are likely due to insufficient sample sizes and therefore low statistical power to detect an effect (discussed in **Chapters 9** and **10**). In this Chapter, I will not consider these null findings any further.

20 Sorokowksi et al. (2012) investigated the Yali tribe of West Papua and found that height was not related to any measure of reproductive success in females ($N = 54$).

21 Sorokowksi et al. (2012) did not find a relationship between height and reproductive success in males from the Yali tribe of West Papua ($N = 52$), while Stearns and colleagues (2012) found that, in a large sample of US men ($N = 2,655$ males, plus two generations of descendants of those males), men of average height had most offspring.

offspring in two studied populations, and curvilinearly related to reproductive success in five studies. Male height was not negatively related to reproductive success in any Western population. One study reporting a positive effect (Pawlowski et al., 2000) did not test for non-linear effects, while the other study reporting a positive effect concerned the West-Point graduates, which may be a particularly biased sample (discussed in **Chapter 10**). Accordingly, I conclude that the most likely relationship between height and reproductive success in Western populations is that average height men have the highest reproductive success. One final word of caution: all the observed curvilinear effects of height were found in US populations, and as such cannot be considered fully independent of each other.

Theoretical reasons why selection pressures on height may be population dependent

Selection pressures can differ substantially among populations and/or over time. Siepielski et al. (2009), collecting over 5,500 estimates of selection pressures on a variety of morphological traits, found considerable year to year variation in both the strength and direction of selection on these traits, and this may also hold true for height. Moreover, on the basis of life history theory, one would not expect a given height to be favourable across all environments. As discussed previously, the trade-off between growth, survival and reproduction is, in fact, expected to give rise to different adaptive values of body size depending on the population. Bigger most certainly is not always better (Sear, 2010). Negative relationships between male height and reproductive success may be a consequence of the previously discussed life history trade-offs men face: temperature, nutritional stress, manoeuvrability through forests, and high adult mortality have all been suggested as examples of ecological factors that may favour short stature.

A potential reason for the variation in selection pressures on female height in non-Western populations, for instance, can be partly explained by the relationship between female height and child survival. In line with previous findings on the relationship between maternal stature and child survival (42 developing countries: Monden and Smits, 2009; 54 low- to middle-income countries: Özaltin et al., 2010; but see Devi et al., 1985), we found that female height was consistently positively related to child survival in non-Western populations (with one exception: Devi et al., 1985; **Table 9.3**). Even in our Western sample, taller women had children who were more likely to survive to adulthood (**Figure 9.1a**). In an environment with few resources, height is likely to be a reflection of health, nutritional status, and greater access to resources (Sear et al., 2004; Silventoinen, 2003), all of which have a positive influence on the survival of children. If child mortality is high, the positive relationship between female height and child survival will result in more surviving offspring, and potentially in more reproductive success for taller women. Indeed, in all studies that found a positive association between height and the number of surviving children, maternal height was positively associated with child survival. Thus, the reason why taller women have higher reproductive success in non-Western populations is most readily explained by the increased survival probability of offspring produced by taller women (Martorell et al., 1981).

Why do average height men and short women have highest reproductive success in Western populations?

The issue of whether evolutionary processes, in particular natural selection, act on contemporary humans is a controversial topic among scientists and the general public. People readily identify all kinds of human inventions that make the modern world very different from our conception of the ancestral past. iPads, night clubs, and Big Macs, to name but a few, are most readily identified as very recent inventions, but there are also more evolutionarily relevant factors such as below-replacement fertility, high longevity, and contraceptive use that call into question the likely impact of evolutionary forces on modern humans. Even among those applying evolutionary theory to humans, there are many who consider the study of current reproductive behavior to be a futile exercise, and "*... a surprising lapse in many excellent evolutionary researchers' thought...*" (Cosmides & Tooby, 1997, p. 293), and that those who choose to do so "*merely draw metaphysical inspiration from Darwinism*" (Symons, 1990 quoting John Tooby; p. 427). The underlying premise here is that adaptive behaviour may not be (or even should not be) expected to occur, given that the psychological and physiological mechanisms that underpin our reproductive behavior evolved under conditions that were very different from those we currently experience (i.e., that this is a mismatch between our naturally selected 'ancestral' behavior and our modern-day environment).

Oral contraceptive use is often presented as a prime example of the way in which modern day technologies impede our "biological imperative", and is thought to be one of the primary causes of low fertility in contemporary populations (Barkow & Burley, 1980). Yet both evolutionary and economic demographers have shown that the transition toward smaller family size started long before effective birth control technology was available (Borgerhoff Mulder, 1998). Furthermore, a recent study in rural Ethiopia found that 96% of the women adopting contraceptives for the first time had already reproduced, and had nearly four children on average at the point at which they began to control their fertility in this way (Alvergne et al., 2011). Thus, it appears that contraceptives are mainly used to facilitate individuals' (biological) imperative to control their own fertility and limit family size (in ways that may potentially serve an adaptive function), rather than simply causing a maladaptive reduction in fertility.

Increased health and low mortality among affluent populations are also considered to be prime examples of why evolution has come to an end in the self-proclaimed pinnacle of evolutionary achievement that we call *Homo sapiens*. Indeed, shortly after publication of '*On the Origin of Species*', the consensus among scientists was that natural selection has ceased to operate on humans because of modern hygiene and medical practices. A rather obvious flaw in this reasoning, of course, is that selection not only operates through differences in survival, but also through differences in reproduction. For natural selection to exert an influence, the only premise to be met is that differences in traits related to reproduction (and survival) covary genetically with differences in biological fitness. The question is, then, an empirical one: do these factors covary in modern populations? The answer to this is a clear yes. For example, in both a French Canadian population (women married between 1799 and 1940; Milot et al., 2011) and a contemporary US population (currently living men and women born in 1948; Stearns et al., 2012), age at first birth covaried genetically with fitness, such that descendants in both populations were predicted to be genetically predisposed to have their first child earlier. There is, therefore, strong and robust evidence that natural selection acts on contemporary human populations (Courtiol et al., 2012; Milot et al., 2011; Stearns et al., 2012).

Findings of this nature thus form the crux of the debate over current adaptiveness versus past adaptation: put simply, they show that, although differences between current and ancestral environments can be readily identified, these differences do not inevitably and necessarily lead to maladaptive behaviour or imply that evolution has ceased to act. Furthermore, they indicate that seemingly maladaptive behavior (e.g., contraceptive use) must be investigated comprehensively from both an evolutionary and demographic perspective before we can conclude that the effects of such behaviour actively reduce fitness. Having said this, I also wish to stress that an adaptive mismatch is, to some degree, inevitable whenever the environment undergoes change (particularly if such changes occur rapidly) and organisms are then forced to adjust via a process of selection (and/or learning). Humans may be particularly prone to such a mismatch because of the way in which we effect our own changes on the environment via culturally-mediated niche-constructing activities, and not just as a consequence of 'natural' changes in the surrounding environment. The extent to which any particular behaviour is (mal)adaptive is therefore an empirical issue, and can only be assessed by long-term multi-generational longitudinal studies (Stearns et al., 2010). This is especially important to consider given that the adaptive value of some behaviors may only manifest after several generations (Hill & Reeve, 2004). Put simply, maladaptiveness cannot simply be deduced from purely theoretical arguments concerning putative differences between modern day environments and hypothesized ancestral environments.

Applying these notions to the case of stature: if the human environment has changed to such an extent that analyses of current adaptiveness represent a 'lapse in thought', then one would not expect to find consistent relationships between biological traits and reproductive success. Yet, height is consistently related to reproductive success in Western populations, even when controlling for education and income, and is therefore suggestive of an underlying biological process of evolutionary significance. Given this, I now turn to functional explanations for the negative relationship between female height and number of children.

Why do shorter women have most reproductive success?

The negative relationship between female height and reproductive success can be explained, in part, by the trade-off between the investment of energy in growth versus reproduction (Allal et al., 2004; Stearns, 2000). For example, women who conceive their first child at a very young age reach a lower adult height. The energetic burden on the body exerted by gestation, parturition and lactation, combined with the associated physiological changes the body undergoes during a reproductive event, all reduce the energy available for growth. Nevertheless, even among those women who reach their final adult height prior to first conception, a negative relationship between height and number of offspring persists (**Chapter 9**). Some of this remaining variation can also be explained by the above trade-off, however: shorter women do appear to invest more in reproduction than in growth as they both reach menarche earlier and reproduce at a younger age than women of taller stature. Thus, shorter women may be more likely to be 'ready for reproduction' at an earlier age than their taller counterparts. Age at first reproduction is a crucial factor in explaining reproductive success among women; indeed, one of the most consistent selection pressures on women in contemporary populations is an early age at first birth. Thus, selection may favour women who invest more in reproduction than in growth, and short women may thus reap a biological advantage in terms of achieving higher reproductive success. Adding even more weight to the idea that a trade-off between growth and reproduction can account for the observed selection pressure on female height is the fact that a genetic correlation exists between female height and age at first birth. That is, women who bear their first child at an early age also show a genetic predisposition to be shorter than average (Stearns et al., 2012). Thus, both the phenotypic (i.e., the life history trade-off) and genetic correlation between height and age at first birth partly explains why shorter women attain higher reproductive success in contemporary populations.

Finally, the ability to attract a mate should be considered when examining an individual's mating and reproductive success. Taller women were more likely to remain unmarried and, among those that did marry, those women who were taller married latest (**Chapter 9**). This is qualitatively consistent with studies of mate choice, which suggest that average height women are considered to be more attractive than taller women (Courtiol et al., 2010b; **Chapter 6**). In contrast, average height women are considered to be more attractive than shorter women (**Figure 6.4b**), yet shorter women marry earliest. Age at marriage cannot, of course, be considered to represent an accurate proxy of mate attractiveness or value. Rather, it may equally well signify the selectivity of the woman herself. Perhaps shorter women are more likely to say 'yes' to the first suitor who approaches them on bended knee, whereas taller women remain more selective and are less likely to 'settle', perhaps even to the extent that they never find an acceptable mate, and so remain unmarried. Given that shorter women are genetically inclined to bear children at an earlier age, it seems plausible that this same biological inclination affects other aspects of psychology and behaviour, such that shorter women also express a desire to have children at an earlier age and therefore show greater motivation to find a committed partner and begin a family when still very young.

Why do average height men have most reproductive success?

Perhaps the most surprising finding with respect to observed selection pressures is that taller men have fewer children than average height men in our sample. This is surprising given the advantage of greater male height in both intra- and inter-sexual selection (**Chapters 2-6**). Taller men are healthier, have higher status, have higher income, win more contests, are most desired in a speed-dating setting and end up with most women for potential dates than shorter men. Why, then, do taller men have fewer children?

It must be noted that demographic data sets often have a number of limitations. First, many of these databases are likely to be biased because of (i) the method of sampling used (e.g., sampling only parents; **Chapter 8**), (ii) biased participant response (i.e., who is willing to participate in the study), or (iii) a biased 'drop-out' rate (i.e., who remains in the study as a full participant and provides all data). There are also other, more specific, biases: the Wisconsin Longitudinal Study, for instance, consists of men who finished high-school, and is therefore biased towards well-educated people. As 25% of the population in the period covered by this sample was predicted not to have graduated from high-school, this study over-represents the more educated sector of society. This is important because education is related to height, and so the sample may also be biased towards those who are taller than average. Indeed, the average height in sample (179.20 cm) was somewhat taller than the national average of white men born in the same age cohort (176.7; although it is difficult to assess how the national average compares to the average height of Wisconsin men at that time; **Chapter 10**). Despite this, I would argue that limitations of the sample are unlikely to affect my interpretation that average height men have most reproductive success, for three reasons. First, the statistical confidence interval of the optimum height included both our sample average and the national average, allowing me to place some confidence in the notion that average height men have the highest reproductive success. Second, even if the sample excludes a somewhat shorter sub-population (because these men were less educated), this still cannot explain why men above the optimum or average height had significantly fewer children. Third, the curvilinear effect of height found in this sample has also been observed in other populations, which do not suffer from being biased toward better educated men and women (e.g., Stearns et al., 2012; of course, this does not exclude the possibility that these samples may be biased in other domains). In conclusion, then, it seems unlikely that the observed curvilinear effect of height is a consequence of potential biases in the sample used in my study.

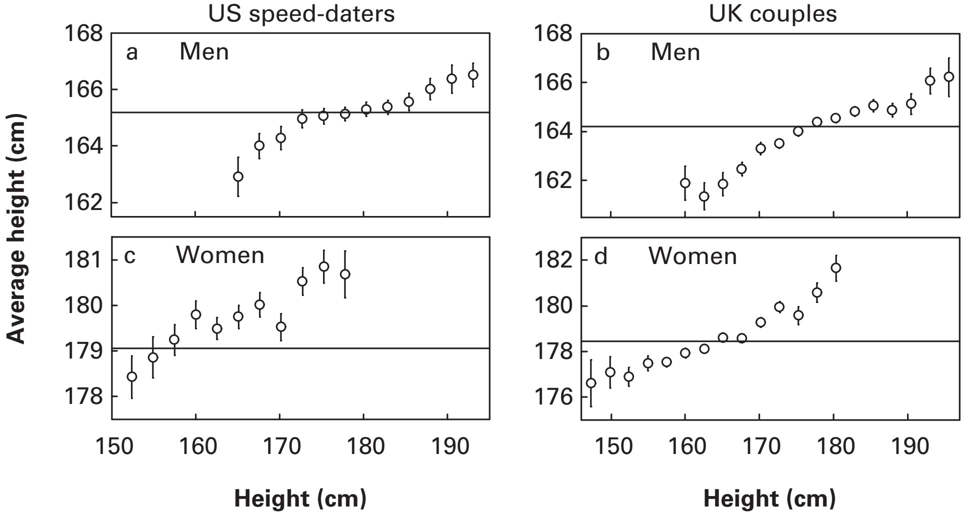
A second methodological problem is that male fertility is notoriously difficult to measure (Rendall et al., 1999). Illustrative of this problem is that, in many studies, women report a significantly higher number of children than men; a problem also noted in the Wisconsin sample (**Chapter 11**). Biologically speaking, it is impossible for more children to be born to women than to men. This difference in the number of children produced by each sex is most likely to be explained by the under-reporting of previous marital and non-marital births by men, and an under-representation of previously married men compared to previously married women in the sample. An additional issue is that extra-pair children born to men are extremely unlikely to be picked up by standard sampling procedures. Thus, some men may have produced children via extra-pair relations, while other men are likely to be raising children that are not genetically related to them. Both of these issues may affect the relationship between reproductive success and height; previous studies have shown that taller men are at an advantage in the mating and marriage market and, because of their increased attractiveness, may be considered more attractive as an extra-pair partner. Rates of non-paternity have been shown to be very low, however (less than 3% as reviewed by Anderson, 2006), and, as such, are unlikely to have grave consequences with respect to the results reported here. Overall, then, methodological biases undoubtedly affect the measurement of male reproductive success, and these biases are not easily overcome. Nevertheless, the consistency with which studies have shown that average height men have greater reproductive success (at least in US populations) suggests strongly that shorter and taller men fall short with respect to biological fitness.

The life history trade-off between growth and reproduction, which seems to partially explain female stature and reproductive success, may similarly affect male height. Selection seems to favour a younger age at first birth in men, and such selection may also affect growth and maturation (Stearns et al., 2012). The resulting curvilinear relationship of reproductive success and height may therefore be a consequence of both positive selection on height through, for example, health, attractiveness and income, combined with negative selection on height with respect to earlier age at first birth. This is, however, purely speculative. In addition to the relationship between growth and reproduction, height may be (genetically) correlated to other traits under selection (Lande & Arnold, 1983). Thus, the specific relationship between stature and reproductive success may be a consequence of selection on other traits related to height, such that average height men attain highest reproductive success. Unfortunately, these potential traits are not yet readily identified.

Men of average height attain their higher reproductive success at least partly as a consequence of marrying at a younger age. As with women, the biological significance of age at first marriage is difficult to assess. It can be interpreted as a cue for attractiveness and mate value, but this interpretation is at odds with both stated mate preferences (**Chapter 5**) and male speed-dating success (**Chapter 6; Figure 6.4c**). In addition, this represents only half the story: the likely fertility (or reproductive potential) of men's marriage partners matters as much, if not more, to their eventual reproductive success. As such, average height men may attain higher reproductive success, not only by marrying at a younger age, but also by marrying women with higher reproductive value. In **Chapters 5** and **6**, I showed that shorter women prefer men much taller than themselves, but this does not equate to a preference for tall men per se. Indeed, shorter women prefer men of average height (**Figures 5.1** and **6.1**). Similarly, taller men prefer women who are shorter than they are, but not necessarily short women. These assortative preferences are therefore likely to result in assortative mating for height (**Chapters 5-7**). More importantly, however, these specific partner height preferences in relation to one's own height may result in shorter women being more likely to be paired with a partner of average height than to one of taller stature. There is some evidence to support this notion: first, shorter women are most likely to match with average height men at speed-dating events and second, shorter women are more likely to have average height and shorter men as actual partners than taller men (**Box 1**). Thus, the increased reproductive success of average height men compared to taller men may be a consequence of their increased likelihood of pairing with shorter women, who produce a larger number of children. Following this line of reasoning, one could then argue that shorter men, who are also most likely to be coupled to shorter women (**Box 1**; **Chapter 7**), should also have increased reproductive success. Reduced reproductive success in shorter men may, however, be a consequence of other factors disfavouring short height, such as being less preferred as a mate, obtaining a mate of lesser quality, lower health status, or fewer resources. In other words, the curvilinear pattern between height and reproductive success is unlikely to be a consequence of a single selection pressure, but is more likely to be the result of competing pressures that act differentially along the height continuum to produce the observed effects on male reproductive success.

I should again stress, however, that the above explanations remain speculative. There is hope, however. With the dawn of genome wide association studies and phenomics, future studies should be better equipped to assess both phenotypic and genetic correlations between height and a variety of other traits, along with the potential trade-offs that occur between them. As more and better information of this nature becomes available, it seems likely that a clearer picture of the manner in which height translates into reproductive success will arise.

BOX 1
HOW DO PEOPLE PAIR UP BY HEIGHT?



The average height (± *SE*) of the individuals with whom an individual of a given height is paired. The left panels (a, c) contain data from the sample of US speed-daters (**Chapter 6**; see Figure 6.6), whereas the right panels (b, d) are based on data from the sample of UK parents (**Chapters 7** and **8**; *N* = 10,664; only White couples included for this graph). The top panels reflect the average height of women with whom men were (a) matched and (b) partnered. The bottom panels reflect the average height of men with whom women were (c) matched and (d) partnered. The horizontal line in each graph represents the average height of the opposite-sex.

DO GENES PLAY A ROLE IN BETWEEN-POPULATION HEIGHT DIFFERENCES?

Given the varying selection pressures on height between populations, and the high heritability of height, it would not be surprising if some of the many genes involved in the regulation of stature differ in frequency across populations (McEvoy & Visscher, 2009; Visscher et al., 2008). To date, very few studies have addressed this issue. Notable exceptions are two recent studies that demonstrate that the difference in height observed between the Baka pygmies of Cameroon and a taller neighbouring non-Pygmy population (Becker et al., 2011; Jarvis et al., 2012) may have a genetic component. Both studies examined the genetic similarity between these populations, and showed that Pygmy individuals that are genetically more similar to non-Pygmy individuals (i.e., higher levels of genetic admixture) are taller. These studies thus suggest that differences in stature between Pygmy and neighbouring populations in Cameroon are likely to have a genetic component. Jarvis et al. (2012) further extended these findings in Pygmies by providing evidence for positive selection on genes that previously have been shown to underlie variation in height in European populations. These findings thus suggest that selection has actively favoured shorter stature among pygmy populations, acting partly on the same array of genes to those that influence height among Europeans.

Additional evidence for genetic factors underlying population differences in height come from a GWA study in a Korean population (Cho et al., 2009). Several loci previously identified in European populations were also detected in this sample. Most pertinently, one of the genes with the largest effects on stature observed in Europeans (HMGA2) was also associated with height in the Korean population, although its effect was much smaller and the frequency of the 'height-raising' allele in the population was lower. These findings suggest that genetic differences may, in part, explain why Koreans are, on average, shorter than Europeans (Cho et al., 2009).

Genetic differences between populations can arise as a consequence of two distinct evolutionary forces. When genetic variants are unrelated to biological fitness, 'genetic drift', which refers to a changes in gene variants in a population due to chance, may result in some populations containing a higher frequency of 'short' compared to 'tall' alleles for non-adaptive reasons (McEvoy & Visscher, 2009); this is especially likely to be the case if the population undergoes any kind of bottleneck that results in a sharp reduction in population size. When genetic variants *are* related to biological fitness, as I established in the previous section ('Selection pressures on human height'), then active selection may take place on these variants. Thus, selection (either positive or negative) on genetic variants associated with stature may cause differences in height between populations.

There is evidence that height differences between Northern- and Southern European countries (with the latter being shorter) are a consequence of past selection on stature (Turchin et al., 2012). Height-increasing alleles found to occur at higher frequencies in Northern than in Southern Europeans, and the strength of these effects suggest them to be a consequence of selection on gene variants associated with height, rather than of genetic drift. Thus, adult height differences across populations of European descent are not driven solely by environmental differences but retain a signature of differential selection in the past. Whether these genetic differences were a consequence of selection favouring height in Northern European populations or disfavouring height in Southern Europeans (or both) cannot, at present, be established.

Only one study has been able to directly assess the genetic response to selection on height (Byars et al., 2010). Making use of a sample of US women from the longest running multi-generational study in medical history, these authors showed that natural selection has acted on female height: shorter women had the highest lifetime reproductive success[22]. More pertinently, the descendants of these women are predicted to be on average slightly shorter than they would have been in the absence of selection.

Although the differences in average height between populations have traditionally been interpreted as a result of different environmental influence on stature, in this section I have presented evidence that some of this variation is very likely to have a genetic basis. Selection pressures furthermore vary in direction, but also in strength between populations, which can give rise to these population differences in stature. Depending on the strength and direction of selection on both male and female height, a population will respond by increasing or decreasing in height. The above findings - that natural selection consistently favours both shorter female height and average male height in US men and women (**Chapters 9-11**) - may therefore shed light on the curious case of the reverse trend in height seen among North-Americans over the course of the last century: once the tallest in the world, the average height of US men and women has fallen in comparison to other affluent populations since the 1950s. Thus, in addition to environmental factors (such as social inequality), natural selection may well be another factor limiting the height of North-Americans.

The people from the Netherlands have been a constant thread throughout my writings, and it seems appropriate to end this synthesis with them. Since the 1860s, the Dutch have increased 20 cm in height, currently towering over all other countries in the world. Furthermore, whereas in most North-European countries the secular trend in height has slowed down or stopped, the Dutch keep growing taller. Perhaps in addition to the excellent social welfare and health care system, the lower labour participation rates of women, and the excessive use of milk, evolution is also pushing the Dutch to ever increasing heights...

22 The selection gradient in this study was nearly identical to that observed in the Wisconsin Longitudinal Study (**Chapter 9**).

CHAPTER 2

HIGH AND MIGHTY

Height increases authority in professional football refereeing

Gert Stulp
Abraham P. Buunk
Simon Verhulst
Thomas V. Pollet

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10: 588-601

ABSTRACT

Throughout the animal kingdom, larger males are more likely to attain social dominance. Several lines of evidence suggest that this relationship extends to humans, as height is positively related to dominance, status and authority. We hypothesized that height is also a determinant of authority in professional refereeing. According to the International Football Association Board, FIFA, football ("soccer") referees have full authority to enforce the laws of the game and should use their body language to show authority and to help control the match. We show that height is indeed positively related to authority status: referees were taller than their assistants (who merely have an advisory role) in both a national (French League) and an international (World Cup 2010) tournament. Furthermore, using data from the German League, we found that height was positively associated with authoritative behavior. Taller referees were better able to maintain control of the game by giving fewer fouls, thereby increasing the "flow of the game". Referee height was also positively associated with perceived referee competence, as taller referees were assigned to matches in which the visiting team had a higher ranking. Thus, height appears to be positively related to authority in professional refereeing.

INTRODUCTION

Throughout the animal kingdom, larger males are more likely to attain social dominance (Andersson, 1994; Archer, 1988; Ellis, 1994; Isaac, 2005), which is the ability to acquire resources in the presence of others through either agonistic or affiliative strategies (Pellegrini & Bartini, 2001). Several lines of evidence suggest that this positive relationship between body size and social dominance extends to humans. First of all, taller men are more likely to win physical fights as they are physically stronger (Sell et al., 2009), have an enhanced capacity to deliver potentially damaging strikes (Carrier, 2011), and react more aggressively in sports (Webster & Xu, 2011). Additionally, taller men are less sensitive to cues of dominance in other men (Watkins et al., 2010) and respond with less jealousy towards socially and physically dominant rivals than do shorter men (Buunk et al., 2008). These findings suggest that it is more important for shorter men, as compared to taller men, to accurately gauge a rival's dominance given the higher costs associated with engaging in a fight if a competitor is miscategorized. Similarly, taller men could be (or perceive themselves to be) better able to deter dominant rivals, which would reduce the need for jealousy.

Perceptions of height and dominance are also closely related. Taller men are perceived as more dominant than shorter men (Montepare, 1995), and, vice versa, more dominant men are estimated as taller than less dominant men (Dannenmaier & Thumin 1964; Marsh et al., 2009). Similarly, the losing candidates in political elections are judged as shorter, whereas the winning candidates are judged as taller than they were perceived to be before the election (Higham & Carment, 1992). People also judge politicians whom they support as taller than politicians whom they oppose (Sorokowski, 2010). Perceptions of height also affect behavior. Huang and colleagues (2002), for example, manipulated the camera angle in a negotiation task and found that men who were perceived as taller were more influential in the task than men who were perceived as shorter. The positive relationship between size and perceived dominance is even apparent in very young children: Thomsen, Frankenhuis and Carey (2011) showed that children as young as ten months old recognize that size plays a role in dominance contests, and are "surprised" by (i.e., pay more attention to) a situation in which a smaller individual dominates a larger individual.

Perhaps because of their increased physical (Sell et al., 2009), behavioral (Watkins et al., 2010) and/or perceived dominance (Marsh et al., 2009), height is positively related to access to actual resources in humans. This is supported by the findings that taller individuals (particularly men) are more likely to have higher starting salaries (Loh, 1993), higher overall income (Judge and Cable, 2004), and are more likely to be promoted (Melamed & Bozionelos, 1992) than shorter men. Not surprisingly therefore, height is positively related to authority status. For example, when one's dominance is exercised legitimately, taller individuals are more likely than shorter individuals to occupy a leadership or managerial position (Gawley et al., 2009; Stogdill, 1948). These findings extend to politics, because since 1896, U.S. citizens have always elected a President whose height was considerably above average (Judge & Cable, 2004). Moreover, Presidents whose presidency was considered "great" were taller than those whose presidency was considered a "failure" (Sommers, 2002). Thus, taller men are more likely to obtain a position of authority, and when they do, are considered more successful.

Giving the above findings, we hypothesized that male height may also be related to authority in a different setting: professional football ("soccer") refereeing. According to the International Football Association Board, FIFA, football referees have full authority to enforce the laws of the game and can use their body language to show authority and help control the match *(Laws of the Game*; FIFA, 2012). Similarly, the website of the British Football Referees' Association (2010) states that a referee always has to "*keep control [of the game], by bending his authority to encourage the flow of the game*". These recommendations are not surprising, given the fact that referees have to deal with verbal and physical aggression not only from players, but also from coaches, and spectators (Folkesson et al., 2002). With almost every blow of the whistle, half of the players, coaches and crowd are likely to disagree with the referee's decision.

We examined whether height was related to authority and authoritative behavior in professional refereeing. First, we examined whether or not referees were taller than their assistants (who merely have an advisory role) in the French professional League (Study 1) as well as during the 2010 World Cup that took place in South Africa (Study 2). Furthermore, we investigated whether there was an association between referee height and authoritative behavior on the football pitch. A recent study by Van Quaquebeke and Giessner (2010) investigated the association between height and dominance in football players. In this study, taller players were perceived as committing more fouls than shorter players. We hypothesize that, apart from player height, referee height is also related to authority and dominance on the pitch (Study 3). We predicted that relatively taller referees would be better able to maintain control of the game (i.e., players would be more wary of committing fouls or retaliating towards other players) and would increase the "flow of the game" by having to give fewer fouls (Study 3). Furthermore, we predicted that the allocation of referees to matches by the football league is contingent on referee height, with taller referees being appointed to more important matches.

Study 1: Ligue 1 (French Professional league) referees

MATERIAL AND METHODS

The aim of our first study was to investigate the relationship between height and status success in professional refereeing. We collected data on assistant referees ($N = 64$) and referees ($N = 38$) from six seasons of Ligue 1 (2004/2005 to 2009/2010), the top French football league from the website http://www.worldfootball.net/. One individual acted as both referee and assistant referee during this period; he was classified as a referee in our analyses. We chose the French league because all referee heights and the majority of assistant referee heights were available (only five out of 69 heights of assistant referees were missing; for consistency with Study 3, we preferred to have data on the German league (Bundesliga). Unfortunately, for this league, more than one third of all assistant referees' heights were missing). Independent sample *t*-tests were performed to test whether head referees were significantly taller than their assistants.

RESULTS

Referees were on average 4.09 cm taller than assistant referees (Figure 2.1a; *t*-test; $M = 179.71$; $SD = 5.49$ cm versus $M = 175.62$; $SD = 7.32$ cm; $t(100) = 2.98$; $p = .004$; $d = 0.62$). No difference in age was found between referees ($M = 41.00$ years; $SD = 5.39$) and assistant referees ($M = 41.41$ years, $SD = 5.83$; *t*-test; $t(102) = 0.35$; $p = .724$, $d = 0.07$). The effect of height can thus not be attributed to the association between age and height.

Study 2: World Cup referees

MATERIAL AND METHODS

To replicate our finding for the French league we collected data from the FIFA-website (www.fifa.com) on all referees and assistant referees who officiated in the 64 matches of the 2010 World Cup in South Africa. In total, 29 trios consisting of one referee ($N = 29$) and two assistant referees ($N = 58$) were invited for the World Cup. Referees were either assigned as an "active" referee or as "stand-in" referee (fourth official) during a match. Similarly, assistant referees were either assigned as an "active" assistant referee or as "stand-in" assistant referee (fifth official). The fourth official is the primary replacement of the referee when he is unable to continue officiating, whereas the fifth official is the primary replacement of the assistant referee.

Only four individuals were assigned exclusively as referee during the tournament. Thirteen officials acted more often as referee than as fourth official, seven acted more often as fourth official than referee, and five acted only as fourth official. With respect to the assistant referees and fifth officials: twenty-two officials acted exclusively as assistant referee, seventeen acted more as assistant referee than as fifth official, nine acted more often as fifth official than assistant referee, and ten acted only as fifth officials. Referees or fourth officials never officiated as an assistant referee or fifth official and no assistant referee or fifth official ever officiated as referee or fourth official. We classified officials on the basis of their most common overall assignment throughout the tournament (e.g., an individual officiating as an assistant referee more often than as a fifth official was classified as an assistant referee). This led to the following classification of officials: 17 referees, 12 fourth officials, 39 assistant referees, and 19 fifth officials.

We tested whether there was a difference in height between referees and assistant referees and between "active" and "stand-in" (i.e., the 4th and 5th official) referees. Given that height varies between countries, and that referees and assistant referees were invited in trios, often with individuals from the same or neighboring countries, we included the trio as a random effect. Inclusion of such a random effect rules out that the effect found for height is an artifact of between-country variation in height.

RESULTS

In 26 out of the 29 invited trios, the referee was taller than at least one assistant referee, and in 17 trios the referee was taller than both assistants. The invited 29 referees were on average 4.31 cm taller than the 58 invited assistant referees (*t*-test; $t(85) = 2.94$; $p = .004$, $d = 0.68$). When taking into account the overall assignment of the officials, the between-country variation in height and the age of the officials, referees were estimated 4.17 cm taller than assistant referees (Linear mixed model parameter estimate (± *SE*): -4.17 ± 1.14; $\chi^2(1, N = 87) = 12.37$; $p = .0004$; see Table 2.1 and Figure 2.1b).

There was no significant difference in height between the "active" official and their potential "stand-in" (-0.38 ± 1.72; $\chi^2(1, N = 87) = 0.05$; $p = .82$; Table 2.1). Age was not significantly related to height ($p = .14$; Table 2.1). The height effect can thus not be attributed to the association between age and height. Parameter estimates for the full model can be found in Table 2.1.

We also investigated whether height was related to the years of international experience a referee had. Taller referees had fewer years of international experience prior to the World Cup (Pearson $r = -.39$; $p = .037$; $N = 27$). After controlling for the age of the referee in a partial correlation, the relationship between height and experience became marginally significant ($r = -.37$; $p = .051$; $N = 26$). For assistant referees, there was no relationship between experience and height ($r = .15$; $p = .25$; $N = 56$).

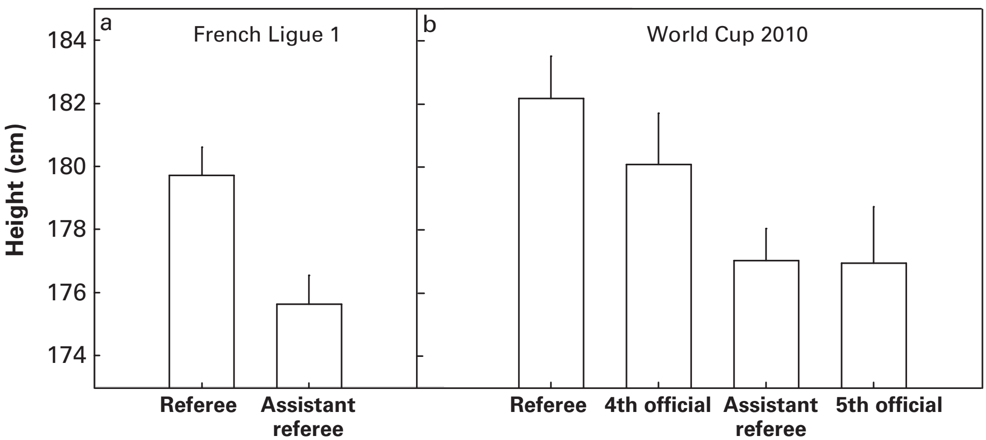

Figure 2.1: Results from Study 1 and 2: The average height (+ *SE*) in centimeters of (a) the referees and assistant referees in the French league and (b) of the referees, fourth officials, assistant referees and fifth officials during the 2010 World Cup.

Table 2.1: Results from Study 2: Linear mixed model parameter estimates (± *SE*) of the effects of age (years), type of referee, 'active' versus 'stand-in' referee and referee trio (see text) on height.

	Height (cm)
Intercept	$1.81*10^{3}$ (± 1.38)***
Referee versus assistant referee[a]	-4.17 (± 1.14)***
'Active' versus 'stand-in' referee[a]	$-3.80*10^{-1}$ (± 1.72)
Age (centered)	$2.75*10^{-1}$ (± $1.88*10^{-1}$)
Random effect referee trio	$1.63*10^{1}$ (± 4.03)[b]
Residual error variance	$2.42*10^{1}$ (± 4.91)[b]

[a] Referee and 'Active' referee are the reference categories.
[b] Standard deviation instead of standard error.
****p* < .001.

Study 3: Bundesliga (German First Division) Referees

MATERIAL AND METHODS

The aim of our third study was to investigate whether authoritative behavior and competence was related to height and experience of a referee. We used football data purchased from Impire AG, a company that specializes in collecting professional sports data (www.impire.de). Available data comprised 1,530 matches from five seasons (2004/2005 to 2008/2009) of the Bundesliga, the highest professional German football division. For each match the referee's identity (N = 28), his height and experience (number of seasons refereeing in the Bundesliga) were available, as well as the average rank of the home and visiting team in the seasons 2004/2005 through to 2008/2009 (1=highest, 18=lowest), the total number of fouls given by the referee, and the number of yellow and red cards that were administered to players. In football, a red card is given for a severe foul, and will result in direct expulsion of the player for the remainder of the match. Two yellow cards, for less severe fouls, will also result in a red card, and hence expulsion. The foul data only include illegal physical contacts towards other players (e.g., unfair tackles), and no other illegal actions that are penalized by the referee (e.g., handball and offside). For all analyses, we included *referee*, the *home team* and the *visiting team* as random factors and *height*, *Bundesliga experience* and *age of referee* as covariates. As referee age was highly correlated with referee experience (r = .83; p < .0001; N = 26), we did not include referee age in the reported models. Including age in the models did not change any of our results, as age never

Table 2.2: Results from Study 3: Descriptive statistics of the 28 referees and 1,530 matches in five Bundesliga seasons (2004/2005 to 2008/2009).

	Mean (± *SD*)	Minimum	Maximum
Referees (N = 28)			
Height (cm)	185.18 (± 5.79)	178	197
Age (years)[a]	35.39 (± 5.27)	22	46
Bundesliga experience (years)[a]	6.25 (± 5.08)	1	17
Matches (N = 1,530)			
Number of fouls	36.86 (± 7.76)	13	70
Number of cards	4.08 (± 2.03)	0	11

[a] Age and experience at the first match played during seasons 2004/2005 to 2008/2009.

reached statistical significance (all $p > .16$). We tested whether referee height was predictive of measures of authority and control during a game, such as the number of fouls and the number of cards given.

Furthermore, we investigated whether referee height was predictive of the perceived competence of the referee, by examining whether these factors influenced the likelihood of being assigned to matches in which the home or visiting team was high ranking (controlling for respectively the visiting and home team by adding them as a random factor). All analyses were performed in R version 2.11.1 (R Development Core Team, 2008), using the lmer package. In the following we defined "tall" or "experienced" as one standard deviation above the respective mean, and "short" or "inexperienced" as one standard deviation below the respective mean.

Table 2.3: Results from Study 3: Generalized linear mixed model parameter estimates (± *SE*) of the effects of height (centered), experience (centered), rank home team, rank visiting team and referee on the total number of fouls in a game (linear) and the total number of cards (Poisson).

	# Fouls	# Cards
Intercept	$3.66*10^{1}$ (± 1.01)***	1.46 (± $4.65*10^{-2}$)***
Rank Home Team	$1.39*10^{-1}$ (± $4.26*10^{-2}$)**	$5.33*10^{-3}$ (± $2.86*10^{-3}$)
Rank Visiting Team	$-7.42*10^{-2}$ (± $4.35*10^{-2}$)	$-1.29*10^{-2}$ (± $2.91*10^{-3}$)***
Experience (years)	$-7.51*10^{-1}$ (± $1.14*10^{-1}$)***	$-8.44*10^{-3}$ (± $4.65*10^{-3}$)
Height (cm)	$-3.28*10^{-1}$ (± $1.46*10^{-1}$)*	$3.34*10^{-3}$ (± $4.35*10^{-3}$)
Random effect referee	$1.59*10^{1}$ (± 3.99)[a]	$8.31*10^{-3}$ (± $9.12*10^{-2}$)[a]
Residual error variance	$5.39*10^{1}$ (± 7.34)[a]	[b]

[a] Standard deviation instead of standard error.

[b] There is no residual error variance in Poisson mixed models because the variance is constrained to the mean.

*$p < .05$; **$p < .01$; ***$p < .001$.

RESULTS

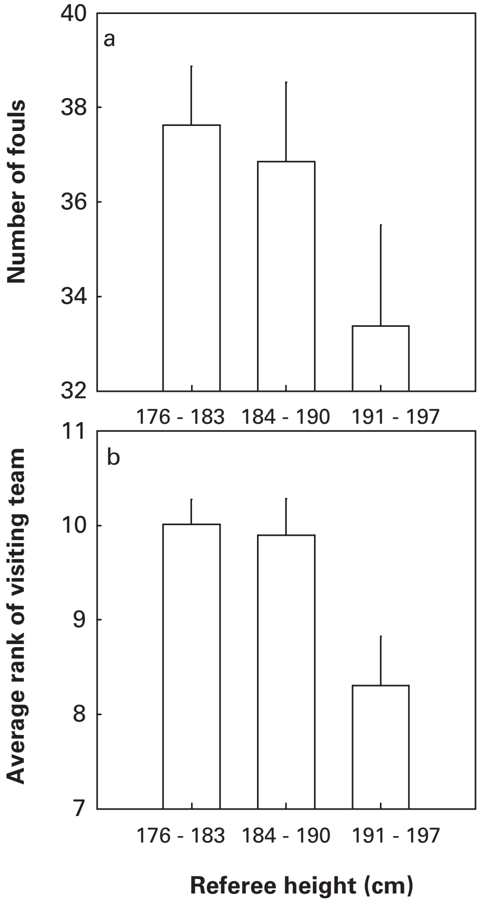

Figure 2.2: Results from Study 3: Least square means (+ *SE*) of the effect of referee height in cm (in three equal height range groups) on (a) the number of fouls, and (b) the average rank of the visiting team (lower rank means better team).

Referees were on average 185.18 centimeters tall ($SD = 5.79$) and had on average 6.25 years of Bundesliga experience ($SD = 5.08$) at the start of the seasons 2004/2005 to 2008/2009 (see Table 2.2 for descriptive statistics).

Referee height was also associated with measures of authoritative behavior during a match. Controlling for the ranks of the playing teams, both referee experience (-0.75 ± 0.11; $\chi^2(1, N = 1{,}530) = 27.45$; $p < .0001$) and height (-0.33 ± 0.15; $\chi^2(1, N = 1{,}530) = 5.26$; $p = .022$; Figure 2.2a) were negatively associated with the number of fouls in a match (see Table 2.3 for all parameter estimates), indicating that taller and more experienced referees assigned less fouls and thus interrupted the game less. Experienced referees gave on average 7.63 fewer fouls compared to inexperienced referees. Tall referees gave on average 3.79 fewer fouls than short referees. Experience and height were not significantly associated with the number of cards given in a match (Table 2.3).

Both *years of Bundesliga experience* (-0.18 ± 0.04; $\chi^2(1, N = 1{,}530) = 17.60$; $p < .0001$) and *height* (-0.08 ± 0.04; $\chi^2(1, N = 1{,}530) = 4.32$; $p = .038$; Figure 2.2b) negatively predicted the average rank of the visiting team, but not of the home team (see Table 2.4 for all parameter estimates). Thus, more experienced and taller referees, as opposed to respectively inexperienced and shorter referees, were assigned to matches where the visiting team had a better performance over these five years (higher ranking means lower average rank). More experienced compared to less experienced and taller compared to shorter referees were assigned to matches in which the visiting team on average was ranked 1.83 and 0.96 higher, respectively (out of 18 teams).

Table 2.4: Results from Study 3: Linear mixed model parameter estimates (± *SE*) of the effects of experience (centered), height (centered), and referee on the rank of the home and visiting team.

	Rank[a] home team	**Rank[a] visiting team**
Intercept	9.54 (± $1.77*10^{-1}$)***	9.71 (± $2.13*10^{-1}$)***
Experience (years)	$-1.69*10^{-2}$ (± $3.66*10^{-2}$)	$-1.81*10^{-1}$ (± $4.21*10^{-2}$)***
Height (cm)	$-1.10*10^{-3}$ (± $3.37*10^{-2}$)	$-8.22*10^{-2}$ (± $4.04*10^{-2}$)*
Random effect referee	$4.02*10^{-1}$ (± $6.34*10^{-1}$)	$7.59*10^{-1}$ (± $8.71*10^{-1}$)
Residual error variance	$1.98*10^{1}$ (± 4.45)[b]	$1.90*10^{1}$ (± 4.36)[b]

[a] Average rank of the team in the last 5 seasons of Bundesliga. Lower means better, as 1 is the top rank and 18 the bottom rank.
[b] Standard deviation instead of standard error.
*p < .05; ***p < .001.

DISCUSSION

In this study, we have shown that referees, the leading officials in football, are taller than their assistant referees in both a national (French professional football league) and an international (World Cup 2010) setting. These novel findings are in line with predictions based on previous studies reporting a positive association between height and authority (Gawley et al., 2009; Judge & Cable, 2004).

In addition, we found evidence that the height of referees was associated with their (perceived) competence. First of all, we found that taller referees had relatively less international experience than shorter referees prior to their invitation to the World Cup. Thus, a tall referee required less experience to be promoted to referee at the highest level. Second, we found that taller and more experienced referees were assigned to matches in which the visiting team had a better performance over the study period in the German League. Hence, as more competent referees are more likely to be assigned to matches with higher ranking teams, both experience and height appear to be indicators of this (perceived) competence. The reason why no effect of height and experience was found on the rank of the home team can be explained by how referees in the Bundesliga are assigned. A referee is registered to a particular region within Germany and is not allowed to officiate in any matches in which teams from that particular region are playing (DFB, 2010). However, for logistical reasons, referees are likely to be assigned to matches in regions neighboring their own. Therefore, the region where the referee is registered constrains the set of home teams that he can be assigned to, and hence the ranks of these home teams he can be assigned to.

We also found evidence that the height of referees was associated with their effectiveness and authority in the field. An important aspect of refereeing, according to the British Football Referees' Association (2010) is to "*keep control [of the game], by bending his authority to encourage the flow of the game*". Taller compared to shorter referees gave fewer fouls, and thus increased the "flow in the game". Apparently, taller referees are better able to control the game by "bending their authority", resulting in players committing fewer fouls (i.e., players would be more wary of committing fouls or less inclined to retaliate towards other players), or they resolved them in another way (e.g., deciding to "play advantage" instead of stopping the game for a foul, because the fouled team still has the advantage in the situation, or by warning players in another way). Similarly, more experienced referees also awarded fewer fouls than less experienced referees. It is worth noting that in the Bundesliga, for both the number of given fouls and the rank of the visiting team, the effect of two extra centimeters in height was comparable to approximately one extra year of experience.

Instead of the increased "flow" or control of the game by taller referees, the negative association between referee height and the number of fouls could also mean that taller referees either notice fewer fouls, or that they are more lenient. Some evidence suggests however, that these alternative explanations are unlikely. Noticing fewer fouls would indicate poor refereeing, as the main job of the referee is to notice and penalize fouls. As mentioned above, referee height was positively associated with measures of the perceived competence of the referee (e.g., being assigned to matches with higher-ranked teams), rendering it unlikely that taller referees are less likely to notice foul play. Additionally, more experienced referees also awarded fewer fouls. As experience is a likely determinant of competence (Dohmen, 2008; Nevill et al., 2002), the fact that more experienced and taller referees awarded fewer fouls suggests that, awarding fewer fouls is likely to be a sign of competence rather than incompetence. It is also unlikely that the positive relationship between height and number of fouls arises because taller referees are more lenient as no differences were found in the number of cards given by taller referees compared to shorter referees (if anything taller referees were less lenient as they gave fewer fouls than shorter referees, yet handed out similar numbers of cards).

Again, these results were mirrored by the effects of experience: no differences were found in the number of cards handed out by experienced referees compared to less experienced referees. A possible explanation for the finding that both stature and experience are related to the number of fouls but not the number of cards, is that there may simply be too little variation in the number of cards given and hence the possibility to find an effect of height and experience may be reduced. Additionally, perhaps interrupting the game by calling a foul is a more subjective decision than the decision of whether or not a player deserves a card, for which there may be more strict guidelines (FIFA, 2010). In conclusion, the most likely explanation for why taller (or more experienced) referees give less fouls, is that due to the authority a tall (or experienced) referee induces, he can increase the "flow" of the game.

The present study does not address the process underlying the association between height and authority. It could arise as a consequence of the association between height and actual ability of the referees. Previous studies have proposed several hypotheses explaining this association, including the positive relationship between height and cognitive ability (explained by common factors such as genes or nutrition; Silventoinen et al., 2006), health (Silventoinen et al., 1999), participation in social activities in young adulthood (Persico et al., 2004), and self-esteem (Judge & Cable, 2004). The association between height and authority in referees may also be a consequence of the *perception* of the referees by others. Taller people may be perceived as more competent, authoritative, or dominant (Judge & Cable, 2004; Marsh et al., 2009; Young & French, 1996). Further research is necessary to determine the causal pathways through which height induces (perceived) authority across different settings.

The higher perceived competence of taller men (Judge & Cable, 2004; Young & French, 1996) is likely to lead to discrimination against shorter men. Cinnirella and Winter (2009) showed that in the labor market employer discrimination with respect to height was likely as height was positively related to income in *employees* (i.e., subordinate to their *employers*) and, in contrast, this relationship was not found in self-employed workers (i.e., who have no manager above them and hence are not at risk of discrimination). The finding that taller referees were assigned to higher quality matches could be a consequence of a similar type of discrimination. When actual competence is not related to height and our subconscious biases act to discriminate against short individuals, society should consider policies to guard against this form of discrimination.

ACKNOWLEDGEMENTS

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CHAPTER 3

TALL CLAIMS?

Sense and nonsense about the importance of height of US presidents

Gert Stulp
Abraham P. Buunk
Simon Verhulst
Thomas V. Pollet

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ABSTRACT

According to both the scientific literature and popular media, all one needs to win a US presidential election is to be taller than one's opponent. Yet, such claims are often based on an arbitrary selection of elections, and inadequate statistical analysis. Using data on all presidential elections, we show that height is indeed an important factor in the US presidential elections. Candidates that were taller than their opponents received more popular votes, although they were not significantly more likely to win the actual election. Taller presidents were also more likely to be reelected. In addition, presidents were, on average, much taller than men from the same birth cohort. The advantage of taller candidates is potentially explained by perceptions associated with height: taller presidents are rated by experts as 'greater', and having more leadership and communication skills. We conclude that height is an important characteristic in choosing and evaluating political leaders.

INTRODUCTION

"At 5'10'' (on a warm day) the author is neither presidential nor destined for even near-greatness"

Paul M. Sommers, 2002.

Presidential height and election outcomes: fact or fiction?

According to conventional wisdom, US presidential elections are often won by the taller of the two candidates. Indeed, US presidential height is a popular topic among essayists (Adams, 1992; Baker, 2007; Carnahan, 2004; Mathews, 1999; Page, 2004; Rolirad, 2004) and popular science writers (Borgmann, 1965; Gillis, 1982). In his book "*Too tall, too small*" for example, Gillis (1982) reported that, in the twenty presidential elections held between 1904 and 1980, the overwhelming majority (80%) was won by the taller of the two candidates. Similarly, Borgmann (1965) claimed that the shorter candidate lost all presidential elections except one between 1888 and 1960.

Similar claims are found in the scientific literature, often drawing on these more popular accounts. Jackson and Ervin (1992), for example, cite Gillis (1982), and report that taller candidates fare better in presidential elections than shorter ones. Sorokowski (2010) similarly cites Gillis (1982), stating that *'between 1900 and 1968, the taller candidate always came first'*. Using a different sample of elections, Higham and Carment (1992) conclude that US presidents elected between 1905 and 1980 were significantly taller than their defeated opponents. Employing yet another sample of elections, namely those between 1952 and 2000, Persico, Postlewaite and Silverman (2004) state that in '*the past 13 US presidential elections the taller candidate has won 10 times*'. Finally, Murray and Schmitz (2011) conclude, based on more quantitative data from all elections, that *'the taller of the two major-party presidential candidates between 1789 and 2008 won the presidency in 58 percent of elections'.*

Despite the apparently overwhelming evidence suggesting that height matters, it is also clear that the figures reported by different authors vary substantially (e.g., from the 58% reported by Murray & Schmitz (2011) to the 100% of all elections reported by Sorokowski (2010)). Such variability may, in turn, be related to methodological issues that also cast doubt on this general conclusion. A problem common to most of these studies is the selective sampling of elections, which inevitably leads to different results. It is notable that the criteria used to select particular time periods usually goes unreported, and appears to be entirely arbitrary. What if all those elections falling outside the selected sample were won by the shorter candidate? An additional methodological issue is the recurrent lack of statistical testing. Does the higher percentage of taller winners actually deviate from that expected by chance (especially when the percentage difference is rather small, e.g., the 58% reported by Murray & Schmitz 2011)? A humorous example of the consequences of selective sampling of presidential elections and lack of statistical testing is given by Adams (1992), who argues that the longer-name-hypothesis should be given equal weight to the height-advantage-hypothesis: '*Of the 22 elections between 1876 and 1960, the candidate with more letters in his last name won the popular vote 20 times*.' In other words, it is very easy to identify features that predict election outcomes, given arbitrary selection of time periods and an absence of any form of statistical analysis, but it seems unlikely that such features are representative of all elections.

Not all studies suffer from these methodological limitations, however. McCann (2001), for instance, provides evidence for a statistical relationship between presidential height and political success. Using all elections for which data were available (1824 to 1992), he found that taller presidents received relatively more support (measured by popular votes) than shorter presidents. Additionally, he showed that in times of social, economic or societal threat, the winning presidential candidates were taller. Thus, taller presidents received more votes than shorter presidents, and were more likely to be chosen as leaders during difficult periods.

Taking a slightly different approach, a number of studies have compared presidential height to the average height of the population. Judge and Cable (2004), for instance, note that *'not since 1896 have U.S. citizens elected a president whose height was below average'*. This leaves unanswered, however, the nature of the relationship existing prior to 1896. Persico and his colleagues (2004) attempted to provide an answer to this by comparing the heights of all presidents (up to G.W. Bush) to the heights of military men born in the year when the president took office. They showed that presidents tend to be distinctly taller than the average man in the military. One limitation here, however, is that, because of the secular trend of increasing height over time, using the heights of men *born* in the year when the president took office overestimates the height of the existing *adult* male population in that same year (a point which the authors themselves acknowledge; Persico et al., 2004). In this study, we attempt to address the methodological and statistical limitations present in the previous work. First, however, we address why height might be related to presidential success.

Why does height matter?

The importance of height to US presidential election success is in line with other research showing that height is related to leadership qualities. Taller people, particularly men, are more likely to emerge as leaders in a group and more often occupy a leadership or managerial position (Gawley et al., 2009; Stogdill, 1948). Height is also positively related to measures of professional and educational achievement (Cavelaars et al., 2000; Judge & Cable, 2004; Silventoinen et al., 2004; **Chapters 2, 9,** and **10**). More specifically, with respect to professional success, taller men have higher starting salaries (Loh, 1993), are more likely to be promoted (Melamed & Bozionelos, 1992) and have higher overall income (Judge & Cable, 2004).

A possible pathway through which taller men have an advantage in obtaining a leadership position, is that height is positively associated with interpersonal dominance: 'an individual's potential for asserting power and authority over more submissive members of his or her group' (Maner and Baker, 2007). Taller men are physically stronger (Carrier, 2011; Sell et al., 2009), are less sensitive to cues of dominance of other men (Watkins et al., 2010) and respond with less jealousy towards socially and physically dominant rivals than shorter men do (Buunk et al., 2008). It is possible, therefore, that taller men are more likely to emerge as leaders and attain high social status within groups and more broadly within society due to their increased dominance status.

The association between perceptions of height and dominance can also be related to one school of thought in the embodied cognition literature, which argues that humans ground their conceptual thinking in terms of bodily morphology and action (Schubert, 2005). For example, we automatically interpret words like "up", "above" and "large" with authority, dominance, and power (Giessner & Schubert, 2007; Schubert, 2005), whereas words like "down", "below" and "small" are associated with subordinance, submission, and powerlessness. These associations are also apparent in our every-day colloquial expressions; the term "big man", for instance, commonly denotes a person of authority and importance across both historical time and cross-culturally. The notion of a "Big man", according to Ellis (1992, p. 279; citing Brown and Chia-Yun (no date)) is 'a conflation of physical size and social rank and that "big men" are consistently *big* men, tall in stature'. Moreover, this link between height and rank (or social status/leadership) has deep evolutionary roots: throughout the animal kingdom, larger males are more likely to win fights (Archer, 1988) and to attain social dominance (Andersson, 1994; Ellis, 1994). Overall, then, there are a number of converging lines of evidence to suggest that height is related to leadership and dominance in biologically significant ways. Given this link between actual dominance and height, it is perhaps not surprising that taller men are also *perceived* to be more dominant than shorter men (Montepare, 1995), and, equally, that more dominant or high-status men are estimated to be taller than less dominant or low-status men (Dannenmaier & Thumin, 1964; Marsh et al., 2009; Wilson, 1968). The relation between perceived size and dominance is already apparent in very young children. Thomsen et al. (2011) found that children as young as ten months old recognize that size plays a role in dominance contests, and are 'surprised' by (i.e., pay more attention to) a situation in which a smaller individual dominates a larger individual.

The robust relationships observed between height and dominance, and the manner in which dominance influences perceived height (and vice versa), shed light on why height might exert an influence on people's voting decisions. Indeed, there is evidence to suggest that such relationships are important. Kassarjian (1963), for instance, found that people's voting intentions correlated with the *perceived* height of presidents: prior to the 1960 election between Kennedy and Nixon, 68.1% of those who planned to vote for Kennedy believed Kennedy to be taller, whereas only 47.3% of those who planned to vote for Nixon thought Kennedy was taller (Kennedy was actually slightly taller than Nixon). Similarly, Ward (1967) found that self-reported liking for President Lyndon B. Johnson was significantly correlated with his estimated height. Another striking example is reported by Singleton (1978): after Nixon fell from grace and was forced to leave office, people estimated that his successor, Jimmy Carter, was taller than the disgraced former president. In reality, Nixon was over five centimeters taller than Carter. More generally, the losing candidates in political elections are judged to be shorter, whereas winners are judged as taller than they were prior to elections (Higham & Carment, 1992). People also judge the politicians that they support to be taller than the politicians they oppose (Sorokowski, 2010).

A more direct example that people value height in their leaders comes from a recent study by Murray and Schmitz (2011) that asked people to draw their "ideal national leader" and a "typical citizen". People from various cultures drew their ideal leader as taller than the typical citizen. This is in line with an earlier study by Werner (1982) who found that, in both US and Brazilian populations, individuals ranked height as an important characteristic of leaders. Murray and Schmitz (2011) also found that taller males were more likely to think of themselves as qualified to be a leader and were more interested in pursuing a leadership position than shorter males. These findings are in line with an earlier meta-analysis on the positive effect of height on occupational success, which found that this positive relationship was partly explained by the increased self-esteem of taller individuals (Judge & Cable, 2004). In other words, people not only value height in their leaders, but taller people are also more likely to pursue a leadership position, partly because they have higher self-esteem.

As one might expect, given these general findings, height is also related to *perceptions* of presidential greatness. Presidents considered to be “great” were taller than presidents considered a “failure” and were perceived as having more ‘leadership qualities’ than their shorter counterparts (Sommers, 2002). Thus, perceived presidential height is a function of both voting intentions and liking, while perceived greatness and leadership ability are a function of actual president height. These findings suggest that height is an important characteristic for US presidents and that people are likely influenced by an individual’s stature when choosing and evaluating their leaders.

This study

In the first two studies reported here, we address the methodological and statistical limitations identified in previous work. Specifically, in Study 1, we examine the association between height and electoral outcomes using data from all US presidential elections, and we employ a more sophisticated statistical approach to test whether taller candidates are more likely to be elected. In addition to using the binary outcome of electoral success, we also examine the link between height and the electoral success as measured by the percentage of popular votes received. This is a numerically more informative measure, as it incorporates the actual magnitude of the election success, rather than simply a win-lose outcome measure. Finally, we investigate whether height plays a role in the reelection of presidents. In Study 2, we compare the heights of elected presidents to the average height of men born in the same birth cohort as a way to test whether presidents are taller than the average for their generation. Based on the previous work discussed above, we hypothesized that the taller candidate is more likely to win elections and reelections as well as to receive a higher share of popular votes. Additionally, we expected presidential candidates to be taller than the average male in the population. In Study 3, we extend previous research by examining five recent polls on perceptions of 'presidential greatness' and various other characteristics, such as leadership, communications skills, and quality of foreign policy. Height was hypothesized to be most strongly related to measures of perceived leadership quality, which would potentially explain the higher electoral success of taller presidential candidates.

Study 1: The role of presidential height in electoral success

MATERIAL AND METHODS

Data

We collected the heights of the US presidents and their opponents from Books LLC (2010), which compiled the data from www.wikipedia.org. We used several sources to check the reliability of the height data we collected. Using a subsample, we found that our collected heights correlated strongly with the heights of a previous research paper on presidential height and greatness (Sommers (2002); Pearson $r = .98$; $p < .0001$; $N = 37$). For data on the outcomes of the elections, and the percentage of popular votes received, we used http://uselectionatlas.org/RESULTS/. We included the heights of all candidates from all major parties (Democratic, Republican, Democratic-Republican, Federalist and Whig party), as well as candidates of other parties provided that they received more than 10% of the electoral votes.

Since 1789, there have been 56 US presidential elections. For eleven elections, we were unable to determine whether the taller candidate won. For election years 1804, 1808, 1816, and 1868, heights were not available for all candidates. For election years 1832, 1884, 1940, and 1992, the presidential candidates were of similar height, so there was no taller candidate. Lastly, in the elections years 1789, 1792, and 1820 the chosen president ran (effectively) unopposed. Excluding these elections leaves 45 elections for analyses.

For the elections in 1796, 1800, and 1808, both parties (Democratic-Republican and Federalist parties) had multiple candidates. For these elections, we included the candidates with the most electoral votes from both parties in the analyses. In 1824, all four candidates were from the Democratic-Republican party, and we included all of these candidates in our analyses. In 1836 and 1860, the height of one candidate was unavailable. In both cases, these candidates were least popular (out of four candidates) in terms of popular votes (2.74% and 12.62% respectively). We therefore included these two elections, using data for the three remaining candidates.

Not all elections can be considered statistically independent, given that, in twenty-eight of fifty-six elections a candidate had already held office as president. With respect to height, this is even more pronounced, as height is related to the chance of reelection (see below). Therefore, we repeated our analyses, including only those elections in which neither candidate had previously held office. This left twenty-three elections available for analyses.

Modeling the election outcomes

Using a binomial test to test the proportion of winning taller candidates against 0.5 is not possible, as in five elections (1824, 1836, 1856, 1860, and 1912) there were more than two candidates (in 1824 there were four presidential candidates). Therefore, we tested whether the taller candidates were more likely to win the election using a randomization test. To this end, we simulated 10,000 sets of 45 elections, randomly deciding the candidate that won each election. Thus, we were able to determine a frequency distribution of how many elections, from a total of forty-five, the tallest candidates would win by chance. We then compared this distribution (of 'likelihoods' of the number of times the taller candidate won) to the actual number of times the tallest candidate won, and determine the likelihood of finding such a result by chance.

Level of support for the president

We investigated whether height influenced electoral success in terms of popular votes. As there were more than two candidates for five elections, we expressed electoral success as the ratio of popular votes for the president to that of the most-popular opponent (i.e., the percentage of popular votes to the president divided by the sum of percentage of popular votes for the president and the percentage of popular votes for the most popular opponent.) We correlated the height of the elected president, the height of the most successful opponent in terms of popular votes, and the relative presidential height (height president divided by height most popular opponent) with this ratio. The elections in which the candidates were of equal height could also be included in this analysis, bringing the sample size to forty-nine elections.

Reelection

We examined whether presidential height was related to the likelihood of reelection. We divided presidents into those who were and those who were not reelected at their first attempt of reelection. In total, twenty-five presidents ever sought reelection after they had been elected president, of which fifteen were reelected.

All analyses were run in R version 2.12.1 (R Development Core Team, 2008).

RESULTS

Is the taller candidate more likely to win an election?

In 45 elections, the taller candidate was elected president 26 times (58%; as reported by Murray and Schmitz (2011)). Simulating random elections, we found that the tallest candidate was most likely to win 21 times when elections were random with respect to height (the median value of taller presidents winning in 10,000 samples was 21; see supplementary Figure S3.1a). The deviation between the random expectation of 21 and 50% of 45 is due to the fact that 5 of the elections had more than two candidates. We found that the tallest candidate won 26 times or more in 1,142 out of 10,000 random samples (see supplementary Figure S3.1a). The 26 times that the tallest president actually won an election is therefore not significantly different from chance at the α = .05 level (p = .1142). This p-value concerns the directional hypothesis that taller candidates are more likely to win the election, not the hypothesis that height is related to election outcomes, and as such is one-tailed. Needless to say, if we assume a two-tailed test, there is even less evidence that the taller candidate is more likely to win than we would expect based on chance.

When examining the differences in height between elected presidents and their tallest competitors, we found that elected presidents were not significantly taller than their competitors across all elections (mean difference (± SD) = .289 (± 10.79) cm; paired samples t-test: $t(44)$ = .180; p = .858; d = 0.0267). This is in contrast to the claim of Higham and Carment (1992). Given that this discrepancy could potentially be explained by the fact that previous studies showing an effect of height on US election results (including Higham and Carment 1992) used a sample covering more recent elections, we therefore tested whether election year was related to the likelihood of the taller candidate winning the election. A logistic regression revealed that taller candidates were indeed more likely to win in more recent elections compared to earlier elections,

(B (± SE) = .0102 (± .00550); *Odds ratio*: 1.01; $p = .064$; *Nagelkerke* $R^2 = .107$).

When we considered only those elections in which both candidates had never been elected president, the effect of height was even further reduced: only 12 out of 23 elections (52.2%) were won by the taller opponent. When simulating these 23 elections, we found that the taller candidate won 12 times or more in only 3,990 out of 10,000 elections (see supplementary Figure S3.1b). Thus, the 12 times that the taller presidential candidate was elected in reality is not significantly different from chance ($p = .3990$).

Is height related to popular votes?

In most presidential elections, the candidate with the majority of electoral votes (and thus elected president) also had the majority of popular votes. In four cases (1824, 1876, 1888, and 2000), however, the elected president had fewer popular votes than his opponent. The most recent occurrence was the election of George W. Bush over Al Gore in 2000. Interestingly, in each of these four elections, it was the shorter candidate that won the presidency. We therefore reran the above simulations using the candidate who received the majority of popular votes as the outcome, instead of the winner of the election. In 42 elections (the first three elections were not based on popular votes; two of those elections were won by the shorter candidate), the taller candidates won the popular vote 28 times (67%). We found that the taller candidate would be expected to win 28 times or more by chance in only 97 out of 10,000 random electionsThus, the taller candidate was significantly more likely ($p < .0097$) to receive the majority of popular votes.

In addition to investigating whether the binary outcome of an election (i.e., who received the majority of popular votes) was related to who was taller, we also tested whether the relative amount of support (calculated using the formula: (% of votes for president) / (% of votes for president) + (% of votes for the runner up)) was influenced by relative height (i.e., how much taller or shorter the elected president was in comparison to his most popular opponent). An additional four elections were available for these analyses compared to the analysis above (in which the presidential candidates were of similar height). Relative presidential height (president height divided by opponent height) was positively associated with the proportion of popular votes ($r = .393$; $p = .007$; $N = 46$; Figure 3.1). Thus, 15.4% of the variation in popular support was explained by the relative heights of the candidates, with the relatively taller candidates receiving more support. Examining the absolute height of the candidates, we

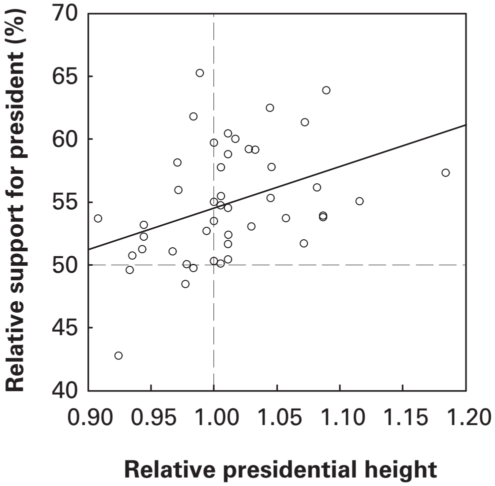

Figure 3.1: The effect of the relative height of the president (president height divided by height most successful opponent) on the ratio of popular votes (% popular votes for president divided by % popular votes president and most successful opponent combined). A relative height of 1 (dashed vertical line) indicates that candidates were of equal height. A ratio of popular votes of 0.5 (dashed horizontal line) indicates that candidates had equal amount of popular votes. With increasing height differences, the relative support for the president increased (the solid line is the regression line).

found that presidential height correlated positively with the proportion of popular votes received ($r = .365$; $p = .013$; $N = 46$), indicating that taller presidents received more support as measured by popular votes (in line with McCann (2001)). The absolute height of the runner-up candidate was negatively, but not significantly, related to the proportion of popular votes for the president ($r = -.214$; $p = .154$; $N = 46$), which suggests that the height of the most successful opponent of the president had a negative effect on the support for the president. Controlling for election year did not change these results (respectively partial $r = .387$; $p = .009$; partial $r = .356$; $p = .016$; partial $r = -.248$; $p = .100$; all $df = 43$).

Excluding those elections in which one of the candidates had previously been president did not change this result: relative presidential height also correlated with the ratio of popular votes in this reduced sample ($r = .467$; $p = .028$; $N = 22$). Similarly, the proportion of popular votes was positively related to presidential height in this sample (non-significantly, but the correlation coefficient was very similar; $r = .325$; $p = .141$; $N = 22$) and negatively related to the height of the most popular opponent ($r = -.420$; $p = .052$; $N = 22$).

Is presidential height related to the likelihood of reelection?

The fifteen presidents that were reelected were, on average, 5.47 cm taller than the ten presidents that were not reelected (181.87 ± 8.00 cm versus 176.40 ± 6.87 cm; Figure 3.2). Visual inspection revealed one outlier in the reelected presidents: President James Madison, with a stature of 168 cm. To accommodate this distribution, we analyzed the group differences using a non-parametric test, and found a significant difference (*Mann-Whitney U* = 39.5; z = 1.98; p = .048). Thus, we conclude that reelected presidents were taller than presidents who were not reelected.

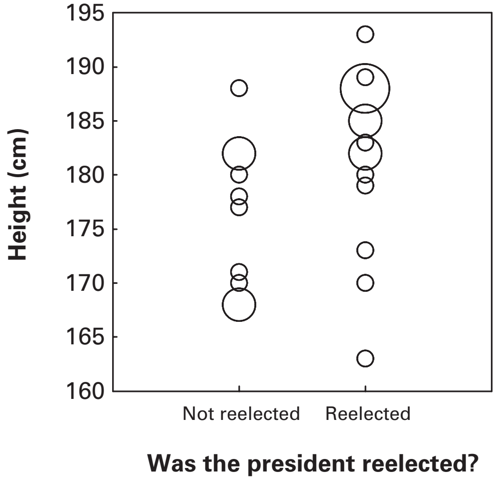

Figure 3.2: Height in centimeter of presidents who were (N = 15) and were not (N = 10) reelected. Diameter of the circles is proportional to N. Presidents who were reelected were taller than presidents who were not reelected.

Study 2: Comparing presidential height to the average height in the population

MATERIAL AND METHODS

We compared the heights of the presidents to the average height of Caucasian men from the same birth cohort, taken from military records (Steckel, 2002). We used this source because these data were available for all relevant birth cohorts (age was binned into ten year bins from 1710 to 1920; from 1920 onwards heights were available per five year bins). It is perhaps dubious to take the average height of Caucasian men as a control group for President Obama. However, African American men are only slightly shorter (3 millimeters) than Caucasian American men in birth cohorts 1960-1965 (President Obama's birth year is 1961; Komlos & Lauderdale, 2007). Moreover, even this slight difference means that our test in this case is conservative, and is biased against our hypothesis rather than toward it. For every president, we calculated the average height of all the losing candidates that each particular president ran against. We also compared this average height of the losing candidates to the average height of Caucasian men from the same birth cohort as that of the relevant president.

RESULTS

Only seven of 43 presidents (James Madison, Benjamin Harrison, Martin Van Buren, William McKinley, John Adams, John Quincy Adams, and Zachary Taylor) were shorter than Caucasian military men from the same birth cohort (Figure 3.3), which is significantly fewer than expected by chance (*Binomial test*: $p < .0001$; test proportion $g = .84$). On average, presidents were 7.23 (±7.10) cm taller than their birth cohort (*one sample t-test:* $t(42) = 6.675$; $p < .0001$; $d = 1.02$). James Madison (president: 1809-1817) was the shortest president relative to his cohort (9.2 cm shorter than average military height) and Lyndon B. Johnson (president: 1963-1969) was relatively tallest (23.0 cm taller). Interestingly, the most recent president of below average height was William McKinley in 1896 (2.2 cm below average height). In line with this observation, the difference between presidential height and the average birth cohort height correlated positively with election year ($r = .319$; $p = .037$; $N = 43$). Thus, the more recent the election, the more likely it is that the president will be taller than other men of his age.

When comparing the average heights of the losing presidential candidates to the height of the general population, we found that in only 6 of 37 cases was the (average) height of the unsuccessful candidate shorter than the height of the general population (*Binomial test*: $p < .0001$; test proportion $g = .84$). On average, losing presidential candidates were 6.95 ($SD = 6.43$) cm taller than the general population (*one sample t-test: t(36)* $= 6.579$; $p < .0001$; $d = 1.08$). Thus, both winning and losing presidential candidates were taller than other men of their age.

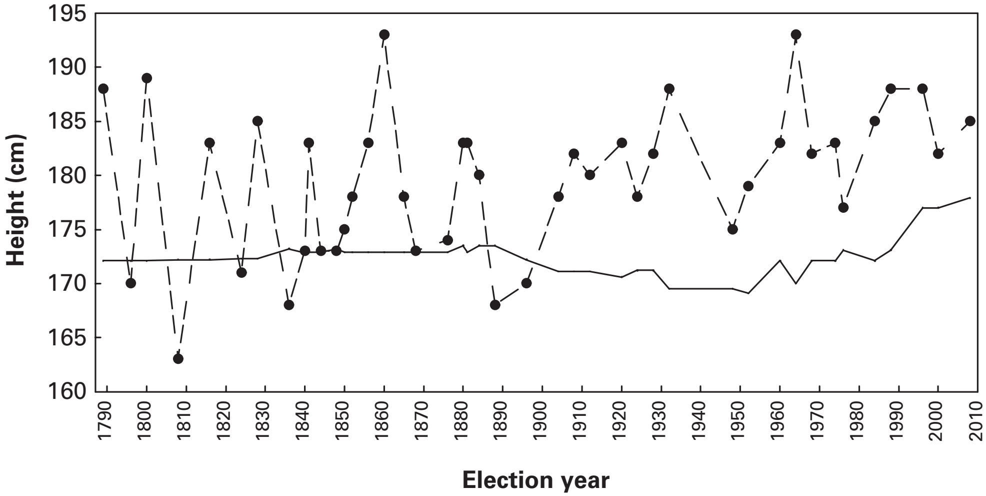

Figure 3.3: Presidential height (dotted line) and the average height of Caucasian military men from the same birth cohort (solid line) for different election years.

Table 3.1: Details from five recent surveys on presidential greatness.

Poll	Year	Experts	Presidents not included	Rated characteristics
Wall Street journal[a]	2005	85 historians, political scientists, law professors and economists[b]	William Harrison, James X. Garfield[c], Barrack H. Obama	Overall greatness
The Times (London)[d]	2008	8 of newspaper's top international and political commentators	Barrack H. Obama	Overall greatness
C-SPAN (Cable-Satellite Public Affairs Network)[e]	2009	64 historians and professional observers of the presidency	Barrack H. Obama	Public persuasion, crisis leadership, economic management, moral authority, international relations, administrative skills, relations with congress, vision/setting agenda, pursued equal justice for all, and performance within context of times. Overall greatness: the average score of the above ten ratings
Siena[f]	2010	238 presidential scholars		Background (family, education, experience), party leadership, communication ability (speak, write), relationship with congress, court appointments, handling of US economy, luck, ability to compromise, willing to take risks, executive appointments, overall ability, imagination, domestic accomplishments, integrity, executive ability, foreign policy accomplishments, leadership ability, intelligence, avoid crucial mistakes, your present overall view. Overall greatness: the average score of the above twenty ratings
USPC (United States Presidency Centre)[g]	2011	47 UK scholars of United States history, politics/government, and foreign policy[h]	William Harrison, James X. Garfield[c]	Vision and agenda-setting, domestic leadership, foreign policy leadership, moral authority, and historical legacy. Overall greatness: the average score of the above five ratings

[a] http://reagan.procon.org/view.resource.php?resourceID=003860 [b] The results of the survey were ideologically balanced, as Democratic- and Republican-leaning scholars were given equal weight. [c] William Henry Harrison and James X. Garfield were excluded in these polls because of the short durations of their presidency. Participants also had to make a preliminary interim assessment of Barack Obama. [d] http://www.timesonline.co.uk/tol/news/world/us_and_americas/us_elections/article5030539.ece [e] http://legacy.c-span.org/PresidentialSurvey/presidential-leadership-survey.aspx [f] http://www.siena.edu/uploadedfiles/home/parents_and_community/community_page/sri/independent_research/Presidents%202010%20Rank%20by%20Category.pdf [g] http://americas.sas.ac.uk/research/survey/aims.htm [h] This is the first official survey on Presidential Greatness outside the US (conducted in the United Kingdom).

Study 3: Perceptions related to presidential height

MATERIAL AND METHODS

For the perceptions of greatness and more specific presidential characteristics, we collected data from five recent surveys on presidential greatness, which took place between 2005 and 2011. See Table 3.1 for the details of these surveys. We correlated presidential height with the overall scores of all five surveys. We also correlated presidential height with the individual qualities rated by the experts for three surveys: C-SPAN 2009, Siena 2010, and USPC 2011 poll. To integrate the information we assigned the different characteristics to seven distinct categories (Leadership, Communication, Performance / Ability, Vision, Policy / Content, Moral authority, Other). As all the ratings were simple rankings, we conducted Spearman's rank correlations (r_s). For ease of interpretation, we reverse coded the ranks, such that a positive correlation coefficient between height and overall greatness, for example, means that taller presidents were considered to be greater. Given the secular trend in average height over time, we controlled for election year in all our analyses.

RESULTS

Presidential height and greatness

On average, taller presidents were rated as greater than shorter presidents, as indicated by the positive correlation between presidential height (controlling for election year) and the average rank score of the five surveys (including the

Table 3.2: Partial Spearman's rho correlation coefficients (r_s, controlled for election year) for the relationship between presidential height and five recent polls of presidential greatness (highest rank means 'greatest').

Poll	r_s	*p*	*df*
Wall street journal 2005	.296	.067	37
Times 2008	.285	.071	39
C-SPAN 2009	.322	.040	39
Siena 2010	.314	.043	40
USPC 2011[a]	.316	.050	37
USPC 2011 incl. Obama[a]	.339	.032	38
Average score[b]	.328	.034	40

[a] President Obama was not included in the original survey results, but data on Obama was collected and reported and we included these intermediate results.

[b] The average score of the above polls (only the USPC 2011 poll with President Obama was included in this score).

current President Obama in the USPC 2011 poll; Table 3.2; Figure 3.4). Examining the individual polls separately, we found that presidential height, controlling for election year, correlated positively with presidential greatness in each of the five surveys (Table 3.2; $.032 < p < .071$; two out of five were marginally significant). Results from the USPC survey with and without the current President were significantly related to presidential height (Table 3.2). Rankings in the different surveys correlated strongly with each other (all $r_s > .886$, $p < .0001$).

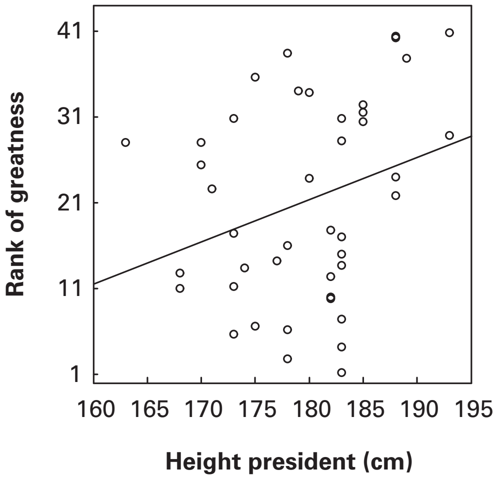

Figure 3.4: The effect of presidential height (cm) on rank of greatness as judged by historians (43 = highest rank = 'greatest' president). The rank of greatness was the average rank of the five most recent polls. Taller presidents were considered 'greater' than shorter presidents (r_s = .328; the ordinary least squares regression (solid) line is added for ease of interpretation).

To which specific qualities is presidential height related?

For three polls (C-SPAN, Siena and USPC), overall greatness is the sum of the rankings of individual characteristics. By correlating height to these individual characteristics, we could examine which specific characteristics led taller presidents to be perceived as greater. Again, results from the three different surveys were very similar (Table 3.3). All eight measures of leadership correlated positively with presidential height (one was marginally significant; Table 3.3), and were among the largest in magnitude. Similarly, all measures falling under the category of 'Communication' and all measures falling under the category 'Performance / Ability' were related positively to presidential height. 'Vision' also seemed positively related to presidential height, but two out of three of these correlations did not reach significance. Height was largely unrelated to 'Policy / Content' (most measures non-significant), and completely unrelated to measures of 'Moral authority' (all four measures non-significant). In the category 'Other', height was only significantly related to luck. Thus, taller presidents were consistently judged as being better leaders, having better communication abilities, and having a higher overall performance. These characteristics led taller presidents to be considered 'greater'.

3

Table 3.3: Partial Spearman's correlation coefficients (r_s, controlled for election year; significant coefficients in bold) for the relationship between presidential height and several qualities from the SIENA (S), C-SPAN (C) and USPC (U) polls.

Common theme	Perceived quality (Poll)	r_s	p^a
Leadership	Party Leadership (S)	**.329**	.033
	Leadership (S)	**.361**	.019
	Crisis Leadership (C)	**.321**	.041
	Domestic Leadership (U)	**.378**	.016
	Executive Ability (S)	**.359**	.019
	Willing To Take Risks (S)	**.326**	.035
	Administration Skills (C)	.289	.067
Communication	Relationship With Congress (S)	**.352**	.022
	Relationship With Congress (C)	**.369**	.017
	Communication Ability (S)	.298	.055
	Public Persuasion (C)	**.319**	.042
	Ability To Compromise (S)	**.322**	.038
Performance / Ability	Overall Greatness[b] (S)	.299	.054
	Overall Ability (S)	**.314**	.043
	Domestic Accomplishments (S)	**.354**	.022
	Performance In Time (C)	**.326**	.038
	Historical Legacy (U)	**.331**	.037
Vision	Vision (C)	.239	.133
	Vision (U)	**.357**	.024
	Imagination (S)	.298	.055
Policy / Content	Handling Economy (S)	.261	.094
	Economic Management (C)	.272	.085
	Court Appointments (S)	.219	.164
	Executive Appointments (S)	**.306**	.048
	Foreign Policy (S)	.194	.219
	International Relationships (C)	.232	.145
	Foreign Policy (U)	.255	.113
Moral authority	Moral Authority (C)	.166	.301
	Moral Authority (U)	.181	.263
	Fight for Equal Justice (C)	.153	.340
	Integrity (S)	.002	.990
Other	Luck (S)	**.319**	.039
	Avoid Crucial Mistakes (S)	.197	.211
	Intelligence (S)	.174	.269
	Background (S)	.140	.377

[a] *p*-value based on the following degrees of freedom: 40 *df* for SIENA poll, 39 *df* for C_SPAN poll (excluded President Obama), and 38 *df* for USPC poll (excluding Presidents W.H. Harrison and J.A. Garfield, who were president for only a very brief period).
[b] Experts were asked for 'their present overall view'. This latter score was incorporated in the final overall score (see Table 3.1).

DISCUSSION

Using a variety of measures, our results show that height plays an important role in determining the electoral success of US presidential candidates and presidents seeking reelection. First, presidential height, and in particular the relative difference in height between the elected candidate and the runner-up, was a significant predictor of the relative amount of electoral support. In particular, candidates who were much taller than their candidates received more popular votes, with the relative difference in height explaining 15% of the variation in electoral support. Not surprisingly then, taller candidates were also generally more likely to receive the majority of popular votes. In fact, in all four cases in which a candidate was elected as president without receiving the majority of the popular vote, the elected president was shorter than the candidate that did. In conclusion, not only does *being* taller give a candidate an advantage in terms of popular votes, but the magnitude of the height difference between a candidate and his opponent also has an effect on political support. In addition to the finding that height is associated with the number of popular votes received, we have shown, for the first time, that reelected presidents were significantly taller (about 5.5 centimeters) than presidents who did not succeed in getting reelected.

Contrary to popular wisdom, and despite the correlation between relative height and success in receiving the popular vote we found that taller candidates were not more likely to win US presidential elections. In only 26 of 45 (58%) elections did the taller candidate win, a finding that does not differ statistically from chance. Why, then, is the notion that the taller candidate wins so widespread? As we noted in the introduction, many of the previous studies investigating this phenomenon have used a highly specific, (self-) selected sample of elections, and very few have analyzed statistically the relationship between stature and election outcomes. Using all elections for which data were available we found, in contrast to one of the few studies that perform any kind of statistical analysis (Higham & Carment, 1992), that elected presidents were not significantly taller than defeated presidential candidates. This discrepancy results from selecting more recent elections as opposed to earlier ones, as we found that the chance of the taller candidate winning has tended to increase as we approach the present day. That is, for more recent elections, height more strongly predicts election outcome (see below for a more detailed discussion of this finding).

The finding that taller candidates are not more likely to win the elections, but receive more electoral support may initially seem contradictory. This pattern can be explained, however, by the fact that taller presidents were more likely to win by an overwhelming majority, while shorter candidates commonly achieve their electoral success through marginal gains. In summary, stature was a clear predictor of support by popular votes and the likelihood of reelection, but height did not statistically predict the most important aspect of an election, namely its outcome.

Our results also showed that elected presidents were, on average, over 7 cm taller than the average Caucasian US male of their generation, whereas only 7 out of 43 presidents were shorter than average. Not only were presidents taller than other men from the same cohort, but the losing presidential candidates were also 7 cm taller on average, indicating that all presidential candidates are substantially taller than the average US male. Of course, we must note that no data were available on the average height of the general male population (i.e., non-military men) and we do not know whether this would affect our results. It seems very unlikely, however, that the non-military men are on average 7 cm taller than military men, which is what it would take to nullify our finding. Furthermore, until recently all men were required to join the military, and hence the military men were a representative sample of the (healthy) general population. In addition, our results are in line with previous studies documenting a positive association between height and education (Silventoinen et al., 2004), income (Judge & Cable, 2004), social status (Ellis, 1994), and authority status (Gawley et al., 2009) in the general population. Thus, as presidents tend to be well educated, have a high income, a high social status and hold one of the most important positions in the world, it is not surprising that they are taller than the average for the population. The finding that both winning and losing presidential candidates were much taller on average than males from the general population may be a consequence of previous selection for height in these candidates at lower levels of government (for instance, as governor, senator or congressman). The finding that height plays such an important role in the presidential elections is therefore even more striking, given that the sample of candidates is already biased towards taller height.

Another interesting finding of our study was that taller candidates were more likely to win more recent elections, and that more recent presidents were relatively taller compared to population height than earlier presidents. In fact, the last time a president was chosen who was shorter than the population average was in 1896: William McKinley, who was 'ridiculed by the press as a "little boy"' (Judge & Cable, 2004). Taken together, these findings suggest that presidential candidate height has become more important in recent times. A potential explanation for this trend is the increasing exposure of candidates in the broadcast media (Drew & Weaver, 2006), making differences in height more visible to the public. Some evidence to support this is provided by Gentzkow, Shapiro and Sinkinson (2009), who showed that, for the period 1869 to 1928, the number of available newspapers affected presidential turnout (the ratio of votes cast to the number of eligible voters), in such a way that one additional newspaper increased presidential turnout by 0.3 percentage points. That is, newspapers had large effects on participation by increasing the 'visibility' of candidates to the population at large. Gentzkow et al. (2009) also showed that the effect of newspapers diminished with the introduction of radio and television, suggesting these alternative sources of information began to have relatively greater impact, particularly television which allowed voters to assess the candidate's physical appearance in addition to what they said.

A classic example of the role of presidential physical appearance is the first televised presidential debates between Kennedy and Nixon: voters who had seen the presidential debate on television were more likely to think that Kennedy had 'won' the debate, a result attributed to the apparent physical discomfort displayed by Nixon, who was sweating profusely throughout the event. Voters who had only heard the presidential debate on the radio, and were unaware of Nixon's appearance, were more likely (or at least equally likely) to think Nixon came out on top (Davey, 2008; but note this assumes that television and radio audiences are random samples of citizens (Smith, 2010)).

It therefore seems likely that the importance of the physical appearance of the candidates, including their height, is likely to be more pronounced in an age with a greater number of alternative forms of visual media. In fact, one of the most contested matters in televised presidential debates is the relative height of the candidates (Schroeder, 2008), with, among other things, ramps being used to make presidential candidates appear to be similar in stature during televised debates (e.g., the 1988 televised debate between George Bush and the much shorter Michael Dukakis). Whether this solution actually benefits the shorter candidates is doubtful, however. Schroeder (2008) concludes: 'At the close of the debate, when Dukakis stepped down from his podium to shake Bush's hand, the height difference between the two men seemed all the more pronounced.' Thus, although this explanation is speculative, the increasing exposure of the candidates and politics in the media may explain the increasing strength of the relationship between height and electoral success.

Our third study showed that taller presidents are perceived as 'greater' than shorter presidents (in line with McCann (1992) and Sommers (2002)). This association between height and presidential greatness was mainly a result of a relationship with perceived leadership abilities: taller presidents were considered to be better leaders than shorter presidents. Taller presidents were also considered to have better communication abilities and rated as showing higher overall performance. Thus, height seems to be a characteristic which is valued in political leaders. Also in other domains than politics, a relationship between height and leadership is found, as taller people, particularly men are more likely to emerge as leaders in a group and more often occupy a leadership or managerial position (Gawley et al., 2009; Stogdill, 1948).

Why is height related to perceptions of leadership? A recent study hypothesized that height would be related to leadership through at least three distinct pathways: via perceptions of dominance, health and intelligence (Blaker et al., in press). In this study, participants rated a picture of a short and a tall man and woman on the aforementioned characteristics, as well as rating the individual depicted on how much they looked like a leader. Height was strongly related to perceptions of leadership in men. This relationship was most strongly mediated by dominance, but also by health and intelligence. Thus, taller men were more likely to be perceived as leaders partly because they were perceived as more dominant, healthier and more intelligent. Interestingly, height was still significantly positively related to leadership after controlling for all three of these pathways.

Physical attractiveness may be another component through which height influences leadership qualities, as height is also positively related to male attractiveness (Courtiol et al., 2010b) and more attractive individuals are more likely to emerge as leaders (Goktepe & Schneier, 1989). The finding that taller presidential candidates are more successful may similarly be a consequence of the positive relationship between height and attractiveness, and perceptions of dominance, health, and intelligence. Further research is necessary to examine the direct versus indirect benefits of height for (perceptions of) male leadership.

In contrast, the relationship between height and perceptions of leadership in women, is completely mediated by the positive relationship between stature and perceived intelligence. Blaker et al. (in press) found that height was not related to perceptions of dominance and health, although these two variables did predict perceptions of leadership in women. Additionally, the relationship between height and leadership is weaker in women compared to men (Blaker et al., in press). This is in line with findings on the relationship between height and measures of social status: both male and female height are positively related to measures of social status (Judge & Cable, 2004), but the magnitude of the relationship is significantly stronger for men than for women. The increased attractiveness of average height women (Courtiol et al., 2010b) also adds another layer of complexity to the association between height and leadership. Nonetheless, female height is related to (perceptions of) leadership, although the effect of height is stronger in men.

Combined with the results of two recent studies investigating perceptions of leadership in relation to height (Blaker et al., in press; Murray & Schmitz, 2011), the present results suggest that height is an important characteristic for choosing and evaluating political leaders. These results therefore signify the importance of considering biological underpinnings of human behavior, which, until recently, have largely been ignored in the social sciences (Murray & Schmitz, 2011). The importance of biological variables is emphasized by our finding that as much as 15% of the variation in (relative) votes can be explained by the difference in height between candidates, suggesting that it is important to also consider biology when aiming to understand relations between leadership and human behavior in general. Thus, biological traits, such as height, deserve a more prominent role in leadership theories (Bass, 2008; Bass & Riggio, 2006; Murray & Schmitz, 2011). The perception of increased leadership qualities in taller individuals is in line with the higher perceived competence associated with increased stature (Young and French, 1996). The 'halo' effects of increased stature are therefore likely to lead to discrimination in favor of taller men and to the detriment of shorter men (**Chapter 2**). There is, in fact, some evidence to suggest that such 'heightism' occurs: taller men tend to have higher starting salaries than shorter men, after controlling for previous qualifications (Loh, 1993). Height also tends to be positively related to income in employed workers (i.e., subordinate to employers) but not in self-employed workers (i.e., those who are not subordinate to employers and therefore experience no risk of discrimination; Cinnirella and Winter, 2009). Under conditions when true competence is not associated with height, but our subconscious biases cause us to discriminate against short individuals, it seems reasonable to suggest that society should consider policies to guard against this form of discrimination.

Any discussion of the biological underpinnings of particular traits obviously raises the issue of whether such patterns are universal across humans or specific to particular cultures. There is, in fact, some evidence to suggest that height is valued in political leaders cross-culturally (Bernard, 1928; Werner, 1982). Indeed, people from diverse populations are more likely to depict their ideal political leader as taller than a regular citizen (Murray & Schmitz, 2011). More cross-cultural research is needed, however, to establish the extent to which height preferences and other leadership characteristics extend to non-Western populations. Preferred leadership characteristics are known to vary across cultures (Gerstner & Day, 1994), and these preferences likely depend on the socio-cultural dimensions of the populations in question, such as the degree of preferred individualism, masculinity, or equality (Ardichvili & Kuchinke, 2002). It seems likely that preferences for taller leaders similarly may be contingent on these socio-cultural dimensions.

A limitation of the current study is that we collected heights of the presidents and their opponents from public databases. Although our height data were almost identical to the heights used in a previous research paper (Sommers, 2002), we could not verify the height of the opponents in a similar way. As several studies have shown that perceived competence or status alter perceptions of height (Dannenmaier & Thumin, 1964; Marsh et al., 2009), there is at least the theoretical possibility that assessments of candidate height by historians is biased, in such a way that opponents who did poorly were underestimated in height or were perceived as shorter than the elected presidents. This limitation is particularly likely to hold true for earlier elections, as accurate, objective measures of height were less likely to be obtained than for more recent elections (for instance, because of the lower number or lack of available pictures and videos of these candidates). This line of reasoning as explanation for our results is in contradiction to our actual findings, however: in more recent elections, for which height data are likely to be more accurate, taller candidates were even more likely to win than in earlier elections. Thus, we consider it unlikely that our findings are a result of biased perceptions of the heights of the candidates.

In conclusion, we have shown that the common conception that taller US presidential candidates are more likely to win elections is not supported by the data. There are, however, reasons to believe that candidate height will significantly predict election outcomes in the future. Presidential candidate height has, for instance, become more important in recent times. More importantly, taller presidents received greater levels of support as measured by the popular vote, and they were more likely to be reelected. Presidents are also much taller than men from their birth cohort and taller presidents are perceived as 'greater' and better leaders than shorter presidents. Apparently, people really do prefer to elect leaders that they can look up to.

SUPPLEMENTARY MATERIAL

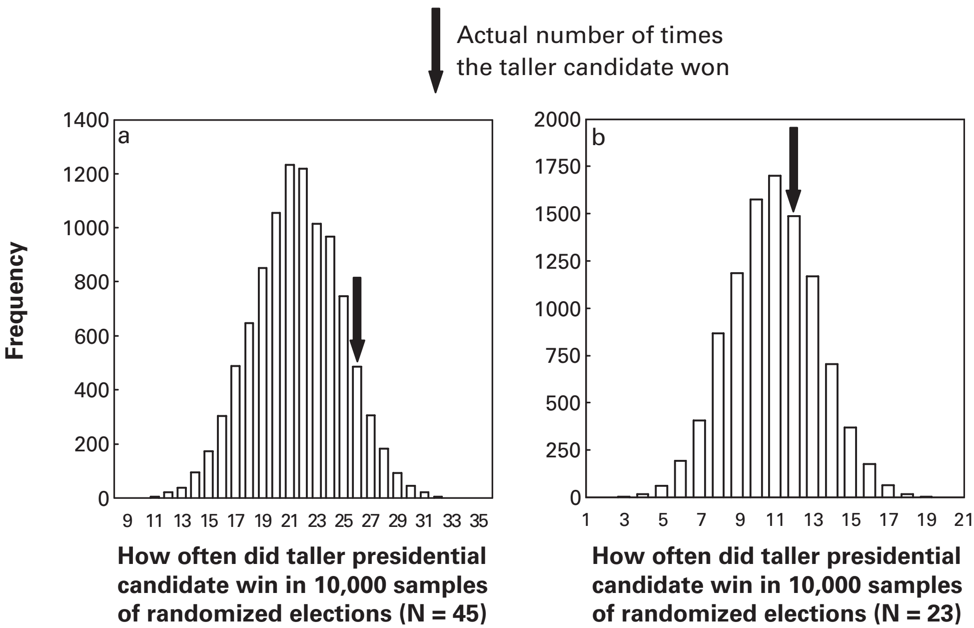

Figure S3.1: Histogram of the number of times the taller presidential candidate won in 10,000 sets of randomized elections and the actual number of times the taller presidential candidate actually won (black arrow) for (a) all elections (N = 45) and (b) all elections (N = 23) in which none of the candidates had been president previously. Taller candidates were not significantly more likely to win the elections.

CHAPTER 4

Human height is positively related to interpersonal dominance in both verbal and non-verbal dyadic interactions

Gert Stulp
Abraham P. Buunk
Simon Verhulst
Thomas V. Pollet

Submitted

ABSTRACT

Taller stature is cross-culturally related to increased social status, the cause of which is unclear. A potential explanation is that taller individuals are more likely to win a dyadic confrontation with a competitor (i.e., are more dominant), which leads to higher social rank. In three naturalistic observational studies, we show that height indeed predicts interpersonal dominance during brief dyadic interactions, such as the likelihood of giving way in a narrow passage (Study 1 & 2), the likelihood of colliding with another individual (Study 2), and the likelihood of maintaining a linear path and so entering another individual's personal space (Study 3). We complement these findings with an experimental approach which shows that the effect of height also extends to longer, verbal interactions between individuals: taller individuals were more persuasive than their shorter counterparts in a negotiation game (Study 4). We conclude that human height is positively related to interpersonal dominance.

INTRODUCTION

Both historically and cross-culturally, the term "big man" has been used to denote an individual of both high social status and physical stature. According to Ellis (1992, p. 279), the phrase is '*a conflation of physical size and social rank and ... "big men" are consistently big men, tall in stature*' (see also Van Vugt et al., 2008). For most of human evolution, it seems likely that "big men" experienced increased social status (i.e., increased access to resources) due to their physical superiority in competition with others. Along similar lines, among contemporary human populations, height is positively related to proxies of social status, such as leadership, professional achievement, education, and income (Gawley et al., 2009; Judge & Cable, 2004; Stogdill, 1948; **Chapters 2**, **3**, **9** and **10**).

Despite overwhelming evidence that human stature is positively related to social status in both men and women in Western societies, the proximate mechanisms that underpin this phenomenon remain obscure. Several hypotheses to explain this relationship have been proposed, including the increased cognitive ability associated with greater height (explained by factors such as genes or nutrition: Silventoinen et al., 2004), the increased health problems associated with shorter stature (Silventoinen et al., 1999), and the observation that taller individuals appear to experience better childhood environments (i.e., parental resources; Persico et al., 2004). All these hypotheses, however, interpret the correlation between height and social status to be indirect; that is, the relationship is mediated by those factors, like improved nutrition and health, that are both a cause and consequence of higher social status in and of themselves. Instead, we consider the possibility that height *directly* influences the likelihood of attaining higher social status. More specifically, we hypothesize that taller people achieve higher social status as a result of their increased interpersonal dominance during confrontations with competitors. Dominance in the animal kingdom is defined as 'an attribute of the pattern of repeated, agonistic interactions between two individuals, characterized by a consistent outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation' (Drews, 1993, p. 283). Although dominance as such is a relative measure (based on repeated interactions), and not an absolute property of an individual, in this study we will refer to interpersonal dominance as the likelihood of an individual winning a dyadic confrontation. We hypothesize that the probability of winning a confrontation increases with height of the individual in relation to their opponent. The form and function of such confrontations can be as diverse as the society in which they occur, and although the advantage of winning one confrontation may be small, the cumulative effect of many such advantages may be instrumental to achieving higher social status.

The hypothesis that body size is related to dominance echoes findings in the animal kingdom. Darwin (1871) was among the first to suggest that males were larger than females in most mammals because such large size was advantageous in contests over mates (Darwin, 1871; p. 260), and later studies have confirmed that size is indeed important in intra-sexual competition. Among mammals, larger males are usually more likely to win fights from smaller males (Archer, 1988), which leads to higher social rank and increased social dominance, and, consequently, increased access to females (Andersson, 1994; Ellis, 1994). Recently, Puts (2010) argued that, although inter-sexual selection (i.e., mate choice) has been considered the main driver of sexual selection in humans, differences in body size, strength, and aggressiveness between the sexes are probably better be explained in terms of intra-sexual competition. Thus, sexual dimorphism in stature may well be a consequence of past intra-sexual competition between males.

Among humans, there is also some evidence to suggest that height is related to physical dominance (Ellis, 1994): taller men are physically stronger (Carrier, 2011; Puts, 2010; Sell et al., 2009); physically more aggressive (Archer & Thanzami, 2007); show better fighting ability (Archer & Thanzami, 2007; Sell et al., 2009; von Rueden et al., 2008), and feel less threatened by physically dominant men (Buunk et al., 2008). However, physical strength and fighting ability may seem unlikely determinants of social status in modern Western societies, given that individuals are prohibited by law from using force against another individual (Puts, 2010). Nevertheless, we suggest that height is associated with dominance in contemporary populations, resulting in taller individuals being more likely to win (non-physical) confrontations against shorter individuals, albeit in more subtle ways.

How, then, could human height directly influence the probability of winning non-physical confrontations? First, even though the use of force is prohibited by law, the increased physical strength (Sell et al., 2009) and fighting ability (von Rueden et al., 2008) of taller individuals may be perceived as more threatening during a contest, even when that contest is non-physical. Taller people are also perceived as more competent, authoritative, and dominant (Cinnirella & Winter, 2009; Judge & Cable, 2004; Marsh et al., 2009; Young & French, 1996). Such height-dependent perceptions may then contribute to the increased dominance of taller individuals if shorter individuals act on their perceptions, and treat those who are taller as more competent, authoritative, and dominant than they are, and so yield to them in competitive situations.

Height may also affect how people perceive themselves, and so influence behaviour (which as noted, in part reflects how other people treat them). For instance, taller individuals, particularly among men, have higher levels of self-esteem than shorter individuals (Judge & Cable, 2004), which may result in taller individuals displaying more self-confidence in social interactions. Increased self-esteem may itself be a consequence of experiencing more favourable contest outcomes earlier in life. Children as young as ten months old recognize that size plays a role in dominance contests (Thomsen et al., 2011), and there is some evidence to suggest that taller individuals win more contests/confrontations during childhood and young adulthood than shorter individuals: taller children win more aggressive bouts on the playground (Pellegrini et al., 2007) and are less likely to be a victim of bullying (Voss & Mulligan, 2000). It has also been shown that taller teenagers participate more in social activities, which in turn has been shown to have long-term effects on social status in later life (Persico et al., 2004). Thus, the cumulative effects of the positive contest outcomes experienced by taller individuals throughout development are likely to contribute to increased self-esteem and hence increased dominance in adulthood.

In this paper, we examine whether stature is positively related to interpersonal dominance in subtle non-physical contests, via a series of both observational and experimental studies. In Study 1, we examined whether height influenced the probability of yielding to another individual when passing through a narrow passage-way. In Study 2, we investigated whether people gave way to confederates of varying height, who walked against the stream of pedestrian traffic in a busy shopping street. In Study 3, we examined whether the height of a pedestrian influenced his or her behavior towards a confederate who was partially blocking the pedestrian's pathway. In all three studies, we hypothesized that height would be positively related to dominance, such that taller individuals would be less likely to yield to those who were shorter. Studies 1-3 focus on non-verbal interactions, and in Study 4 we investigated experimentally whether height was related to dominance in an extended verbal interaction, by monitoring individuals completing a game of negotiation. Here we also predicted that taller individuals would be less likely to yield than shorter individuals, and so achieve an outcome that was closer to their view than to those of their opponent.

Study 1: Taking precedence and giving way on a narrow sidewalk

INTRODUCTION

Imagine a situation where two individuals from opposite directions simultaneously attempt to pass through a narrow passage way that only accommodates the passing of a single individual. Which individual is more likely to take precedence and which individual is more likely to give way? We hypothesized that in real-life examples of this 'chicken game' (e.g., Cohen & Nisbett, 1996), taller individuals would be more likely to take precedence and that shorter individuals would more likely to give way, and allow taller individuals to pass first.

MATERIAL AND METHODS

Procedure

We observed pedestrians entering and leaving a supermarket in a mid-size European city (Brugstraat in Groningen, the Netherlands). To do so, pedestrians had to walk through a narrow passage on a sidewalk (Figure 4.1a). The passage was too narrow for two individuals to pass through simultaneously. Thus, when two individuals approaching from opposite directions attempted to pass, one individual was required to give way (Figure 4.1a). In the first

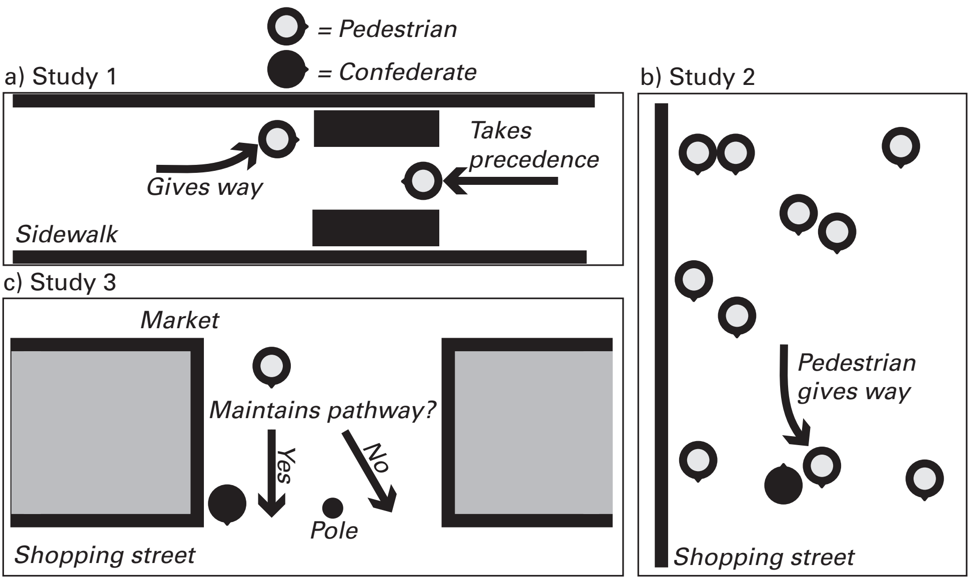

Figure 4.1: The set-up from (a) Study 1, (b) Study 2, and (c) Study 3.

part of our experiment, we made use of narrowness of passageway resulting from temporary scaffolding (because of construction work). After the scaffolding was removed, we used bicycles to create a similarly narrow passage. All observations were performed by pairs of observers (comprised of a total of six different observers). The observers stood on the opposite side of the street, outside of the direct line of sight of the pedestrians. For each pair, the observers agreed on both the height and age of each individual, and on which individual took precedence and which individual gave way. Individual height was estimated using chalk lines marked on the wall next to the passage way. The lines were marked in ten cm increments from 160 to 200 cm. A pilot experiment demonstrated that this method of estimating height was reliable between raters as high inter-rater reliability correlations across all raters indicated (all Pearson $r > .95$; $p < .0001$). Groups and individuals pushing either bicycles or buggies were not included in the observations. All observers were aware of the aims of the study. All the research reported in this document was approved by the psychology ethics committee of the University of Groningen.

Analyses

In total, we observed 92 pairs of individuals trying to pass through the passage-way at exactly the same time on six different observation days (on six different days during 12.00-13.30 and 17.00-19.00, mid-April). We only included same-sex pairs ($N = 50$ pairs). Heights were estimated to be equal in 4 of these 50 pairs, and these were excluded from the analyses, leaving 46 pairs (28 male pairs and 18 female pairs). A paired samples *t*-test was used to test whether those who took precedence were taller than those who yielded and gave way. To test for differences in the effect of height depending on the sex of the pair, we used a General Linear Model, with the difference in height between the individuals as a dependent variable and sex as a fixed factor. This analysis is equivalent to a paired samples *t*-test when no fixed factors are included in the GLM and only an intercept is fitted. Because age is related to height and differences in age between the individuals in the pair may influence who yields, we also controlled for the difference in perceived age in the GLM. Additionally, we reran the analyses only including couples in which the perceived age differences did not exceed 15 years. Including the pair of observing experimenters as a random effect did not influence the results, nor did the method by which the passageway was narrowed (scaffolding versus bicycles; results not reported). All analyses were performed using R, version 2.13.1.

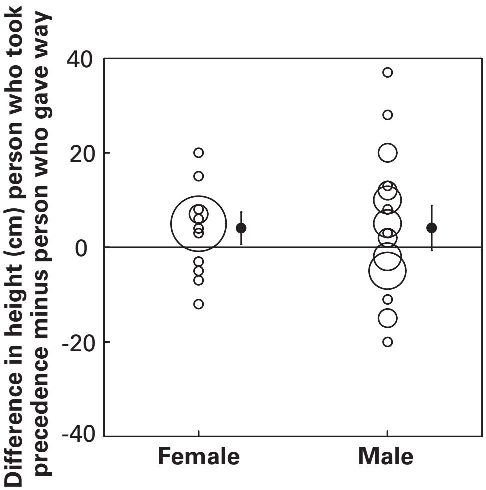

Figure 4.2: Results from Study 1: Priority of access in relation to difference in height (cm) (individual who took precedence – individual who gave way) for female and male pairs. The diameter of the open circles indicates sample size. The black dots and bar represent the *mean* and 95% confidence interval.

RESULTS

Men who took precedence were estimated to be 181.32 (*SD* = 10.77) cm in height, on average, whereas men who gave way were estimated to be 177.21 (*SD* = 5.55) cm. Similarly, women who took precedence were estimated to 171.11 (*SD* = 7.59) cm tall on average, whereas women who gave way were estimated to be 167.06 (*SD* = 6.23) cm on average. Combining male and female pairs revealed that individuals who took precedence were significantly taller (4.09 (*SD* = 10.96) cm) than those who gave way (paired samples t-test: $t(45) = 2.53$; $p = .015$; $d = 0.37$; Figure 4.2). Similarly, taller individuals (67%) were significantly more likely than shorter individuals (33%) to take precedence (Binomial test: $N = 46$; $p = .026$).

A GLM with the difference in height as a dependent variable, revealed that there was neither a significant effect of sex ($F(1, 44) < .001$; $p = .99$; *partial* $\eta^2 < .01$), nor could this effect be attributed to the difference in perceived age ($F(1, 44) = .65$; $p = .42$; *partial* $\eta^2 = .01$). In other words, the strength of the effect of height was similar for men and women and was not driven by the effect of age. Restricting the analyses to pairs where the perceived age difference was estimated to be less than 15 years resulted in a stronger effect of height (mean difference = 5.66 cm (*SD* = 10.74); $t(31) = 2.98$; $p = .006$; $d = 0.53$). Again, there was no significant sex difference with respect height ($F(1, 30) < 1.900$; $p = .18$; *partial* $\eta^2 = .060$), although the effect of height was, on average, 1.90 (*SE* = 3.809) cm stronger for men. Similarly, with this age range restriction, taller individuals were even more likely (75%) than shorter individuals (25%) to take precedence (Binomial test; $N = 32$; $p = .007$).

DISCUSSION

Taller individuals were more likely to take precedence when entering a narrow passage wide enough only for a single individual to pass. This effect was independent of both sex and perceived age. To the best of our knowledge, this is the first evidence that height differences affect the outcome of a brief dyadic interaction in a naturalistic setting. Given the nature of the observational set-up, we were, however, unable to assess whether this effect was because taller individuals actively take precedence, shorter individuals are more likely to give way, or both. In a follow-up study, therefore, we investigated how pedestrians reacted towards confederates of varying height, as they walked along a busy shopping street.

Study 2: Giving way and collisions in a busy shopping street

INTRODUCTION

On busy shopping streets people walk in a variety of directions at a variety of speeds heading toward a variety of destinations. Yet, for the most part, people obey an implicit rule that they should walk on the "right" side of the street. As a result, pedestrian traffic self-organises, and the overwhelming majority of people on the same side of the street will walk in the same direction. What happens when an individual violates this norm and walks against the flow of pedestrian traffic? More pertinently to our aims here, does the height of the person violating this norm influence how people react? In our second study, we therefore investigated whether pedestrians would be more likely to give way to, and less likely to bump into, a taller individual who walked against the flow of pedestrian traffic than they would to a shorter individual.

MATERIAL AND METHODS

Procedure

Confederates of varying height walked up and down a crowded shopping street of a mid-size European town (Herestraat in Groningen, the Netherlands). They were instructed to walk in a straight line, against the flow of pedestrian traffic (i.e., walking on the left side of the street) and to not look oncoming pedestrians in the eye, but to gaze either at shop windows or into the middle distance.

One observer (of which there were six in total; the same individuals also acted as confederates) observed the sex of each pedestrian encountered, whether the pedestrian gave way to the confederate (i.e., the pedestrian would move to one side and onto a different heading, in order to avoid a collision with the pedestrian), and whether the participants collided with the confederate (Figure 4.1b). We defined a collision as any physical contact between a pedestrian and the confederate. When it was evident that the pedestrian was not going to step aside for the confederate and a collision was imminent, the confederate would then step aside. When a collision occurred, the confederate would apologize to the participant. Heights and ages of the participants were not recorded, as this was too difficult to assess accurately by the experimenter, who also had to maneuver through the busy shopping street, and avoid colliding with pedestrians. All confederates were dressed in a similar fashion (jeans and dark jacket). Eight female confederates (with heights of: 160, 161, 171, 172, 175, 177, 183 and 183 cm) and seven male confederates (with heights of: 170, 177, 180, 185, 200, and 200 cm) participated in the study, and all were aware of the study's aims.

Analyses

Logistic mixed models were used to analyse the data. The binomial dependent variables were (a) whether the participant gave way to the confederate (i.e., stepped aside) and (b) whether a collision occurred. As independent factors, we included confederate height and sex, and the sex of the pedestrian. Confederate identity was included as a random factor because observations within a confederate cannot be assumed to be independent. Including the identity of the observer as a random factor did not change our results (results not reported). We determined the R^2 for the full model (i.e., *conditional* R^2) based on the methods by Nakagawa & Schielzeth (2012). Furthermore, we determined the R^2 of the effect of height for each variable (i.e., the *marginal* R^2), to compare their magnitude.

RESULTS

In total, we observed 1,018 pedestrians in the shopping street on eleven different days (only at busy hours; 14-17 and 19-21 on Thursday evenings). Controlling for height, we found that pedestrians were more likely to give way to female than to male confederates (Table 4.1). For a woman of 180 cm, 76% of individuals were predicted to step aside, whereas for a man of the same height, the value was 65%. Height was positively related to the chance of giv-

Table 4.1: Results from Study 2: Logistic mixed model parameter estimates (± *SE*) for the effect of the height, sex of the confederate, sex of the pedestrian, and their interactions on the likelihood that the pedestrian would (i) give way to the confederate or (ii) collide with the confederate (*N* = 1,108). Non-independence due to confederate ID was modelled as a random intercept.

	Likelihood that confederate was given way		**Likelihood of collision with confederate**	
	Parameter estimate (± *SE*)	*p*-value	Parameter estimate (± *SE*)	*p*-value
Intercept	-7.72 ± 2.04	.0002	4.91 ± 2.27	.030
Sex confederate[a]	-0.54 ± 0.26	.039	0.56 ± 0.31	.073
Sex participant[a]	--[b]	--	-0.46 ± 0.20	.021
Sex conf. x Sex pp.	--[b]	--	0.50 ± 0.28	.069
Height	0.049 ± 0.012	<.0001	-0.031 ± 0.013	.017
Random intercept[c]	0.093 ± 0.31		0.14 ± 0.38	
R^2 [d]	.085		.078	

[a] Reference category is male.
[b] Non-significant (both *p* > .38) and therefore not included in the final model.
[c] Intercept at the level of confederate; variance estimate ± *SD*.
[d] R^2 for the full model; based on the methods by (Nakagawa & Schielzeth, in press; i.e., *conditional* R^2).

ing way by the pedestrian in both sexes (Figure 4.3a, b). For our shortest female (160 cm) and male (170 cm) confederates, our model predicted that 55% and 54% of pedestrians would step aside, respectively. In contrast, for our tallest female (183 cm) and male (200 cm) confederates, this value was increased to 79% and 84% respectively. No significant interaction was found between confederate height and sex (*p* = .87). Examining the amount of variation explained by height, we found that 7.0% of the variation in giving way in men was explained by height, whereas for women this value was 4.8%. The sex of the participant had no effect on the chance of giving way (*p* = .97), nor did it interact with either confederate height (*p* = .18) or the sex of the confederate (*p* = .38). In conclusion, pedestrians were more likely to yield and give way to taller compared to shorter individuals, and this was equally true for men and women, although the effect was slightly stronger for men.

Confederate height was negatively related to the chance of a collision (Table 4.1; Figure 4.3c, d). That is, pedestrians were more likely to collide with shorter confederates than with taller confederates. The lack of a significant interaction between sex and height of the confederate (*p* = .81), again suggests that the effect of height was similar for men and women. Height in men explained 3.3% of the variance in collision probability (*marginal* R^2), whereas female confederate height explained 1.5% of the variance. We also found a marginally significant interaction between the sex of the confederate and the sex of the pedestrian, such that male pedestrians were less likely to collide with female confederates (Table 4.1).

For our shortest female confederate (160 cm), our model predicted that 48% of women and 37% men would collide with the confederate respectively, while for our tallest female confederate (183 cm) our model predicted that only 31% of women and 22% of men would collide. There was no difference in rate of collision between the sexes when a male confederate was walking against the stream of people. For our shortest male confederate (170 cm), our model predicted that 54% of women and 55% of men respectively would collide with

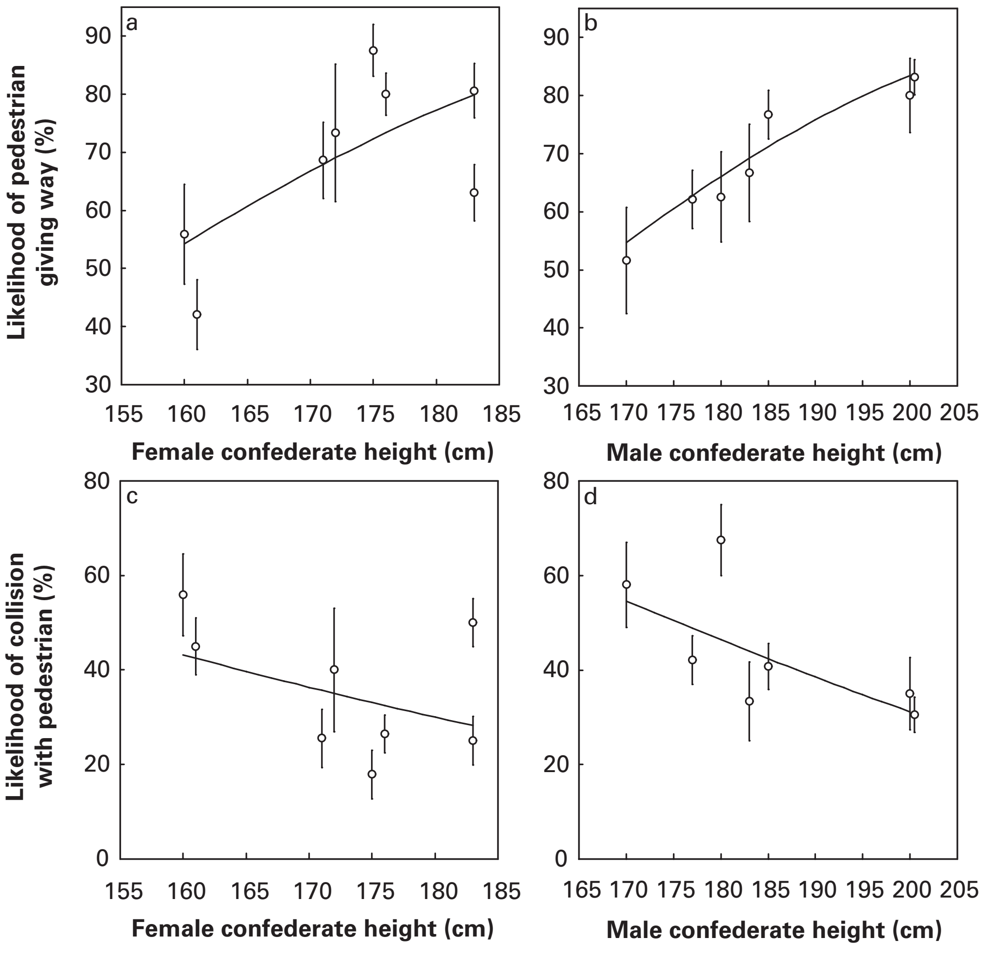

Figure 4.3: Results from Study 2: The effect of confederate height on the likelihood that a pedestrian gave way (top panels; a, b) or collided with (bottom panels; c, d) a female confederate (left panels; a, c) or male confederate (right panels; b, d).

the confederate, whereas for our tallest male confederate (200 cm), our model predicted that only 32% of women and 33% of men would collide. There was no significant interaction between the height of the confederate and the sex of the participant (p = .33), nor did we find a three-way interaction between the height of the confederate, the sex of the confederate and the sex of the pedestrian on the likelihood of a collision (p = .97). In summary, shorter confederates were more likely to collide with pedestrians than were taller individuals. In addition, male pedestrians were less likely to collide with female confederates than they were with males.

DISCUSSION

Pedestrians were more likely to yield to taller than to shorter confederates by giving way and stepping aside. This was equally true for both male and female confederates. In addition, when examining a more confrontational measure of dominance - actual physical contact - we found that taller confederates were less likely to collide with pedestrians than shorter ones. We also observed a gender-related norm in the shopping street: male pedestrians were less likely to collide with female than male confederates. In line with the findings of Study 1, therefore, we found that an individual's height influenced strongly the behavior of others in a dyadic encounter in a naturalistic setting. In Study 3, we assessed yet another behavioural measure of dominance: the social distance adopted by people of different heights when passing by an unknown individual in a confined space.

Study 3: Maintaining one's pathway in a narrow passage

INTRODUCTION

In general, people try to avoid invading someone else's personal space, and ensure they pass by others at a socially acceptable distance. What happens, however, when an unknown individual partly blocks your pathway? Do people choose to remain on their original heading, thereby passing by such individuals in close proximity, or do they divert from their chosen path, thereby giving a wider berth to the blocking individual? In this study, we tested whether the height of the passing pedestrian, would significantly influence the path chosen. We hypothesized that taller pedestrians would be less likely to yield and divert from their path.

MATERIAL AND METHODS

Procedure

The study was set in a passageway for pedestrians between a market and the main shopping street of the same European city (Koude Gat in Groningen, the Netherlands). The passageway was narrow (approximately 2.5 m wide) and contained a small pole in the middle of the passage near the shopping street (Figure 4.1c). The pole acts as a 'guide' to ensure people walk through the passage on the 'right' side. Thus, people coming from the market and entering the shopping street mostly walk on one side of the passage (and pole), whereas people going to the market from the shopping street usually walk on the other side of the passage (and pole; Figure 4.3). Taking advantage of this set-up, we positioned a confederate in a way that partially blocked the passage for those pedestrians walking from the market towards the shopping street. More specifically, the confederate was asked to lean against the wall in the vicinity of the pole, thus leaving only around one meter of space between the confederate and the pole through which pedestrians could pass. We examined whether pedestrians would maintain their original path, and so pass the confederate at sufficiently close proximity to invade their personal space (Figure 4.1c), or whether they would yield to the confederate by deviating from their original path (and so passing the confederate on the 'wrong' side of the pole). This set-up thus provided a clear and unambiguous measure of path deviation by allowing us to record simply on which side of the pole a given pedestrian chose to walk in order to pass through the passage. Observations were conducted on ten different days (between April 24th and June 5th; between 11.00-17.00 h).

In each observation session, the blocking confederate was instructed to lean against the wall, with his or her right arm resting against the wall, so that they were facing towards the shopping street and away from the pedestrian. They were instructed to play with a mobile phone to make their behavior appear more natural. Four female confederates (with heights of 171, 175, 176, and 183 cm) and three male confederates (with heights of 177, 185, and 200 cm) participated in the study. As the main focus of the study was the height of the pedestrians, rather than that of the confederates (as was the case in Study 2), we used fewer confederates, and their individual heights did not cover the entire height range. It is possible, however, that confederate height may influence the behavior of the pedestrians, and therefore we included it in our analyses.

Two observers simultaneously recorded the behavior of the pedestrians coming from the market and walking through the passage, approaching the confederate from behind. One researcher recorded the height, sex and perceived age of each pedestrian, whereas the other researcher recorded whether or not pedestrians maintained their path (i.e., they recorded which side of the pole the pedestrian chose to pass the blocking confederate). The observers were positioned behind a corner, out of the line of sight of the pedestrians. To our knowledge, pedestrians were completely unaware of the presence of the observers while walking through the passage way. Individuals walking in groups or with a bicycle or a buggy were not recorded. We also did not record the behaviour of pedestrians when other pedestrians were walking through the passageway, as this resulted in further blocking of the pathway in addition to our confederates, and the basis of pedestrian movement decisions with respect to the confederate became ambiguous. All confederates and research assistants were aware of the aims of the study.

Due to local conditions of this experimental-set up, we could not make use of chalk markings on the wall to estimate pedestrian height. Instead, observers estimated height without any reference points. Although this method is less accurate than our first study, we do not consider this to be a major problem, for two reasons. First, all our research assistants were trained during our first study to make accurate height estimations. Second, two researchers rated a subset of pedestrians on height, and inter-rater correlation was high (Pearson $r = .83$, $p < .0001$, $N = 50$).

Analyses

We used logistic mixed models to analyse the data, with the chosen path of the pedestrian (i.e., whether the pedestrian was observed to deviate from his or her path) as the dependent variable. We included height and sex of the participant, and the sex of the confederate, as fixed effects, and we included confederate identity as a random effect because observations within a confederate may not be independent. Including observer identity as a random effect did not change our results (results not reported). We standardized the estimated height of pedestrians within each sex in order to better compare the effect of height between the sexes: a shift of one standard deviation therefore means the same for both men and women in this study.

RESULTS

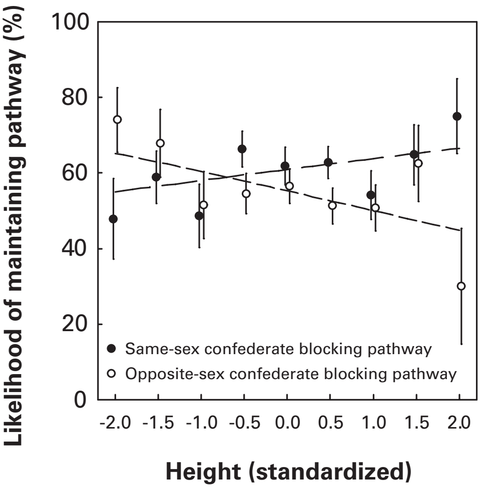

Figure 4.4: Results from Study 3: The effect of the pedestrian height (standardized) on the likelihood of maintaining one's path (*mean* ± *SE*) and thereby passing close by an opposite-sex or same-sex confederate who was partially blocking the pedestrian's pathway (see Figure 4.1c).

Preliminary analysis indicated that people of both sexes behaved differently depending on whether there was a same-sex or opposite sex confederate. Rather than including the sex of the confederate in our analyses, we instead included a binary variable that specified whether the confederate was of the same sex as the pedestrian. We found a significant interaction between height of the pedestrian and confederate sex on the likelihood of passing by the confederate without deviating from their path (Table 4.2). When the confederate was of the opposite sex, taller individuals were more likely to yield and deviate from their path than shorter individuals (p = .030; Table 4.2; Figure 4.4). A short woman (two *SD* below height) was predicted to pass by the confederate without deviating from her path with a likelihood of 68%, whereas for a tall woman (two *SD* above height) this was reduced to 49%. For men, these same values were 62% versus 41%. In contrast, and in line with our hypothesis, when the confederate was of the same sex, taller pedestrians were more likely to maintain their path without deviation compared to shorter individuals (parameter estimate for slope (± *SE*) = .12 (± .09); p = .17; obtained by reverse coding the variable in the analysis). For women, the likelihood that a tall individual would pass the confederate in close proximity without any deviation was 69% versus 56% for a short individual. For men, these values were 62% versus 51% respectively. The positive and negative slopes for pedestrian height depending on whether the confederate was of the same sex did not differ statistically in magnitude as evidenced by the overlapping standard errors of both estimates.

This two-way interaction did not differ by sex as evidenced by the fact that there was no significant three-way interaction between sex of the pedestrian, whether the confederate was of the same sex, and height (p = .47). Thus, the effect of pedestrian height on the likelihood of path deviation

Table 4.2: Results from Study 3: Logistic mixed model parameter estimates (± *SE*) for the likelihood of passing by the confederate without deviating from path in relation to sex and height of the pedestrian, whether the confederate was of the same sex as the pedestrian, and their interaction (*N* = 1,056). Non-independence due to confederate ID was modelled as a random intercept.

	Likelihood that pedestrian passed by without deviating from path	
	Parameter estimate (± *SE*)	*p*-value
Intercept	0.36 ± 0.11	.002
Sex participant[a]	-0.30 ± 0.13	.019
Confederate same-sex[b]	0.20 ± 0.13	.120
Height participant	-0.21 ± 0.095	.030
Height x same sex	0.32 ± 0.13	.011
Random intercept[c]	0.005 ± 0.072	
R^2 [d]	.021	

[a] Reference category is female.

[a] Reference category is 'confederate of different sex as participant'.

[c] Intercept at the level of confederate; variance estimate ± *SD.*

[d] R^2 for the full model; based on the methods by (Nakagawa & Schielzeth, in press; i.e., *conditional* R^2).

did not differ for male and female pedestrians. The two-way interaction between pedestrian height and same-sex confederate did, however, explain twice as much of the variance for men (R^2 = .016; determined using the methodology of Nakagawa & Schielzeth, 2012) than women (R^2 = .008). In general, men were significantly more likely to deviate from their path than women (Table 4.2). Against our expectation, the height of the confederate had no significant effect on whether the pedestrian would maintain his or her path (p = .86), and nor did the perceived age of the pedestrian (p = .18).

Overall then, for both male and female pedestrians, height was related to the likelihood of path deviation: taller individuals were more likely to pass the confederate in close proximity without deviating from their path. This effect of height was, however, dependent on the sex of the confederate blocking the pathway. Taller pedestrians were more likely to maintain their path when the confederate was of same sex, whereas shorter pedestrians were more likely to maintain their path when the confederate was of the opposite sex.

DISCUSSION

Our results show that, when pedestrians were confronted by an individual of the same sex partially blocking their pathway, taller individuals were less likely to yield and so more likely to pass by within closer proximity than shorter individuals. This finding is in line with our first two experiments, providing further corroboration that height in both men and women is positively related to dominance in brief confrontations in a naturalistic setting.

When an opposite-sex individual was blocking the pathway, however, the exact opposite pattern was found: taller pedestrians were more likely to deviate from their path than were shorter individuals. The finding that pedestrians react differently to confederates depending on their sex (also apparent in Study 2), is not surprising. It seems entirely reasonable to expect that, in same-sex interactions, competition will be more pronounced, whereas gender norms and mate choice concerns are more likely to dominate in opposite-sex interactions. Indeed, interpersonal attraction has been shown to be related to proximity between two individuals (Fisher & Byrne, 1975; Sundstrom & Altman, 1976), such that those attracted to one another are in closer proximity.

This pattern of results raises the question of why height should be related to how individuals behave in opposite-sex encounters. One potential explanation relates to the absolute increase in physical size of taller men and women, not only in the horizontal dimension, but also in the vertical dimension (because of reasons of allometry). Taller and wider individuals perhaps choose to pass by the confederate at larger distances so as to ensure a lack of physical contact and maintain a certain minimum distance. That is, because taller men and women perceive that they are more likely, to pass the confederate at an unacceptable (or at least uncomfortable) degree of proximity, they instead choose to deviate from their original pathway in order to ensure that this does not occur. In contrast, shorter individuals, who are also less likely to be broad, may be able to pass by the confederate at a distance that is neither perceptually nor absolutely socially unacceptable. Although this argument is speculative, our study does provide some evidence in support: on average, men were more likely to yield and deviate from their pathway than were women. Because men are on average larger than women, the distance at which they pass by a stranger may be higher correspondingly. Indeed, our finding that men were more likely to avoid close proximity conforms to a plethora of research indicating that men require a larger amount of personal space, and greatly dislike any intrusion into this space (Camperio Ciani & Malaman 2002; Kenner & Katsimaglis 1993).

We did not find a statistically significant effect of the height of the confederate blocking the passage way on the likelihood of the pedestrian to maintain its path. This could be explained potentially by the fact that the heights of the confederates were made less salient by the fact that were instructed to lean against the wall, with their head slightly tilted to look at their phone. Furthermore, we may have used too few confederates (e.g., three males and four females) to detect statistical effects for variations in height in relation to this posture.

Study 4: Persuasion during dyadic negotiating

INTRODUCTION

In brief (non-verbal) encounters, taller individuals are less likely to give way compared to shorter individuals. The costs of giving in are, however, very low in such studies and the effect of height may be less pronounced when the stakes of the outcome of the interaction are higher. Furthermore, this effect may disappear altogether when verbal contact is extended between individuals (i.e., when individuals are better able to assess the dominance of the other). We examined, therefore, whether height played a role during a negotiation game. In this game, participants first had to solve a task individually, following which they had to solve the same task again, while partnered with a same-sex individual. We examined which partner was better able at persuading the other that their solution was better, and therefore who was more likely to give way, and so admit that their original contribution had been less valuable. The negotiation task we used - the Arctic survival task - has previously been used to examine social influence in a dyadic task (Huang et al., 2002): when competitors were perceived to be tall (by being filmed from below), they had more influence during the task, than when competitors were perceived to be short (by being filmed from above). Based on our own previous results as well as those of Huang et al.'s (2002) study, we hypothesized that taller individuals would have a larger impact on joint decisions during the negotiation task than shorter individuals.

MATERIAL AND METHODS

Sample and procedure

Participants were Dutch biology students taking part in a compulsory practical in 2010 (N = 145). The average and median birth year of the participants was 1991 (SD = 1.256; minimum = 1987; maximum = 1994). Participants were randomly assigned to same-sex pairs, resulting in 45 female and 27 male pairs (one female participant could not be assigned to a pair). One of four experimenters would accompany a randomly chosen pair to a testing room (a total of three rooms were used for this purpose). Participants were instructed to complete the Arctic survival task (see below) individually, ranking twelve items in order of importance for survival within five minutes. There was no contact between the participants during this period.

After the individual task had been completed, participants were instructed to undertake the task again as a pair. Participants stood at a table (to make the effect of height more salient), with their individual ranking sheets before them. On the table were twelve cards representing the individual items from the task, which the participants were asked to place in order of importance. In this second round of the task, the ranking was negotiated by the participants, who had to agree on their ideal ranking by discussing their views. To give the participants an incentive to participate, but without giving away the purpose of our study (i.e., the competition between the individuals), participants were informed that that the pair with the ranking most similar to an expert ranking (see below) would win 50 Euros (about 60 US dollars). Each pair had five minutes to solve the task, after which the experimenter entered the testing room and ended the task. After the task was completed, the height of the participants was measured using a tape measure.

Arctic survival task

The Arctic survival task (retrieved from: http://scoutingweb.com/scoutingweb/SubPages/SurvivalGame.htm) starts with a brief description explaining that you and your companions have survived a crash in a very cold area, and that the nearest town is more than twenty miles away. The following twelve items have been saved from the crash: a ball of steel wool; a small axe; a loaded pistol; a can of Crisco shortening; newspapers; a cigarette lighter (without fluid); extra clothing; a large piece of canvas; a sectional air map; whisky; a compass, and chocolate bars. Participants are then asked to rank these twelve items in order of importance for survival. The instructions and list of items were translated to Dutch.

Analyses

For all participants in the study, we calculated how negotiated pair-wise rankings diverged from the original rankings made by each participant individually. To this end, for each item, we calculated the absolute difference in the rank assigned individually, and the rank assigned as a pair (e.g., ranking the pistol as 1 as an individual but 7 as a pair, resulted in a difference score of 6). To provide an overall score for each individual, we then summed the difference rankings for all items, with a higher score indicating that a participant was less able to maintain his or her individual ranking, and a lower score indicating that an individual was capable of maintaining his or her rankings following negotiation (minimum: 2 rank differences; maximum: 60 rank differences). As a dependent variable in our GLM, we used the difference in the ability to maintain one's ranking. Our independent variable of interest was the difference in height between participants. We subtracted the height of the individual on the left of the standing table (which was randomly assigned) from the height of the individual on the right of the standing table. We also included a measure of initial agreement between individuals in a pair, which was calculated as the absolute difference in rank assigned to each item by each individual in the pair (similar to the above calculation). High initial agreement meant that participants tended to converge on those items they deemed most important for survival, whereas low agreement indicated that their independent rankings diverged from each other. Because participants may have had previous knowledge of this game (or at least the concept involved), for every participant, we also calculated how close his or her scores were to an expert ranking (which was only available to us). The deviation from the expert rankings could be used to account for any previous knowledge of the game, and we then calculated the difference between individuals in each pair with respect to these scores. One female pair had identical initial rankings, and one member of a different female pair did not complete the individual task. We excluded these two pairs for analyses, leaving 43 female and 27 male pairs.

RESULTS

When controlling for differences in previous knowledge and the initial agreement of the participants, we found no effect of height on the ability to maintain one's own rankings (B = -.203 (*SE* = .214); $F(1, 66) = .902$; $p = .346$; partial η^2 = .013). However, a significant interaction was found between the height difference between participants and the initial difference in rankings on participant's ability to maintain their own rankings ($p = .029$; Table 4.3): that is, when the initial agreement between the participants was low (i.e., the individual rankings were more dissimilar), taller individuals exerted more influence over the order of rankings in the paired negotiation task, while there was no discernible height effect when initial agreement was high (Figure 4.5). When considering a simple categorical distinction of which partner was taller in a negotiating

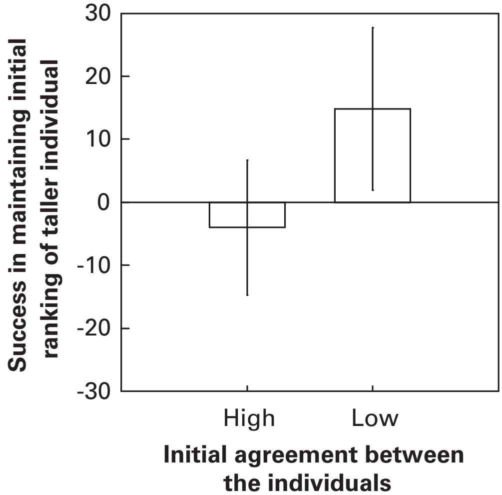

Figure 4.5: Results from Study 4: The difference in success at maintaining initial rankings for the taller compared to the shorter individual in a negotiating pair (*mean* ± *SE)*. A higher score indicates that the taller individual was more successful at maintaining his or her ranking. Only when the differences in initial individual scores were high (low agreement on rankings) did height matter. High versus low agreement was based on median split.

pair (i.e., avoiding absolute height difference), we again found a significant interaction between height of the participant and initial agreement (B = -1.121 (*SE* = .439); $F(1, 65) = 6.522$; $p = .013$; partial $\eta^2 = .091$).

Potential differences in existing knowledge of the participants (as measured by the difference in similarity between the individual rankings and those of an expert ranking) also had a significant effect on the ability to maintain one's initial rankings (Table 4.3), suggesting that individuals with previous knowledge or better insight were able to perform better, and so were better able to defend their choices. There was no main effect of sex of the couple ($F(1, 65) = .255$; $p = .651$; partial $\eta^2 = .004$), nor did the sex of the couple interact with height ($F(1, 64) = .004$; $p = .953$; partial $\eta^2 < .001$). In other words, the effect of height difference on negotiation success was similar for both sexes. The amount of variance explained by the interaction term, however, was more than twice as large for men than for women (partial $\eta^2 = .136$ versus partial $\eta^2 = .062$, respectively).

Table 4.3: Result from Study 4: GLM parameter estimates for the effect of the difference in previous knowledge, the initial agreement, the difference in height, and their interaction on the ability to maintain one's ranking.

	B ± *SE*	***p*-value**	**partial η^2**
Intercept	-11.703 ± 9.506	.223	.023
Difference in previous knowledge	0.351 ± 0.171	.044	.061
Difference initial individual rankings	0.221 ± 0.222	.323	.015
Difference in height (cm)	2.113 ± 1.060	.050	.058
Interaction between difference in individual rankings and the difference in height	-0.054 ± 0.024	.029	.071

DISCUSSION

In line with the results from our previous three studies, we found that height was positively related to dominance in an extended verbal interaction with a same-sex individual. Taller men and women were more likely to persuade their negotiating partners that their view of on rankings was better, whereas shorter men and women were more likely to yield with respect to their views. This effect of height was only apparent, however, when the participants were very different with respect to their initial rankings.

GENERAL DISCUSSION

Our results show that height is related to interpersonal dominance in a variety of social settings, which we assessed in both verbal and non-verbal interactions. In our first study, we showed that taller individuals were more likely to take precedence over shorter individuals when they were simultaneously approaching a narrow passage. Similar patterns were then observed in our second study (Study 2), when individuals of varying height walked against the flow of people in a busy shopping street. Pedestrians were more likely to give way to a tall oncoming confederate than to a short confederate. Furthermore, pedestrians were less likely to collide with a taller rather than shorter individual. Gender specific behaviour was also observed in this shopping street: men were less likely to collide with a female confederate than a male confederate. In our third observational study, we found that, when confronted by a same-sex individual partly blocking their pathway, taller pedestrians were more likely to maintain their path, thereby passing the blocking individual within close proximity, compared to short individuals. When the blocking individual was of the opposite sex, however, the opposite pattern was found: shorter individuals were more likely to maintain their path compared to taller individuals. Therefore, in all three observational studies, we found clear evidence to support the notion that human height is positively related to interpersonal dominance (at least when that person is confronted by a same-sex individual). In our fourth study, we showed that taller individuals also possessed higher dominance in a laboratory- based setting involving a dyadic, verbal interaction. More specifically, height was positively related to the ability to standing one's ground in a negotiating task. These results are in line with a previous study that made use of the Arctic survival task (Huang et al., 2002). In summary, the results from our four studies indicate that height is indeed positively related to interpersonal dominance, in both verbal and non-verbal interactions.

The increased dominance of taller men and women is likely to result from both perceptions of the self and the perceptions of others. Indeed, taller people are perceived as more dominant (Cinnirella & Winter, 2009; Judge & Cable, 2004; Marsh et al., 2009; Young & French, 1996), and some of these biases are already apparent in very young children (Thomsen et al., 2011). Perhaps because of these perceptions, pedestrians were more likely give way and less likely to collide with taller confederates compared to shorter confederates (Study 2). These different perceptions of and behaviors towards taller compared to shorter individuals may subsequently lead to increased self-esteem in taller individuals (Judge & Cable, 2004), which in turn is likely to affect their dominance. Indeed, an individual's height also determined his or her behavior towards a confederate blocking their path (Study 3). Future studies could therefore address the extent to which the relationship between height and interpersonal dominance is mediated by an individual's direct perception of their own dominance in relation to height, versus the behaviour of others toward them in relation to their height. Manipulating height in a behavioral study with actual people (e.g., such as wearing higher shoes), without changing any other variables is difficult. Studies using virtual reality techniques may be best suited to this purpose, as the heights of individuals' avatars can be manipulated without participants' awareness.

Although the effect of height on dominance did not significantly differ between the sexes in any of our studies, the effects of height were consistently stronger for men than for women. This is in line with findings on the relationship between height and social status. While both male and female height are positively related to measures of social status (Judge & Cable, 2004), the magnitude of this relationship is significantly stronger for men than for women. Similarly, a recent study showed that perceptions of leadership were more closely related to height for men, than for women (Blaker et al., in press). In addition, this study found that male height was positively associated with perceived dominance, health, and intelligence, whereas female height was associated only with perceived intelligence (Blaker et al., in press). Height also has a differential effect on attractiveness for men and women: whereas taller men are considered more attractive, women of average height are rated as most attractive in preference studies (reviewed by Courtiol et al., 2010b). Overall, then, it seems clear that taller individuals are more likely to be dominant, but male height makes a more significant contribution to this assessment than does female height, and this potentially can be explained by the relationship between height and perceptions of dominance, intelligence, health, and attractiveness (e.g., Blaker et al., in press).

A limitation of our behavioural studies is that we were only able to estimate the heights and ages of the pedestrians, rather than recording their actual heights and ages. Although perceptions of age have been shown to be highly accurate (Rhodes, 2009) and were not of central interest to our study, perceptual distortions of height in relation to status and dominance are well documented. For instance, individuals who are higher in status or who behave in a more dominant fashion are perceived as taller than individuals who are lower in status or who behave submissively (Marsh et al., 2009; Wilson, 1968). Similarly, taller individuals are perceived as more dominant than shorter individuals (Blaker et al., in press; Marsh et al., 2009). These findings may pose a problem for our observational studies, as height estimations were made during overt dominance interactions, and estimations of dominant behavior (e.g., refusing to yield, collisions) were made while the height of the individuals involved was known (Study 1, 2). Our results could therefore be a consequence of perceptual distortions on the part of the observers, rather than an actual behavioural effect related to height. However, we believe that our results are unlikely to be a consequence of these perceptual distortions for several reasons. First, in Study 4, height was positively related to dominance, but a perceptual distortion could not have occurred: our measure of dominance was a quantitative objective measure of behavior (i.e., the ability to maintain one's own preference ranking) rather than a perceived measure, and the heights of the individuals were measured rather than estimated. Second, several of our measures could be easily and unambiguously be assessed, such as the heights of the pedestrians relative to markings on a wall (Study 1); whether any physical contact occurred between the participant and the pedestrian (Study 2) and which side of a pole a pedestrian would pass (Study 3). Finally, it is difficult to see how perceptual distortions of height could lead to the observed three-way interaction in our third study, as our behavioral measure of dominance was differentially affected by height, in a manner that was also dependent on the sex of the confederate blocking the pathway. For all these reasons, we believe it is unlikely that our results are merely a consequence of a perceptual distortion of height in relation to dominance, or perceptual distortions of dominance on the basis of height. The use of video cameras to record interactions that can then be scored by observers blind to the aims of the study may circumvent some of these problems. It is, however, increasingly difficult to perform such studies without the awareness of the participants and ethical concerns with respect to privacy laws.

A second limitation of our behavioural studies is that all experimenters and confederates were aware of the aims of the study. It would be very difficult to devise our studies in such a way that experimenters could remain blind to these aims (particularly in Study 1 and 3). In addition, the recording of the heights (and age) of pedestrians and their behavioral interactions was taxing for observers, and adding 'foil' variables could compromise study accuracy and precision with respect to the key variables of interest. The aim of our three observational studies was therefore guessed easily, and we chose, therefore, to inform all experimenters and confederates. The use of video cameras may again circumvent some of these problems. Again, no such limitation held for Study 4, in which we also showed that height was positively related to interpersonal dominance.

Overall, our findings suggest that, even in the absence of overt physical aggression, height influences the outcome of verbal and non-verbal confrontations between individuals. In contrast to those hypotheses that suggest height and social status are correlated via intervening variables such as improved health and nutrition, our results demonstrate that height directly influences the probability of winning social confrontations. Thus, the increased social status and upward social mobility (Bielicki & Charzewski, 1983) of taller individuals in modern society may occur, at least in part, as a consequence of their increased interpersonal dominance.

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CHAPTER 5

Women want taller men more than men want shorter women

Gert Stulp
Abraham P. Buunk
Thomas V. Pollet

Personality and Individual
Differences (in press)

ABSTRACT

Physical characteristics, such as height, play an important role in human mate preferences. Satisfaction with one's own height and one's partner height seem likely to be related to these preferences. Using a student sample (*N* = 650), we show that women are not only more selective, but also more consistent, than men, in their partner height preferences. Women prefer, on average, a larger height difference between themselves and their partner (i.e., males being much taller than themselves) than men do. This effect is even more pronounced when examining satisfaction with actual partner height: women were most satisfied when their partner was 23 cm taller, whereas men were most satisfied when they were 8 cm taller than their partner. Next, using data from our sample and that of a previously published study (*N* = 58,223), we showed that, for men height is more important to the expression of satisfaction with one's own height than it is for women. Furthermore, slightly above average height women and tall men are most satisfied with their height. We conclude that satisfaction with one´s own height is at least partly a consequence of how the opposite sex expresses partner height preference and satisfaction with partner height.

INTRODUCTION

Height in couples

Physical characteristics play an important role in human mate choice (Barber, 1995; Kurzban & Weeden, 2005), and human height was among the first of these physical characteristics to be studied. As early as 1903, Pearson and Lee observed that heights between partners were more similar than heights between non-partners in a British sample (Pearson & Lee, 1903). This pattern has been labelled assortative mating, i.e., the existence of a positive correlation between partner characteristics, and has been observed for height in many populations (see Spuhler, 1982 for review).

In addition to the positive assortment of height in couples, heterosexual couples seem to follow another non-random pattern with respect to their height preferences, namely that the male is taller than his partner. Gillis & Avis (1980) were the first to document this male-taller norm: in married couples from both the UK and US, the woman was shorter than her husband more frequently than would be expected by chance.

Observed mating patterns with respect to height are likely to be a consequence of mate preferences for stature within each sex (Courtiol et al., 2010b). Indeed, much research has focussed on the role of height in partner preferences (see below). Given the role of height in mate preferences and mate choice, one would expect that satisfaction with one's own height would be at least partly contingent on the preferences shown by the opposite sex, but surprisingly few studies have addressed whether this holds true. Similarly, satisfaction with the height of one's partner is also likely to be related to the actual height of the partner. The aim of the current study, therefore, was threefold. First, we aimed to replicate previous findings with respect to preferences for partner height differences (Courtiol et al., 2010b; Fink et al., 2007; Pawlowski, 2003; Salska et al., 2008), using a more detailed series of questions. Our second aim was to examine satisfaction with one´s own height in both sexes, whereas our third aim was to investigate to what extent partner height influences satisfaction with one´s partner's height.

Preferences for romantic partner height

Preferences for partner height have been studied in a variety of settings, such as lab-based experiments (reviewed in Courtiol et al., 2010b), responses to online advertisements (Pawlowski & Koziel, 2002), and speed-dating (Kurzban & Weeden, 2005). In line with findings on actual couples, these studies consistently have found that both men and women's height is correlated with their expressed preferences for partner height and that both men and women prefer to be in couples where the man is taller than woman, i.e., a male-taller norm (Fink et al., 2007; Pawlowski, 2003). These studies also suggest that women prefer men who are not too tall and that men prefer women who are not too short (Salska et al., 2008). Courtiol and colleagues (2010b) furthermore showed that different preferences in men and women resulted in a mating market where tall, but not too tall, men were most preferred by the opposite sex, whereas average height women were most preferred by men. Preferences for partner height differences are furthermore dependent on one´s own height. Pawlowski (2003) was the first to show that both shorter men and taller women tend to prefer smaller partner height differences than taller men and shorter women, who both prefer larger partner height differences.

Satisfaction with height

It would seem likely that the preferences of the opposite sex will be reflected in satisfaction with one´s own height, yet this assumption has rarely been formally tested. Perhaps the most extreme example of dissatisfaction with height is the existence of hormone therapies in order to reduce or increase one´s adult height. Whereas hormone therapies are used for both sexes to increase height (Allen, 2006), therapies to reduce growth are more common for women (Pyett et al., 2005). The choice for hormone therapy is often based on the decision of the parents or a physician rather than that of the child, and many hormonally treated tall women are dissatisfied with the decision that was made for them (Pyett et al., 2005). Tall untreated women, in contrast, are not necessarily dissatisfied with their height (Lever et al., 2007). A more thorough understanding of how satisfaction with one's own height is affected by an individual's height is important when hormone therapies, with its potentially grave side effects, are considered.

This study

As noted above, the first aim of our study was to replicate previous findings with respect to preferences for partner height. Our second aim was to examine satisfaction with one´s own stature and we expected height to be more important with respect to explaining satisfaction with one's own height for men compared to women. Furthermore, we hypothesized that individuals would be most satisfied with their own heights when this height was the one most preferred by the opposite sex. Our final aim was to investigate to what extent partner height influences satisfaction with one’s partner height, and we hypothesized that partner height is more important for women than for men.

MATERIAL AND METHODS

Participants and protocol

All participants were first year psychology students from a large European university who participated in exchange for course credits (N = 693). Participants who did not report on their sexual orientation (N = 8), or those that reported to have a homosexual (N = 7) or bisexual (N = 26) sexual orientation were excluded from all analyses, as we were solely interested in heterosexual partner height preferences. Two individuals were excluded who did not report their own height (N = 2). After exclusion, our total sample included 650 participants (461 women). Table 5.1 contains the descriptive statistics for the sample. Participants provided the following socio-demographic information: age, sex, height, weight, ethnicity and sexual orientation. Because most students were either Dutch or German, we coded Ethnicity as either Dutch, German or Other (see Table 5.1). Participants then answered a series of questions concerning their partner height preferences; we asked about their (i) ideally preferred, (ii) minimally acceptable, and (iii) maximally acceptable partner height (all in cm). We also asked about their relationship status (single or in a relationship). If the participants indicated that they had a romantic partner, they were then asked to report on (i) their partner´s actual height, and (ii) their satisfaction with their partner´s height. Last, all participants indicated their degree of satisfaction with their own height. Satisfaction was measured on a 100-point scale, anchored at 50.

Statistical analysis

For virtually all the independent sample t-tests we performed, we dealt with unequal variances (as indicated by the Levene’s test). In these cases, we determined the Cohen’s d by dividimg the mean difference between groups by the standard deviation from the group with the largest sample size. We indicate only when a t-test was performed under the assumption of equal variances. Controlling for age and ethnicity did not change any of our reported results (results not shown).

In order to investigate the validity of our results with respect to height satisfaction, we compared our findings to those of Lever et al. (2007) (based on the methodology of Frederick et al., 2006, who examined satisfaction with height in 59,632 individuals that completed a 'Sex and Body Image Survey' on either MSNBC.com or Elle.com). In the Lever et al. sample, individuals were asked: "How do you feel about your height?" and could respond with three options: "I wish I were taller", "I wish I were shorter", and "I feel okay about my height". We analysed the data using a logistic regression, with the binary dependent variable coded as whether the participant felt okay or not about his or her height. All analyses were performed in SPSS 17.0.

RESULTS

Sample description

The 461 women in our sample reported an average height (± *SD*) of 170.94 (± 5.926) cm, and the 189 men reported an average of 184.60 (± 7.960) cm tall ($t(277.28) = 21.29$; $p < .0001$; $d = 2.30$) (Table 5.1).

Table 5.1: Descriptive statistics of sample (*Frequencies* or *Means* ± *SD*).

	Men (*N* = 189)	**Women (*N* = 461)**
Age (years)	20.96 ± 2.751	19.96 ± 2.778
Height (cm)	184.60 ± 7.960	170.94 ± 5.926
Nationality		
Dutch	108	297
German	64	137
Other	17	27
Relationship status		
Single	104	230
In relationship	85	231

Preferences for partner height

Preferred partner height

An individual's height correlated significantly and positively with preferred partner height in both men (r = .47; p < .001; N = 188) and women (r = .54; p < .001; N = 461), indicating a preference for assortment: taller men and women preferred taller partners than shorter men and women (Figure 5.1). Next, we calculated the preferred differences between one´s own height and that of one´s partner. We found that male height was positively correlated (r = .69; p < .001; N = 188) and that female height was negatively correlated with preferred partner height difference (r = -.49; p < .001; N = 461). Thus, taller men and shorter women preferred larger height differences, i.e., the male partner being much taller, whereas shorter men and taller women preferred smaller height differences, i.e., the male partner being only slightly taller. On average, women preferred a larger partner height difference (13.45 cm ± 5.61) than men (12.11 ± 7.44; t(277.81) = 2.23; p = .027; d = .239). Interestingly, there was significantly more variation in men's preferences compared to those of women (Levene's test for equality of variances: F = 11.23; p = .001).

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Minimally and maximally acceptable partner height

With respect to the minimally acceptable partner height (Figure 5.1), we found that women on average were prepared to accept a height difference of 3.72 cm (± 5.54) whereas men were prepared to accept a difference of -0.053 cm (± 7.29); a significant difference (t(277.20) = 6.37; p < .0001; d = 0.68). One sample t-tests revealed that the minimally acceptable partner height was significantly different from zero for women (t(460) =14.41; p < .0001; d = 0.67), but not for men (t(186) = 0.10; p = .92; d = -0.007). Thus, women and not men, are the ones who prefer to be in a couple in which the man is taller than the woman (i.e., the male-taller norm). Again, the variation in the minimally acceptable height was greater for men than women (F = 8.99; p = .003).

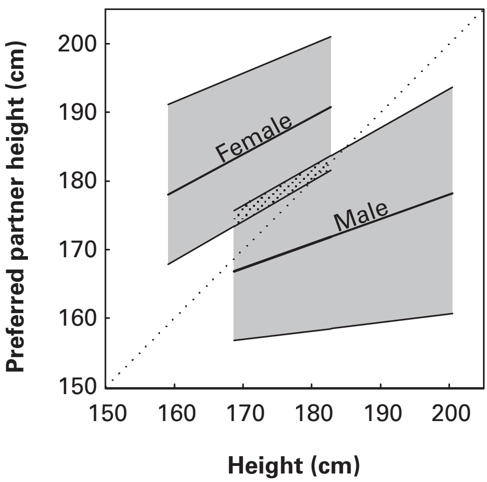

Figure 5.1: Regression lines for preferred (thick line), minimally acceptable (lower line) and maximally acceptable (upper line) partner height for males and females. Data is plotted for the range ± 2 *SD*.

When asked about their maximally acceptable partner height (Figure 5.1), we found that women were, on average, prepared to consider a maximally acceptable partner height difference of 25.15 (± 8.13) cm compared to that of 25.94 (± 12.23) cm for men, indicating a male-not-too-tall norm. This difference was not significant, however ($t(252.28) = 0.81$; $p = .42$; $d = 0.097$). There was more variation in maximally accepted height in men than in women ($F = 15.66$; $p = .0001$).

The acceptable height range

Next, we examined whether men and women differed in their selectivity with respect to partner height. In order to do so, we calculated the difference in acceptable partner height range (i.e., the difference between the maximally and minimally acceptable partner height) between men and women. On average, men accepted a significantly larger height range (25.85 cm ± 12.55) than women (21.38 ± 8.76; $t(257.71) = 4.42$; $p < .001$; $d = 0.51$; Figure 5.1). Again, there was more variation among men than in women ($F = 10.20$; $p = .001$).

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Following from this, we then investigated whether men and women were more tolerant towards heights above or below their preferred partner height. To do so, we examined the difference between the maximally acceptable and preferred partner height and the difference between the minimally acceptable height and preferred partner height. For men, the maximally acceptable height was, on average, 12.06 cm (± 5.76) away from preferred partner height, whereas the minimally acceptable height was, on average, 13.79 cm (± 9.01) away from preferred partner height; a significant difference (paired sample *t*-test: $t(183) = 2.78$; $p = .006$; $d = 0.21$). In contrast, for women, the difference between the maximally acceptable height and preferred partner height was 11.67 (± 6.52) cm whereas the difference between minimally acceptable height and preferred partner height was 9.70 (± 4.48) cm; again, a significant difference ($t(457) = -6.06$; $p < .0001$; $d = 0.28$). This indicates that women were more accepting of heights above their preferred partner height than to heights below their preferred partner height, whereas men showed the reverse pattern, and were more tolerant towards heights below, rather than above, their preferred height.

Satisfaction with one´s own height

Our sample

Regression analyses revealed that both male and female height were curvilinearly related to satisfaction with one´s own height (Table 5.2). The male optimum of the curve was at a height of 193.74 cm (9.15 cm above average) and the female optimum at a height of 175.97 cm (5.03 cm above average). From Figure 5.2a, it is clear that satisfaction with male height increases until average height is reached, after which satisfaction remains constant with increasing height. For women, those of average height and slightly above average height appear more satisfied than those who are either shorter than aver-

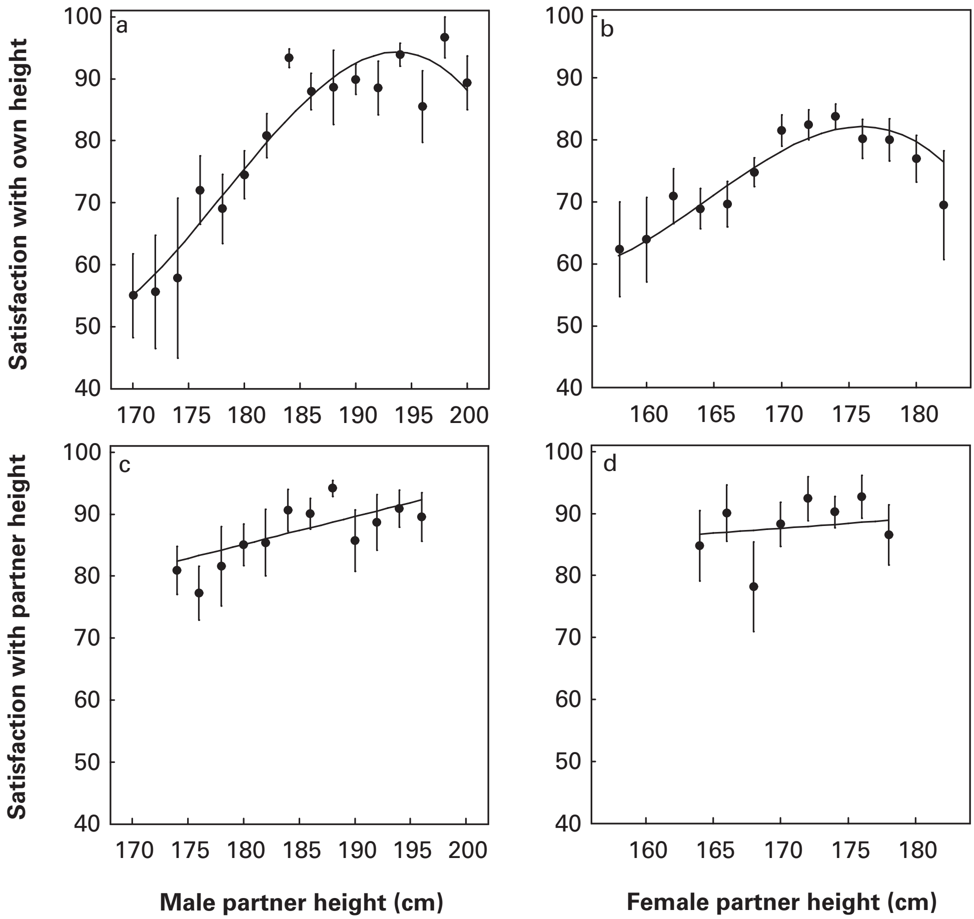

Figure 5.2: *Mean* (± *SE*) satisfaction with own height for (a) men and (b) women and *mean* satisfaction with male partner height by women (c) and female partner height by men (d). Lines are OLS regressions.

Table 5.2: Regression parameter estimates (*B* ± *SE*; *p*-value in brackets) for the effect of height on satisfaction with own height.

	Our sample[a]		Sample from Lever et al., 2007[b]	
	Men	Women	Men	Women
Intercept	84.80 ± 1.44 (<.0001)	79.23 ± 1.13 (<.0001)	1721.33 ± 57.13 (<.0001)	1223.73 ± 102.92 (<.0001)
Height	1.83 ± 0.25 (<.0001)	1.06 ± 0.24 (<.0001)	-29.14 ± 0.95 (<.0001)	-22.61 ± 1.85 (<.0001)
Height^2	-0.058 ± 0.013 (<.0001)	-0.076 ± 0.019 (<.0001)	0.16 ± 0.005 (<.0001)	0.14 ± 0.011 (<.0001)
Height^3	-0.0030 ± 0.0011 (.00528)	-0.0039 ± 0.0018 (.0310)	-0.0003 ±0.00001 (<.0001)	-0.0003 ± 0.00002 (<.0001)
R^2	.320	.072	.319	.144
Optimum (cm)	193.74	175.97	195.28	177.21

[a] Linear regression; height was centered; R^2 is adjusted R^2.
[b] Logistic regression; R^2 is Nagelkerke R^2.

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age or tall (Figure 5.2b). For men, height explained 32.0% of the variance in satisfaction with own height, whereas for women the amount of explained variance was only 7.2% (Table 5.2). Thus, actual height explained around four times as much of the variance in male satisfaction with their height than it did for females (Figure 5.2a, b).

An analysis of the data provided by Lever et al., (2007)

Very similar results were obtained when analysing the data provided by Lever et al., (2007). Logistic regression revealed that height was curvilinearly related to the statement 'I feel okay about my height' (Table 5.2). The optima were also very comparable to our results, as men were most satisfied at a height of 195.28 cm and women at a height of 177.21 cm (Table 5.2). Again, satisfaction with one´s own height was much more dependent on actual height for men than for women (by a factor of 2), corroborated our results by those from a much larger sample.

Actual partner height

Height and relationship status

Eighty-five out of 189 men and 231 out of 461 women were in a relationship. No significant height differences were found between single and partnered men (mean difference: .19 ± 1.17 cm; $t(187) = 0.17$; $p = .87$; $d = 0.25$; equal variances assumed) or women (-0.47 ± 0.55 cm; $t(459) = -0.86$; $p = .39$; $d = 0.080$;

equal variances assumed). Single men and women seemed somewhat less restrictive towards preferred partner height than partnered men and women: on average, the accepted height range was wider (although only marginally significant) in single men (mean difference: 3.32 ±1.85 cm; $t(182) = 1.80$; $p = .074$; $d = 0.27$; equal variances assumed) and women (1.50 ±0.17 cm; $t(456) = -1.84$; p = .067; $d = 0.17$; equal variances assumed) compared to partnered men and women, respectively.

Satisfaction with partner height and partner height differences

Participant height correlated positively with reported height of their partner in both men ($r = .19$; $p = .081$; $N = 84$) and women ($r = .29$; $p < .0001$; $N = 231$). Thus, taller men tended to be paired with taller women. In women, partner height correlated with reported satisfaction with partner height ($r = .19$; $p = .004$; $N = 231$). Thus, women with tall partners reported higher satisfaction (Figure 5.2c). For men, no association between partner height and satisfaction with partner height was found ($r = .065$; $N = 84$; $p = .56$; Figure 5.2d). No quadratic effects were found (all p > .31).

We also examined whether partner height differences predicted satisfaction with partner height. For both men and women, partner height differences were curvilinearly related to partner height satisfaction (Figure 5.3; Table 5.3; although for men this relationship was marginally significant). Whereas the optimum of the curve for men was at 8.26 cm (Table 5.3; Figure 5.3), the optimum of the curve for women was at 22.59 cm. Thus, men were most satisfied when their partner was slightly shorter than themselves, whereas women were most satisfied when their partner was much taller than themselves. Partner height differences were more important in explaining partner height satisfaction in women than in men, accounting for around three times as much of the explained variance (women: $R^2 = .103$; men: $R^2 = .029$).

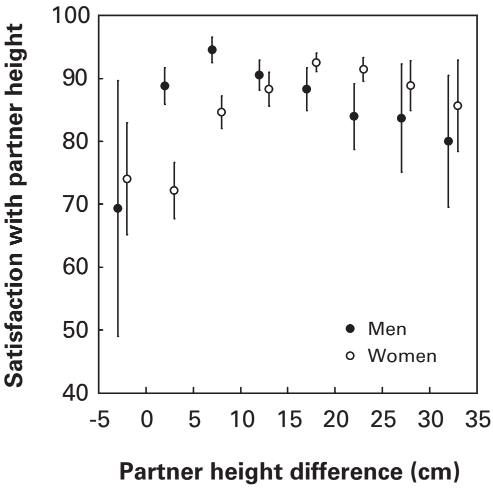

Figure 5.3: *Mean* (± *SE*) satisfaction with partner height based on partner height differences.

Table 5.3: Linear regression parameter estimates (± *SE*; *p*-value in brackets) for the effect of partner height differences on satisfaction with partner height.

	Men	Women
Intercept	88.76 ± 3.06 (<.0001)	75.36 ± 2.41 (<.0001)
Partner height difference	0.30 ± 0.32 (.341)	1.46 ± 0.37 (<.0001)
Partner height difference^2	-0.018 ± 0.010 (.070)	-0.032 ± 0.012 (.007)
Adjusted R^2	.029	.103
Optimum (cm)	8.26	22.59

DISCUSSION

In line with previous studies (e.g., Courtiol et al., 2010b), we found support for positive assortative mating preferences for height: taller individuals preferred taller romantic partners. Additionally, both men and women prefer to be in a couple where the man was taller than the woman, but not too tall (similar to Salska et al., 2008). The male taller preference, however, was most pronounced in women. Women, but not men, considered partner heights unacceptable if they resulted in the female partner being taller than the male. This was also evident from the finding that women were more tolerant towards male partner heights that were above their preferred height than towards heights that were below their preferred height. Thus, our data suggest that the male-taller norm as observed in married couples in Western societies (Gillis & Avis, 1980; Sear, 2006; **Chapter 7**) is more likely to be driven by women rather than by men.

Similar to Pawlowski (2003), we found that preferred partner height was a function of one's own height: taller men and shorter women preferred larger differences between their own height and that of their partner (i.e., a male partner slightly taller than themselves). In contrast, as shorter men and taller women preferred smaller differences between their own height and that of their partner (i.e., again, for the male partner to be slightly taller). Additionally, we found that women preferred larger height differences than men, which resulted in a conflict over preferences between the sexes (in line with Courtiol et al., 2010b). Mutual mate choice is thus likely to result in couples where the height preferences of either the male partner, the female partner, or indeed both, are not optimally satisfied.

We extended these findings by showing that women were more restrictive with respect to the preferred stature of their partner than men in two respects. First, women display less variation across all the measures of partner preference that we investigated compared to men, suggesting that women reach greater consensus with respect to preferred partner height. Second, women were more restrictive in their range of acceptable heights compared to men. That is, women were more likely to rule out certain heights as completely unacceptable. Together these results suggest that women place a greater value on their partner's height than men.

The notion that women are more selective in terms of partner height is also supported by the finding that partner height explained substantially more variance in satisfaction with partner height for women than men. Women were found to report more satisfaction when were partnered with taller rather than shorter men. No such effects were observed in men, however, suggesting that their partner's height was less important to them. Moreover, men and women differed strongly with respect to the partner height difference they found most satisfactory: men were most satisfied with their partner's height when they were slightly taller than their female partner (i.e., 8 cm), whereas women were most satisfied with their partner height when they were substantially shorter than their male partner (i.e., 23 cm). In our sample, then, we can conclude that women place more value on partner height than do men, and men and women do not agree on what constitutes the 'ideal' height difference.

Given that women place more value on partner height than men do, it is not surprising that we also found, using data from two samples, that height was much more important in explaining satisfaction with one's own height for men than for women. Furthermore, men who were taller than average reported the highest level of satisfaction with their own height, whereas shorter men reported the least amount of satisfaction. The finding that shorter men were least satisfied with their height can be understood from our findings on mate preferences: women preferred greater height differences; were more tolerant with respect to heights above their preferred height, but less tolerant towards those below and, most importantly, women were most satisfied with their partner's height when he was tall. The increased satisfaction with their own height among taller men is also in line with studies indicating that tall men have higher self-esteem (Judge & Cable, 2004), display less jealousy towards other men (Buunk et al., 2008), and display higher levels of subjective well-being (Carrieri & De Paola, 2012).

In women, we found that those of average height and those of above average height were the most satisfied with their own height. This curvilinear effect of height on satisfaction with respect to one's own stature is in line with previous research suggesting that women of average height are least jealous (Buunk et al., 2008), and least competitive towards other women (Buunk et al., 2009). The finding that shorter, rather than taller, women are less satisfied with their height (Lever et al., 2007) may reflect the finding that men were most satisfied with their partner's height when she was only slightly shorter, rather than being much shorter. This finding is obviously pertinent when considering the decision to administer growth suppression treatments to girls who are exceptionally tall for their age.

An obvious limitation of our study is that we used a sample of predominantly White European psychology undergraduates. Although previous studies from a number of Western societies and using a wide range of methodologies and samples (Courtiol et al., 2010b; Fink et al., 2007; Pawlowski & Koziel, 2002; Re & Perrett, 2012; Salska et al., 2008; Swami et al., 2008) have all yielded the same consistent mate preferences with respect to height, studies from non-Western samples suggest that preferences and choice for partner height are not universal (Sear, 2006; Sorokowski & Butovskaya, 2012). Thus, although it is likely that our results can be generalized to Western populations, they are unlikely to do so for non-Western populations.

Another potential limitation is the methodology of relying on self-report with respect to height. People may not be very accurate at assessing height and they are also likely to round their responses to questions of this kind: indeed, in our sample, 71% reported their ideal partner height with a 'rounded' number (i.e., a number ending with a zero or a five). These problems are, however, much more likely to result in a rather noisy data set, rather than to generate a systematic biases with respect to height preferences. Another limitation is that we have assumed that preferences for partner height translate into mate choice in the real world. Mating preferences are only one element in the process of mate choice and pair formation, and many other factors also play a role (Courtiol et al., 2010a; **Chapter 7**). Despite these caveats, we have shown quite clearly that satisfaction with one's own height is contingent on the preference for partner height expressed by the opposite sex, suggesting that, to at least some degree, mating preferences are expressed in actual choice and pairing.

CHAPTER 6

THE HEIGHT OF CHOOSINESS

mutual mate choice for stature results in sub-optimal pair formation for both sexes

Gert Stulp
Abraham P. Buunk
Robert Kurzban
Simon Verhulst

Animal Behaviour (accepted)

ABSTRACT

Mutual mate choice is prevalent in humans, where both males and females have a say in their choice of partner. How the choices made by one sex constrain the choice of the other remains poorly understood, however, because human studies have mostly limited themselves to measuring preferences. We used a sample of 5,782 speed-daters making 128,104 choices to link preferences for partner height to actual choice and the formation of a match (the mutual expression of interest to meet again). We show that sexual conflict at the level of preferences is translated into choice: women were most likely to choose a speed-dater 25 cm taller than themselves, whereas men were most likely to choose women only 7 cm shorter than themselves. As a consequence, matches were most likely at an intermediate height difference (19 cm) that differed significantly from the preferred height difference of both sexes. Thus, our study reveals how mutual mate choice can result in sub-optimal pair formation for both sexes, highlighting the importance of assessing the mate choice process in its entirety.

INTRODUCTION

You can't always get what you want,
But if you try sometimes you just might find
You get what you need

Rolling Stones

Finding a suitable mating partner to form a reproductive unit is complex, due to the many factors that prevent an individual from obtaining its preferred partner. Mate availability is, naturally, the first hurdle to overcome (Widemo & Sæther, 1999), but even when numerous potential mates are available, animals often lack the time and energy to assess them all, leading to inevitable compromises (Fawcett & Johstone, 2003; Reynolds & Gross, 1990; Widemo & Sæther, 1999). Furthermore, it is unlikely that all the traits displayed by a potential mate will be ideally preferred when multiple traits are considered during mate selection (Buss et al., 1990; Fawcett & Johnstone, 2003). Some preferred characteristics may even trade-off against each other: for instance, attractiveness may trade-off against parental investment (Magrath & Komdeur, 2003). Thus, there is no reason to expect that mate preferences will be completely realized in choice. Even when a choice is made, successful pair formation is not guaranteed especially if mutual mate choice occurs (Baldauf et al., 2009; Johnstone et al., 1996), or when same-sex rivals prevent an animal form obtaining a chosen mate (Wong & Candolin, 2005). Finally, even successful pair formation always entails the risk that, at some point in the future, the partner may move to a more attractive alternative (Rusbult & Buunk, 1993). Thus, little can be predicted about the mating pattern of a population from mating preferences alone (Courtiol et al., 2010a).

The study of mate choice, however, has focused mainly on preferences, which is understandable given the difficulty of tracking actual choice and pairing (Courtiol et al., 2010a). Thus, it remains unclear how preferences translate to choice and subsequent pairing. We examined the relationships between preference, choice and pairing among humans using data from speed-dating events, focusing on partner height as preference variable. During a speed-dating event, participants meet approximately 10 to 30 individuals in a series of 3 to 7 minute 'dates' after which they indicate on a score form whether they are interested in further contact ('Yes'/ 'No'). When a Yes is reciprocated they make a 'Match', and contact details are subsequently provided to enable participants to arrange a more traditional date if desired (Finkel & Eastwick, 2008; Kurzban & Weeden, 2005, 2007; Lenton & Francesconi, 2011). Although such 'matches' do not inevitably lead to the formation of an actual relationship, people who made at least one match during speed-dating had a 10.9% chance of engaging in sexual intercourse within six weeks of the event, while the chance of a more serious relationship after one year was 7.2% (Asendorpf et al., 2011). This suggests that speed-dating is an ecologically relevant setting to study pair formation.

By enabling observation of all stages of mate assessment in a single venue, where many potential mates are assessed face-to-face and in real-time, speed-dating presents a distinct advantage over self-report questionnaire- or vignette-based studies: it has both much greater ecological validity, and it allows factors like availability of mates and mutual mate choice to be assessed accurately. More importantly, speed-dating allows researchers to determine how mate preferences translate into the choices that individuals actually make, and whether these choices translate into successful pair formation. We thus treated the speed-dating venue as a 'model system' that enabled us to interrogate human mate choice processes in a manner directly comparable to those of other species. To this end, we operationalized definitions related to preference, choice and pairing as used in the mate choice literature for use within a speed-dating context (Table 6.1).

Previous studies have addressed the interplay between preferences, choice, and pairing in speed-dating, but none have considered all three processes in concert. Such studies have shown that stated preferences are generally poor predictors of choice during speed-dating, in that many 'non-preferred' individuals are also chosen (Eastwick & Finkel, 2008; Eastwick et al., 2011; Kurzban & Weeden, 2007; Todd et al., 2007). Preferences also fail to predict which potential mates are pursued after a speed-dating event (Eastwick & Finkel, 2008). Other studies investigated the choices made during speed-dating events, and found that these choices were only weakly reciprocated between partners (Back et al., 2011; Luo & Zhang, 2009). Our study setting has several advantages over previous study settings. First, we had the opportunity to examine preference, choice and pairing in tandem. We used height as a mate characteristic, which is particularly suitable trait to study, because: i) it is an easily verified objective measure (in contrast to other measures important in human mate choice, such as kindness or reported income), ii) both sexes show preferences for stature in a partner (reviewed in Courtiol et al., 2010b), and iii) stature is related to actual pairing: partner heights correlate positively (Silventoinen et al., 2003; Spuh-

Table 6.1: Definitions of preference measures, choice and pairing drawn from the literature and the operational definitions used in a speed-dating context.

Variable	General (short) definition	Operational definition
Preference ranking[a]	The ranking of mates based on the trait value with respect to likelihood of mating	The stated minimal and maximal preferred height
Strength[b]	The degree to which deviations from the ideally preferred trait value are disfavoured	The decrease in the probability of responding 'Yes' to a speed-dater whose height deviates from the chooser's acceptable height range preference.
Responsiveness[b]	The probability that an individual will respond positively to any mate, independently of trait value	The probability of responding 'Yes' to any speed-dater encountered during an event, independently of their height.
Tolerance[b]	The range of trait values considered acceptable by a choosing individual	The standard deviation of the mean of those heights to which a 'Yes' response was given.
Choice	Positive response to sampled mates.	Whether a given speed-dater gave a "Yes" response.
Pair Formation	The formation of a pair to reproduce.	Whether a "Yes" response was reciprocated, and a "Match" formed.

[a] In humans, preference rankings are established somewhat differently from those of other animals (but see Courtiol et al. (2010a, 2010b) for notable exceptions). Non-human animals are usually presented with repeated binary choices between two potential mates that differ in the trait of interest, and the measure of preference is indicated by some form of interest shown by the 'chooser'.
[b] Based on Fowler-Finn & Rodríguez (2012).

ler, 1982) and men are taller than their partner more often than expected by chance alone (Gillis & Avis, 1980; **Chapter 7** and **8**). Another advantage of our study is that a clearly defined partner preference was available (i.e., preferred partner height), allowing a direct comparison with the response to heights. This is a distinct advance over previous studies, where preferences have most commonly been measured using a subjective scale (e.g., rate on a scale how important physical attractiveness is in an ideal romantic partner; see Kurzban & Weeden (2005) for a notable exception). Finally, because we could combine the specific preferences and choices of both sexes simultaneously, we were able to assess potential conflicts over partner height, and so examine how mutual mate choice affects final pairing.

We first examined preferences for partner height, predicting on the basis of previous research that the preference functions for height in both sexes would not align, thereby creating a sexual conflict over partner height (Baldauf et al., 2009; Courtiol et al., 2010b; Table 6.1). Having established these preferences, we tested (i) whether stated preferences for partner height translated into actual choice during speed-dating and (ii) whether height was related to responsiveness and desirability. Based on the preferences and choices of speed-daters, we determined both strength of preference and tolerance with respect to height, and examined how these depended on sex and own height. Finally, we tested whether (iii) the conflict between the sexes over stated height preferences affected choice and pair formation.

MATERIAL AND METHODS

Speed-dating

We used data collected by HurryDate, a firm organizing speed-date events across North America. The procedure has been described elsewhere (Kurzban & Weeden, 2005, 2007). In short, men and women are invited in groups of usually up to 50 and with equal sex ratio. Events are stratified by age (25 –35 and 35 – 45 are typical). During an event, all men interact with all women for three minutes per date after which both parties discretely register their interest in the other person by indicating either 'Yes' or 'No' on a designated scorecard. These are subsequently stored by HurryDate and checked for 'matches': cases in which both male and female indicated 'Yes' to one another. Subsequently, participants are informed who their matches are, can view these individuals' online profiles, and send emails to their matches. Our sample consisted of single men and women paying a fee to attend the event, indicating that these individuals were genuinely searching for a mate, which contrasts with many other studies in which speed-daters received a reward for participating in the form of e.g., money or course credits. HurryDate collects survey data from their participants including their own height and a preferred height range (i.e., a minimal and maximal preferred height).

During a HurryDate event, women usually remain seated while the men rotate. Given this pattern, women's height may be more difficult for men to assess than vice versa. However, before the speed-dating event starts, the speed-daters spend several minutes interacting while standing, allowing assessments of height. Moreover, height is also readily assessed from cues while sitting, as standing height correlates strongly with both sitting height ($r = 0.94$) and arm length ($r = .94$; Torres, Martinez, & Manço, 2003). In addition, the face can also be used as a cue to height (Re & Perrett, 2012). Thus we assume that men had sufficient opportunity to assess the height of their female dates.

Sample

We included all events in which full information was available for all choices made by all participants in that event (i.e., full information on who said 'Yes' to whom). We excluded all events in which (a) one of the individuals said 'Yes' to an unknown individual; (b) when a 'Match' was reported even though both individuals had not said 'Yes' to one another; (c) when 'Yes' was said to an individual of the same sex (HurryDate sessions are specifically designed for heterosexuals); and (d) when the total number of participants in the event was lower than fifteen. This gave us a total of 174 speed-dating events with full information on who said 'Yes' to whom in which 5,782 individuals (N = 3,024 females) made 128,104 choices, resulting in 9,072 'matches'.

Analyses

All analyses were performed separately for the two sexes. We examined the individual preferences for partner height and how these related to an individual's height using Pearson r correlations and t-tests were calculated to examine sex differences (using Cohen's d as our measure of effect size). We examined whether height (or differences in height) affected the chance of either giving or receiving a 'Yes' response using mixed models with binomial error distribution, in which individuals of both sexes and 'event' were included as random effects (i.e., three random effects in total). Height and preferences for height were reported in inches, and hence we used this unit of measurement in all analyses, but for the graphs we converted these data to cm. All analyses were performed using the lme4 package in R, version 2.13.1 (R Development Core Team, 2008). All percentages mentioned in the results section are predictions from mixed models based on the fixed effects, which were calculated based on the formula in Diggle et al. (2002). Confidence intervals for optima were based on 1,000 re-analyses of the data using the functions *simulate* and *refit* in R.

RESULTS

Overall sample

An average of 36.97 (SD = 10.82) individuals participated in the 174 speed-dating events, in which an average of 18.17 ± 5.18 were women and 18.80 ± 6.06 were men. Average height for men was 179.06 (SD = 6.87) cm (154 men did not report height), and 165.20 (SD = 6.72) cm for women (172 women did not report height). See supplementary Tables S6.1 and S6.2 for more descriptive statistics.

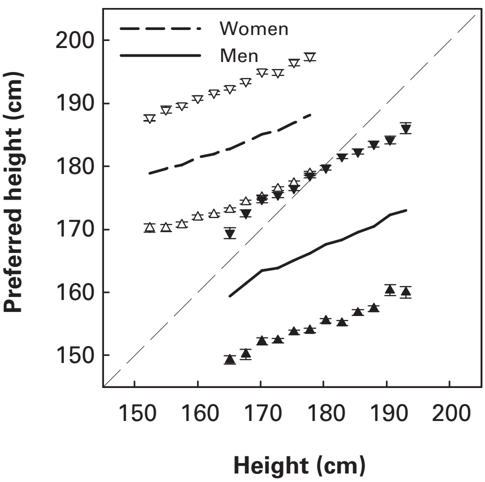

Figure 6.1: Minimum and maximum preferred height (*means* ± *SE*) in relation to subject height for men (filled triangles) and women (open triangles). The lines reflect the midpoint between the minimally and maximally preferred height. For men, bins below 65" and above 75" were collapsed, and for women bins below 60" and above 70".

Stated preferences for partner height

P*reference ranking* with respect to height was studied using the minimum and maximum preferred height. Men were more likely (761 out of 2,601; 29.26%) than women (167 out of 2,847; 5.87%) to report a very low minimally preferred height (4 foot ≈ 122 cm; ($\chi^2(1)=526.28$; $p < .0001$). In contrast, women were more likely (844 out of 2847; 42.14%) than men (623 out of 2,601; 23.95%) to report a very high maximally preferred height (7 foot ≈ 222 cm; $\chi^2(1)=22.39$; $p < .0001$). We considered the very low minimally (4 foot) and very high maximally (7 foot) preferred height to indicate that there was no limit to the height of an acceptable partner, and therefore excluded these individuals from the following analysis. The preferred height range (maximally preferred minus minimally preferred height) was larger in men than in women (men, mean ± *SD*: 24.43 ± 8.43 cm; $N = 1,770$; women: 18.72 ±7.08 cm; $N = 1,996$; $t(3,470.13) = 22.33$; $p < .0001$; $d = 0.74$). Height correlated positively with minimally and maximally preferred height in both sexes (Figure 6.1; men: min.: $r = 0.35$; $p < .0001$; $N = 1,822$; max.: $r = 0.52$; $p < .0001$; $N = 1,957$; women: min.: $r = 0.40$; $p < .0001$; $N = 2,653$; max.: $r = 0.42$; $p < .0001$; $N = 1,983$).

Women preferred larger within-pair height differences than men. Men's minimally preferred height difference was 0.021 (*SD* = 6.65) cm (indicating that on average men prefer to be a minimum of 0.021 cm taller than a woman), whereas women indicated a significantly larger minimum height difference of 8.30 (*SD* = 6.95) cm ($t(4,314.21) = 40.96$; $p < .0001$; $d = 1.21$). A one sample t-test against zero revealed that women ($t(2,652) = 61.45$; $p < .0001$; $d = 1.19$), but not men ($t(1,956) = 0.14$; $p = .890$; $d = 0.003$) preferred to be in a couple in which the male was taller. With respect to the maximum preferred height difference, we again found a significant contrast between the sexes: on average, men preferred smaller maximum within-pair height differences than women (respectively 24.67 (*SD* = 7.44) cm versus 27.94 cm (± 6.54); $t(3,637.69) = 14.28$;

p < .0001; *d* = 0.47).

Knowing the distribution of both individual *preference rankings* and actual heights enabled us to identify the potential direction and intensity of inter-sexual selection acting on height (Fawcett & Johstone, 2003). To this end, we first calculated how many opposite sex individuals would accept a partner of a given height, in the sense that his/her height was between the reported minimum and maximum preferred height of opposite sex participants. We then calculated the total number of individuals that were of acceptable height for these opposite-sex individuals. In these calculations, we also included individuals with very low minimal or high maximal preferred heights. The ratio of these values gives the number of same-sex people that an individual of a given height would face as competition per opposite-sex person. For instance, a man of 177.8 cm (70 inches) would fall within the preferred height range of 2,458 women. These 2,458 women on average would accept 2,101 other men. Thus, a man of 177.8 cm would compete with, on average, 2,101/ 2,458 = 0.85 men (see supplementary Tables S3 and S4 for these calculations for all heights). Short men faced the greatest number of competitors (Figure 6.2), whereas men of average height had the fewest competitors. Very tall men had more competitors than average height men, but fewer than short men. Relatively short and tall women face more competition than average height women, but variation in competition across women is much lower than across men (Figure 6.2). This reflects our finding that the male preferred height range is, on average, larger than the female preferred height range.

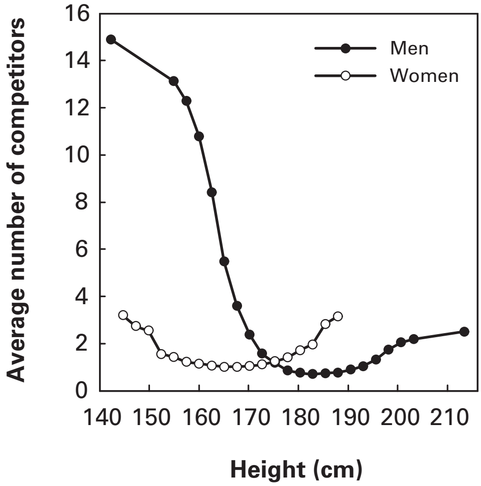

Figure 6.2: The number of competitors in the speed-date population for men and women in relation to their height. High values indicate that the number of individuals of a given height is high relative to the number of opposite sex individuals for whom that height falls within the acceptable height range. See text and supplementary Tables S3 and S4 for further information.

6

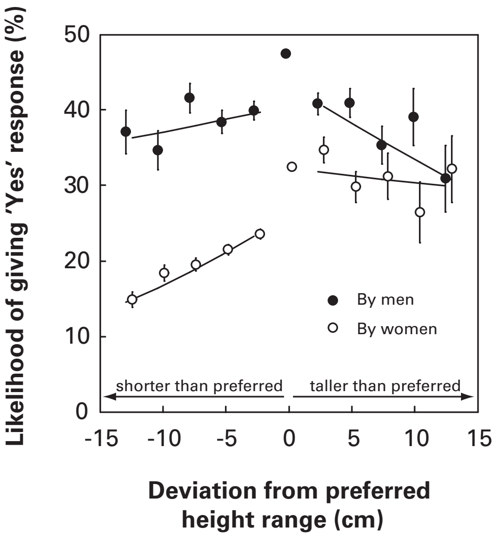

Figure 6.3:The *strength* of the height preference: the chance of giving a 'Yes' response with increased deviation from the preferred height range for men and women (*mean* ± *SE*). Bins below -7″ and above 7″ were collapsed. The likelihood of giving a 'Yes' response when the height fell within the height range is plotted for comparison.

Strength of preference in relation to height

To establish the strength of the preferences with respect to height we analysed the relationship between preferred height range and choice. Strength was assessed on two levels, and both analyses showed that women had a stronger preference than men. First, we examined the likelihood that an individual said 'Yes' to a speed-dater who fell *within* the reported preferred height range of that individual. For men, the estimated likelihood of saying 'Yes' to a preferred individual with respect to height was 47.9%, whereas for a non-preferred individual this was reduced to 42.8% (logistic regression; $Z = 7.62$; $p < .0001$). For women, these same values were 32.2% for a preferred individual versus 25.4% for a non-preferred individual ($Z = 13.63$; $p < .0001$): a significantly greater decrease than seen in men (interaction-term: $Z = 3.10$; $p = .002$). Second, for those speed-daters who fell outside the preferred height range of a choosing individual, we assessed the extent to which the magnitude of the deviation from the preferred height range influenced the chance of saying 'yes'. For men, we found that the likelihood of saying 'Yes' to an individual who fell 1 inch (2.54 cm) outside the preferred height range was predicted to be 40.0%, whereas this likelihood decreased by 5.7% when the individual fell 5 inches (12.7 cm) outside the preferred range ($Z = 3.01$; $p = .003$; Figure 6.3). For women, we found that the likelihood of saying 'Yes' to an individual who fell 1 inch (2.54 cm) outside the preferred height range was predicted to be 24.8%, while 5 inches decreased it by 8.0% ($Z = 7.87$; $p < .0001$). A significant interaction was found between sex and the deviation from the preferred height range ($Z = 2.14$; $p = .016$), indicating that preference strength was stronger in women than men. Examining the *strength* of preference separately towards heights above and below the preferred height range, we found that women disfavoured heights that were shorter than preferred more than those taller than preferred (interaction-term: $Z = 3.02$; $p = .003$; Figure 6.3). The reverse was true for men: men tended to disfavour women who were taller than preferred more than women shorter than preferred (interaction-term: $Z = 1.66$; $p = .097$). This pattern was significantly different between the sexes (interaction-term: $Z = 3.33$; $p = .001$).

Tolerance in relation to height

The standard deviation of heights to which a 'Yes' response was given (including only those that responded with 'Yes' more than once), was on average 2.45(± 0.73) for men and 2.35 (± 1.00) women, a small but significant difference ($t(5203) = 5.24$; $p < .0001$; $d = 0.15$). This reinforces the above results on strength of preferences, with women displaying a significant tendency to choose a narrower range of mates during speed-dating than men. This measure of tolerance also correlated weakly but significantly with the reported preferred height range in men (Spearman's $rho = .070$; $p = .004$; $N = 1{,}691$) and women (Spearman's $rho = .064$; $p = .009$; $N = 1{,}690$), indicating that individuals who reported a narrower preferred height range also showed less variability with respect to which heights were given a 'Yes' response.

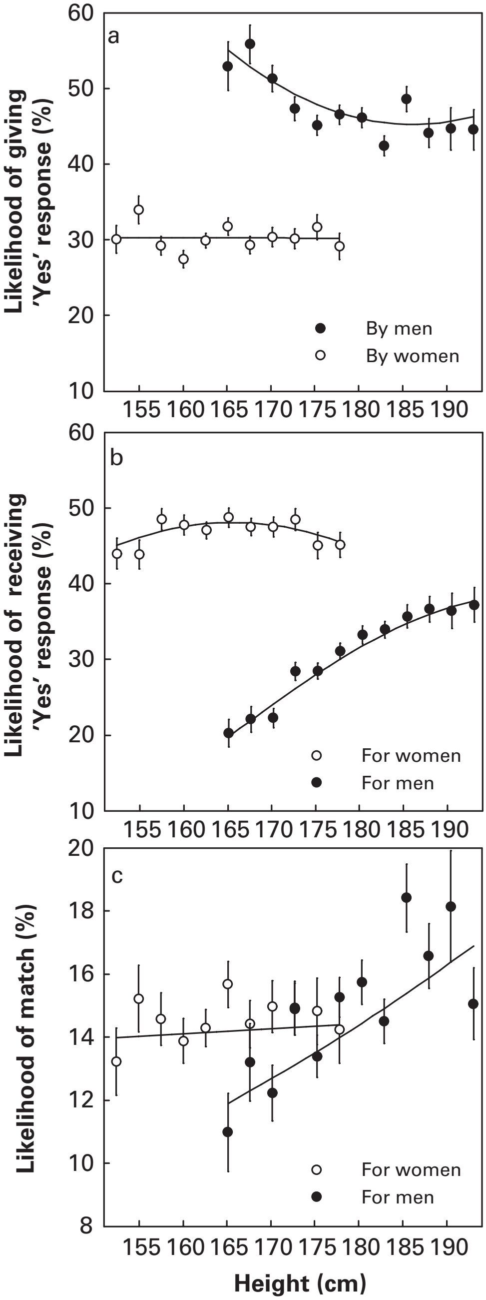

Figure 6.4: The effect of male and female height on a) the likelihood of giving a 'Yes' response, b) the likelihood of receiving a 'Yes' response, and c) the likelihood of a match (all *mean* ± *SE*). For men, bins below 65" and above 75" were collapsed, and for women bins below 60" and above 70".

Responsiveness, desirability and pair formation in relation to height

Overall, we found that, for both men and women, those who reported a wider preferred height range were also more responsive in general (men: $Z = 4.73$; $p < .0001$; women: $Z = 8.63$; $p < .0001$). Furthermore, men were more responsive than women: on average, they said 'Yes' to 47.4% of women, whereas for women this value was substantially lower at 30.2% ($Z = -20.85$; $p < .0001$).

Taller men were less responsive themselves, but more likely to receive a 'Yes' response from women (which we refer to as 'desirability'). Both relationships were curvilinear, with minimum responsiveness at 7.2 cm above average height (95% *CI* = 3.4 – 18.9), and maximum desirability at 21.3 cm (95% *CI* = 12.9 – 64.0) above average height (Table 6.2; Figure 6.4a, b). The desirability effect was stronger than the responsiveness effect and hence taller men were more likely to form a pair, i.e., were more likely to end up with a 'Match' (Table 6.2; Figure 6.4c).

Female height was not significantly related to either responsiveness or pair formation (Table 6.2; Figure 6.4a, c). However, average height women were

Table 6.2: The effect of male and female height (in inches; *mean*-centered) on the likelihood of giving a 'Yes' response, receiving a 'Yes' response, and having a match during speed-dating. Table entries show binomial logistic mixed model parameter estimates (± *SE*) and the associated *p*-value (in brackets).

	Likelihood of giving 'Yes' response		Likelihood of receiving 'Yes' response		Likelihood of match	
	Male	Female	Male	Female	Male	Female
Intercept	-0.22 ± 0.052 (<.0001)	-1.23 ± 0.043 (<.0001)	-1.18 ± 0.046 (<.0001)	-0.12 ± 0.053 (.026)	-2.27 ± 0.034 (<.0001)	-2.27 ± 0.034 (<.0001)
Height	-0.050 ± 0.012 (<.0001)	-0.00049 ± 0.010 (.962)	0.12 ± 0.010 (<.0001)	0.002112 ± 0.010 (.834)	0.047 ± 0.0084 (<.0001)	0.0041 ± 0.0083 (.619)
Height^2	0.0088 ± 0.0027 (.0014)	[b]	-0.0071 ± 0.0024 (.0025)	-0.0070 ± 0.0030 (.020)	[b]	[b]
Random effects[a]						
Choosing individual ID	2.23 ± 1.49	1.66 ± 1.29	1.76 ± 1.33	2.31 ± 1.52	0.79 ± 0.89	0.81 ± 0.90
Chosen individual ID	1.63 ± 1.28	1.58 ± 1.26	1.48 ± 1.21	1.61 ± 1.27	0.85 ± 0.92	0.83 ± 0.91
Event ID	0.13 ± 0.36	0.086 ± 0.29	0.081 ± 0.28	0.13 ± 0.36	0.056 ± 0.24	0.054 ± 0.23

[a] Parameter estimate for variance components (± *SD*).
[b] $p > .159$.

slightly more desirable, as indicated by a significant quadratic effect of female height on the chance of receiving a 'Yes' response (Table 6.2; Figure 6.4b). The most frequently chosen female height was 0.38 cm (95% *CI* = -5.1 – 6.4) above average height. Thus, average height women were chosen more often.

Do stated preferences predict pair formation?

To assess the extent to which stated preferences were actually realized in resulting 'Matches', we examined the likelihood of a match with someone who fell within a chooser's preferred height range compared to someone who fell outside this range. The likelihood of a match with a preferred individual with respect to height was 14.7% when men were choosing, whereas for a non-preferred individual this was reduced to 11.4% ($Z = 6.98$; $p < .0001$). When women were choosing, this was 15.3% versus 12.0% ($Z = 8.88$; $p < .0001$).

Does the conflict over preferred height differences between the sexes influence choice and pair formation?

As partner preferences are dependent on one's own height (Figure 6.1), relative height difference may be more informative with respect to the chance of giving a 'Yes' response than assessment of potential partner height alone. We found curvilinear effects for both men and women on the chance of giving a 'Yes' response with respect to partner height differences (male minus female height; Table 6.3; Figure 6.5). For men, a 'Yes' response was most likely when

Table 6.3: The effect of the difference in height (male minus female height; in inches) on the likelihood of giving a 'Yes' response by men and women, and the chance of a match. Table entries show binomial logistic mixed model parameter estimates (± *SE*) and the associated *p*-value (in brackets).

	Likelihood of giving 'Yes' response		**Likelihood of match**
	Male	Female	
Intercept	-0.11 ± 0.065 (.081)	-1.67 ± 0.061 (<.0001)	-2.47 ± 0.051 (<.0001)
Height difference	0.021 ± 0.011 (.052)	0.14 ± 0.011 (<.0001)	0.085 ± 0.011 (<.0001)
Height difference^2	-0.0038 ± 0.0007 (<.0001)	-0.0072 ± 0.0008 (<.0001)	-0.0057 ± 0.0008 (<.0001)
Random effects[a]			
Choosing individual ID	2.29 ± 1.51	1.71 ± 1.31	0.83 ± 0.91
Chosen individual ID	1.63 ± 1.27	1.50 ± 1.22	0.81 ± 0.90
Event ID	0.13 ± 0.35	0.089 ± 0.30	0.060 ± 0.25

[a] Parameter estimate for variance components (± *SD*).

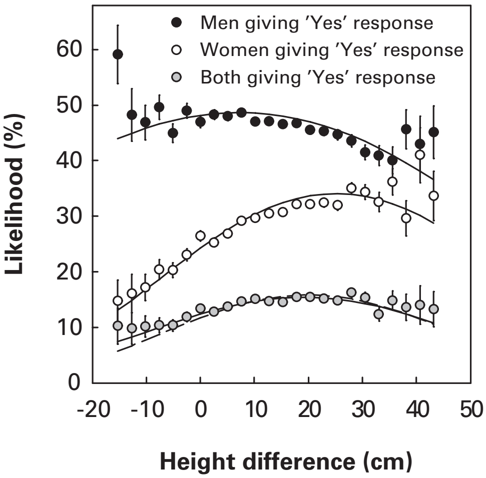

Figure 6.5: Height differences (male minus female height) and the likelihood of giving a 'Yes' response by men and women, and the likelihood of a match (all *mean* ± *SE*). Bins below -6" and above 17" were collapsed. The broken line represents the multiplication of the curves representing the likelihood of giving a 'Yes' response for both men and women.

the woman was 7.1 cm (95% *CI* = 1.0 - 12.2) shorter than themselves, significantly lower than the average height difference of 13.9 cm between men and women in our sample. Women, in contrast, were most likely to give a 'Yes' response when the man was 25.1 cm taller (95% *CI* = 22.1 – 28.8). This height difference was significantly larger than the average height difference in the matches and also substantially larger than the male optimum.

We then calculated the height difference with the highest likelihood of a match (i.e., mutual score of 'Yes'). We found an optimum of 19.2 cm (95% *CI* = 16.2 – 22.8) which falls in between the most chosen value for both men (7.1 cm) and women (25.1 cm), and which was also significantly greater than the average height difference (Table 6.3; Figure 6.5). When we multiply the curve of the men giving a 'Yes' response (with respect to the height differences) with that of the female curve, we obtain a curve indicating the chance of a 'Match' when the chance of a 'Yes' being reciprocated is independent (i.e., the likelihood of having a 'Yes' response reciprocated is equal to that non-reciprocated). This estimated curve was very similar to the observed height distribution of the matches (Figure 6.5), suggesting that men and women were not more likely to give a 'Yes' response to an individual who gave them a 'Yes' response in turn – thus there is no evidence to suggest that a given couple feels a 'click' with one another.

Resulting mating patterns with respect to height

The heights of the matched individuals were positively, but weakly, correlated ($r = .069$; $p < .0001$; $N = 8{,}361$ matches). In contrast, there was no significant correlation between the height of speed-dating couples that did not match ($r = -.006$; $p = .189$; $N = 49{,}372$), implying that the correlation between heights of matched partners was not due to variation in height across speed-dating events. These correlations, however, include multiple data points per individual. Therefore, we also correlated the height of an individual to the average height of all matches of that individual (Figure 6.6). Both male (r = .128; p < .0001; N = 2,206) and female (r = .105; p < .0001; N = 2,381) height correlated positively with this average height, providing some indication of assortative mating: taller individuals tended to be matched with taller individuals in both sexes, but average height men were more likely to be matched with shorter females (Figure 6.6). Thus, assortative mating for height was tempered by female choice for men much taller themselves, with the result that men of average height, rather than shorter men, were more likely to be matched with shorter women. Indeed, short men were much less likely overall to find a match during speed dating events (Figure 6.4c).

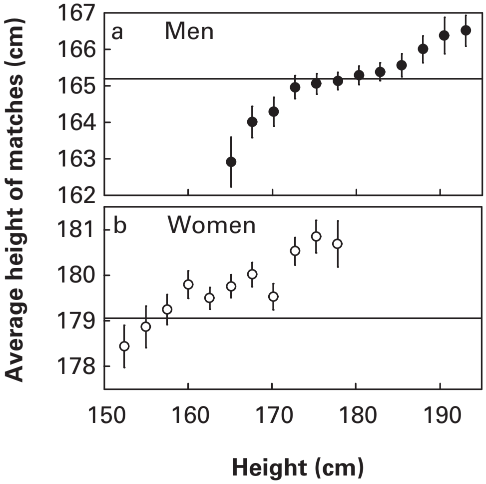

Figure 6.6: The average height (± *SE*) of the individuals with whom an individual of a given height is paired. For every individual we calculated the average height of all individuals matched with (see text). The horizontal line represents the average height of the opposite-sex.

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DISCUSSION

Studies of mate choice are generally restricted to the assessment of preferences, thereby neglecting the subsequent processes that lead to actual pair formation. In contrast, we addressed simultaneously how preferences for partner height were translated into actual choice, and how choice then translated into pairing. With respect to the relationship between preferences and choice, we found that non-preferred potential partners with respect to height still had a high (albeit reduced) chance of being chosen (42.8% and 25.4% for respectively men and women). This is line with previous speed-dating studies, most of which report that partner preferences are not strong predictors of choice during speed-dating (Eastwick & Finkel, 2008; Eastwick et al., 2011; Kurzban & Weeden, 2007; Todd et al., 2007). As already noted, there are many reasons why preferences should not be expected to predict choice simply as a matter of course, such as mate availability, preference trade-offs and competition. In this context, however, it seems worth mentioning a human-specific reason why choices may deviate from expressed preferences: the validity of verbally expressed mate preferences. For instance, humans may not be able to express their own preferences accurately, or they may feel compelled to give social desirable answers (Eastwick et al., 2011; Todd et al., 2007). Additionally, and perhaps most crucially, the setting in which preferences are established may not conform to the situation in which preferences are actually expressed. Unfortunately, we are not able to assess any of these with our present study, but it is worth bearing in mind that other psychological processes besides those relating strictly to mating decisions may explain some of the deviation of choice from preference.

Despite the imperfect mapping of preferences onto choice, we found that women's preferences were more strongly related to choice than those of men. Women reported a narrower preferred height range than men, and they were also less likely to choose men that fell outside this range (i.e., women had a higher *strength* of preference). Similarly, there was less variation in the heights chosen by women compared to men (i.e., women also had a lower *tolerance*). Finally, women were less *responsive* overall (i.e., lower chance of giving a 'Yes' response) than men, which mirrors findings from previous research (e.g., Eastwick & Finkel, 2008; Kurzban & Weeden, 2005; Todd et al., 2007), but there was no influence of a woman's own height on her responsiveness (in line with Kurzban & Weeden, 2005). Female height did however influence their desirability: average height women were most desired during speed-dating. Furthermore, based on the preferences for height expressed by men and the actual height distribution of women, it was clear that average height women also had the fewest number of rivals to compete with compared to shorter and taller women. These effects were generally small, however, and did not translate into actual success, as female height was unrelated to the chance of match. A contrasting pattern of results was obtained for men, where an individual's own height had a significant influence on their *responsiveness*: specifically, taller men were less responsive than shorter men. The lower responsiveness by taller men can partly be explained by their increased desirability, as taller men were most often given a 'Yes' response by women and had to compete with fewer rivals than shorter men. Thus, the increased popularity of and reduced competition for taller men compared to shorter men may functionally explain their decreased responsiveness during speed-dating. Despite being less responsive, taller man were most likely to end up with a match. Taken together, these results demonstrate that height is considered more important by women as a mate choice characteristic, and that men's 'mating success' is therefore more dependent on their height than that of women. Thus female mate choice is likely a contributor to the evolution of human sexual size dimorphism.

Stated preferences for height differences also revealed a conflict between the sexes. In general, women preferred their partner to be much taller, whereas men preferred their partner to be only slightly shorter. Furthermore, women preferred to be in a couple in which the man was minimally taller than the women, whereas the same was not true for men. These stated preferences were also reflected in choice: men were most likely to choose only small partner height differences, including those height differences in which the woman was taller than the choosing men. Women, in contrast, were most likely to choose very larger partner height differences, and least likely to choose small partner height differences, particularly those that would result in the man being shorter. Further evidence that women disfavour men shorter than themselves is also shown by the differences in their *strength* of preference: women strongly disfavoured men who were shorter, but not those who were taller, than their preferred height range (Figure 6.3). These converging lines of evidence strongly suggest that the male-taller norm observed in actual couples (i.e., males are more often taller than their partner when compared to random mating; Gillis & Avis, 1980; **Chapters 7**) is driven by women rather than by men.

Our most notable finding, however, concerns the manner in which the conflict over partner height difference extended to actual pair formation. While men preferentially chose partners with a height difference that fell significantly below the average height difference between men and women, women chose partners with height differences that were significantly above this average difference (Figure 6.5). This conflict in choice inevitably resulted in pairs in which the height difference between partners was sub-optimal for both sexes, even though all parties were expressing a free choice and rivals did not prevent this choice. Thus, our study shows how mutual mate choice for preferred partners can lead to sub-optimal pair formation, highlighting the value of following the mate choice process beyond the establishment of preferences through to pair formation.

The higher overall "mating success" of taller men in speed-dating is in stark contrast with recent studies indicating that average height men attain highest reproductive success (Stearns et al., 2012; **Chapters 10** and **11**). Our study provides a potential explanation for this finding. The process of mate choice and pair formation resulted in assortative mating for height, but, because women's choices were so strongly directed toward men much taller than themselves, men of average height, rather than shorter men, were most likely to end up paired with shorter women. It should be noted, however, that as shorter men were less likely overall to be paired in our speed-dating sample, the magnitude of assortment for height in matches is lower than that observed among actual couples (Silventoinen et al., 2003; Spuhler, 1982). The higher likelihood of average height men to be coupled with shorter women relative to taller men, therefore, may provide the key to understanding the increased reproductive success of average height men. Studies on the relationship between female height and fertility have consistently shown that the shortest women attain the highest reproductive success (Stearns et al., 2012; reviewed in **Chapter 9**), most likely due to a life-history trade-off between growth and reproduction and the genetic correlation between female height and age at first birth (i.e., those that give birth at a younger age are genetically predisposed to be shorter; Stearns et al., 2012). Our results therefore suggest the intriguing possibility that, in western populations, due to assortative mating for height, taller men are least likely to end up with shorter, more fertile, women because of the manner in which their own and opposite-sex preferences intersect (Figures 6.5 and 6.6). Average height men, in contrast, are most likely to be matched with short women, and this may be instrumental in their achieving higher reproductive success. The reduced reproductive success of shorter men, who are most likely to be paired with shorter women, may be a consequence of other factors disfavouring short height, such as being less preferred as a mate and thereby obtaining a mate of lesser quality, lower health status, lower social status, or fewer resources (see **Chapter 10**). In other words, the curvilinear relationship between height and reproductive success may be the result of competing pressures that act differentially along the height continuum to produce the observed effects on male reproductive success. Clearly, this explanation is speculative, but it does provide a new and plausible mechanism for why average height men achieve highest reproductive success. Moreover, it further emphasizes the value of speed-dating as model system for mate choice processes, because it allows the investigation of individual choice and pairing in a way that potentially can shed light on how these processes affect actual reproductive success.

ACKNOWLEDGEMENTS

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SUPPLEMENTARY MATERIAL

Table S6.1: Descriptive statistics of the events (*N* = 174).

	Mean ± SD	***Minimum***	***Maximum***
# Persons in event	36.79 ± 10.82	15	65
# Men in event	18.80 ± 6.06	6	35
# Women in event	18.17 ± 5.18	7	30
Sex ratio[a]	0.51 ± 0.050	0.35	0.63

[a] # men in event divided by # persons in event.
The correlation between the number of men and women participating in the event was $r = .852$ ($p < .0001$).

Table S6.2: Descriptive statistics of the sample of speed-daters.

	N		***mean ± SD***	***Minimum***	***Maximum***
Female	3,024				
Age		3,019	31.83 ± 5.16	20	53
Height		2,852	165.20 ± 6.72	144.78	187.96
Ethnicity	3,024				
Caucasian		2,305			
Asian		135			
African		107			
Hispanic		125			
Other		83			
Unknown		269			
Male	2,758				
Age male		2,755	34.41 ± 6.06	21	68
Height male		2,604	179.06 ± 6.87	142.24	213.36
Ethnicity	2,758				
Caucasian		2,109			
Asian		138			
African		86			
Hispanic		98			
Other		102			
Unknown		225			

Table S6.3: The average number of competitors per male height (see Figure 6.2)

Male height[a]	Frequency	# Women would accept height[b]	Average # men accepted by these women[c]	Considered too short by # women	Considered too tall by # women	Average # competitors[d]
142.24	1 (0.04%)	171 (6.01%)	2547 (98%)	2676 (93.99%)	0 (0%)	14.89
154.94	1 (0.04%)	194 (6.81%)	2547 (98%)	2653 (93.19%)	0 (0%)	13.12
157.48	4 (0.15%)	207 (7.27%)	2542 (98%)	2640 (92.73%)	0 (0%)	12.27
160.02	6 (0.23%)	235 (8.25%)	2533 (97%)	2612 (91.75%)	0 (0%)	10.78
162.56	11 (0.42%)	298 (10.47%)	2508 (96%)	2549 (89.53%)	0 (0%)	8.41
165.1	42 (1.61%)	455 (15.98%)	2490 (96%)	2392 (84.02%)	0 (0%)	5.47
167.64	107 (4.11%)	685 (24.06%)	2463 (95%)	2162 (75.94%)	0 (0%)	3.59
170.18	175 (6.72%)	1014 (35.62%)	2412 (93%)	1833 (64.38%)	0 (0%)	2.38
172.72	258 (9.91%)	1486 (52.2%)	2334 (90%)	1360 (47.77%)	1 (0.04%)	1.57
175.26	312 (11.98%)	1891 (66.42%)	2244 (86%)	954 (33.51%)	2 (0.07%)	1.19
177.8	397 (15.25%)	2458 (86.34%)	2102 (81%)	385 (13.52%)	4 (0.14%)	0.85
180.34	351 (13.48%)	2689 (94.45%)	2029 (78%)	150 (5.27%)	8 (0.28%)	0.75
182.88	389 (14.94%)	2803 (98.45%)	1980 (76%)	18 (0.63%)	26 (0.91%)	0.71
185.42	209 (8.03%)	2676 (93.99%)	1982 (76%)	4 (0.14%)	167 (5.87%)	0.74
187.96	174 (6.68%)	2590 (90.97%)	1983 (76%)	0 (0%)	257 (9.03%)	0.77
190.5	80 (3.07%)	2243 (78.78%)	1994 (77%)	0 (0%)	604 (21.22%)	0.89
193.04	53 (2.04%)	1929 (67.76%)	2001 (77%)	0 (0%)	918 (32.24%)	1.04
195.58	17 (0.65%)	1536 (53.95%)	2025 (78%)	0 (0%)	1311 (46.05%)	1.32
198.12	10 (0.38%)	1185 (41.62%)	2063 (79%)	0 (0%)	1662 (58.38%)	1.74
200.66	4 (0.15%)	1016 (35.69%)	2085 (80%)	0 (0%)	1831 (64.31%)	2.05
203.2	1 (0.04%)	959 (33.68%)	2096 (81%)	0 (0%)	1888 (66.32%)	2.18
213.36	2 (0.08%)	844 (29.65%)	2110 (81%)	0 (0%)	2003 (70.35%)	2.50

[a] Height in cm (originally reported in inches).

[b] The number of women who included that particular male height in their preferred height range.

[c] The average number of men liked by all the women who included that particular male height in their preferred height range.

[d] The average number of competitors was a function of how many women would accept a man of a given height and the average number of men that were accepted by these women. Thus: the average number of *other* men accepted by the women (average number preferred minus 1) divided by the number of women who would accept them.

Table S6.4: The average number of competitors per female height (see Figure 6.2)

Female height[a]	Frequency	# Men would accept[b]	Average # women accepted by these men[c]	Considered too short by # men	Considered too tall by # men	Average # competitors[d]
144.78	1 (0.04%)	863 (33.18%)	2760 (96.77%)	1738 (66.82%)	0 (0%)	3.20
147.32	9 (0.32%)	1000 (38.45%)	2736 (95.92%)	1601 (61.55%)	0 (0%)	2.73
149.86	17 (0.6%)	1070 (41.14%)	2725 (95.53%)	1531 (58.86%)	0 (0%)	2.55
152.4	85 (2.98%)	1740 (66.9%)	2706 (94.89%)	861 (33.1%)	0 (0%)	1.55
154.94	124 (4.35%)	1887 (72.55%)	2695 (94.49%)	714 (27.45%)	0 (0%)	1.43
157.48	277 (9.71%)	2181 (83.85%)	2666 (93.47%)	420 (16.15%)	0 (0%)	1.22
160.02	304 (10.66%)	2303 (88.54%)	2644 (92.72%)	297 (11.42%)	1 (0.04%)	1.15
162.56	455 (15.95%)	2446 (94.04%)	2606 (91.37%)	151 (5.81%)	4 (0.15%)	1.06
165.1	363 (12.73%)	2532 (97.35%)	2570 (90.1%)	58 (2.23%)	11 (0.42%)	1.01
167.64	380 (13.32%)	2532 (97.35%)	2564 (89.9%)	21 (0.81%)	48 (1.85%)	1.01
170.18	305 (10.69%)	2468 (94.89%)	2574 (90.26%)	8 (0.31%)	125 (4.81%)	1.04
172.72	219 (7.68%)	2329 (89.54%)	2592 (90.88%)	3 (0.12%)	269 (10.34%)	1.11
175.26	169 (5.93%)	2099 (80.7%)	2614 (91.64%)	1 (0.04%)	501 (19.26%)	1.24
177.8	100 (3.51%)	1862 (71.59%)	2628 (92.13%)	0 (0%)	739 (28.41%)	1.41
180.34	32 (1.12%)	1537 (59.09%)	2641 (92.61%)	0 (0%)	1064 (40.91%)	1.72
182.88	10 (0.35%)	1356 (52.13%)	2660 (93.27%)	0 (0%)	1245 (47.87%)	1.96
185.42	1 (0.04%)	949 (36.49%)	2682 (94.03%)	0 (0%)	1652 (63.51%)	2.82
187.96	1 (0.04%)	859 (33.03%)	2704 (94.82%)	0 (0%)	1742 (66.97%)	3.15

[a] Height in cm (originally reported in inches).

[b] The number of men who included that particular female height in their preferred height range

[c] The average number of women liked by all the men who included that particular female height in their preferred height range

[d] The average number of competitors was a function of how many men would accept a woman of a given height and the average number of women that were accepted by these men. Thus: the average number of *other* women accepted by the men (average number preferred minus 1) divided by the number of men who would accept them

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CHAPTER 7

Are human mating preferences with respect to height reflected in actual pairings?

Gert Stulp
Abraham P. Buunk
Thomas V. Pollet
Daniel Nettle
Simon Verhulst

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ABSTRACT

Pair formation, acquiring a mate to form a reproductive unit, is a complex process. Mating preferences are a step in this process. However, due to constraining factors such as availability of mates, rival competition, and mutual mate choice, preferred characteristics may not be realised in the actual partner. People value height in their partner and we investigated to what extent preferences for height are realised in actual couples. We used data from the Millennium Cohort Study (UK) and compared the distribution of height difference in actual couples to simulations of random mating to test how established mate preferences map on to actual mating patterns. In line with mate preferences, we found evidence for: (i) assortative mating (r = .18), (ii) the male-taller norm, and, for the first time, (iii) for the male-not-too-tall norm. Couples where the male partner was shorter, or over 20 cm taller than the female partner, occurred at lower frequency in actual couples than expected by chance, but the magnitude of these effects was modest. We also investigated another preference rule, namely that short women (and tall men) prefer large height differences with their partner, whereas tall women (and short men) prefer small height differences. These patterns were also observed in our population, although the strengths of these associations were weaker than previously reported strength of preferences. We conclude that while preferences for partner height generally translate into actual pairing, they do so only modestly.

INTRODUCTION

Finding a mate to form a reproductive unit is a complex process but an important factor in determining an individual's Darwinian fitness. Mating preferences, the propensity to mate with certain phenotypes (Jennions & Petrie, 1997), are an important part of pair formation. However, due to constraints in the mating process the preferred partner characteristics may differ from actual partner characteristics when a pair is formed. For instance, limited availability of mates and hence severe competition with rivals may prevent one from ending up with the desired partner (Widemo & Sæther, 1999). In addition to such constraints, the risk of being deserted for a better option after pair formation may make it strategically optimal to forego mating options with members of the opposite sex that are preferred by many, to ensure a long-term pair bond (Riebel et al., 2010). This consideration arises because even when a pair is formed, the availability of attractive alternatives is a determinant of the stability of that pair (Houston et al., 2005; Rusbult & Buunk, 1993).

In addition, many characteristics are taken into account when choosing a mate (Candolin, 2003), which likely results in choosing a mate with some preferred, but other less-preferred characteristics, even when choice is without constraints. A mismatch between actual and preferred mate characteristics is even more pronounced when a desired characteristic is traded off against another one, implying that selecting on one desired characteristic reduces the likelihood of obtaining a different preferred characteristic (as suggested for example for parental investment and genetic quality; Magrath & Komdeur, 2003; Waynforth, 1999). An additional obstacle for obtaining a preferred partner arises when there is mutual mate choice, in which case the preferences and choice of the opposite sex further complicate the mating process (Johnstone et al., 1996). All of the above reasons may lead to pair formation where both individuals have a less than ideally preferred partner.

Although it seems likely that the translation of preferences into actual partner characteristics will be constrained, causing a mismatch between preferences and actual mating patterns, this mismatch has been little studied. Here we test whether preference rules with respect to human height are translated in actual pairings. Human height is a partner characteristic that is valued by both men and women and preferences for partner height have been well studied (reviewed in Courtiol et al., 2010b). Although the above preferences have consistently been shown in Western populations using a variety of methodologies, partner height preferences and choice may be different in non-Western populations (Sear & Marlowe, 2009; Sear, 2006; Sorokowski & Butovskaya, 2012; Sorokowski et al., 2011; see Sear, 2010 for potential causes for these differences). In this paper, we focus exclusively on Western mating preferences for height, and below we describe these in more detail before going on to test whether these preference rules are translated in actual pairings.

Assortative mating

In both men and women, questionnaire based data suggests that with increasing height the preferred partner height also increases (Courtiol et al., 2010b), indicating preferences for assortative mating. Similar patterns have been found in responses to online advertisements (Pawlowski & Koziel, 2002) and in speed dating events (Kurzban & Weeden, 2005). Assortative preferences for height seem to be realised in actual couples (Gillis & Avis, 1980; Mcmanus & Mascie-Taylor, 1984; Oreffice & Quintana-Domeque, 2010; Silventoinen, et al., 2003; Spuhler, 1982). Spuhler (1982), for instance, reviewed assortative mating with respect to physical height in 28 populations and found an average between partner height correlation of .2.

Male-taller norm (female-shorter norm)

In general, women prefer men taller than themselves and, conversely, men prefer women shorter than themselves (Courtiol et al., 2010b; Fink et al., 2007; Pawlowski, 2003; Salska et al., 2008). Again, preferences are reflected in actual pairs as the male-taller norm is also found in actual couples (Gillis & Avis, 1980). Gillis and Avis (1980) found that in only 1 out of 720 US/UK couples, the female was taller. Because women are on average shorter than men, chance predicts that the occurrence of couples in which the female is taller is 2 out of 100, 14 times higher than the observed 1 out of 720 (see Sear (2006) for a recent study replicating this finding in a Western population).

Male-not-too-tall norm (female-not-too-short norm)

Not only do men and women prefer the male to be taller than the woman in a romantic couple, they also prefer the male not to be too tall relative to the woman: the male-not-too-tall norm (Courtiol et al., 2010b; Fink et al., 2007; Pawlowski, 2003; Salska et al., 2008). In a sample of undergraduates selecting dates, the largest reported acceptable height difference for both sexes was the male being 17% taller than the female (Salska et al., 2008). The extent to which the male-not-too-tall norm is expressed in actual couples is currently unknown, and in the present study we address this issue.

Preferred partner height differences are dependent on one's own height

According to Pawlowski (2003), preferred partner height difference depends on an individual's own height: both shorter men and taller women prefer smaller partner height differences than taller men and shorter women do, who prefer larger partner height differences. However, it is not known whether these preferences for partner height differences are realised in actual couples, and we therefore also address this issue.

To test to what extent the above described rules with respect to preferences for partner height are realised in actual couples, we compared the distribution of actual couple heights to the distribution of couple height expected when mating was random with respect to height. With this technique, we were able to statistically assess simultaneously the male-taller norm, the male-not-too-tall norm, and whether preferred partner height differences are dependent on one's own height. We compare our estimates to those previously reported on partner height preferences, to assess how well preferences translate into choice (Courtiol et al., 2010b). Although assortative mating, the male-taller norm, and the male-not-too-tall norm may be considered as distinct preference rules, this need not be the case. For instance, strict adherence of individuals to assortative mating would lead to a male-taller and male-not-too tall norm on the population level. Through simulation techniques, we examined how enforcing either a male-taller norm, or a male-not-too-tall norm would affect the strength of assortative mating.

MATERIAL AND METHODS

Sample

We used data from the Millennium Cohort Study (MCS), a survey that gathered information from the parents of 18,819 babies born in the United Kingdom in 2000. See (Hansen, 2008; Plewis, 2007) for a detailed description. In brief: parents were interviewed when their babies were 9 months old. The sample was selected from a random sample of electoral wards, disproportionately stratified to ensure adequate representation of all four regions of the UK, areas with higher minority ethnic populations, and deprived areas (Dex & Joshi, 2004; Hansen, 2008; Plewis, 2007). The overall response rate was 68% (Dex &

Joshi, 2004). Height of the mother and father were self-reported. Self-reported measures of height have been shown to be reliable in women of reproductive age (Brunner Huber, 2007). For the analyses presented here, we included all heterosexual parents for which both heights were available (12,502 cases). Women were on average 163.75 ± 6.97 (mean ± standard deviation) and men 177.86 ± 7.42 centimetres tall. The average Parental Height Difference was 14.11 ± 9.25 centimetres. Because height is related to ethnicity, and there is strong assortative mating for ethnicity we re-analyzed our data restricting our sample to Caucasian parents (N = 10,664). This led to very similar results (results not reported).

Analysis

We investigated whether and how the observed distribution of Parental Height Differences (PHD; male height minus female height in cm) differed from the distribution expected under random mating over height. To obtain an estimate of PHD under random mating, we generated 10,000 samples in R (R Development Core Team, 2008), each sample being a complete randomization of the 12,502 couples (and thus their heights). We compared the distribution of PHD resulting from these random samples to the PHD distribution in the original population, to examine the differences between the observed heights and the heights in random mating. In order to do so, we divided the range of PHD in the original population and the 10,000 random samples in 5 centimetre bins, and counted the occurrences of these bins in both the original population and the random samples (bins with fewer than 75 cases were collapsed resulting in a lower bound cut-off bin of <-15 cm and a higher bound cut-off bin of >35 cm). For instance, the bin 15 to 20 cm, indicating that the male partner was 15 to 20 cm taller than the female, occurred exactly 2,586 times in the original population. The median value (50th percentile) of occurrences of this bin in the 10,000 random samples was 2,464. This indicates that the most likely number of occurrences (median of 10,000 samples) of the bin 15-20 cm is 2,465 when mating with respect to height is random, which suggests that this bin occurred more often in the original population than expected under random mating. Ninety-five per cent of the occurrences of this bin in the 10,000 samples fell between 2,382 (the 2.5th percentile) and 2,549 (the 97.5th percentile). The actual value (2,586) falls outside this range, indicating that this specific bin occurred significantly more often in the original population compared to what would happen when mating was random with respect to height.

A specific *p* value for the difference between the original and the random samples was determined by what proportion of the 10,000 samples the occurrence of the bins were higher, equal or lower than the actual occurrences of these bins. For instance, the bin 15 to 20 cm was found to be equally or less frequent than 2,586 (the number of occurrences of this bin in the original sample) in only 21 of the 10,000 samples. Thus, the occurrence of this bin is significantly different from random mating with a *p*-value of 21/10,000 is 0.0021. As This *p*-value concerns the directional hypothesis that the height bin is *either* over- or underrepresented compared to the original sample, not the hypothesis that the height bin has a different frequency in the random samples compared to the original sample, and as such is one tailed.

For every PHD bin, we also calculated the 'relative likelihood of pairing', the frequency of observing a particular PHD bin in the original population relative to random mating, by dividing the number of occurrences in the actual population of that PHD bin by the median number of occurrences of that PHD bin in the random samples. For example, the frequency of the PHD bin 15 to 20 cm was 2,586 in the actual original population, which we divided by 2,464 (median occurrence in 10,000 samples of random mating), yielding and 1.05 implying this PHD bin is 5% more frequent than expected by chance. A relative likelihood of pairing greater (*lower*) than one means that the PHD bin is more (*less*) likely to occur in the actual population than expected by random mating.

RESULTS

Assortative mating, the male-taller norm, and the male-not-too-tall norm

We first examined whether the assortative mating, the male-taller norm, and the male-not-too-tall norm over height were apparent in our sample. In line with earlier studies (Gillis & Avis, 1980; Mcmanus & Mascie-Taylor, 1984; Oreffice & Quintana-Domeque, 2010; Silventoinen et al., 2003; Spuhler, 1982), we found that taller women had taller partners, indicating assortative mating with respect to height ($r = .18$; $p < .0001$; Figure 7.1). For every cm increase in female height, partner height on average increased with 0.19 cm (i.e., the slope of the regression line; linear regression: B (± *SE*) = 0.19 ± 0.01; $p < .0001$; intercept (± *SE*) = 147.34 ± 1.54; $p < .0001$). Similarly, for every cm increase in male height, the female partner is predicted to increase with 0.17 cm (linear regression: B (± *SE*) = 0.17 ± 0.01; $p < .0001$). Courtiol et al. (2010b) provide estimates for their assortative preference functions (i.e., the slope of the preference function), and find that, for women, an increase of 0.77 cm per cm (95% *CI*

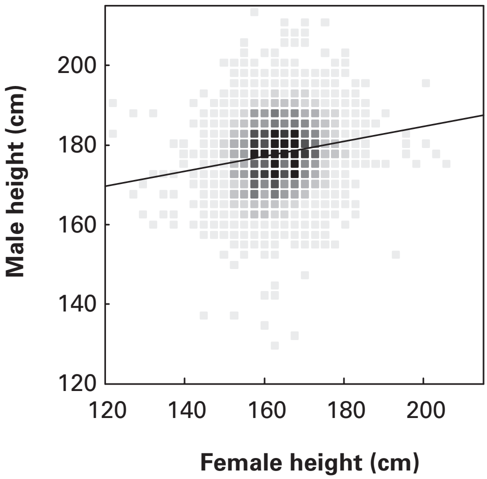

Figure 7.1: The positive correlation ($r = .18$) between female and male height. Lumination indicates frequency of occurrence (lightest color <20 couples; darkest color >200 couples).

= 0.51-1.03) own height is preferred, whereas for men an increase of 0.60 cm per cm (95% *CI* = 0.37-0.84) own height is preferred. Thus, while taking into account that the estimates for the preference functions were taken from a different populations with potential differences in average heights and variation in height, the slopes of the preference functions are substantially and significantly larger in magnitude than the slopes of assortative mating in our sample. This suggests that the assortative preference for height is only weakly realized in actual couples.

Comparing the actual occurrences of the PHD bins in the population (Figure 7.2a) to the expectation under random mating provided clear evidence for the male-taller norm being reflected in actual pairings (Table 7.1; Figure 7.2b). Adherence to the male-taller norm was evident in these data since men were taller than their partners in 92.5% of the couples, significantly more often than the expected 89.8% when mating was random with respect to height ($p < .0001$; Table 7.1). The male-taller norm was thus violated in 10.2% of the couples when mating was random, while in the original population this norm was violated in 7.5% of the couples, a 26% reduction (Table 7.1). Furthermore, bins in which the female was substantially taller than the male (> 5 cm) were much less likely to occur compared to random mating than bins in which the females was only slightly taller than the male (Table 7.1; Figure 7.2b), indicating that when the male-taller norm was violated it was most likely violated only slightly.

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The male-not-too-tall norm was also reflected in the actual pairings: bins in which the male was 25 or more cm taller than their partner occurred significantly less often in the original population (13.9%) than expected when mating was random with respect to height (15.7%; Table 7.1; Figure 7.2b). Thus, 15.7% of the couples was predicted to violate the male-not-too-tall norm when mating was random (with the assumption that the norm lies at a PHD of 25 cm), while in the original population this norm was violated in 13.9% of the couples, a reduction of 12%. The intermediate range of PHD, in which the male

Table 7.1: Occurrences of similar height partners (♂ =♀), male taller (♂ > ♀) and male shorter (♂ < ♀) compared to female, and Parental Height Differences (PHD; male height – female height) in bins of 5 centimetre in couples from the Millennium Cohort Study (MCS) and in the 10,000 samples of random mating.

	MCS	**10,000 Random samples**			
		Median	95% data range	Difference[a]	Rel. likel. pairing[b]
♂ < ♀	511	811	772-851	<.0001	0.63
♂ =♀	425	460	420-499	.0442	0.92
♂ > ♀	11566	11231	11185-11277	<.0001	1.03
PHD (cm)					
< -10	78	167	147-189	<.0001	0.47
-10 to -5	192	330	299-362	<.0001	0.58
-5 to -0	241	314	282-348	<.0001	0.78
0 to 5	1058	1090	1034-1146	.1372	0.97
5 to 10	2032	1807	1736-1880	<.0001	1.12
10 to 15	2663	2395	2314-2478	<.0001	1.11
15 to 20	2586	2464	2382-2549	.0021	1.05
20 to 25	1917	1969	1896-2044	.0820	0.97
25 to 30	1101	1175	1118-1232	.0056	0.94
30 to 35	461	527	488-567	.0002	0.88
> 35	173	262	238-287	.0001	0.66

[a] *p*-value for difference of occurrence of bin between original sample and 10,000 samples of random mating sample (see text).

[b] The Relative likelihood of pairing is the number of occurrences of a bin (second column) divided by the median occurrences of this bin (third column) in the random samples.

was 5 to 20 cm taller than their female partner, occurred more often in the original population compared to random mating (Table 7.1; Figure 7.2b). Similar to the male-taller norm, we found that when the male-not-too-tall norm was violated, it was most likely violated only slightly (Table 7.1; Figure 7.2b). Thus, a height difference of 25-30 cm was relatively more likely to occur than a height difference of 30-35 cm, but both were observed less often than expected by chance (Table 7.1; Figure 7.2b).

In conclusion, in line with reported partner height preferences (Courtiol et al., 2010b), we found evidence for assortative mating, the male-taller norm and the male-not-too-tall norm. However, the level of assortative mating (r = .18) is moderate, and the male-taller norm was violated in only 26% fewer pairs than expected by chance. Similarly, in 13.9% of the couples, the male-not-too-tall norm (i.e., > 25 cm height difference) was violated, only 12% less than expected by chance. Thus, these preference rules are only weakly translated into actual couple formation.

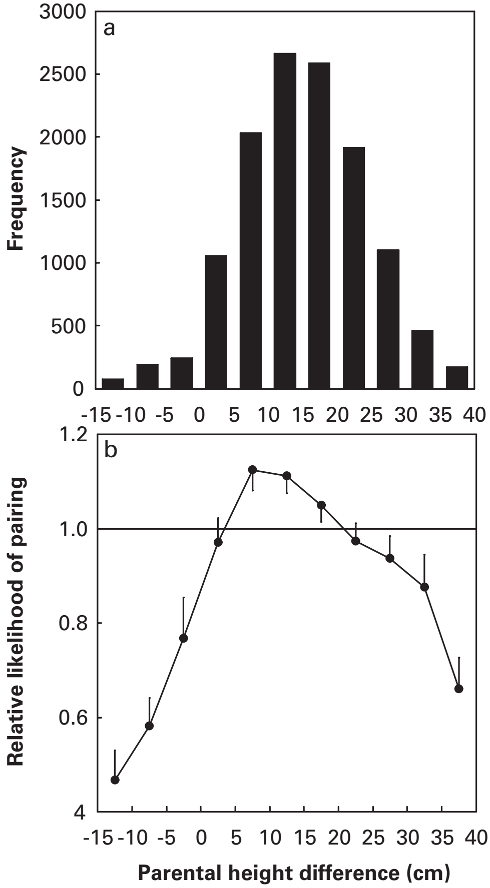

Figure 7.2: (a) The frequency distribution of parental height differences (PHD) in bins of 5 cm, and (b) the relative likelihood of pairing in these bins, which is the frequency of the bins in the original population divided by the median (± 97.5% upper/lower limit) occurrences of that bin in the 10,000 samples of random mating (see text). A number greater (*lower*) than one (solid horizontal line) means that the PHD bin is more (*less*) likely to occur in the original population than expected by random mating.

Preferred partner height differences are dependent on one's own height

On the basis of reported preferences for partner height differences (Pawlowski, 2003), we predicted that, when preferences are translated into actual mating patterns, taller compared to shorter men would have large partner height differences (i.e., the man being much taller than the woman). Similarly, we predicted that taller women compared to shorter women would have smaller partner height differences (i.e., the man being only slightly taller than the woman). We indeed found that taller men had greater partner height differences than shorter men, as indicated by a positive correlation between male height and PHD (r = .67). Similarly, we found that shorter women had greater parental height differences than taller women (r = -.61). However, this pattern is also observed when we randomly pair individuals. In 10,000 simulations of random pairing we find a median correlation of r = .73 (95% *CI* = .72 to .74) for the relationship between male height and PHD and a median of r = -.68 (95% *CI* = -.69 to -.68) for this relationship in women. Thus, purely random mating with respect to height generates a pattern in which taller men (and shorter women) have larger height differences than shorter men (and taller women).

To assess how well this preference rule is realized in actual couples, we again compared the estimates of our slopes from the relationship between own height and PHD to those reported in (Courtiol et al., 2010b). For every cm increase in female height, we showed that partner height on average increased with 0.19 cm (see above), which equals to a decrease of 0.81 cm in partner height differences. Similarly, for every cm increase in male height, we showed that partner height on average increased with 0.17 cm (see above), which equals to an increase of 0.84 cm in partner height differences. In contrast, the slopes for the preference function with respect to partner height differences for women is -0.23 cm per cm own height, and for men 0.4 cm (Courtiol et al., 2010b). Thus, the slopes from the preference function were substantially smaller in magnitude from the slopes observed in the couples. For women, on the one hand, we found that with increasing height the parental height differences *decreased more* than actually preferred. For men, on the other hand, we found that with increasing height the parental height differences *increased more* than preferred. In conclusion, and again taking into account that we have used estimates from a preference function of a different population, which can differ in both slope and intercept of the preference function from our population, we found that realized partner height differences are in line with preferences for partner height differences, although the difference in slopes suggest that the realized height differences are different from ideally preferred.

Non-mutual exclusive rules

Although we have treated assortative mating, the male-taller norm and the male-not-too-tall norm as distinct rules, they are not completely independent. For example, strict assortative mating (as in: always select a partner with a PHD that conforms to the average height difference between the sexes) would lead to strong adherence to both the male-taller and the male-not-too tall norm. Likewise, adhering to the male-taller norm will by itself generate assortative mating with respect to height. To examine the relationships between these norms on the one hand, and assortative mating on the other hand, we randomly coupled partners in 10,000 generated samples, while forcing either a male-taller norm ('as a female accept any partner taller than you') or a male-not-too-tall norm ('as a female accept any partner that is less than 25 cm taller than you'). We chose a value of 25 cm, because all bins above this value were significantly underrepresented in our population (Figure 7.1b). Because of the sequential nature of pairing in our algorithm, women that 'chose' last may not be able to find a partner that conforms to the norm, leaving them single. In the two times 10,000 samples (one for each norm), the percentage of unpaired individuals we observed ranged from 0 to 0.1%, which we considered low enough to ignore and we therefore excluded the unpaired individuals from our analyses. When forcing a male-taller norm, we observed a median correlation between partner heights of *r* = .34 (95% range: .33-.35), which was almost twice as high as the correlation of assortative mating in the population (*r* = .18). When a male-not-too-tall norm was enforced we observed an even higher median correlation between partner heights of *r* = .47 (95% range: .46-.48). Increasing the value of the norm (i.e., > 25 cm) lowers the median correlation, whereas decreasing this value increases it (results not reported). In conclusion, adhering to either a male-taller norm or a male-not-too-tall norm results in significant positive assortment for height, much stronger than observed in the actual population. This indicates that either norm in isolation would suffice to generate the pattern of assortative mating for height found in the population.

DISCUSSION

Preferences with respect to specific characteristics are an important ingredient of pair-formation, but multiple constraints (see Introduction) may prevent the realisation of such preferences when forming a pair. In this study, using simulations in which we randomized pairings, we examined whether previously documented preference rules for partner height were realised in actual couples. Firstly, we replicated the well-known finding that there is assortative mating with respect to height (Figure 7.1). We also replicated the finding of a male-taller norm (Figure 7.2), as men were more frequently taller than their partner than expected by chance. We extended this finding by showing that couples in which the man is much shorter than the woman are relatively less likely to occur than couples in which the man is only slightly shorter than the woman. Thus, when the male-taller norm is violated, it is mostly violated only slightly. A male-not-too-tall norm has previously been documented as a preference (Courtiol et al., 2010b; Fink et al., 2007; Pawlowski, 2003; Salska et al., 2008), and we show, to our best knowledge for the first time, that this norm is translated in actual pairing (Figure 7.2). Couples in which the male was more than 25 cm taller than the female partner, were rarer than expected by chance. Furthermore, similar to the male-taller norm, when the male-not-too-tall norm was violated, it was most likely violated only slightly (e.g., a partner height difference of 30 cm was relatively more likely to occur than a partner height difference of 35 cm, but both were less likely to occur than expected by chance). Lastly, in line with preferences for partner height differences, we found that shorter women and taller men were more likely to have greater partner height differences, whereas shorter men and taller women were more likely to have smaller partner height differences.

Although all known preference rules for height were qualitatively realised in actual couples, these effects were generally modest when compared to random mating. There may be several reasons for why an individual's preferred partner characteristics differs from actual partner characteristics (see introduction). Men and women, for instance, do not agree on their preferred partner height, as women prefer larger partner height differences than men. Mutual mate choice is thus likely to produce couples in which partner height preferences for either the male, or the female, or both are not optimally satisfied. Furthermore, height is but one of many characteristic valued in a mate (Buss et al., 1990), and the strength of the preference for height in comparison to other preferred traits determines final pairing with respect to height (Courtiol et al., 2010a). Even if choice is unconstrained, it is unlikely that a mate exists that satisfies all preferences.

The observed non-random pairing with respect to height need not be a consequence of mating preferences with respect to height (Courtiol et al., 2010a, b). It could also arise when assortment took place on a different characteristic but related to height (e.g., ethnicity and education). For instance, when there are differences in height between sub-populations, and individuals are more likely to pair within sub-populations than between sub-populations, than assortative mating for height could arise on the population level without playing a role in the pairing within sub-populations. Educational levels, for instance, may be considered as sub-populations. Height is positively related to education (Silventoinen et al., 2004), and assortative mating for education is widely observed (Oreffice & Quintana-Domeque, 2010). Thus, the correlation between partner heights might therefore at least in part be a consequence of the correlation between the educational attainments of the partners. It seems unlikely however, that these associations can fully explain the observed patterns. Firstly, the variation in height differences is much larger within a sub-population than between sub-populations (e.g., between 1-3 cm; Cavelaars et al., 2000). Therefore, that height differences above 25 cm occur less often than expected by chance (i.e., the male-not-too-tall norm), is unlikely to be due to sub-population effects, because height differences between sub-populations are much smaller (Cavelaars et al., 2000). Secondly, assortative pairing for other characteristics than height is unlikely to result in a male-taller norm. For these two reasons we believe it is unlikely that the non-random pairing with respect to height is a consequence assortative mating for other characteristics.

Due to the nature of our sample (i.e., parents) we excluded childless pairs, which may limit the generality of our conclusions because the proportion of childlessness is known to be related to height (**Chapters 9** and **10**). We do, however, believe that the inclusion of childless individuals would not change our results qualitatively for two reasons. Firstly, relationships between height and measures of reproductive success are weak, typically explaining less than 1% of the variance (**Chapters 9** and **10**). Thus the effect of being childless on the height distributions in our sample will be very small.

In conclusion, we have shown that all documented general preference patterns for partner height are on average at least qualitatively realised in actual pairings. We note however that compared to random mating the magnitude of these effects was generally low, suggesting that mating preferences were only partially realised. These results are in line with a recent study that showed that traits considered strongly related to attractiveness, such as height, are not necessarily strongly related to actual pairing (Courtiol et al., 2010a).

CHAPTER 8

Parental height differences predict the need for an emergency Caesarean section

Gert Stulp
Simon Verhulst
Thomas V. Pollet
Daniel Nettle
Abraham P. Buunk

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ABSTRACT

More than 30% of all pregnancies in the UK require some form of assistance at delivery, with one of the more severe forms of assistance being an emergency Caesarean section (ECS). Previously it has been shown that the likelihood of a delivery via ECS is positively associated with the birth weight and size of the newborn and negatively with maternal height. Paternal height affects skeletal growth and mass of the fetus, and thus might also affect pregnancy outcomes. We hypothesized that the effect of newborn birth weight on the risk of ECS would decrease with increasing maternal height. Similarly, we predicted that there would be an increase in ECS risk as a function of paternal height, but that this effect would be relative to maternal height (i.e., parental height differences). We used data from the Millennium Cohort Study: a large-scale survey (N = 18,819 births) with data on babies born and their parents from the United Kingdom surveyed 9 to 12-months after birth. We found that in primiparous women, both maternal height and parental height differences interacted with birth weight and predicted the likelihood of an ECS. When carrying a heavy newborn, the risk of ECS was more than doubled for short women (46.3%) compared to tall women (21.7%), in agreement with earlier findings. For women of average height carrying a heavy newborn while having a relatively short compared to tall partner reduced the risk by 6.7%. In conclusion, the size of the baby, the height of the mother and parental height differences affect the likelihood of an ECS in primiparous women.

INTRODUCTION

Obstructed labor, a failure to progress due to a mismatch between fetal size and the mother's pelvis (Neilson et al., 2003), accounts for 8% of maternal deaths worldwide. Only a minor part of these maternal deaths, i.e., the death of a woman during or shortly after pregnancy (WHO, 2005), occur in the developed world, but obstructed labor is nonetheless a common obstetrical problem. For example, in England more than 30% of all pregnancies require some form of assistance at delivery (NHS, 2005), of which an emergency Caesarean section (ECS) is the most common form (12.7% of all deliveries).

Short maternal stature is associated with adverse pregnancy outcomes, such as stillbirths (Bresler, 1962), low birth weight newborns (Camilleri, 1981), low APGAR scores (a quick assessment of health directly after delivery, based on Appearance, Pulse, Grimace, Activity and Respiration; Kappel et al., 1987), and perinatal mortality (Thomson & Billewicz, 1963). Despite having smaller neonates (Camilleri, 1981; Chan & Lao, 2009), shorter mothers are also at a higher risk for obstructed labor, resulting in an assisted delivery, in particular ECS (Kirchengast & Hartmann, 2007; WHO, 2005). Obstructed labor is related to the narrower pelvises of shorter women (Adadevoh et al., 1989; Awonuga et al., 2007; Baird, 1949), through which the head (i.e., cephalopelvic disproportion) or shoulders (Trevathan & Rosenberg, 2000; Sandmire & O'Halloin, 1988) of the baby is hindered.

Fetus size is also a well-known risk factor for obstructed labor. Heavier and larger newborns increase the likelihood of difficult deliveries (such as an ECS; Kirchengast & Hartmann, 2007; Nesbitt et al., 1998; Parrish et al., 1994; Read et al., 1994; Shy et al., 2000; Turner et al., 1990; Witter et al., 1995) or assisted deliveries resulting from shoulder dystocia (Langer et al., 1991; Nesbitt et al., 1998; Sandmire & O'Halloin, 1988). A short woman with a heavy and/or large newborn seems particularly at risk for obstructed labor (Brabin et al., 2002; James & Chiswick, 1979; Merchant et al., 2001; Shy et al., 2000). In contrast, for taller women, for whom the increased size of the newborn is less likely to lead to obstructed labor (Brabin et al., 2002; Merchant et al., 2001), a low birth weight newborn seems more predictive of adverse pregnancy outcomes (Shy et al., 2000). In the latter situation, operative deliveries are more a result of fetal distress, preeclampsia, or fetal malformations, rather than size-related obstetrical problems (Shy et al., 2000).

Although the effects of maternal height and birth weight on ECS risk are well established, it is currently unknown whether or not there is an effect of paternal height on the likelihood of having an ECS. Paternal height may influence pregnancy outcomes, as it has a positive effect on neonatal body size (Catalano et al., 1995; Knight et al., 2005). Whereas the height of the mother is especially associated with the size of the newborn through the adiposity of the fetus, the height of the father predicts skeletal growth and fat-free mass of the newborn (Catalano et al., 1995; Knight et al., 2005; Shields et al., 2006; Veena et al., 2004). Specifically, research has shown an effect of paternal height on neonatal fat-free mass, but not on fat mass (Catalano et al., 1995; Knight et al., 2005), on the length of the baby (Knight et al., 2005; Veena et al., 2004), on neonatal bone mineral content (Godfrey et al., 2001), on placental volume (Wills et al., 2010), and on head circumference (Knight et al., 2005; Veena et al., 2004). This is relevant because the skeletal structure of the baby is more predictive of birth problems than birth weight (Kirchengast & Hartmann, 2007; Merchant et al., 2001). For instance, head circumference is more important in predicting problems at delivery than birth weight (James & Chiswick, 1979; Merchant et al., 2001). The effect of paternal height on the structural size of the baby may therefore affect the risk for adverse pregnancy outcomes.

Much of the research on size and complications at birth in humans is mirrored by research on obstetric complications in animal research. In cattle, feto-pelvic disproportion, the disproportion between calf size and the size of the birth canal of the cow is the major cause of problems at birth (Bellows et al., 1982; Colburn et al., 1997; Mee, 2008). In line with the findings on humans, both the size of the cow as well as the size of the calf is a determinant of difficult delivery (Bellows et al., 1982; Colburn et al., 1997; Mee, 2008). Furthermore, the sire also affects this risk, as pairing cows to sires bred for heavy birth weight calves (versus low birth weight calves; Bellows et al., 1982; Colburn et al., 1997) and sires bred for meat (which are bigger, versus bred for dairy; Barkema et al., 1992) increases the risk of difficult delivery. Additionally, as found in humans, the skeletal size of the calf seems more important than the birth weight of the calf for the risk of difficult delivery (Colburn et al., 1997).

In this study, our aim was to test the hypothesis that in addition to maternal height and birth weight, paternal height also affects the risk of ECS. We use the Millennium Cohort Study (MCS) to test this hypothesis. In line with previous findings (Brabin et al., 2002; James & Chiswick, 1979; Merchant et al., 2001; Shy et al., 2000), we predict that maternal height would interact with birth weight, such that a relatively short woman with a heavy newborn would be most at risk. Furthermore, we extend earlier findings and hypothesize that paternal height also influences the risk for ECS, but that the effect of paternal height would be dependent on the height of the mother. We predict that with increasing parental height differences, the risk for ECS would increase.

MATERIAL AND METHODS

The Millennium Cohort Study (MCS) is a survey that gathered information from the parents of 18,819 babies born in the year 2000/2001 in the United Kingdom. Interviews were carried out when the babies were around 9–12 months. Detailed information on the pregnancy and birth was collected as well as anthropometric (maternal and paternal height, age, and birth weight), social and economic information (all self-reported) from the mother and where possible from the father. Self-reported measures of height have been shown to be very reliable in women of reproductive age (Brunner Huber, 2007). The sample was selected from a random sample of electoral wards, disproportionately stratified to ensure adequate representation of all four regions of the UK, areas with higher minority ethnic populations, and deprived areas. The overall response rate was 68% (Dex & Joshi, 2004). We used the first Wave of data from the MCS.

For the analyses presented here, we only included White parents for which height data were available who had their first, singleton child (of which the birth weight was available), leaving 4,365 cases. Only White parents were included in the analyses as ethnicity relates to maternal pelvic size, which might influence the risk of ECS (Chan & Lao, 2009). We chose to include only first births, because parity has been shown to be a strong determinant of ECS (Mocanu et al., 2000; Parrish et al., 1994). This was also evident in our sample, as primiparous women had an average risk of 27%, whereas parous women only had a risk of 9% for an ECS. In addition, obstetrical problems resulting from the large size of the newborn are largely confined to primiparous women (Mocanu et al., 2000; Parrish et al., 1994). For instance, when delivering a macrosomic baby (i.e., an extremely heavy newborn; >4.5 kg), 39.8% of primiparous women had a normal vaginal delivery, whereas 24.2% had an ECS (Mocanu et al., 2000). In contrast, 81% of multiparous women had a normal vaginal delivery when delivering a macrosomic baby, and only 5.7% had an ECS (Mocanu et al., 2000). Therefore, we restricted our sample to primiparous women.

We performed logistic regressions on our key dependent variable; whether the delivery was normal (i.e., vaginal without complications) or by ECS, leaving in total 3,165 cases. We excluded Caesarean delivery on request (*N* = 266), assisted breech delivery (*N* = 9), assisted forceps (*N* = 376), assisted vacuum extraction (*N* = 503), water births (*N* = 11) and other problems without specification (*N* = 5). However, including these cases (i.e., resulting in a dependent variable vaginal without complications versus any form of assistance) did not change our key results. To examine the effects of maternal and paternal height on birth weight, we performed a linear regression. All analyses were performed in SPSS 17.0.

Occurrence of the various pregnancy outcomes in the Millennium cohort was comparable to national statistics. In our entire sample the occurrence of a normal vaginal delivery and ECS were 68.5% and 12.2% respectively, whereas the national statistics for England for 2000 to 2001 are 66.6% and 12.7% respectively (NHS, 2005).

RESULTS

Descriptive statistics

Table 8.1 provides descriptive statistics of the entire cohort as well as our restricted sample of White couples with singleton, first births for which information on maternal and paternal height and birth weight of the newborn was

Table 8.1: Characteristics (*mean* ± *SD* or %) of the entire cohort and the sample used for our analyses.

	Entire sample		**Restricted sample**	
		N		*N*
Maternal height (cm)	163.5 ± 7.0	18,217	164.4 ± 6.9	3,165
Paternal height (cm)	177.8 ± 7.4	12,617	178.7 ± 7.4	3,165
PHD[a] (cm)	14.1 ± 9.2	12,617	14.3 ± 9.5	3,165
Birth weight (kg)	3.34 ± 0.6	18,484	3.34 ± 0.6	3,165
Delivery outcomes:				
Normal delivery	68.5%	12,666	73.1%	2,314
Emergency CS	12.2%	2,260	26.9%	851
Planned CS	9.4%	1,742		
Other forms of assistance[b]	9.9%	1,828		

The sample used for analyses was White parents (for which height data were available) who had their first, singleton child (of which birth weight was available) through a normal vaginal delivery or an emergency Caesarean section.

[a] PHD; Parental height differences (paternal minus maternal height).

[b] Other forms of assistance were: assisted breech delivery, assisted forceps, assisted vacuum extraction, water births and other problems without specification.

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Table 8.2: Linear regression parameter estimates of the effects of maternal height and paternal height on birth weight.

	B (± SE)	**β**
Intercept	$-1.48*10^{-1}$ ($\pm 3.23*10^{-1}$)	
Maternal height	$1.32*10^{-2}$ ($\pm 1.46*10^{-3}$)***	0.158
Paternal height	$7.41*10^{-3}$ ($\pm 1.37*10^{-3}$)***	0.095
N	3,165	

Maternal and paternal height in centimeters, birth weight in kilograms.
****p* <.0001.

available (see supplementary Tables S8.1 for more descriptive statistics on the sample used for our analyses). As expected, maternal and paternal height were positively correlated, indicating that taller women had taller partners (Pearson $r = 0.11$; $p < .0001$; $N = 3{,}165$). Furthermore, taller mothers and fathers had heavier newborns, as both maternal and paternal height positively and independently affected the birth weight of the newborn, with the maternal effect being 66% stronger than the paternal effect (Table 8.2).

Effects of birth weight

Logistic regression revealed a quadratic effect of birth weight on the likelihood of having an ECS: both low and high birth weight newborns had an increased risk for ECS compared to average weight newborns (Table 8.3a; Figure 8.1). The lowest risk of 21.8% (the minimum of the quadratic curve) was found at a birth weight of 3.1 kg, which was 0.2 kg below average.

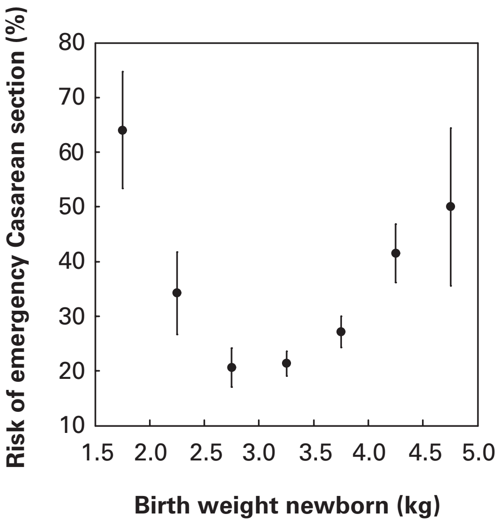

Figure 8.1: The effect of birth weight (*means* and 95% confidence intervals of raw data) on the risk of ECS. Birth weight in bins of 0.5 kg and bins lower than 2.5 and higher than 4.5 kg were pooled. The confidence interval was determined using the Agresti-Coull method (Agresti & Coull, 1998).

Effects of maternal height

Controlling for birth weight, maternal height had a negative effect on the occurrence of ECS. Shorter women were more likely to have had ECS compared to taller women, and this was a decelerating pattern as indicated by a significant quadratic effect of height (Table 8.3b; Figure 8.2a). Maternal height interacted with birth

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weight (Table 8.3c; Figure 8.2b), indicating that the risk resulting from the size of the newborn depended on the height of the mother. To illustrate these findings, Table 8.4a provides model predictions for the interaction between maternal height and birth weight. As expected, the highest risk for an ECS arises when short women carry heavy babies. Short women (below mean - 1 *SD*)

Table 8.3: Logistic regression parameter estimates (± *SE*) of the effects of maternal height, height^2, birth weight, birth weight^2, parental height differences and their interactions on the probability of an emergency Caesarean section.

Model	a	b	c	d	e	f
Intercept	4.46 (±6.60*10^{-1}) ***	54.25 (±15.03) ***	46.50 (± 15.21) **	44.16 (±15.40) **	114.75 (±29.03) ***	116.53 (± 29.01) ***
Birth weight	-3.75 (±4.14*10^{-1}) ***	-4.03 (±4.20*10^{-1}) ***	3.76 (±1.67) *	4.23 (±1.69) *	4.63 (±1.72) **	1.36 (±2.31)
Birth weight^2 [a]	6.14*10^{-1} (±6.47*10^{-2}) ***	6.76*10^{-1} (±6.61*10^{-2}) ***	7.30*10^{-1} (±6.87*10^{-2}) ***	7.25*10^{-1} (±7.03*10^{-2}) ***	7.32*10^{-1} (±7.06*10^{-2}) ***	7.10*10^{-1} (±7.14*10^{-2}) ***
Mat. Height		-5.51*10^{-1} (±1.83*10^{-1}) **	-6.15*10^{-1} (±1.84*10^{-1}) ***	-6.03*10^{-1} (±1.86*10^{-1}) ***	-1.45 (±3.50*10^{-1}) ***	-1.40 (±3.50*10^{-1}) ***
Mat. height^2 [a]		1.51*10^{-3} (±5.57*10^{-4}) **	2.21*10^{-3} (±5.75*10^{-4}) **	2.22*10^{-3} (±5.80*10^{-4}) **	4.76*10^{-3} (± 1.07*10^{-3}) ***	4.44*10^{-3} (± 1.08*10^{-3}) ***
Mat. height * Birth weight[a]			-4.95*10^{-1} (±1.03*10^{-2}) ***	-5.22*10^{-1} (±1.05*10^{-2}) ***	-5.49*10^{-1} (±1.07*10^{-2}) ***	-3.60*10^{-1} (±1.39*10^{-2}) **
PHD				5.21*10^{-3} (±5.70*10^{-3})	-2.21 (±5.61*10^{-1}) ***	-2.28 (±5.62*10^{-1}) ***
Height * PHD					2.61*10^{-2} (±6.89*10^{-3}) ***	2.64*10^{-2} (±6.90*10^{-3}) ***
Height^2 * PHD					-7.65*10^{-5} (±2.14*10^{-5}) ***	-7.85*10^{-5} (±2.14*10^{-5}) ***
PHD * Birth weight						2.07*10^{-2} (±9.79*10^{-3}) *
N	3,275	3,275	3,275	3,165	3,165	3,165

Height in centimeters, weight in kilograms. PHD is parental height differences (=paternal height – maternal height).

**p* <.05; ***p* <.01; ****p* <.001 (significance based on Wald test statistic with *df*=1).

[a] We also ran models which included all two-way interactions with maternal height^2 and birth weight^2. None of these terms were significant (all p >.12). We always included the underlying (interaction with the) linear term when including a(n interaction with a) squared term in the model.

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were more than twice as likely to need an ECS (46.3% versus 21.7%) than tall women (above mean +1 *SD*) when carrying a heavy newborn (above mean +1 *SD*). Generally, with increasing birth weight the risk of ECS also increased, but in tall women the risk of having ECS when carrying an average weight newborn was marginally lower compared to when having a light weight newborn (respectively 16.6% and 18.7%; Table 8.4a, see supplementary Table S8.2 and Figure S8.1 for model predictions across the entire range of female height).

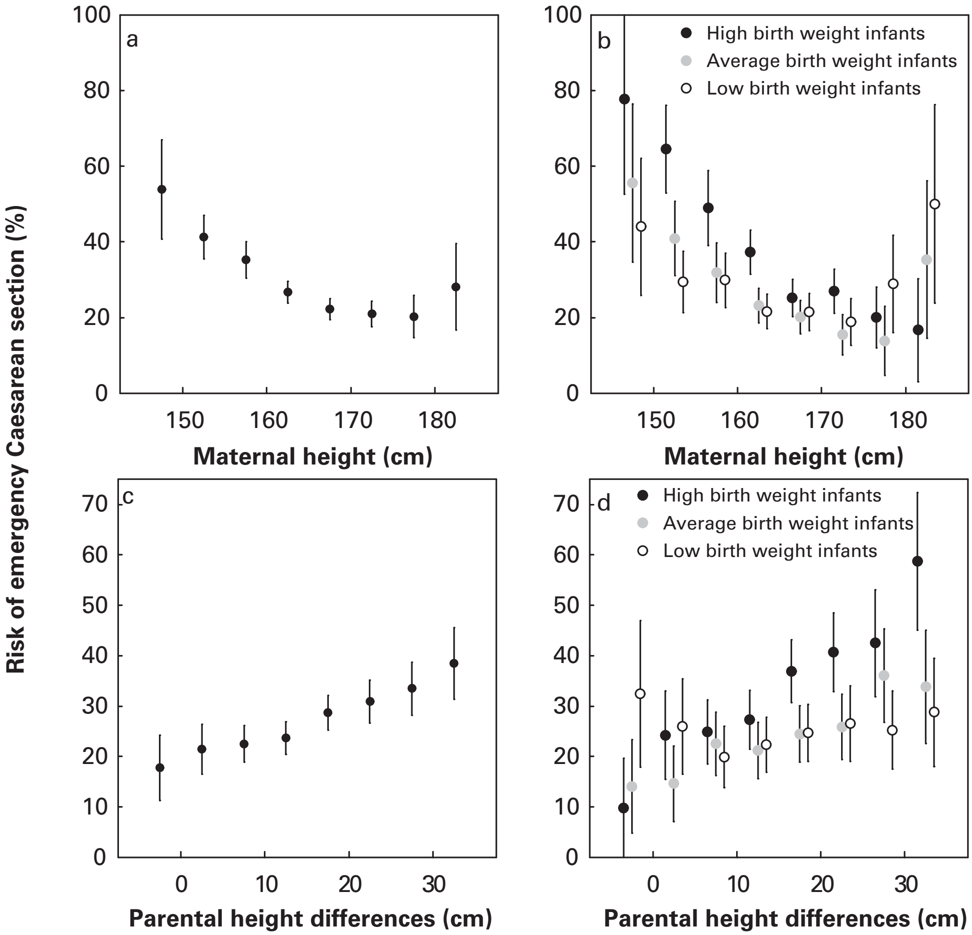

Figure 8.2: The effect of maternal height, parental height differences and birth weight on ECS risk. The effects (*means* and 95% confidence interval of raw data) are shown for (a) maternal height, (b) maternal height and birth weight (c) parental height differences and (d) parental height differences and birth weight. Height is divided into bins of 5 cm (bins lower than 145 for maternal height and -5 cm for parental height differences and higher than 180 and 35 cm were pooled) and birth weight was divided into tertiles. The confidence interval was determined using the Agresti-Coull method (Agresti & Coull, 1998).

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Effects of parental height differences

Having established that effects of previously identified risk factors (i.e., maternal height and birth weight) on ECS risk are present in the Millennium Cohort Study, we extended the analyses to examine the effects of parental height differences (PHD; paternal minus maternal height) on ECS risk. Logistic regression revealed that, when controlling for maternal height, birth weight and their interactions, there was no main effect of PHD on ECS risk (Table 8.3d). PHD did, however, affect the risk of ECS, as it significantly interacted with the squared effect of maternal height (Table 8.3e). With increasing PHD, the risk of an ECS increased (Figure 8.2c), but the effect of PHD was restricted to women of average height and tall women (Table 8.3e; see supplementary Table S8.2 and Figure S8.2 for model predictions of the effect of PHD in short, average height and tall women). There was no effect of PHD in short women, most likely because the risk for ECS in these women was already very high (i.e., a ceiling effect; supplementary Figure S8.2).

In addition to the interaction of PHD with maternal height, PHD also interacted with birth weight (Table 8.3f, Figure 8.2d). With increasing PHD the risk of ECS increased, but only when the mother was carrying heavy newborns or newborns of average weight but not when carrying relatively light newborns (Figure 8.2d). Table 8.4b provides model predictions for the effect of PHD and birth weight on the occurrence of an ECS for average height women (see supplementary Table S8.2 and Figure S8.3 for model predictions of the effect of PHD when mothers carry light, average weight and high birth weight newborns). Average height women were most at risk for an ECS (32.6%) when carrying a heavy newborn and having a relatively tall partner (large PHD; Table 8.4b). The lowest observed risk for average height women was 18.6%, when having small PHD and a baby of average weight.

Having a relatively tall compared to short partner increased the risk for ECS in average height women when carrying a heavy (from 25.9% to 32.6%) or average weighing newborn (from 18.6% to 20.9%; Table 8.4b). For average height women carrying light weight newborns, increasing PHD hardly changed the likelihood of an ECS (from 19.2% to 18.8%).

The effect of the interactions between maternal height, birth weight and PHD on the risk of ECS remained significant after controlling for maternal and paternal age, self-perceived health, socio-economic status, education, household income, sex of the baby, and gestation time (see supplementary Table S8.3 for parameter estimates). Newborns with low or high birth weight probably increase ECS risk for different reasons, but when excluding low birth

Table 8.4: Model predictions for the risk (%) of an emergency Caesarean section for (a) short, average height, and tall mothers and, (b)average height women with small, average, and large parental height differences for low, average and high birth weight newborns.

		Birth weight newborn				
a		Low	Average	High	*RR*[a]	*OR*[a]
Maternal height	Short	24.5	29.4	46.3	1.89	2.66
	Average	19.7	20.5	30.6	1.55	1.80
	Tall	18.7	16.6	21.7	1.16	1.20
	RR[b]	1.31	1.78	2.13		
	OR[b]	1.41	2.10	3.11		
b		Low	Average	High	*RR*[a]	*OR*[a]
Parental height differences	Small	19.2	18.6	25.9	1.35	1.47
	Average	18.9	19.7	29.1	1.54	1.76
	Large	18.8	20.9	32.6	1.73	2.09
	RR[c]	0.98	1.12	1.26		
	OR[c]	0.97	1.16	1.38		

Short and small refers to *mean* – *SD*, average refers to *mean*, and tall and large refers to *mean* + *SD*. Relative risks (*RR*) and Odds ratios (*OR*) are calculated based on the percentages.
[a] Comparison between high and low birth weight newborns.
[b] Comparison between short and tall mothers.
[c] Comparison between large and small parental height differences.

weight newborns (below 2.5 kg; Brabin et al., 2002; Parrish et al., 1994) from the analysis the results were very similar (supplementary Table S8.4). This suggests that the effects documented are not driven by newborns with very low birth weights.

Effects of maternal height and parental height differences independent of birth weight

Given that birth weight is obtained only after birth, and can hence not serve as practical predictor of ECS risk in a clinical setting, we performed additional analyses in which we excluded birth weight (and the interactions with it) to obtain clinical relevant estimates of the effects of maternal height and parental height differences. In line with the results above, logistic regressions revealed a significant squared effect of maternal height (Table 8.5a). A woman of average height has a 24.9% chance of having ECS at the birth of her first child. Women one standard deviation below average have a risk of 32.7% (an increase of 7.8%), whereas women one standard deviation above average 21.0% (a decrease of 3.9%). There is a 1.56 (32.6%/21.0%) greater probability of ECS for short compared to tall mothers.

Table 8.5: Logistic regression parameter estimates (± *SE*) of the effects of maternal height, height^2, parental height differences and their interactions on the probability of an emergency Caesarean section.

Model	a	b	c
Intercept	49.56 (±14.54)***	47.53 (±14.70)**	100.85 (±28.07)***
Height	$-5.73*10^{-1}$ ($\pm1.77*10^{-1}$)**	$-5.57*10^{-1}$ ($\pm1.79*10^{-1}$)**	-1.19 ($\pm3.34*10^{-1}$)***
Height^2	$1.61*10^{-3}$ ($\pm5.38*10^{-4}$)**	$1.58*10^{-3}$ ($\pm5.43*10^{-4}$)**	$3.48*10^{-3}$ ($\pm9.91*10^{-4}$)**
PHD		$7.54*10^{-3}$ ($\pm5.54*10^{-3}$)	-1.74 ($\pm5.55*10^{-1}$)**
Height * PHD			$2.09*10^{-2}$ ($\pm6.79*10^{-3}$)**
Height^2 * PHD			$-6.19*10^{-5}$ ($\pm2.10*10^{-5}$)**
N	3,275	3,165	3,165

Height in centimeters, weight in kilograms. PHD is parental height differences (=paternal height – maternal height).
**p <.01; ***p <.001 (significance based on Wald test statistic with df=1).

Similarly, the interaction between maternal height and parental height differences (PHD) remained significant when excluding birth weight from the analyses (Table 8.5c). A woman of average height with an average PHD, has a 24.7% chance of having undergone ECS. Having a PHD one standard deviation below average would reduce this risk to 22.6% and a PHD difference one standard deviation above average would increase the risk to 26.9% for a woman of average height (see supplementary Table S8.5 for model predictions of the effect of PHD for short, average height and tall women). There is a 1.19 (26.9%/22.6%) higher probability of ECS for women of average height with larger compared to smaller partner height differences. Thus, women with a relatively tall partner were more likely to have had an ECS, also when effects of newborn weight are ignored.

DISCUSSION

In this study, we have shown that the size of the newborn, the height of the mother and parental height differences all predict the risk of an emergency Caesarean section in primiparous women. We replicated the finding that both lower and higher birth weight newborns increase the risk of ECS (Parrish et al., 1994; Witter et al., 1995; Shy et al., 2000). Whereas the increased risk for heavy weight newborns is likely to be a consequence of size-related obstetrical problems, the increased risk for low birth weight newborns may be more a result of fetal distress, preeclampsia and fetal malformations rather than size-related obstetrical problems (Shy et al., 2000). In line with previous studies (Kirchengast & Hartmann, 2007; McGuinness & Trivedi, 1999), we also found that shorter women are at a higher risk for an ECS and that with increasing height the decrease in risk became progressively weaker. Maternal height interacted with birth weight: shorter women were especially susceptible to the effect of newborn weight on ECS risk (in line with earlier studies Brabin et al., 2002; James & Chiswick, 1979; Merchant et al., 2001; Shy et al., 2000). When carrying a heavy newborn (one *SD* above average weight), short women were more than twice as likely to need an ECS than tall women. For taller women, for which the overall risk of ECS is lowest, the increased size of the baby had little effect on ECS risk and a low birth weight newborn seems more predictive of an adverse pregnancy outcome for reasons discussed above.

Furthermore, to our best knowledge, we documented for the first time that the height of the father, specifically parental height differences, also affected the occurrence of ECS. The effect of the parental height differences on ECS was, however, dependent on the height of the mother and the birth weight of the newborn. Women with tall compared to short partners relative to their own height, had an increased ECS risk when carrying an average weight and heavy newborn, but not when carrying a light weight newborn, and this effect was most pronounced in average height and tall women. For shorter women, the overall ECS risk was highest, and parental height differences had little additional influence on ECS risk. Average height and tall women giving birth to a heavy newborn were at higher risk when their partners were relatively tall (respectively 32.6% and 25.0%) compared to short (respectively 25.9% and 19.4%). As the structural size of the baby has been shown to be more important in predicting problems at birth than birth weight (Merchant et al., 2001) and the height of the father predicts the structural size rather than the adiposity of the fetus (Catalano et al., 1995; Knight et al., 2005), having a tall partner relative to the height of the mother, will result in a relatively larger (in structural size) fetus for that mother, which in turn increases the risk for ECS. Particularly, having a high birth weight newborn with large PHD suggests that the structural size of this baby is large, which causes most problems for the delivery. The mismatch between the size of the fetus and the mother results in adverse pregnancy outcomes Brabin et al., 2002; James & Chiswick, 1979; Merchant et al., 2001; Shy et al., 2000). Unfortunately, in our sample no data were available on the structural size (e.g., head circumference, length) of the newborn, and we thus have no finer grained measures to further substantiate our results.

The finding that differences in height between father and mother influence pregnancy outcomes partly explains the increased risk of assisted deliveries for shorter women. Shorter women have partners who are on average much taller than themselves and with increasing female height, the difference in height between partners decreases strongly. Thus, the higher risk for adverse pregnancy outcomes for shorter women is partly due to the fact that they are more likely to have a partner much taller than themselves.

The finding that parental height differences predict the need for ECS is also consistent with a study investigating cross-national variation in height differences between the sexes (Guegan et al., 2000). This study found that "maternal death caused by deliveries and complications of pregnancy (a variable known to be size related) could be a key determinant explaining variation in sexual stature dimorphism [sex differences in height] across populations" (Guegan et al., 2000; p. 2529). According to these authors, tall mothers would more likely survive childbirth, which would result in females getting taller relative to males, thereby decreasing the average height differences between the sexes. Based on our data, the reverse association is also likely: the cross-national variation in height differences between the sexes might explain the variation in maternal deaths caused by deliveries and complications during pregnancy. When average height differences between the sexes are large, fetuses would be relatively large for the mothers carrying them, resulting in more complications at birth.

A potential limitation of our study is the nature of the sample, in particular the oversampling of individuals from deprived areas. However, controlling for socio-economic status with several indicators (household income, National Vocational Qualifications (NVQ levels) / National Statistics Socio-economic Classifications (NS-SEC)) did not change our results, which suggests that the effects of maternal and parental height differences on the risk of ECS are independent of socioeconomic status. Another limitation is that the data are self-reported, through interviews approximately 9 months after birth. However, national health statistics regarding rates of assisted deliveries for England in 2000–2001 are comparable to the rates in our sample. In addition, it seems unlikely that there is a systematic error in reporting problems at birth associated with height: there is little reason to assume that women of a certain height or women with a partner of a certain height would be more likely to over- or underreport complications such as an ECS.

The incidence of ECS may be an imperfect index of obstructed labor, as a physician bias related to maternal height might have occurred (Van Roosmalen & Brand, 1992). The need for assistance at delivery may be overrated for short women, due to physicians' expectations of difficulty at delivery. This potential bias might have influenced our results for the risk of ECS for short women, but it seems an unlikely explanation for the effects of the parental height differences on ECS risk as this effect is also present for women of average height and for tall women.

From a functional perspective, documented preferences for partner height among men and women (e.g., Courtiol et al., 2010b; Pawlowski, 2003) are consistent with our finding that parental height differences predict the likelihood of ECS. Whereas women prefer men taller, but not too tall, men prefer women shorter but not too short. Our results suggest that these mate preferences could be adaptive as a male partner too tall or a female partner too short will both result in an increased risk for obstructed labor.

ACKNOWLEDGEMENTS

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SUPPLEMENTARY MATERIAL

Table S8.1: Characteristics (*mean* ± *SD* or %) of the sample used for our analyses.

	Mean ± SD/%	**Min**	**Max**	**N**
Maternal height (cm)	164.4 ± 6.9	121.9	203.2	3,165
Paternal height (cm)	178.7 ± 7.4	132.1	213.36	3,165
PHD[a] (cm)	14.3 ± 9.5	-35.6	68.6	3,165
Birth weight (kg)	3.34 ± 0.6	0.71	6.78	3,165
Delivery outcomes				3,165
Normal delivery	73.1%			2,314
Emergency CS	26.9%			851
Age mother (yrs)	27.1 ± 5.6	13	48	3,165
Age father (yrs)	30.1 ± 6.3	15	57	3,160
Household income				3,008
0-3,100 £	1.0%			30
3,100-10,400 £	11.4%			344
10,400-20,800 £	34.6%			1042
20,800-31,200 £	26.5%			797
31,200-52,000 £	19.1%			575
> 52,000 £	7.3%			220
Health mother[b]				3,165
Excellent	36.7%			1,161
Good	52.0%			1,645
Fair	9.6%			305
Poor	1.7%			54
Health father[b]				3,165
Excellent	36.1%			1,141
Good	51.6%			1,633
Fair	10.6%			334
Poor	1.8%			57
NS-SEC mother[c]				3,069
Managerial and professional occupations	39.3%			1,205
Intermediate occupations	22.5%			689
Small employers and own account workers	3.2%			99
Lower supervisory and technical occupations	5.3%			162
(Semi-)routine occupations / No work	29.8%			914
NS-SEC father[c]				3,115
Managerial and professional occupations	41.8%			1,302
Intermediate occupations	5.8%			180
Small employers and own account workers	10.3%			322
Lower supervisory and technical occupations	16.4%			512
(Semi-)routine occupations / No work	25.7%			799

Table S8.1: continued.

	Mean ± SD/%	Min	Max	N
Education mother[d]				3,128
None of these qualifications	5.6%			174
NVQ Level 1	7.0%			219
NVQ Level 2	30.1%			942
NVQ Level 3	17.9%			560
NVQ Level 4	35.1%			1,097
NVQ Level 5	4.3%			136
Education father[d]				3,115
None of these qualifications	9.3%			234
NVQ Level 1	7.5%			955
NVQ Level 2	30.7%			553
NVQ Level 3	17.8%			935
NVQ Level 4	30.0%			147
NVQ Level 5	4.7%			
Gestation time (days)	278 ± 14.7	170	296	3,165
Sex baby				3,165
Male	52.2%			1,651
Female	47.8%			1,514

The sample used for analyses was White parents (for which height data were available) who had their first, singleton child (of which birth weight was available) through a normal vaginal delivery or an ECS.
[a] PHD; Parental Height Differences (paternal minus maternal height).
[b] Self-perceived health.
[c] The National Statistics Socio-economic Classification. The reference category was 'managerial and professional occupations' (http://www.ons.gov.uk/about-statistics/classifications/current/ns-sec/index.html).
[d] National Vocational Qualifications. (http://www.direct.gov.uk/en/EducationAndLearning/QualificationsExplained/DG_10039029).

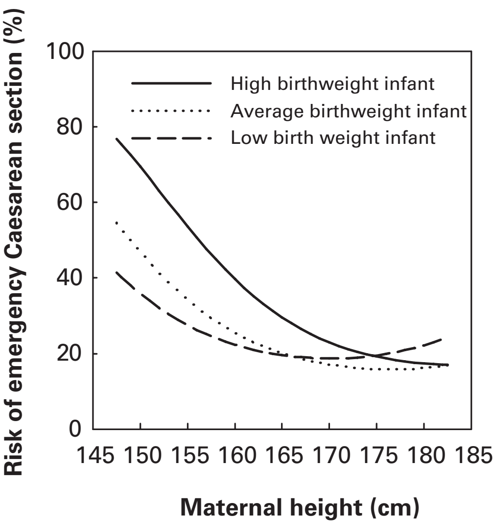

Figure S8.1: Model predictions for the effect of maternal height on the risk (%) of an emergency Caesarean section for mothers carrying low (*mean – SD*), average (*mean*) and high (*mean + SD*) birth weight newborns.

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Table S8.2: Model predictions for the risk (%) of an emergency Caesarean section for low (*mean – SD*), average (*mean*) and high (*mean + SD*) birth weight newborns having (a) short (*mean – SD*), average height (*mean*), and tall (*mean + SD*) mothers and (b) small (*mean – SD*), average (*mean*), and large (*mean + SD*) parental height differences for short, average height (c) and tall mothers (d).

		Birth weight newborn				
a)		Low	Average	High	*RR*[a]	*OR*[a]
Maternal height	Short	24.5	29.4	46.3	1.89	2.65
	Average	19.7	20.5	30.6	1.55	1.79
	Tall	18.7	16.6	21.7	1.16	1.21
	RR[b]	1.31	1.78	2.13		
	OR[b]	1.41	2.10	3.11		
b) Short women						
Parental height differences	Small	27.4	29.5	42.6	1.55	1.96
	Average	26.0	29.8	45.1	1.73	2.34
	Large	24.7	30.1	47.7	1.93	2.78
	RR[c]	0.90	1.02	1.12		
	OR[c]	0.87	1.03	1.23		
c) Average height women						
Parental height differences	Small	19.2	18.6	25.9	1.35	1.47
	Average	18.9	19.7	29.1	1.53	1.75
	Large	18.8	20.9	32.6	1.73	2.09
	RR[c]	0.98	1.12	1.25		
	OR[c]	0.97	1.16	1.38		
d) Tall women						
Parental height differences	Small	17.9	15.3	19.4	1.09	1.11
	Average	17.7	16.3	22.1	1.25	1.32
	Large	17.5	17.3	25.0	1.43	1.57
	RR[c]	0.98	1.13	1.29		
	OR[c]	0.97	1.16	1.38		

Relative risks (*RR*) and Odds ratios (*OR*) are calculated based on the percentages.
[a] Comparison between high and low birth weight newborns.
[b] Comparison between short and tall mothers.
[c] Comparison between high and low parental height differences.

Table S8.3: Logistic regression parameter estimates (± *SE*) of the effects of maternal height, height^2, parental height differences (PHD), birth weight, their interactions, and control variables on the probability of an emergency Caesarean section.

	Maternal height	**PHD**
Intercept	55.13 ± 16.75**	121.60 ± 33.14***
Birth weight (kg)	3.77 (± 1.83)*	$3.95*10^{-1}$ (± $2.68*10^{-1}$)
Birth weight^2	$7.80*10^{-1}$ (± $8.34*10^{-2}$)***	$7.80*10^{-1}$ (± $8.34*10^{-2}$)***
Height (cm)	$-7.55*10^{-1}$ (± $2.01*10^{-1}$)***	-1.48 (± $3.99*10^{-1}$)***
Height^2	$2.65*10^{-3}$ (± $6.25*10^{-4}$)***	$4.63*10^{-3}$ (± $1.22*10^{-4}$)***
Height * Birth Weight	$-5.16*10^{-2}$ (± $1.12*10^{-2}$)***	$-3.24*10^{-2}$ (± $1.61*10^{-2}$)*
PHD (cm)		-2.51 (± $5.90*10^{-1}$)***
Height * PHD		$2.93*10^{-2}$ (± $7.21*10^{-3}$)***
Height^2 * PHD		$-8.83*10^{-5}$ (± $2.24*10^{-5}$)***
PHD * Birth weight		$4.88*10^{-2}$ (± $8.86*10^{-3}$)***
Age mother (yrs)	$1.02*10^{-1}$ (± $1.01*10^{-2}$)***	$1.08*10^{-1}$ (± $1.29*10^{-2}$)***
Age father (yrs)		$1.49*10^{-3}$ (± $1.04*10^{-2}$)
Household income[b]		
3,100-10,400 £	$-5.32*10^{-1}$ (± $5.08*10^{-1}$)	$-4.72*10^{-1}$ (± $5.60*10^{-1}$)
10,400-20,800 £	$-4.70*10^{-1}$ (± $4.86*10^{-1}$)	$-4.46*10^{-1}$ (± $5.37*10^{-1}$)
20,800-31,200 £	$-4.49*10^{-1}$ (± $4.90*10^{-1}$)	$-4.75*10^{-1}$ (± $5.41*10^{-1}$)
31,200-52,000 £	$-5.05*10^{-1}$ (± $4.95*10^{-1}$)	$-4.85*10^{-1}$ (± $5.46*10^{-1}$)
> 52,000 £	$-3.07*10^{-1}$ (± $4.10*10^{-1}$)	$-2.79*10^{-1}$ (± $5.62*10^{-1}$)
Health mother[c]		
Good	$1.79*10^{-1}$ (± $9.71*10^{-2}$)	$1.77*10^{-1}$ (± $1.02*10^{-1}$)
Fair	$3.37*10^{-1}$ (± $1.61*10^{-1}$)*	$3.77*10^{-1}$ (± $1.67*10^{-1}$)*
Poor	$5.06*10^{-1}$ (± $3.43*10^{-1}$)	$4.51*10^{-1}$ (± $3.59*10^{-1}$)
Health father[c]		
Good		$9.66*10^{-3}$ (± $1.01*10^{-1}$)
Fair		$-1.19*10^{-2}$ (± $1.70*10^{-1}$)
Poor		$-8.80*10^{-1}$ (± $4.78*10^{-1}$)
NS-SEC mother[d]		
Intermediate occupations	$1.42*10^{-1}$ (± $1.26*10^{-1}$)	$1.96*10^{-1}$ (± $1.31*10^{-1}$)
Small employers / own account workers	$-1.03*10^{-1}$ (± $2.63*10^{-1}$)	$-3.10*10^{-3}$ (± $2.74*10^{-1}$)
Lower supervisory / technical occupations	$3.06*10^{-1}$ (± $2.23*10^{-1}$)	$1.12*10^{-1}$ (± $2.30*10^{-1}$)
(Semi-)routine occupations / No work	$6.52*10^{-2}$ (± $1.43*10^{-1}$)	$1.20*10^{-1}$ (± $1.49*10^{-1}$)
NS-SEC father[d]		
Intermediate occupations		$-1.59*10^{-1}$ (± $2.13*10^{-1}$)
Small employers / own account workers		$-3.32*10^{-2}$ (± $1.79*10^{-1}$)
Lower supervisory / technical occupations		$-3.86*10^{-2}$ (± $1.49*10^{-1}$)
(Semi-)routine occupations / No work		$3.45*10^{-2}$ (± $1.48*10^{-1}$)
Education mother[e]		

Table S8.3: continued.

	Maternal height	PHD
NVQ Level 1	$-6.76*10^{-2}$ (± $2.93*10^{-1}$)	$-2.53*10^{-1}$ (± $3.14*10^{-1}$)
NVQ Level 2	$3.08*10^{-1}$ (± $2.47*10^{-1}$)	$-3.10*10^{-2}$ (± $2.63*10^{-1}$)
NVQ Level 3	$7.78*10^{-3}$ (± $2.58*10^{-1}$)	$-9.18*10^{-3}$ (± $2.75*10^{-1}$)
NVQ Level 4	$-6.26*10^{-3}$ (± $2.56*10^{-1}$)	$-3.59*10^{-2}$ (± $2.74*10^{-1}$)
NVQ Level 5	$-6.38*10^{-2}$ (± $3.20*10^{-1}$)	$-4.59*10^{-2}$ (± $3.48*10^{-1}$)
Education father[e]		
NVQ Level 1		$3.64*10^{-3}$ (± $2.63*10^{-1}$)
NVQ Level 2		$2.97*10^{-1}$ (± $2.01*10^{-1}$)
NVQ Level 3		$3.62*10^{-1}$ (± $2.17*10^{-1}$)
NVQ Level 4		$7.46*10^{-2}$ (± $2.21*10^{-1}$)
NVQ Level 5		$1.43*10^{-1}$ (± $2.98*10^{-1}$)
Gestation time (days)	$1.68*10^{-3}$ (± $4.51*10^{-3}$)	$1.74*10^{-3}$ (± $4.69*10^{-3}$)
Sex baby[f]	$-1.32*10^{-1}$ (± $8.97*10^{-2}$)	$-1.50*10^{-1}$ (± $9.32*10^{-2}$)
N	2,972	2,817

*p <.05, **p <.01, ***p <.001 (significance based on *Wald* test statistic with df=1).
[a] This interaction was not significant (p >.72). [b] The reference category was income bin 0-3,100 £.
[c] Self-perceived health. The reference category was 'Excellent'. [d] The National Statistics Socio-economic Classification. The reference category was 'managerial and professional occupations' (http://www.ons.gov.uk/about-statistics/classifications/current/ns-sec/index.html). [e] National Vocational Qualifications. The reference category was 'none of these qualifications' (http://www.direct.gov.uk/en/EducationAndLearning/QualificationsExplained/DG_10039029). [f] The reference category was male.

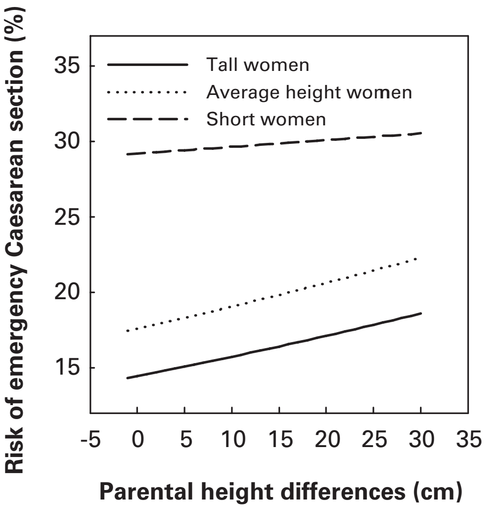

Figure S8.2: Model predictions for the effect of parental height differences on the risk (%) of an emergency Caesarean section for short (*mean– SD*), average (*mean*) and tall (*mean + SD*) mothers carrying an average birth weight newborn.

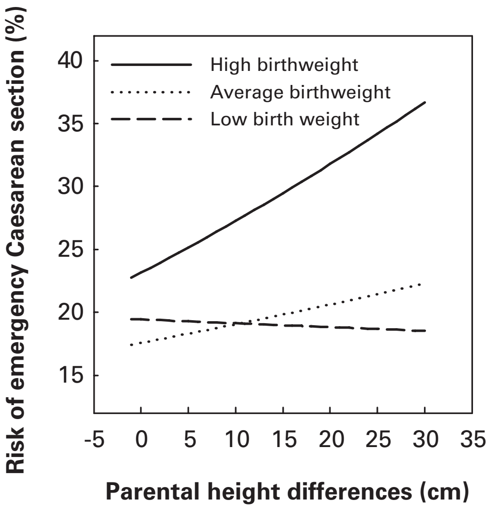

Figure S8.3: Model predictions for the effect of parental height differences on the risk (%) of an emergency Caesarean section for average height mothers carrying low (*mean – SD*), average (*mean*) and high (*mean + SD*) birth weight newborns.

Table S8.4: Logistic regression parameter estimates (± *SE*) of the effects of maternal height (cm), height^2, birth weight (kg), birth weight^2, parental height differences (cm) and their interactions, on the probability of an emergency Caesarean section when light birth weight newborns (< 2.5 kg) are excluded.

	Maternal height	**PHD**
Intercept	46.51 (± 17.22)**	123.12 (± 30.34)***
Birth weight	7.93 (± 2.34)***	4.67 (±3.16)
Birth weight^2	$4.84*10^{-1}$ (± $1.65*10^{-1}$)**	$4.34*10^{-1}$ (± $1.71*10^{-2}$)*
Maternal height	$-7.08*10^{-1}$ (± $2.04*10^{-1}$)***	-1.56 (± $3.66*10^{-1}$)***
Maternal height^2	$2.64*10^{-3}$ (± $6.36*10^{-4}$)***	$5.00*10^{-3}$ (± $1.14*10^{-3}$)***
Maternal height * Birth weight	$-6.33*10^{-2}$ (± $1.45*10^{-2}$)***	$-4.43*10^{-1}$ (± $1.93*10^{-2}$)*
Parental height differences (PHD)		-2.63 (±$5.82*10^{-1}$) ***
Height * PHD		$3.05*10^{-2}$ (± $7.12*10^{-3}$)***
Height^2 * PHD		$-9.14*10^{-5}$ (± $2.21*10^{-5}$)***
PHD * Birth weight		$3.03*10^{-2}$ (±$1.38*10^{-2}$)*
N	3,048	2,944

PHD is parental height differences (=paternal height – maternal height).
*p <.05; **p <.01; ***p <.001 (significance based on *Wald* test statistic with df=1).

8

CHAPTER 9

The effect of female height on reproductive success is negative in Western populations, but more variable in non-Western populations

Gert Stulp
Simon Verhulst
Thomas V. Pollet
Abraham P. Buunk

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ABSTRACT

In this article we examine the association between female height and reproductive success in a US sample and present a review of previous studies on this association. We also outline possible biological explanations for our findings.We used data from a long-term study of 5,326 female Wisconsin high school graduates to examine the association between female height and reproductive success. Twenty-one samples on this association were covered by our literature review. Shorter women had more children surviving to age 18 than taller women, despite increased child mortality in shorter women. Taller women had a higher age at first birth and age at first marriage and reached a higher social status, but the negative effect of height on reproductive success persisted after controlling for these variables. However, while these effects were quite consistent in Western populations, they were not consistently present in non-Western populations. Our review also indicated that child mortality was almost universally higher among shorter women. We conclude that shorter women have a higher number of live births but that final reproductive success depends on the positive effect of height on child survival.

INTRODUCTION

Female height may in various ways be associated with reproductive success. First, shorter women may have more reproductive success than taller women because of the trade-off between investing energy in somatic growth or reproduction (Stearns, 1992). This trade-off is evidenced by the fact that women who have menarche at an earlier age typically reach a shorter adult height than women who have menarche at a later age (McIntyre and Kacerosky, 2011; Okasha et al., 2001). Similarly, women who have their first child at an earlier age are shorter than women who give birth at a later age (Helle, 2008). Thus, taller women seem to become fertile at a later age than shorter women and women who invest energy in reproduction at an early age (e.g., early menarche or child birth) reach a shorter adult height, which may result in a negative relationship between female height and reproductive success. In addition, the positive relationship between height and social status could translate into decreased reproductive success for taller women, and thus into more reproductive success for shorter women. In Western societies, education and income reflect social status and height is positively correlated with education (Cavelaars et al., 2000; Silventoinen et al., 1999), as well as with income (Judge and Cable, 2004). Both education and income are negatively associated with female reproductive success: relatively highly educated women and women with high incomes have less offspring (reviewed in Hopcroft, 2006; Nettle and Pollet, 2008).

The higher potential reproductive success among shorter women, however, may be counteracted by the negative relationship between maternal height and child morbidity and mortality. Shorter women are at a higher risk for complications during pregnancy, such as stillbirths (Bresler, 1962), failure to progress in labor (Sheiner et al., 2005), and the need for Caesarean sections (Kirchengast and Hartmann, 2007; **Chapter 8**). The adverse effect of short height is not limited to complications during pregnancy, but extends to the health of the newborn baby as shorter women are more likely to give birth to infants with a relatively low birth weight (Camilleri, 1981) and with relatively low Apgar scores (a health assessment score directly after delivery; Camilleri, 1981; Casey et al., 2001). Both measures are predictors of child morbidity and mortality (Casey et al., 2001; McIntire et al., 1999). Although little is known about the relationship between height and child mortality in developed countries (although see Bresler, 1962), maternal height is almost universally negatively related to child mortality in developing countries (Monden and Smits, 2009) and in low- to middle-income countries (Özaltin et al., 2010).

To complicate matters further, the increased ability to attract mates by average height women compared to shorter and taller women may translate into decreased reproductive success for both shorter and taller women. Indeed, a recent review of the attractiveness of female height suggests that men prefer partners shorter than themselves, but do not have a general preference for shortness (Courtiol et al., 2010b). These preferences result in women of average height being considered more attractive than either short or tall women. Consistent with this pattern is the curvilinear association between height and jealousy, with average height women being least jealous of attractive rivals (Buunk et al., 2008), and least competitive toward other women (Buunk et al., 2009). Therefore, short as well as tall women may have more difficulty in attracting a partner.

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

MATERIAL AND METHODS

Wisconsin longitudinal study

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

The key variables for this study were height, education, income, number of children ever born, number of children surviving to reproductive age (18 years), age at the birth of the first child, whether the respondent was ever being married and age at first marriage. Only biological children were included in the offspring counts. We combined the data from separate time points to maximize sample size. Thus, when data for a certain variable were missing at one time point, we used data from a different time point for that variable, combining the data into one new variable. For height, education, the number of children ever born and surviving to reproductive age, age at the birth of the first child, and ever being married we used data from 1992 and 2004. In 1992, all women were at least 52-years old, and were thus unlikely to conceive more children. Education was measured as 'how many years of education does the graduate have based on his or her highest degree?' (ranging from high school degree = 12 years of education to postdoctoral education = 21 years of education). We combined data from 1975 and 1992 for age at first marriage. For income we used the 1974 data only (total earnings in US$ last year), because inflation and career development make income more difficult to compare across decades.Statistical analyses were performed using SPSS 16. To examine the associations between height, education and income, we used Pearson correlations. For the effects of height on different measures of reproductive success (number of children ever born, number of children surviving to 18 years, proportion of children surviving until reproductive age, age at the birth of the first child, ever being married, and age at first marriage) we used generalized linear models with the appropriate error distribution (normal, Poisson, or binomial). To test for possible curvilinear effects of height, we included a squared term of height in all models. All tests were two-tailed and the significance level was set to $\alpha = .05$.

Previous research on the relationship between female height and reproductive success

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

For each study, we determined the power to detect the effect of height on number of children, based on the *N* of the study, a *p* level of.05, and a given effect size using G*Power 3, version 3.1.2 (Faul et al., 2007). G*Power is a flexible statistical power analyses program for statistical tests commonly used in social and behavioral research. The effect size used in the power analysis was determined by performing a linear regression on our data regressing number of children on height. Linear regression was used to determine the effect size rather than the Poisson regression applied in the present study, to facilitate comparison with the few studies that performed a regression analysis.

Table 9.1: Characteristics of the women from the Wisconsin Longitudinal Study for whom height was available.

	Mean ± *SD*	Minimum	Maximum	*N*
Height (cm)	164.18 ± 6.26	139.70	198.12	4,059
Education (years)	13.26 ± 1.97	21	21	4,059
Annual income in '74 ($)	17037 ± 18457	0	300,000	3,873
Number of children ever born	2.78 ± 1.65	0	10	4,059
Number of children surviving to 18	2.72 ± 1.63	0	10	4,059
Age at first marriage	21.70 ± 3.62	16	54	3,878
Age at first birth	23.17 ± 3.61	17	47	3,232

RESULTS

Wisconsin longitudinal study

For 4,059 out of 5,326 women, height was available. The descriptive statistics for these women and the sample size available for all variables (and hence analyses) are summarized in Table 9.1. Poisson regression revealed that height had a negative effect on number of children ever born (Table 9.2; Figure 9.1a). Thus, shorter women had more live births than taller women. In contrast, logistic regressions revealed that there was a positive linear effect of maternal height (in cm) on the proportion of children surviving until 18 years (intercept (± *SE*) = -0. 0751 (± 1.80), $p = .967$; B = 0.0244 (± 0.0110), $p = .027$; $N = 3{,}613$). To illustrate this finding we calculated that women one standard deviation below average (157.92 cm) had 97.8% surviving offspring whereas for women of average height (164.18 cm) this was 98.1%. Thus, the relationships between height and child survival and height and number of ever born children are opposite, with the effect of height being positive for child survival but negative for children ever born.

The effect of female height on child survival was small and hence the effect of height on number of children surviving to reproductive age (18 years) was still negative (Table 9.2; Figure 9.1a). Yet, as expected be-

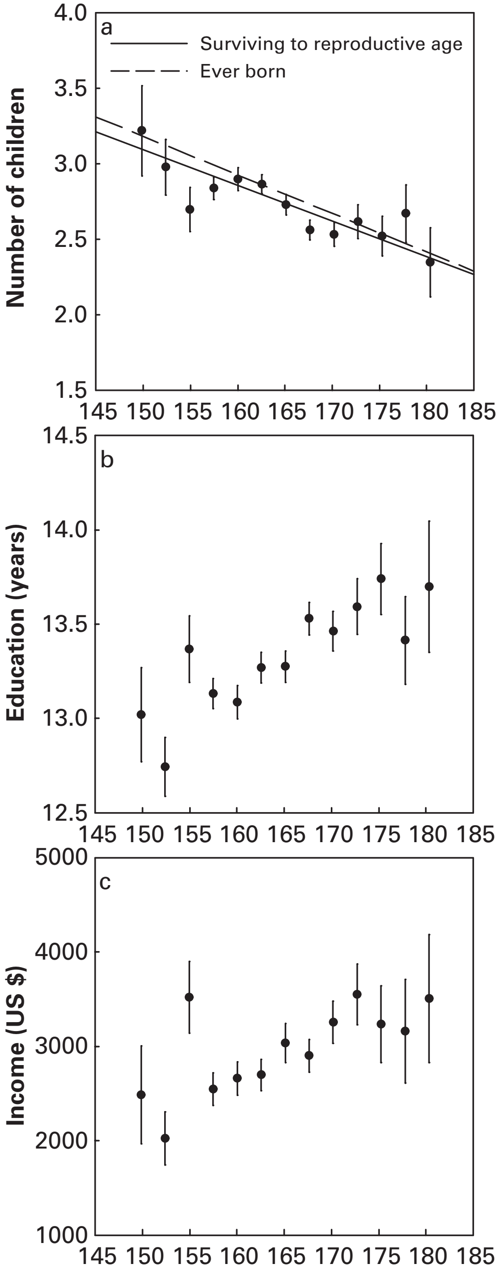

Figure 9.1: The effect of height on (a) the number of children surviving to 18 (with Poisson regression lines), (b) the number of years of education, and (c) annual income (US $) in 1974 binned by inch of height (*mean* ± *SE*). Given that height was measured in inches, we binned data using this unit of measurement (which was converted into cm). Bins below 59" and above 71" were collapsed.

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cause of the positive association between height and child survival the effect of height on number of surviving children was smaller in magnitude than the effect of height on number of children ever born (Figure 9.1a). In industrialized societies, infant and child mortalities are low. In this study, 192 out of 3,613 (5.3%) mothers reported that at least one child had deceased before the age of 18. Hence, there was a strong correlation between number of children ever born and number of children surviving to the age of eighteen years old (r = .98; $p < .0001$; N = 3,613).

Height correlated positively with the age of the mother at the birth of her first child (log-transformed for normality; r = .09; $p < .0001$; N = 3,232), indicating that taller women had their first child at a later age. As women rarely grow in stature after the birth of their first child (Allal et al., 2004), shorter women are perhaps shorter because they have their first child at a younger age, and the negative association between height and reproductive success might be a result of this trade-off between growth and reproduction. Therefore, we re-analyzed the above relationships between height and number of (surviving) children for women who had their first child at an age of 21 and older, when final stature has been reached. These results were very similar (Poisson regression parameter estimate (± *SE*) for height; ever born children: B = -0.00678 (± 0.00189); $p < .001$; N = 2,479; surviving children: B = -0.00625 (± 0.00191); p = .001; N = 2,479).

We also investigated the association between height and the ability to attract mates, namely being married and age at first marriage. There was a trend that women who never married (4%, 165 out of 4,053) were slightly taller than ever married women (t-test: t(4,051) = 1.68; p = .09; Cohen's d = 0.13). In line with this trend, we found that among married women age at first marriage (log-transformed for normality) increased with height (r = .06; $p < .001$; N = 3,878). The negative relationship between height and reproductive success in married women with at least one child, although attenuated, was still significant after controlling for age at first marriage and age at first birth (both log-transformed; Poisson regression parameter estimate (± *SE*) for height; ever born children: B = -0.00374 (± 0.00161); p = .020; N = 3,216; surviving children: B = -0.00335 (± 0.00162); p = .039; N = 3,216).

We repeated the above analyses while including the variables education and income. Height was significantly correlated with both education (Figure 9.1b; r = .08; $p < .0001$; N = 4,059) and income (Figure 9.1c; r = .05; $p < .001$; N = 3,873), but accounted for <1% of the variation in both variables. Although education and income both had a negative effect on the number of children ever born and the number of children surviving to reproductive age, the negative effect of height remained significant (Table 9.2). To compare the effects of height, education and income, we calculated the decrease in number of children when increasing the trait with one standard deviation. Increasing one standard deviation in height reduced the number of ever born children by 3.3%, for education this was 10.7% and for income 20.2%. Thus, the effect of height was approximately three times weaker than the effect of education and about six times weaker than the effect of income. Similarly, for the number of children surviving to the age of 18; increasing one standard deviation in height reduced the number of surviving children by 2.9%, for education this was 10.6% and for income 20.1%. Thus, again the effect of height was approximately three times weaker than the effect of education and about seven times weaker than the effect of income. No significant interactions between height, education and income were found (see supplementary Tables S9.1 and S9.2 for parameter estimates in low income, high income, low education, and high education mothers).

The effect of height on the proportion of surviving children, age at first marriage, and age at the birth of the first child remained significant when controlling for education and income. Furthermore, no significant quadratic effects were found (see supplementary Tables S9.3–9.7 for parameter estimates of the effects of height, height^2, education, and income on all dependent variables).

Table 9.2: Poisson regression parameter estimates (± *SE*) of the effects of height (cm), education (years) and income in 1974 (US $) on number of children ever born and number of children surviving to 18 years.

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

All estimates significant at the p <.001 level, except *p = .0025.

Table 9.3: Studies on the association between female height and reproductive success. *N* indicates sample size. The power is the probability of detecting the effect size estimated by our analyses (r=0.09) at a significance level of α = .05 given the sample size *N* (see text for further explanation).

Study	**Sample**	***N***	**Age**	**Control factors**	**Height effect on repr. success**	**Height effect on child mort.**	**Power**
Mueller (1979)	Families (at least 1 child) from a Malnourished population in Colombia	349	<29-65+	Age, Age^2, SES, SES^2	No [I, a]	-	0.39
Shami & Tahir (1979)	Pakistani women (at least 1 child)	827	?		Curvilinear [I, II, b]	-	
Lasker & Thomas (1976)	Mexican women who have lived in US	147	> 25	Age	No [II]	-	0.19
Mueller et al. (1981)	Mexican women in Mexico or US	121	16-85	Age, Age^2, Residence	No [I]	-	0.17
Martorell et al. (1981)	Malnourished Guatemalan Indian women (at least 1 child)	380	15-47	Age	Positive [I, II, c]	Negative [d]	0.42
Brush et al. (1983)	Papua New Guinean Women	152	21-44	Age	Curvilinear [I, II]	-	0.20
Devi et al. (1985)	Undernourished population of Jalaris, India	291	23-55	Age, # Conceptions	Negative [I, II]	Positive [e]	0.34
Kirchengast & Winkler (1996)	!Kung san women from Namibia	93	18-65	Age	Negative [I, II]	Negative [f]	0.14
Kirchengast & Winkler (1996)	Kavango women from Namibia	85	18-60	Age	Negative [I, II, g]	Negative [f]	0.13
Kirchengast (2000)	!Kung san women from Namibia	65	25-40		Negative [I, II]	Negative [h]	0.11
Sear et al. (2004)	Farming community in rural Gambia (at least 1 child)	216	>50	Age	Positive [I, II]	Negative [i]	0.26
Pollet & Nettle (2008)	Women from stressed environment in rural Guatemala	2571	18-35	Age, Age^2, Ethnicity, Education	Positive [I, j]	Negative [k]	>0.99
Fielding et al. (2008)	Chinese women	6709	>50	Age, Education, Parental possessions	Negative [I, l]	-[m]	>0.99

Table 9.3: Continued.

Study	Sample	*N*	Age	Control factors	Height effect on repr. success	Height effect on child mort.	Power
Clark & Spuhler (1959)	Women from European descent from Michigan, US	324	20-70		No [II, n]	-	0.37
Bailey & Garn (1979)	White females from 10 different states in US	± 1261	45-65	Income	Negative [II, o]	-[p]	0.89
Scott & Bajema (1981)	Females who attended public schools in Boston, US	600	±50-55	Income	No [II, q]	-	0.60
Nettle (2002)	Children born in UK in a certain week in 1958	3554	42	Occupational class, Social class father	Negative[I] [I, r]	-	>0.99
Deady & Law Smith (2006)	White women from UK, US, Canada and Australia	315	>45	Age, Parental income	Negative [III]	-	0.36
Helle (2008)	Finnish women	271	>55	Education, Birth cohort, Area, Height[2]	No [I]	-	0.32
Byars et al. (2009)	Participants from the Framingham Heart study	2227	post-meno pause	Education, Whether native born, Whether smoker, Medicine use	Negative [I, II]	-	0.99
Nenko & Jasienska (2009)	Rural women from Poland (at least 1 child)	328	21-85	Age	No[III]	-	0.37
This study	White women from Wisconsin	4059	>63	Education, Income	Negative [I, II]	Negative	>0.99

We consider populations on the left page non-Western, and those on the right page as Western.

[I] Dependent variable: number of surviving children.

[II] Dependent variable: number of children ever born.

[III] Unknown whether surviving or ever born children wad used as dependent variable.

[a] Instead of height, these authors used a composite measure of many bone measurements. Height was not a strong determinant of this composite measure.

[b] The authors reported no statistical analyses, but women a little above average height had on average most (surviving) offspring.

[c] The authors report a negative relationship between height and ever born children, although this relationship was not significant.

[d] As dependent variables, both number of deceased children and child mortality were used.

[e] The dependent variable was number of post-natal deaths.

[f] The authors found a negative correlation between height and number of deceased children.
[g] The negative relationship between height and number of live births was significant, the relationship with number of surviving children only marginally significant.
[h] A comparison between heights of mother with 0, 1-3 or 4 or more dead children was not significant. However, a clear graph of the negative correlation between height and number of deceased children was provided.
[i] Child mortality was the dependent variable.
[j] The optimum of the curvilinear effect reported by Pollet & Nettle (2008) reported was nearly two standard deviations above average. Thus, for the normal range of ± 2 standard deviations, the relationship between height and reproductive success was positive.
[k] Proportion of surviving children was used as dependent variable. Similar as above, the optimum was nearly two standard deviation above average.
[l] The effect disappeared after controlling for education and parental possessions.
[m] Shorter women had a higher risk for miscarriage.
[n] Mitton (1975) re-analysed this sample only incorporating women older than 40. No effects of height were found.
[o] Taller women had fewer children than shorter women (t-test comparison between short and tall height group).
[p] Short women (<15th percentile) had more stillborn children than tall women (>85th percentile), although this difference was not statistically significant
[q] Childless women were shorter. However, ethnicity was not controlled for.
[r] Nettle (2002) reported a curvilinear effect. However, the optimum was nearly two standard deviations below average. Thus, for the normal range of ± 2 standard deviations, the relationship between height and reproductive success was negative.

Previous research on the relationship between female height and reproductive success

We identified 20 scientific publications reporting the relationship between height and reproductive success measured as number of live born or living children, of which one article included data on two different populations (Kirchengast and Winkler, 1996). Including the present study this brings the total to 22 studies (Table 9.3). A variety of effects of female height on reproductive success were reported, including positive (*N* = 3), negative (*N* = 10; including the present study), null (*N* = 7), and curvilinear effects (*N* = 2).

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In part, this variation in results may be due to methodological factors, such as differences in sampling procedure (for instance including only parous women or including women who have not yet reached the end of their reproductive careers), differences in sample size (and hence statistical power), or differences in the number of predictor variables considered in the statistical analysis (which also affects statistical power). To examine the effect of differences in sample size, we determined for each study the power to detect the effect of height on reproductive success, based on the *N* of the study, a *p* level of 0.05, and an effect size of *r* = .09 (Table 9.3). The latter was taken from a linear regression of number of ever born children on height using the data from the present study. We used ever born children as outcome measure as more studies in our review used this measure rather than the number of surviving children (linear regression of number of surviving children on height resulted in an r of -.08). The choice of this effect size, at least for Western populations seems justified, as one of the few studies that reports an effect size of height on lifetime reproductive success was very similar to ours (r = -.083; Byars et al., 2010). Given these parameters, an N of 966 was needed to obtain a power of 0.80. The fact that the required sample size is so large is mainly due to the low effect size of the relationship we study (low, but not uncommon; Kingsolver et al., 2001). The seven studies that did not find any relationship all had a power smaller than 0.6 to detect r = 0.09. The power decreases even further when samples use wide age ranges (e.g., Mueller et al., 1981), only parous women (e.g., Nenko and Jasienska, 2009) or different ethnicities (e.g., Scott and Bajema, 1982). We will not consider these null findings any further.

Results from Western samples were very similar to each other: every study that found a significant effect, reported a negative association between height and reproductive success (N = 5). More variation was found among the non-Western samples; positive (N = 3), curvilinear (N = 2) as well as negative (N = 5) effects were reported. Brush et al. (1983) found a curvilinear effect of height on the number of children. However, the peak of the curvilinear effect could not be established as appropriate estimates or graphs were not given. This peak could thus have been either to the left or the right of the height distribution, which would substantially alter the interpretation of the results.

Given the variety in results found in non-Western samples, and the fact that these effects were found using substantially smaller samples, for such samples the use of our low effect size and power calculations based on this estimate (r = .09) may not be fully justified. Therefore, we determined the effect size of one of the non-Western studies that was most comparable to our study (using postreproductive women; Sear et al., 2004), and for which appropriate information was available. We found an effect size of r = .16 for the relationship between height and the number of ever born children, which was substantially higher than our effect size and in the opposite direction. Given these parameters, an N of 304 was needed to obtain a power of 0.80. Two of the three non-Western studies that did not find an effect had a power lower than 0.5 to detect this effect size.

DISCUSSION

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

Given that height is related to education (Cavelaars et al., 2000; Silventoinen et al., 1999), and that our sample consisted of female high-school graduates, the observed relationship between height and reproductive success may have been biased. Our review of studies on the relationship between female height and reproductive success, however (Table 9.3), confirmed our finding that across Western populations female height is negatively associated with reproductive success, as five out of nine studies documented a similar negative effect. The four remaining studies in Western populations found no effect of height, which was likely due to small sample size and hence low statistical power to detect an effect of the magnitude we found in our study.

In non-Western populations the relationship between height and reproductive success was more variable. There can be different causes for this variation. One possibility is that there is true variation in selection pressures between populations and over time, which in itself is not unusual (Siepielski et al., 2009). Alternatively, but not mutually exclusive, conclusions across studies may differ for methodological reasons, such as low statistical power (see above) or differences in sampling procedure (e.g., including young women who have likely not ended their reproductive careers). The variation in the non-Western populations can also partly be explained by the relationship between female height and child survival. In line with previous findings on the relationship between female stature and child mortality (42 developing countries: Monden and Smits, 2009; 54 low- to middle-income countries: Özaltin et al., 2010; but see Devi et al., 1985), we found that female height is consistently negatively related to child mortality in non-Western populations (with one exception: Devi et al., 1985). Even in our Western sample, female height was negatively associated with child mortality. In an environment with few resources height might be a reflection of health, nutritional status, and greater access to resources (Sear et al., 2004; Silventoinen, 2003), all of which have a positive influence on the survival of children. If child mortality is high, the positive relationship between female height and child survival will result in more surviving offspring, and potentially in more reproductive success for taller women. Indeed, in all studies that found a positive association between height and the number of surviving children, maternal height was positively associated with child survival. Thus, we conclude that the positive association between height and reproductive success in non-Western populations can be explained by the increased survival probability of offspring from taller women (Martorell et al., 1981).

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

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

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

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

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

Regardless of the mechanism causing the higher reproductive success of shorter women, our findings suggest that in particular in Western populations there is a selection pressure on women favoring lower height. Moreover, the contrast with non-Western populations suggests that this may be a relatively recent development. Whether this will lead to shorter height in the future is uncertain however (but see Byars et al., 2010 for a quantitative prediction for a specific population). First, in addition to the selection pressure on female height within cohorts, as we identified here, there is a secular trend that height increases (Silventoinen, 2003). Second, because offspring height is determined by the genes they inherit from both their parents (Silventoinen, 2003), the selection pressure on height in males also plays a role. We recently showed that average height men obtained higher reproductive success than either taller or shorter men (**Chapter 10**). Thus, predictions on how height will evolve in the future should be based on the integration of the selection pressures acting on height in both sexes, and these predictions likely differ from predictions based on either sex in isolation.

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53706 and at http://www.ssc.wisc.edu/wlsresearch/data/. The opinions expressed herein are those of the authors.

SUPPLEMENTARY MATERIAL

Table S9.1: Poisson regression parameter estimates (± *SE*) of the effect of height (cm) on the number of children ever born and the number of children surviving to 18 years for below median education (only high-school education) and above median education (more than high-school education) mothers.

	Number of children ever born		**Number of children surviving to 18 years**	
	Low education	High education	Low education	High education
Intercept	2.20 (±2.98*10^{-1})****	2.15 (±4.45*10^{-1})****	2.10 (±3.01*10^{-1})****	2.06 (±4.49*10^{-1})****
Height	-6.70*10^{-3} (±1.82*10^{-3})***	-7.83*10^{-3} (±2.70*10^{-3})**	-6.24*10^{-3} (±1.84*10^{-3})***	-7.36*10^{-3} (±2.73*10^{-3})**
N	2,539	1,520	2,539	1,520

***p* <.01, ****p* <.001, *****p* <.0001

Table S9.2: Poisson regression parameter estimates (± *SE*) of the effect of height (cm) on the number of children ever born and the number of children surviving to 18 years for below median income in 1974 (below US $500) and above median income (more than US $500) mothers.

	Number of children ever born		**Number of children surviving to 18 years**	
	Low income	High income	Low income	High income
Intercept	2.74 (±3.46*10^{-1})****	1.65 (±3.76*10^{-1})****	2.58 (±3.50*10^{-1})****	1.60 (±3.79*10^{-1})****
Height	-9.72*10^{-3} (±2.12*10^{-3})****	-4.65*10^{-3} (±2.29*10^{-3})*	-8.89*10^{-3} (±2.14*10^{-3})****	-4.42*10^{-3} (±2.31*10^{-3})[a]
N	1,915	1,958	1,915	1,958

**p* <.05, *****p* <.0001, [a]*p* = .056.

Table S9.3: Poisson regression parameter estimates (± *SE*) of the effects of height (cm), height^2, education (years) and income (US $ in 1974) on number of children ever born.

	Number of children ever born			
Intercept	2.40 (±2.48*10^{-1})****	2.62 (±4.08)	2.77 (±2.60*10^{-1})****	2.77 (±4.21)
Height	-8.39*10^{-3} (±1.51*10^{-3})****	-1.11*10^{-2} (±4.97*10^{-2})	-5.30*10^{-3} (±1.56*10^{-3})***	-5.29*10^{-3} (±5.13*10^{-2})
Height^2		8.14*10^{-6} (±1.51*10^{-4})		2.64*10^{-8} (±1.56*10^{-4})
Education			-5.65*10^{-2} (±5.42*10^{-3})****	-5.65*10^{-2} (±5.42*10^{-3})****
Income			-5.29*10^{-5} (±2.90*10^{-6})****	-5.29*10^{-5} (±2.90*10^{-6})****
N	4,059	4,059	3,873	3,873

****p* <.001, *****p* <.0001.

Table S9.4: Poisson regression parameter estimates (± *SE*) of the effects of height (cm), height^2, education (years) and income (US $ in 1974) on number of children surviving to 18 years.

	Number of children surviving to 18 years			
Intercept	2.30 (±2.50*10^{-1})****	2.25 (±4.13)	2.65 (±2.62*10^{-1})****	2.43 (±4.26)
Height	-7.92*10^{-3} (±1.52*10^{-3})****	-7.25*10^{-3} (±5.03*10^{-2})	-4.75*10^{-3} (±1.57*10^{-3})**	-2.08*10^{-3} (±5.18*10^{-2})
Height^2		-2.03*10^{-6} (±1.53*10^{-4})		8.14*10^{-6} (±1.58*10^{-4})
Education			-5.58*10^{-2} (±5.47*10^{-3})****	-5.58*10^{-2} (±5.47*10^{-3})****
Income			-5.26*10^{-5} (±2.93*10^{-6})****	-5.260*10^{-5} (±2.93*10^{-6})****
N	4,059	4,059	3,873	3,873

***p* <.01, *****p* <.0001.

Table S9.5: Logistic regression parameter estimates (± *SE*) of the effects of height (cm), height^2, education (year) and income (US $ in 1974) on the proportion of children surviving to 18 years.

	Proportion of children surviving to 18 years			
Intercept	-7.51*10^{-2} (±1.80)	-8.79 (±2.90*10^{1})	-1.17*10^{-1} (±1.87)	-2.34 (±3.10*10^{1})
Height	2.44*10^{-2} (±1.10*10^{-2})*	1.31*10^{-1} (±3.55*10^{-1})	2.77*10^{-2} (±1.13*10^{-2})*	4. 12*10^{-2} (±3.80*10^{-1})
Height^2		-3.27*10^{-4} (±1.09*10^{-3})		-4.42*10^{-5} (±1.16*10^{-3})
Education			3.89*10^{-2} (±3.68*10^{-2})	3.89*10^{-2} (±4.15*10^{-2})
Income			1.86*10^{-5} (±2.25*10^{-5})	-1.86*10^{-5} (±2.25*10^{-5})
N	3,613	3,613	3,449	3,449

**p* <.05.

Table S9.6: Linear regression parameter estimates (± *SE*) of the effects of height (cm), height^2, education (years) and income (US $ in 1974) on the age at first marriage (log-transformed).

	Ln(age at first marriage)			
Intercept	2.84 (±6.02*10^{-2})****	3.50 (±9.81*10^{-1})***	2.63 (±5.97*10^{-2})****	3.38 (±9.61*10^{1})***
Height	1.39*10^{-3} (±3.67*10^{-4})***	-6.63*10^{-3} (±1.19*10^{-2})	8.94*10^{-4} (±3.58*10^{-4})***	-8.15*10^{-3} (±1.17*10^{-2})
Height^2		2.44*10^{-5} (±3.62*10^{-5})		2.75*10^{-5} (±3.55*10^{-5})
Education			2.10*10^{-2} (±1.16*10^{-3})****	2.10*10^{-2} (±1.16*10^{-3})****
Income			3.43*10^{-6} (±5.80*10^{-7})****	3.43*10^{-6} (±5.80*10^{-7})****
R^{2a}	0.3%	0.3%	10.3%	10.3%
N	3,878	3,878	3,698	3,698

**p* <.05, ****p* <.001, *****p* <.0001, [a] Adjusted R^2.

Table S9.7: Linear regression parameter estimates (± *SE*) of the effects of height (cm), height², education (years) and income (US $ in 1974) on the age at the birth of the first child (log-transformed).

		Ln(age at the birth of the first child)		
Intercept	2.78 ($\pm 6.59*10^{-2}$)****	3.45 ($\pm 1.08*10^{-1}$)**	2.53 ($\pm 6.52*10^{-2}$)****	3.38 ($\pm 9.61*10^{1}$)**
Height	$2.16*10^{-3}$ ($\pm 4.01*10^{-4}$)****	$-5.99*10^{-3}$ ($\pm 1.31*10^{-2}$)	$1.77*10^{-3}$ ($\pm 3.91*10^{-4}$)****	$-9.65*10^{-3}$ ($\pm 1.29*10^{-2}$)
Height²		$2.48*10^{-5}$ ($\pm 3.98*10^{-5}$)		$3.47*10^{-5}$ ($\pm 3.90*10^{-5}$)
Education			$2.39*10^{-2}$ ($\pm 1.27*10^{-3}$)****	$2.39*10^{-2}$ ($\pm 1.28*10^{-3}$)****
Income			$-2.85*10^{-6}$ ($\pm 6.73*10^{-7}$)****	$-2.85*10^{-6}$ ($\pm 6.73*10^{-7}$)****
R^{2a}	0.9%	0.8%	11.3%	11.1%
N	3,232	3,232	3,094	3,094

**p* <.05, ****p* <.001, *****p* <.0001, [a] Adjusted R^2.

9

CHAPTER 10

A curvilinear effect of height on reproductive success in human males

Gert Stulp
Thomas V. Pollet
Simon Verhulst
Abraham P. Buunk

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ABSTRACT

Human male height is associated with mate choice and intra-sexual competition, and therefore potentially with reproductive success. A literature review (N=18) on the relationship between male height and reproductive success revealed a variety of relationships ranging from negative to curvilinear to positive. Some of the variation in results may stem from methodological issues, such as low power, including men in the sample who have not yet ended their reproductive career, or not controlling for important potential confounders (e.g., education and income). We investigated the associations between height, education, income and the number of surviving children in a large longitudinal sample of men (N=3,578; Wisconsin Longitudinal Study), who likely had ended their reproductive careers (e.g., >64 years). There was a curvilinear association between height and number of children, with men of average height attaining the highest reproductive success. This curvilinear relationship remained after controlling for education and income, which were associated with both reproductive success and height. Average height men also married at a younger age than shorter and taller men, and the effect of height diminished after controlling for this association. Thus, average height men partly achieved higher reproductive success by marrying at a younger age. On the basis of our literature review and our data, we conclude that men of average height most likely have higher reproductive success than either short or tall men.

INTRODUCTION

Body size is among the most conspicuous differences between males and females in many species. In most species of birds and mammals, males are larger than females, with perhaps the most striking example being the southern elephant seal, a species where the male is on average seven times larger than the female (Fairbairn et al. 2007). Such a size dimorphism is often explained in terms of sexual selection through either mate choice, with a preference for larger males by females, or through intra-sexual competition, with an increased advantage of larger males in male–male competition (Andersson 1994; Fairbairn et al. 2007).

Human males are ± 8% larger than females (Gray and Wolfe 1980), and male body size (i.e., height) plays a role in both human mate choice and intra-sexual competition. Women prefer taller rather than shorter men in online dating advertisements (Salska et al. 2008), questionnaire studies (Fink et al. 2007) and lab-based preference studies (reviewed by Courtiol et al. 2010b), and these preferences seem to translate into real word decisions: taller men receive more responses to online dating advertisements (Pawlowski and Koziel 2002), are more likely to obtain a date (Sheppard and Stratham 1989), are more desirable in a speed-dating setting (Kurzban and Weeden 2005), have more attractive female partners (Feingold 1982) and are more likely to be married (Pawlowski et al. 2000). Although male height is related to mate choice in Western societies, recent studies indicate that preferences for taller men are not cross-culturally universal (Sear and Marlowe 2009).

There is also evidence to suggest that male height plays a role in intra-sexual competition. First of all, height is related to physical strength and thereby the chance of winning a physical contest (Sell et al. 2009; Carrier 2011). Second, taller men are less sensitive to cues of dominance in other men (Watkins et al. 2010), and respond with less jealousy towards socially and physically dominant rivals than shorter men (Buunk et al. 2008). Perceptions of height and dominance are also interlinked, as taller men are perceived as more dominant than shorter men and vice versa; dominant men are estimated as taller than less dominant men (Marsh et al. 2009). In addition, men who were perceived as taller were more influential in a negation task (Huang et al. 2002). Together, these findings may partly explain the observed association between height and social status, as taller men more often have a leadership position (Gawley et al. 2009), often emerge as leaders (Stogdill 1948), have higher starting salaries (Loh 1993) and have higher overall income (Judge and Cable 2004).

To be of evolutionary consequence, the advantage of increased height in mate choice and intra-sexual competition should translate into increased reproductive success for taller men. Several studies have examined this relationship without reaching consensus, and we provide a literature review including all studies that we could locate (*N*=18; see Chapter 1 and the supplementary material for the methods of the literature review and a discussion of the findings) on the association between male height and reproductive success (Table 10.1). A variety of effects of male height on reproductive success were reported, including three positive, two negative, eight null and five curvilinear effects. There may be several reasons for this variation. First of all, selection pressures may differ among populations or over time. Siepielski et al. (2009) found considerable year to year variation in both strength and direction of selection for morphological traits, and this may also hold true for height. Variation in reported results can also stem from methodological reasons, such as differences in sampling procedure, in sample size and hence statistical power or in the variables considered in the statistical analysis. With respect to the sampling procedure, we find that several studies used samples that were clearly not representative of the population (e.g., only healthy men, men from low socio-economic class, or ‘troubled boys’), and it is unclear to which extent and how this would affect the results. Sampling procedure can possibly also explain the results of the study which has documented the strongest positive effect of height on reproductive success: Mueller and Mazur (2001) found clear evidence for directional selection for male height among men from the US military academy at West Point with military careers of 20 years or more. This sample is intentionally not representative of the whole population with respect to physical health and condition. More importantly, the physical selection is likely to be stronger on tall men, because for biomechanical reasons it is more difficult for tall men to meet physical requirements of the military such as the minimum number of eight correct pull-ups and 54 push-ups in 2 minutes (Mueller and Mazur 2001); hence, tall men that do meet those requirements may be exceptionally fit even compared to shorter men that meet the same requirements.

In addition, some of the variation in the effects found may be explained by the fact that very few studies were restricted to men who were at least close to having completed their reproductive careers (e.g., over 50 years in developed countries). If the association between male height and reproductive success is mostly determined at a later age, than effects of height are difficult to detect when using a sample of younger men. An additional methodological issue is the low statistical power for detecting an effect due to insufficient sample sizes, as selection gradients are typically low (Kingsolver et al. 2001), and therefore substantial samples are required to detect an effect.

As mentioned previously, male height is positively associated with social status (e.g., education (Silventoinen et al. 1999; Cavelaars et al. 2000) and income (Judge and Cable 2004)), which is an important determinant of male reproductive success (reviewed by Hopcroft 2006). In Western societies, education and income reflect social status but have large, opposing effects on reproductive success (reviewed by Hopcroft 2006; Nettle and Pollet 2008): in men, number of children increases with income but decreases with educational level. Therefore, in investigating male reproductive success, it is crucial to incorporate both education and income. Only very few studies that examined the relationship between height and reproductive success have controlled statistically for education and income (or proxies thereof).

In this study, we examine the relationship between height and reproductive success in a new sample in which some of the previously described limitations are overcome. First of all, we use a large sample of Wisconsin high-school graduates who were followed longitudinally and have likely ended their reproductive careers (i.e., over 60 years old). Second, we have high statistical power to find even weak effects of height, as the total sample included 3,578 men. Third, measures of education and income, both correlates of height, were available to disentangle possible confounding effects. Several (proxy) measures of reproductive success are available, including number of children ever born, number of surviving children, proportion of married offspring and potential proxies of mate value, such as number of marriages and age at first marriage.

MATERIAL AND METHODS

We used the Wisconsin Longitudinal Study (WLS), a long-term study of a random sample of 10,317 men and women, born between 1937 and 1940, who graduated from Wisconsin high schools in 1957 (Wollmering 2006; http://www.ssc.wisc.edu/wlsresearch/). Survey data on a wide variety of topics were collected at several time points (in 1957, 1974, 1992/3 and 2003/4/5), covering almost 50 years of the participants' lives. The WLS sample is broadly representative of white, non-Hispanic American men and women who have completed at least a high-school education. As about 75% of Wisconsin youth graduated from high school in the late 1950s (Wollmering 2006), our sample was biased towards well educated people. In line with the finding that height is positively

Table 10.1: Studies on the association between male height and reproductive success. *N* indicates sample size.

Study	Sample	*N*	Age	Control factors	Height effect on repr. success	Tested for curvilinear effects?
Winkler and Kirchengast (1994)	Healthy !Kung san men from Namibia	114	18-38	Age	No [I,II]	No
Kirchengast and Winkler (1995)	Healthy urban !Kung san men from Namibia	59	18-39	Age	Negative [I,II,a]	No
Kirchengast and Winkler (1995)	Healthy rural !Kung san men from Namibia	78	18-39	Age	Positive [I,II]	No
Kirchengast (2000)	!Kung san men from Namibia	103	25-40	Weight	No [I,II]	No
Sear (2006)	Farming community in rural Gambia	303	>50	Age	No [I,II,b]	Yes
Lasker and Thomas (1976)	Mexican men who have lived in US (± 215)	±215	> 30	Age	No [II]	No
Mueller et al., (1981)	Mexican men in Mexico or US	159	18-96	Age, Age^2, Residence	No [I,c]	No
Goldstein and Kobyliansky (1984)	Mexican families (at least 1 child) in Mexico and US	230	Mother>40		No [I,c]	No
Mueller (1979)	Families (at least 1 child) from a Malnourished population in Colombia	338	<29-65+	Age, Age^2, SES, SES^2	Curvilinear [I,d]	Yes
Shami and Tahir (1979)	Pakistani men (at least 1 child)	860	?		Curvilinear [I,II]	Yes[e]
Fielding et al., (2008)	Chinese men	2620	>50	Age, Education, Parental possessions	Negative [I,f]	No

We consider populations on the left page non-Western, and those on the right page as Western.

[I] Dependent variable: number of surviving children.

[II] Dependent variable: number of children ever born.

[III] Unknown whether surviving or ever born children was used as dependent variable.

[a] Height correlated negatively with number of surviving children, not with number of children ever born.

[b] Tested for curvilinear effects, but parameter estimates and *p*-values were not provided.

[c] Did not test for curvilinear effects, but concluded curvilinear effects on basis of data of both parents (see main text).

[d] Instead of height, these authors used a composite measure of many bone measurements. Height was however, the strongest determinant of this composite measure.

[e] The authors divided height into several height classes, and found that the number of children (both surviving and ever born) was significantly higher when the average range classes were combined together and compared to the other height classes.

[f] This effect disappeared after controlling for education and parental possessions.

[g] A significant positive effect of height was found for urban men, a marginally significant effect for rural men.

Table 10.1: continued.

Study	Sample	*N*	Age	Control factors	Height effect on repr. success	Tested for curvilinear effects?
Pawlowski et al. (2000)	Healthy Polish men	3201	25-60	Age, Residence, Education	Positive [III,g]	No
Nettle (2002)	Children born in UK in a certain week in 1958	4586	42	Education, Occupational class	No [II]	Yes[h]
Clark and Spuhler (1959)	Men from European descent from Michigan, US	136	>40	Head length, Head height	Curvilinear [II,i,j]	Yes
Damon and Thomas (1967)	White Harvard men	2616	>60		Curvilinear [II,k]	Yes
Scott and Bajema (1981)	Males who attended public schools in Boston, US	621	±50-55	Ethnicity, Income	Curvilinear [II,j,l]	Yes
Mueller and Mazur (2001)	US military men	322	>62	Career predictors and parameters	Positive [III]	No
Genovese (2008)	Men from a shelter program for troubled boys	192	19-65		No [I]	No
This study	Wisconsin Longitudinal Study	3578	>64	Education, Income	Curvilinear [I,II]	Yes

[h] Nettle provided us with the results from a linear regression where number of children was regressed on height and height squared. Effects were non-significant.

[i] Mitton (1975) re-analysed the data by Clark and Spuhler (1959) and these results are mentioned in the table. Clark and Spuhler (1959) did not find an effect of height on reproductive success and did not test for curvilinear effects. They used a larger sample than Mitton (1975) (*N*=213), because they included men aged from 25 to 40.

[j] Instead of including a height-squared term to test for non-linear effects, the absolute value of the distance to the mean was used.

[k] We re-analyzed the data by Damon and Thomas (1967) and our results are reported in the table (see supplementary material and Table S10.1). Damon and Thomas (1967) found no effect of height on reproductive success but did not test for curvilinear effects.

[l] A marginally significant curvilinear effect was found. Also a marginally negative effect was found when controlling for ethnicity and when controlling for income. No non-linear effects were tested when controlling for either ethnicity or income.

related to education (Silventoinen et al. 1999), we find that the average height of our sample (179.20 cm) is taller than the average height of white US males from the same birth cohort (176.7 cm; Komlos and Lauderdale 2007). We will address this limitation further in our discussion.

Of particular interest for this study are the height, education, income, number of marriages, age at first marriage, number of children ever born, number of children surviving to reproductive age (18 years), age at birth first child and proportion of adult offspring (> 18 years) who are married (both sons and daughters). Because in the WLS, data were collected at several time points and by several methods (e.g., phone interviews, mail correspondence), and because of non-response, there is not complete information for all measures and sample sizes may differ for different measures.

Only biological children were included in the offspring counts. It was impossible to control for extra-pair paternity, as all data was self-reported by the respondent. For all measures except income and proportion of married offspring, we combined the data of separate time points to maximize sample size. For income we used the data collected in 1974 only (the respondent's total earnings in 1974), because due to inflation, income is incomparable across decades (Pearson correlation with income in 1992; $r = .48$; $p < .0001$; $N = 3{,}723$; Pearson correlation with income in 2004; $r = .39$; $p < .0001$; $N = 3{,}151$). Education was measured as the number of years required to obtain the highest reported level of education (high school degree = 12 years of education; post-doctoral education = 21 years of education). For the proportion of married offspring, we only used data from 2004, as many children would not have reached adulthood when using data from earlier time points.

Statistical analyses were performed using R (version 2.13.1; R Development Core Team, 2011). All tests were two-tailed, and the significance level was set to $\alpha = .05$. To examine the associations between height, education and income, we used Pearson correlations. For the effects of height on different measures of reproductive success, we used Poisson or logistic regression depending on the error distribution. Height squared was included to test for possible curvilinear effects. Whenever a curvilinear effect was found, we determined a confidence interval of the optimum of the effect, by simulating 1,000 responses (using the simulate{stats} function in R) and refitting the statistical model. In this way, 1,000 parameter estimates and hence optima are generated, and we could determine the 95% data range of these 1,000 samples.

RESULTS

For 3,578 out of 4,991 men, height was available. The descriptive statistics for these men and the sample sizes available for all variables (and hence analyses) are summarized in Table 10.2. Poisson regression revealed that height had no significant linear effect on number of children ever born (Table 10.3). However, when we included the squared height in the analyses we found that height had a significant curvilinear effect on the number of children ever born (Table 10.3). Men with a height of 177.42 cm were predicted to have the most ever born children (Table 10.3).

A better approximation of reproductive success is the number of children surviving to adulthood. Because child mortality was low in our sample (only 2.9%, i.e., in 92 out of 3,142 families at least one child died before reaching adulthood), the correlation between number of children ever born and number of children surviving to 18 years was high ($r = .99$; $p < .0001$; $N = 3{,}578$). Moreover, the proportion of children surviving was not related to height (Table 10.3). Not surprisingly therefore, we also found a curvilinear effect of height on children surviving to reproductive age (Table 10. 3; Figure 10.1a).

We also investigated the effect of male height on proxies of mating success: the number of marriages, the chance of being married and age at first marriage. Poisson and logistic regressions showed no linear or curvilinear effects

Table 10.2: Descriptive statistics for all males from the Wisconsin Longitudinal Study for whom height was available.

	Mean ± *SD* / %	**Range**	***N***
Height (cm)	179.21 ± 6.43	143.51-198.12	3,578
Education (years)	14.03 ± 2.51	12-20	3,577
Income in ‘74 (US dollars)	15,867 ± 11,052	0-165,000	3,384
Number of children ever born	2.53 ± 1.51	0-10	3,578
Number of children surviving to age 18	2.51 ± 1.49	0-10	3,578
Percentage ever had child	87.8%		3,578
Age at first birth	25.68 ± 4.38	18-68	2,740
Number of marriages	1.21 ± 0.60	0-6	3,571
Percentage married	95.8%		3,571
Age at first marriage	24.06 ± 4.11	16-53	3,406
Proportion married offspring	77.3%		2,729
Proportion married sons	73.8%		2,235
Proportion married daughters	81.9%		2,182

Table 10.3: Parameter estimates (± *SE*; *p*-value in brackets) for the effect of the intercept, height and height^2 on all dependent measures. *N* is number of cases included in the analyses. *N* is number of cases included in the analyses. Δ*AIC* and Δ*Deviance* are the difference in model fit measure *AIC* and *deviance* respectively between the intercept-only model and the model including height and height^2 (negative values mean better model fit). R^2 is the adjusted explained variance in linear regression. The optimum is determined from parameter estimates, and the *Z*-value is the standardized value (*Z*-transformed). *CI* is the 95% confidence interval for the optimum from 1,000 generated samples (see text).

	Parameter estimates ±*SE* (*p*-value)			***ΔAIC* (*Δdeviance*) / R^2**	**Optimum (*Z*-value)**	**95% *CI* (*Z*-value)**
	Intercept	Height	Height^2			
Number of children ever born[a] (*N*=3,578)	$-1.76*10^{1}$ ±5.63 (0.001774)	$2.09*10^{-1}$ $\pm6.29*10^{-2}$ (0.000897)	$-5.89*10^{-4}$ $\pm1.76*10^{-4}$ (0.000813)	-8.8 (-12.8)	177.43 (-0.28)	173.89-180.20 (-0.83-0.15)
Number of children surviving to 18[a] (*N*=3,578)	$-1.80*10^{1}$ ±5.67 (0.001476)	$2.14*10^{-1} \pm 6.34*10^{-2}$ (0.000745)	$-6.02*10^{-4}$ $\pm1.77*10^{-4}$ (0.000673)	-9.2 (-13.2)	177.41 (-0.28)	173.14-180.18 (-0.94-0.15)
Proportion of children surviving to 18[b] (*N*=3,142)	$-2.69*10^{1}$ $\pm4.51*10^{1}$ (0.551)	$3.57*10^{-1}$ $\pm5.05*10^{-1}$ (0.480)	$-1.01*10^{-3}$ $\pm1.41*10^{-3}$ (0.474)	3.5 (-0.54)		
Ln(age at First birth)[c] (*N*=2,740)	7.21 ±1.51 ($2.04*10^{-6}$)	$-4.53*10^{-2}$ $\pm1.69*10^{-2}$ (0.00758)	$1.29*10^{-04}$ $\pm4.74*10^{-05}$ (0.00663)	0.3%	175.90 (-0.51)	168.11-179.68 (-1.73-0.07)
Number of marriages[a] (*N*=3,571)	$-6.45*10^{-1}$ ±7.61 (0.932)	$7.30*10^{-3}$ $\pm8.51*10^{-2}$ (0.932)	$-1.46*10^{-5}$ $\pm2.38*10^{-4}$ (0.951)	3.2 (-0.8)		
Ever married[b] (*N*=3,571)	$-3.35*10^{1}$ $\pm3.38*10^{1}$ (0.321)	$4.04*10^{-1}$ $\pm3.80*10^{-1}$ (0.288)	$-1.11*10^{-1}$ $\pm1.07*10^{-1}$ (0.298)	2.6 (-1.4)		
Ln(age at first marriage)[c] (*N*=3,406)	9.21 ±1.30 ($1.53*10^{-12}$)	$-6.74*10^{-2}$ $\pm1.45*10^{-2}$ ($3.55*10^{-6}$)	$1.88*10^{-4}$ $\pm4.06*10^{-5}$ ($3.85*10^{-6}$)	0.6%	179.47 (0.04)	177.18-182.20 (-0.32-0.47)
Number of children surviving to 18[a] (only married men) (*N*=3,406)	$-1.540*10^{1}$ ±5.63 (0.00624)	$1.85*10^{-1}$ $\pm6.30*10^{-2}$ (0.00325)	$-5.25*10^{-4}$ $\pm1.76*10^{-4}$ (0.00290)	-6.9 (-10.9)	176.77 (-0.39)	170.71-180.21 (-1.32-0.16)
Number of children surviving to 18[a,d] (only married men, controlled for age at first birth) (*N*=3,406)	$-2.29*10^{-1}$ ±5.63 (0.684)	$9.26*10^{-2}$ $\pm6.27*10^{-2}$ (0.140)	$-2.66*10^{-4}$ $\pm1.75*10^{-4}$ (0.130)	-0.41 (-4.41)[e]		
Proportion of children married[b] (*N*=2,729)	$-1.48*10^{1}$ $\pm1.34*10^{1}$ (0.271)	$1.77*10^{-1}$ $\pm1.50*10^{-1}$ (0.238)	$-4.90*10^{-4}$ $\pm4.21*10^{-4}$ (0.244)	2.4 (-1.6)		
Proportion of sons married[b] (*N*=2,235)	$-1.41*10^{1}$ $\pm1.79*10^{1}$ (0.431)	$1.67*10^{-1}$ $\pm2.01*10^{-1}$ (0.404)	$-4.61*10^{-4}$ $\pm5.61*10^{-4}$ (0.411)	3.2 (-0.84)		
Proportion of daughters married[b] (*N*=2,182)	$-1.69*10^{1}$ $\pm2.05*10^{1}$ (0.410)	$2.03*10^{-1}$ $\pm2.30*10^{-1}$ (0.376)	$-5.60*10^{-4}$ $\pm6.44*10^{-4}$ (0.385)	3.0 (-1.0)		

[a] Poisson regression.
[b] Logistic regression.
[c] Linear regression.
[d] Parameter estimate for age at first birth (log transformed): -1.52 ± 7.86 $*10^{-2}$ ($p<2*10^{-16}$).
[e] Change in *AIC* and *Deviance* in comparison to the model including both the intercept and age at first birth (log-transformed).

Table 10.4: Parameter estimates (± *SE*; *p*-value in brackets) for the effect of the intercept, height, height², education (years) and income (in 100s $) on all measures for which a significant curvilinear effect of height was found. Total *dev* and Total R^2 are respectively the total deviance and total explained adjusted variance from the full model. Δ*DEV* and ΔR^2 is the difference in deviance and R^2 between the full model and the model without the specific term. See legend Table 10.3 for description of *N*, Optimum and 95% *CI*.

	Intercept	**Height**	**Height²**	**Education**	**Income**	**Optimum (*Z*-value)**	**95% *CI* (*Z*-value)**
Number of children ever born[a](*N*=3,384)[c]	$-1.48*10^{1}$ ±5.77 (0.01031)	$1.81*10^{-1}$ $\pm 6.45*10^{-2}$ (0.00506)	$-5.09*10^{-4}$ $\pm 1.80*10^{-4}$ (0.00481)	$-2.91*10^{-2}$ $\pm 4.53*10^{-3}$ ($1.30*10^{-10}$)	$4.76*10^{-4}$ $\pm 8.97*10^{-5}$ ($1.14*10^{-7}$)	177.81 (-0.22)	172.71-181.48 (-1.01-0.35)
Total *dev*= 3694.66		Δ*DEV*= 8.63		Δ*DEV*= 42.14	Δ*DEV*= 25.76		
Number of children surviving to 18[a](*N*=3,384)[c]	$-1.50*10^{1}$ ±5.81 (0.00989)	$1.83*10^{-1}$ $\pm 6.49*10^{-2}$ (0.00488)	$-5.14*10^{-4}$ $\pm 1.82*10^{-4}$ (0.00462)	$-2.85*10^{-2}$ $\pm 4.55*10^{-3}$ ($3.66*10^{-10}$)	$4.74*10^{-4}$ $\pm 9.03*10^{-5}$ ($1.52*10^{-7}$)	177.79 (-0.22)	173.09-181.43 (-0.95-0.35)
Total *dev*= 3667.97		Δ*DEV*= 8.77		Δ*DEV*= 40.06	Δ*DEV*= 25.25		
Ln(age at first birth)[b] (*N*=2,608)[c]	6.63 ±1.49 ($8.92*10^{-6}$)	$-4.09*10^{-2}$ $\pm 1.67*10^{-2}$ (0.01412)	$1.16*10^{-4}$ $\pm 4.66*10^{-5}$ (0.01302)	$1.61*10^{-2}$ $\pm 1.21*10^{-3}$ ($<2*10^{-16}$)	$-7.82*10^{-5}$ $\pm 2.70*10^{-5}$ (0.00382)	176.68 (-0.39)	166.60-181.31 (-1.96-0.33)
Total R^2= 6.50%		ΔR^2= 0.19%		ΔR^2= 6.25%	ΔR^2= 0.27%		
Ln(age at first marriage) [b](*N*=3,229)[c]	8.25 ±1.29 ($1.81*10^{-10}$)	$-5.84*10^{-2}$ $\pm 1.44*10^{-2}$ ($5.34*10^{-5}$)	$1.62*10^{-4}$ $\pm 4.03*10^{-5}$ ($5.87*10^{-5}$)	$1.26*10^{-2}$ $\pm 1.07*10^{-3}$ ($<2*10^{-16}$)	$-1.14*10^{-4}$ $\pm 2.41*10^{-5}$ ($2.43*10^{-6}$)	179.82 (0.10)	177.03-182.89 (-0.34-0.57)
Total R^2= 4.65%		ΔR^2= 0.44%		ΔR^2= 4.11%	ΔR^2= 0.63%		

[a] Poisson regression.
[b] Linear regression.
[c] Sample size was slightly reduced because education and income (for which some cases were missing) were included in the analyses.

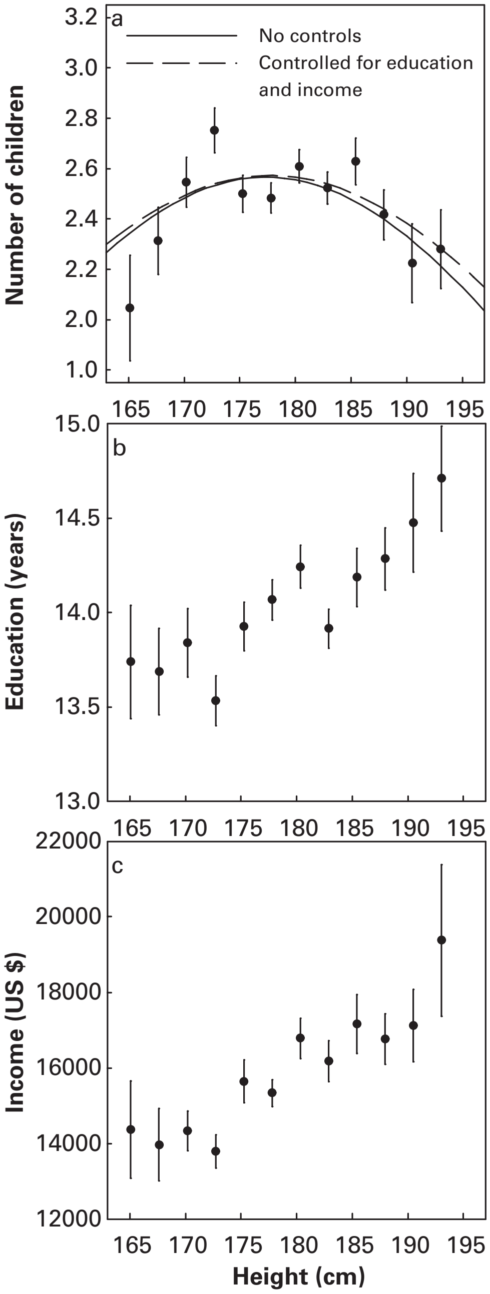

Figure 10.1: The effect of height on (a) the number of children surviving to 18 (with Poisson regression lines), (b) the number of years of education, and (c) annual income (US $) in 1974 binned by inch of height (*mean* ± *SE*). Given that height was measured in inches, we binned data using this unit of measurement (which was converted into cm). Bins below 65″ and above 76″ were collapsed.

of height on the number of marriages or the chance of being married (Table 10.3), but a linear regression on age at first marriage (log transformed to normalize its distribution) revealed that there was a curvilinear relationship between height and age at first marriage; average height men married youngest (Table 10.3). Similar effects of height were found with respect to the age at birth of the first child (Table 10.3). To examine whether the observed relationship between height and age at first marriage could account for the curvilinear effect of height on reproductive success, we re-analyzed this relationship while controlling for the age at first marriage. When excluding non-married men from the analyses, height was still significantly curvilinearly related to reproductive success in married men (Table 10.3). However, when controlling for age at first marriage, height was no longer a significant predictor of reproductive success in married men (Table 10.3), suggesting that age at first marriage can at least partly explain the observed patterns between height and reproductive success.

As height is related to education and income, which both have independent opposite effects on reproductive success, we repeated the analyses in which a significant effect of height was found while including education and income.

As in previous studies, height was positively correlated with both education (Figure 10.1b; $r = .08$; $p < .0001$; $N = 3{,}577$) and income (Figure 10.1c; $r = .09$; $p < .0001$; $N = 3{,}384$). With respect to both the number of children ever born and surviving to reproductive age, education had a significant negative effect, while income had a significant positive effect, but the curvilinear effect of height remained significant when controlling statistically for these factors (Table 10.4). There were no significant two-way or three-way interactions between height, education and income on the number of children ever born or surviving to 18 years.

To compare the relative importance of height, education and income in explaining variation in number of children, we compared the change in deviance when removing the individual terms from the final model (Table 10.4). With respect to the number of children surviving to age 18, we found that the effect of income was about 2.8 times as strong as the effect of height (Income: ΔDeviance for income = 25.25 and ΔDeviance for height = 8.77, respectively). Similarly, the effect of education was 4.5 times stronger than the effect of height and about 1.5 times stronger than the effect of income (ΔDeviance for education = 40.06; see Table 10.4 for similar calculations on the other dependent variables).

We further compared the effects using the parameter estimates. When controlling for education and income, the maximal predicted reproductive success of 2.57 children was obtained by a man of 177.79 cm. Moving one standard deviation in height away from the optimum reduced the number of children by 2.1% (2.52), whereas moving two standard deviations away reduced the number of children by 8.1% (2.36). One standard deviation increase in years of education resulted in a decrease in number of children of 6.9%. For income, one standard deviation increase resulted in an increase of number of children of 5.4%. Therefore, while height is related to reproductive success, its effect is relatively small compared to education or income.

It is possible that a child's reproductive success is dependent on the height of their father. To consider this possibility, we used the proportion of adult children being married. Paternal height was not significantly related to the proportion of married children, proportion of married sons or proportion of married daughters (Table 10.3).

For all significant curvilinear effects we determined the optimum, as well as a confidence interval around this optimum (Table 10.3). All optima were very close the average height of the entire sample (Table 10.3; range 175.90–179.47; range in *Z*-scores -0.51 to 0.04), and all 95% confidence intervals on the optima overlapped the sample average. Thus, optima were not significantly different from the average height in this population.

DISCUSSION

In Wisconsin high-school graduates, average height men, compared to shorter and taller men, attained the highest reproductive success as measured by the number of children ever born and the number of children surviving to reproductive age. Thus, male height is curvilinearly related to reproductive success. In line with previous research, we found that education had a negative effect and that income had a positive effect on reproductive success (reviewed by Hopcroft 2006; Nettle and Pollet 2008). This underlines the importance of considering these two variables separately in a life history context, instead of using a combined social status measure (Hopcroft 2006). The effect of height was modest, being almost three times smaller than the effect of income, and 4.5 times smaller than the effect of education. Therefore, any selection pressure on male height in Western societies is likely relatively small in comparison to the selection on male education and male wealth

The effect of male height on reproductive success could not be attributed to education or income in our sample. Thus, the shape of the curvilinear effect appears not to be a result of a differential effect of education or income across the height continuum. Apparently, being rich or being well educated does not provide the means to compensate for the effect of being short or tall on reproductive success, but neither does being poor or uneducated aggravate these effects. Income and education have pervasive effects on health and lifestyle, and the finding that the effect of height on reproductive success was insensitive to these factors suggests that there is a fundamental underlying biological process causing this effect. These findings are in broad agreement with the suggestion of Mueller et al. (1981) who reported that 'the curvilinear association of fertility and bone [length] does not appear related to socioeconomic factors in this sample' (p. 164), although they did not provide direct quantitative support for this suggestion.

A limitation of our study is that the sample was biased towards well-educated people (i.e., at least high-school education). As one out of four people never graduated from high-school in the 1950s, a part of the population is therefore not included in our sample. Given that height is positively related to education, our sample may have been biased towards taller men. Indeed, the average height in our sample (179.20 cm) was somewhat taller than the national average height of white men born in the same age cohort (176.7 cm; Komlos and Lauderdale 2007). Despite this limitation we still conclude that average height men had more reproductive success than their shorter and taller counterparts, as both the average height of the population as well as the national average height fell within the confidence interval for the estimated optima for number of children surviving to reproductive age (173.54–180.38 cm).

A limitation shared by all studies on the relationship between height and reproductive success, including ours, is that information on extra-marital offspring is lacking. Possibly taller and/or shorter men have more extra-pair offspring, which could offset the lower number of children within their own marriage, and we cannot test this hypothesis with the available data. In fact, we are not aware of any studies that have tested the relationships between height and either extra-pair mating success or the risk of losing fertilizations. However, non-paternity rates have been shown to be very low (around 3% as reviewed by Anderson 2006), making it unlikely that the quadratic association between height and reproductive success could be nullified by extra-pair offspring.

The number of children born to a male is only a proxy for fitness, which should ultimately be measured far into the future. Taller men may, for example, increase their relative reproductive success through increased survival chances of their offspring or the increased ability of their offspring to find a partner. We did not find any evidence for either of these processes, as height was not related to the proportion of children surviving to age 18 or the chance of adult offspring being married (either sons or daughters). For obvious reasons we cannot exclude the possibility that offspring reproductive success depends on paternal height when measured further into the future, but as paternal height was not related to offspring mating success, we anticipate that this possibility is not very likely.

Previous studies on the relationship between male height and reproductive success (Table 10.1) have reported a variety of effects of male height including positive (N = 3), negative (N = 2), no (N = 8) and curvilinear effects (N = 6) as in the present study (for an extensive discussion of the literature review and the variation in results, see Chapter 1). We attribute most of this variation in results to differences in sampling procedure (e.g., biased samples or samples including very young men not likely to have ended their reproductive careers), low power of the majority of studies to detect the relevant effect size and the lack of testing for non-linear relations. The importance of testing for curvilinear effects is apparent from two re-analyses which found significant curvilinear effects, whereas the original studies reported no effect of height (Mitton 1975 re-analyzed Clark and Spuhler 1959; and we re-analyzed Damon and Thomas 1967). Furthermore, two studies conclude that their data show stabilising selection for height, without testing this statistically (Mueller et al. 1981; Goldstein and Kobyliansky 1984). Out of the ten studies considering non-linear effects, eight appear to support a curvilinear relationship. We therefore suggest that the most likely pattern with respect to the association between male height and reproductive success is average height men having most children. Further work remains necessary, however, as especially large samples from non-Western populations measuring reproductive success at the end of a male's reproductive career are lacking.

Given our findings, it is puzzling that tall men are more attractive. Women might be more attracted to taller men because of the direct benefits it would confer to them, as height is universally positively associated with social status (Schumacher 1982; Silventoinen et al. 1999; Cavelaars et al. 2000; Judge and Cable 2004). Also in our study there was a positive association between height and income, but this did not translate into more reproductive success for taller men. In our sample, height was not associated with number of marriages or the chance of being married (in line with findings of a more traditional society: Hadza foragers of Tanzania, Sear and Marlowe 2009). However, average height men did marry at a younger age, suggesting that, to the extent that age of marriage is a proxy for mate value, average height men were more successful in finding a mate than either taller or shorter men. Furthermore, the relationship between height and age at marriage accounted (at least partly) for the effect of height on reproductive success. Thus, average height men attained more reproductive success by marrying at a younger age, potentially due to an increased length of the reproductive window.

The relationship between male height and reproductive success can also occur due to selection on correlated characters (e.g., indirect selection; Lande and Arnold 1983), rather than direct selection on male height. Inclusion of two known correlates of height and reproductive success (education and income) did not affect our estimates of selection on height, but nevertheless other (unknown) correlated factors might underlie or change this relationship. Whether selection on height acts directly or indirectly, the high heritability of height (around 0.8; Visscher et al. 2006) makes it likely that phenotypic selection on height directly affects the many genes coding for height.

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SUPPLEMENTARY MATERIAL

Details and discussion of the literature review

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

We identified seventeen scientific publications reporting the relationship between height and reproductive success measured as number of (living) children, of which one article studied two different populations (Kirchengast & Winkler 1994). Including the present study this brings the total to nineteen studies (Table 10.1). A variety of effects of male height on reproductive success were reported, including positive ($N = 3$), negative ($N = 2$), no ($N = 8$) and curvilinear effects as in the present study (N = 6). There can be different causes for this variation. One possibility is that there is true variation in the selection pressure among populations or over time, which is in itself not unusual. For instance, Siepielski et al. (2009) found considerable year to year variation in both strength and direction of selection for morphological traits, and this may also hold true for height.

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Alternatively, but not mutually exclusive, conclusions may differ for methodological reasons, for example due to differences in sampling procedure, in the variables considered in the statistical analysis, or in the sample size and hence statistical power. As mentioned above, too few studies reported sufficient statistical details to allow for a meta-analysis to test these hypotheses. Instead we therefore discuss each of the possible methodological explanations for the variation in results among the eighteen studies.

With respect to the sampling procedure: A conspicuous difference among the studies is that not all studies were restricted to men who were at least close to have completed their reproductive careers, e.g. over fifty years in developed countries. Thus when the association between male height and reproductive success is mostly determined at a later age, than effects of height are difficult to detect when using a sample of younger men. Some studies used samples that were clearly not representative of the population (e.g. only healthy men, men from low socio-economic class, or 'troubled boys'), but in most cases it is not clear to what extent and in what way this would affect the results. An exception is the study of Mueller & Mazur (2001), who sampled men from the US military Academy at West Point with military careers of 20 years or more, and found a clear positive relationship between height and reproductive success. This sample is intentionally not representative of the whole population with respect to physical health and condition. More importantly, the selection procedure for this academy is likely to be stronger on tall men, because for biomechanical reasons it is more difficult for tall men to meet physical requirements of the military such as the minimum number of eight correct pull-ups and 54 push-ups in two minutes (Mueller & Mazur, 2001), and tall men that do meet those requirements may be exceptionally fit even compared to shorter men that meet the same requirements. Thus the discrepancy in results between the present study and the study of Mueller & Mazur (2001) may well be due to differences in sampling. Studies that used samples from non-western societies may be representative as such, but more difficult to compare with our results. However, also among non-western populations the results are mixed.

With respect to the statistical analysis we find that the studies vary in the variables controlled for when testing the effect of height, and in whether or not height squared was tested. Height is associated with both education and income, which are also associated with reproductive success. As education and income have opposite effects on reproductive success (negative and positive respectively), it is important to control for both of these measures instead of using a combined social status measure. Only two other studies controlled for education and (proxies of) income (Nettle 2002; Fielding et al. 2008). Note however that in our study it made little difference whether or not education and income were controlled for, because the effects of height were largely independent of education and income. Not controlling for these parameters is therefore unlikely to have affected tests of curvilinear effects except that this would have slightly increased the statistical power.

Tests of non-linear effects were reported in only 5 studies (including the present study), but we cannot exclude the possibility that there were unreported non-significant results. Four out of these five studies did find non-linear effects, with Sear (2006) being the exception. Although not reported in his article, Nettle (personal communication) also tested for non-linear effects, and did not find curvilinear effects. One possible reason for the discrepancy between the study from Nettle (2002) and our results, is that Nettle (2002) used a sample of men who might not yet have ended their reproductive careers (i.e. all men of 42 years of age). Furthermore, the average number of children and the variance was much lower in his sample compared to ours (1.81±1.33 versus 2.54 ±1.53 children), potentially making it more difficult to find an effect because of the lower variance. Mueller & Mazur (2001) did not test for non-linearity, but visual inspection of the data suggests this was also unnecessary as graphs clearly displayed a positive linear effect of height on number of children. This may be due to the biased nature of their sample as discussed above, and hence we consider it justified to ignore this result in this context. The importance of testing for non-linear effects becomes clear when considering the re-analyses of two studies in the table. Mitton (1975) re-analyzed the data of Clark & Spuhler (1959) and Damon & Thomas (1967) and found a curvilinear effect in both data sets. Mitton (1975) excluded single and married men without children from his re-analyses of Damon & Thomas (1967), potentially biasing the outcomes. Therefore, we re-analysed the Damon & Thomas (1967) data, with the help of tables provided in Mitton (1975), Vetta (1975), and Damon & Thomas (1967), including single men and married men without children (for details see below). Using Poisson regression, we found a significant curvilinear effect of height on number of children. So after re-analysis we find 6 out of 8 studies in which was tested for non-linearity, show a curvilinear effect of height on reproductive success.

Two studies mention curvilinear effects without actually testing for them. Goldstein and Kobyliansky (1984, p.42) conclude 'According to our data, the peak of fertility tends to be related with modal parental morphological traits'.

Similarly, Mueller et al. (1981) conclude on the basis of their data: '…non-linear associations of anthropometrics and fertility are more likely than directional selection.' (p. 315). In total, thus 8 studies appear to support a curvilinear relationship of male height on reproductive success from the 10 studies considering non-linear effects.

An additional methodological issue is the low statistical power for detecting an effect due to insufficient sample sizes. Selection gradients are typically low (Kingsolver et al. 2001), and therefore substantial samples are required to detect an effect. We calculated the *N* needed to detect the effect size from our study with a power of 0.8 and a *p*-level of 0.05, using G*Power 3 (Erdfelder et al. 1996). We used an effect size of $r = .06$ which was taken from a linear regression of number of children on height and height^2 using the data of the present study (obviously this is a very conservative effect size, as studies with much lower samples sizes observed effects of height). Linear regression was used to determine the effect size rather than the Poisson regression applied in the present study, to facilitate comparison with the few studies that performed a regression analyses, because these studies used linear regressions exclusively. Given these parameters, an *N* of 2,680 was needed to obtain a power of 0.80 to detect a curvilinear effect of height. In addition to our study, Nettle (2002) is the only study with a sample size that exceeds this number. All other studies reporting null findings had much lower sample sizes, with the largest sample being 303 (Sear, 2006). With this sample size, an effect size of $r = .06$, and a p-value of 0.05, this study had a power of 0.14 to detect a curvilinear effect of height. Thus, all studies (except Nettle 2002) reporting no effect of height had a power equal or lower than 0.14. It is therefore not surprising that many studies did not observe selection on male height even when it was tested.

The re-analysis of the Damon & Thomas (1967) study

We re-analyzed the Damon and Thomas (1967) data, with the help of tables provided in Mitton (1975), Vetta (1975), and Damon and Thomas (1967), including single men and married men without children. On the basis of the means and standard deviations of these tables, we generated the data using random number generators. Depending on the underlying distribution of the variable to be generated, we used normal or Poisson random number generators. Using Poisson regression, we found a significant curvilinear effect of height on number of children (Table S10.1). In our re-analysis the height associated with the optimum number of children (177 cm) was close to the average height

(173 cm). To compare the Poisson regression parameter estimates between those of our study (Table 10.3) and those of the re-analysis of the Damon and Thomas (1967) data, a test of the equality of was done using the formula $Z=(b_1-b_2)/(SE_{b1}^2 + SE_{b2}^2)$ (Paternoster et al. 1998). Parameter estimates were not significantly different (Table S10.1).

Table S10.1: Comparison of the Poisson regression parameter estimates (± *SE*; *p*-value in brackets) of the effects of height and height2 on number of children ever born for our study and the re-analyses of Damon and Thomas (1967).

	Our study[a]	**Damon & Thomas (1967)**	**Difference estimates (Z, p)**
Intercept	$-1.76*10^{1} \pm 5.63$ (.001774)	-29.63 ± 9.65 (.002136)	
Height	$2.09*10^{-1} \pm 6.29*10^{-2}$ (.000897)	$3.39*10^{-1} \pm 1.11*10^{-1}$ (.002312)	$Z = -1.02$, $p = .31$
Height^2	$-5.89*10^{-4} \pm 1.76*10^{-4}$ (.000813)	$-9.53*10^{-4} \pm 3.20*10^{-4}$ (.002917)	$Z = 1.00$, $p = .32$
N	3,578	2,616	

a We used the parameter estimates from the analyses on the number of children ever born, as Damon & Thomas (1967) also used this measure of reproductive success.

b The difference between the estimates of our study (Table 10.3) and the re-analysis is expressed in the Z statistic using the formula $Z=(b_1-b_2)/(SE_{b1}^2 + SE_{b2}^2)$ (Paternoster et al. 1998).

10

CHAPTER 11

Intralocus sexual conflict over human height

Gert Stulp
Bram Kuijper
Abraham P. Buunk
Thomas V. Pollet
Simon Verhulst

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ABSTRACT

Intralocus sexual conflict (IASC) occurs when a trait under selection in one sex constrains the other sex from achieving its sex-specific fitness optimum. Selection pressures on body size often differ between the sexes across many species, including humans: among men individuals of average height enjoy the highest reproductive success, while shorter women have the highest reproductive success. Given its high heritability, IASC over human height is likely. Using data from sibling pairs from the Wisconsin Longitudinal Study, we present evidence for IASC over height: in shorter sibling pairs (relatively) more reproductive success (number of children) was obtained through the sister than through the brother of the sibling pair. By contrast, in average height sibling pairs most reproductive success was obtained through the brother relative to the sister. In conclusion, we show that IASC over a heritable, sexually dimorphic physical trait (human height) affects Darwinian fitness in a contemporary human population.

INTRODUCTION

Because of their different life histories, selection pressures often differ between the sexes (Bonduriansky & Chenoweth, 2009; Darwin, 1871; Van Doorn, 2009). Sex-specific selection for different trait optima, sexually antagonistic selection (SAS), can be resolved through the evolution of sexual dimorphism (Cox & Calsbeek, 2009; Fairbairn et al., 2007; Van Doorn, 2009). However, the sexes share most of their genome, which can constrain the evolution of sexual dimorphism, thus preventing the sexes from reaching their sex-specific optima. The resulting intralocus sexual conflict (IASC) can be an important determinant of fitness variation (Cox & Calsbeek, 2009; Van Doorn, 2009) and has been postulated to underlie variation in reproductive success (Camperio-Ciani et al., 2004) and its components (Garver-Apgar et al., 2011) in human populations.

The widespread existence of sexual size dimorphism suggests that IASC is at least partly resolved in response to sex-specific selection on size (Cox & Calsbeek, 2009; Fairbairn et al., 2007). However, IASC will persist when current levels of sexual dimorphism are insufficient to allow both sexes to attain their sexspecific optima, leading to ongoing selection for increased sex-dimorphism (Cox & Calsbeek, 2009). Recent studies suggest that IASC could exist for human height, at least in Western populations, given that the selection pressures on height differ between the sexes. In women, a negative relationship between height and reproductive success is found, selectively favouring those women of short height (reviewed in **Chapter 9**), whereas in men a curvilinear association is more prevalent (reviewed in **Chapter 10**), such that average height men have more reproductive success than either shorter or taller men (see Courtiol et al., 2010b; **Chapters 9** and **10**) for reviews of the potential mechanisms giving rise to these divergent selection pressures). Given the SAS on height and the high heritability of height ($h^2 > 0.8$ in industrialized countries; Silventoinen, 2003), IASC is likely to persist.

In this study, we examined whether there is IASC over human height using data from the Wisconsin Longitudinal Study (WLS). We focus on sets of siblings (the main respondent plus one randomly selected sibling) and postulated that the relative contribution of the brother and sister to the combined reproductive success (i.e., the number of children) depends on height. More specifically, we postulate that in short sibling pairs the sister would contribute most to reproductive success, while the brother would contribute most to reproductive success in average height sibling pairs.

MATERIAL AND METHODS

Sample

The WLS is a long-term study of a random sample of 10,317 men and women, born between 1937 and 1939, who graduated from Wisconsin high schools in 1957 (Wollmering, 2006). Survey data were collected at several time points, covering almost 50 years of the participants' lives—see (**Chapters 9** and **10**; Wollmering, 2006) for discussion of representativeness and other features of this sample. In 1975, respondents of the WLS were asked about their full siblings, and in 1977, 1994 and 2005 one of these siblings (randomly selected) was interviewed. In this study, we included data on the respondents and their selected sibling (we included siblings who were selected in 1975 and responded in 1994). Sex, number of living siblings and year of birth of the sibling were obtained in 1975. Height and the number of biological children ever born (our measure of reproductive success) were obtained by combining data from waves 1994 and 2005, whereas birth order was obtained in 2004 (original respondent) and 2005 (selected sibling). As selection pressures can vary over time and height tends to increase with year of birth, we only include full siblings who differed no more than 10 years in age with the main respondent.

Analyses

We first examined whether selection pressures on the siblings were similar to those previously described (**Chapters 9** and **10**), by using Poisson regressions. To examine IASC, we first standardized height within each sex and calculated the average standardized height across each sibling pair. We used this average to characterize height of both siblings, because it is a better indicator of the phenotype their shared genome codes for than the height of either sibling in isolation. We then regressed reproductive success (number of reported children ever born) against height (squared), sex and their interactions, while controlling for confounding variables (see below). On the basis of our predictions, we expected a significant interaction between height of the sibling pair and the sex of the individual in the sibling pair on reproductive success, indicating IASC. More specifically, we expected an interaction between sex and the squared term of height, because of the curvilinear effect of height found for men (**Chapter 10**). Poisson mixed models were used, with a random intercept at sibling pair level, to account for statistical non-independence of sibling pair members. All analyses were performed in R v. 2.13.1 (R development core team, 2008).

RESULTS

Descriptive statistics for the respondents and their siblings are provided in the supplementary Table S11.1. In total, there were 808 brother–brother, 996 sister–sister and 1,718 opposite-sex sibling pairs. Heights between siblings correlated positively (all *r*'s >.45; see supplementary Table S11.2).

Similar to effects observed in the primary respondents (**Chapters 9** and **10**), we found SAS on height for the siblings of the respondents. In male siblings, height was curvilinearly related to the number of children when controlling for birth year (Poisson parameter estimate (± *SE*) for height: 0.22 (± 0.10); $Z = 2.19$; $p = .028$; for height^2: $-6.20 * 10^{-4}$ ($\pm 2.80 * 10^{-4}$); $Z = -2.22$; $p = .027$). Similarly, we found a negative effect of height on number of children in sisters ($-7.63 * 10^{-3}$ ($\pm 2.33 * 10^{-3}$); $Z = -3.28$; $p = .001$; see supplementary Figure S11.2 and Table S11.3 for full models).

In support of IASC, we found a significant interaction between the average height of the sibling pair (squared) and the sex of the sibling on the number of children (Table 11.1 and Figure 11.1). In shorter sibling pairs (relatively) more reproductive success was obtained through the sister than through the brother of the sibling pair (Figure 11.1). By contrast, in average height sibling pairs

Table 11.1: Mixed model Poisson regression parameter estimates (± *SE*) and *p*-values (based on *Z*-value) for the effect of the average height and height^2 of the sibling pair (standardised), sex of the individual and their interactions on the number of children, while controlling for birth year (centred), birth order and the number of living siblings ($N = 6{,}280$).

	Parameter estimates (± *SE*)	***p*-value**
Intercept	0.827 (± 0.020)	<.001
Sex (ref. cat = male)	0.060 (± 0.023)	.002
Pair height	$-2.68 * 10^{-5}$ (± 0.014)	.998
Pair height^2	-0.037 (± 0.016)	.002
Sex * Pair height	-0.048 (± 0.019)	.011
Sex * Pair height^2	0.042 (± 0.016)	.008
Birth year	-0.032 ($\pm 2.31 * 10^{-3}$)	<.001
Birth order	$-8.36 * 10^{-3}$ ($\pm 6.38 * 10^{-3}$)	.190
# Living siblings	0.040 ($\pm 4.68 * 10^{-5}$)	<.001
Random effect	Parameter estimate (± *SD*)	
Sibling pair	0.010 (± 0.102)	

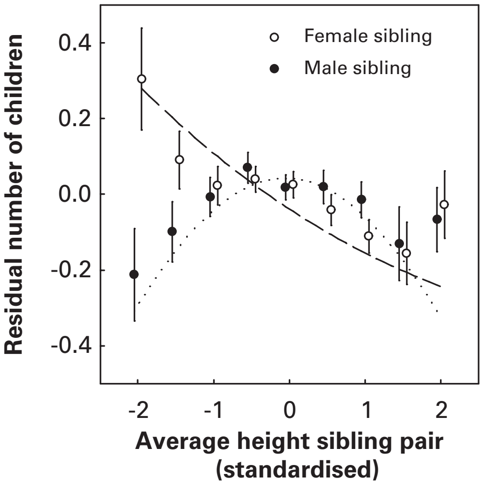

Figure 11.1: Average height of the sibling pair (average over heights standardised per sex) and the number of children (mean residual ± *SE*) through the brother (closed circles) and the sister (open circles; see Table 11.1 for controls; fitted lines calculated for means of covariates). The predicted optimum for males was exactly at average standardized sibling height (0.00). Height was divided in bins of 0.5 *SD*. Bins ≤-2 and ≥2 were pooled. See Figure S11.2 for raw data.

most reproductive success was obtained through the brother relative to the sister. These effects persisted after controlling for birth year, birth order and the number of siblings. Excluding these confounds, restricting the analyses to opposite-sex sibling pairs, using the standardized heights of both siblings in the sibling pair rather than their average height, or doing an analysis similar to Garver-Apgar et al. (2011) yielded very similar results (see supplementary Tables S11.4–11.7).

The lower number of children reported by men compared with women (see the supplementary Table S11.1 and Figure S11.2) is probably a consequence of men under-reporting previous marital and non-marital births, and the under-representation of previously married men compared with previously married women (Rendall et al., 1999). However, we previously showed that male height was not associated with the number of marriages or the likelihood of marriage (**Chapter 10**), making it unlikely that our results will be strongly affected by this limitation. Height may, however, be positively related to success in siring extra-pair children (as discussed in **Chapter 10**), which are likely to be under-reported. Nevertheless, because extra-pair children generally occur at low frequency (Anderson, 2006) and because IASC is most pronounced in short sibling pairs (Figure 11.1) we consider it unlikely that including extra-pair children would change our result.

A potential solution to IASC is biasing the sex-ratio of the offspring (Cox & Calsbeek, 2010), but a logistic regression revealed that the average height of a sibling pair was not related to the proportion of sons in the family, providing no evidence for sex-ratio biasing in response to body size (parameter estimate (± *SE*): -0.22 (± 0.19); $\chi^2(1, N = 3{,}522) = 1.32$; $p = .251$).

DISCUSSION

These results show, to our knowledge for the first time, that SAS on a human trait can result in IASC. In line with previous studies (**Chapters 9** and **10**), we show that shorter women and average height men are obtaining the highest reproductive success, indicative of SAS. These selection pressures are sufficiently different to result in significant IASC as in shorter sibling pairs more reproductive success was obtained through the sister than through the brother of the sibling pair. By contrast, in average height sibling pairs most reproductive success was obtained through the brother relative to the sister. We previously showed that the relationship between height and reproductive success in our sample is representative of contemporary Western populations (**Chapters 9** and **10**) suggesting that IASC is the norm in such populations. The IASC, combined with the high heritability of height (Silventoinen, 2003) indicates that neither sex is likely to evolve their sex-specific optima for height. The extent to which IASC exists in non-Western populations is difficult to assess as selection pressures may differ in these populations (**Chapters 9** and **10**) and heritability's are generally lower in resource poor environments (Silventoinen, 2003).

Despite substantial sexual dimorphism in human height (± 8%; Fairbairn et al., 2007), our result emphasizes that IASC is not fully resolved (in line with Cox & Calsbeek, 2009). Why then does IASC persist over human height? First, height is a highly polygenic trait, and the result of interactions between numerous underlying genes (Visscher et al., 2007) distributed over the autosomal and sex chromosomes. Therefore, sex-linkage of height genes can only partially resolve IASC (Van Doorn, 2009). Additionally, only about one-fifth of all human autosomal gene loci are estimated to be adjacent to binding sites indicative of sex-specific expression (Stewart et al., 2010), rendering it likely that height loci are simply too numerous to all accumulate at upstream DNA binding sites that facilitate sex-specific expression. As a result, it seems unlikely that IASC over height will be resolved rapidly. Biasing the sex ratio provides an alternative means to resolve IASC over body size (Cox & Calsbeek, 2010). Yet, we found no evidence for a relationship between height and sex-ratio (in line with Denny, 2008), using a much larger sample), indicating that, at least with respect to height, humans do not bias their sex-ratio to reduce IASC.

IASC has previously been postulated to underlie variation in reproductive success (and its components) in humans. First, male homosexuality was hypothesized to be a consequence of alleles that are beneficial to female fecundity but detrimental to male fecundity (Camperio-Ciani et al., 2004). Second, variation in sibling attractiveness has also been attributed to IASC (Garver-Apgar et al., 2011): physically and hormonally masculine men and women rated their brothers as more attractive than their sisters. The latter result may be contributing to the IASC observed in our study, as height is associated with attractiveness (Courtiol et al., 2010b). On the basis of these results, one would predict that shorter females and average height males would be favoured by the opposite sex. We extend these studies by showing that SAS acts on a heritable, sexually dimorphic physical characteristic (human height) and results in IASC, affecting Darwinian fitness as measured by number of children.

ACKNOWLEDGEMENTS

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SUPPLEMENTARY MATERIAL

Table S11.1: Descriptive statistics (*mean ± SD*) of the respondents and siblings from the Wisconsin Longitudinal Study (only sibling pairs where the age difference was less than ten years were included).

	Respondent		**Selected Sibling**	
	Male (*N*=1,665)	Female (*N*=1,857)	Male (*N*=1,669)	Female (*N*=1,853)
Height (cm)	179.2 ± 6.5	164.2 ± 6.1	179.0 ± 6.3	164.0 ± 6.1
Birth year	1938.8 ± 0.5	1938.9 ± 0.4	1939.6 ± 5.2	1939.7 ± 5.2
# Children	2.5 ± 1.5	2.8 ± 1.7	2.5 ± 1.6	2.7 ± 1.7

Table S11.2: Pearson correlation coefficients describing the association between sibling heights.

	Pearson *r*	Heritability (h^2)[a]
Brothers (*N*=808)	.475	0.950
Sisters (*N*=996)	.406	0.812
Opposite-sex siblings (*N*=1,718)	.449	0.898

all p < .0001.

[a] To obtain h^2, the correlation coefficient r between heights of full siblings is multiplied by 2. This calculation, however, includes the effect of the shared environment and thus overestimates h^2. These correlation coefficients are reasonably close to what is expected on the basis of the h^2 range reported for height in Western populations (Silventoinen, 2003).

Table S11.3: Poisson regression parameter estimates (± *SE*) and *p*-values (based on *Z*-value) for the effect of height, height², birth year (centered) and birth year² on reproductive success for the male (*N* = 1,669) and female (*N* = 1,853) siblings of the main respondents.

	Male siblings		Female siblings	
	Parameter estimate (± *SE*)	*p*-value	Parameter estimate (± *SE*)	*p*-value
Intercept	-18.48 (± 8.94)	.039	2.25 (± 0.38)	.013
Birth year	-0.030 (± 0.003)	<.001	-0.039 (± 0.003)	<.001
Birth year²	[a]		$-1.32*10^{-3}$ (± $5.25*10^{-4}$)	.012
Height	0.22 (± 0.10)	.028	$-7.63*10^{-3}$ (± $2.33*10^{-3}$)	.001
Height²	$-6.20*10^{-4}$ (± $2.80*10^{-4}$)	.027	[b]	

[a] Squared term of birth year not significant for males (p = .604).

[b] Squared term of height not significant for females (p = .563).

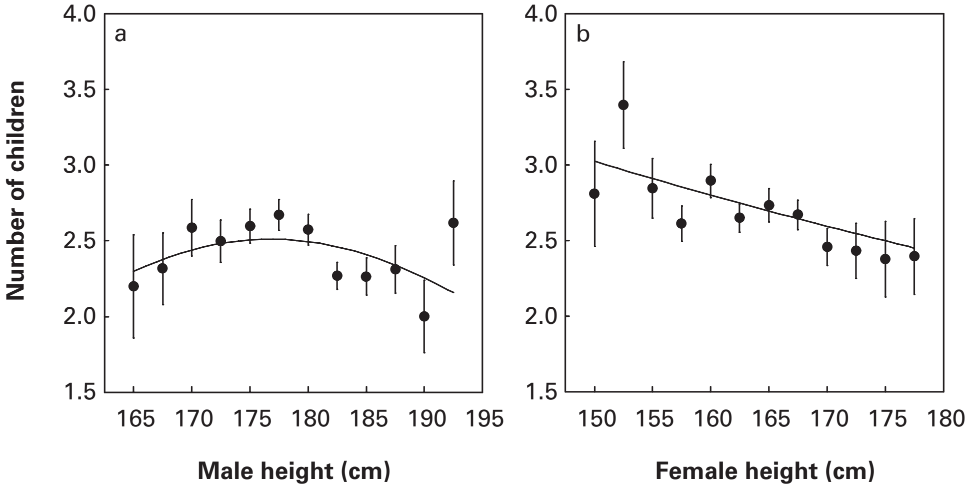

Figure S11.1: The effect of the (a) male and (b) female height (in bins of 2.5 cm) on the number of children ever born for the selected siblings of the main respondents (see main text). For men, bins below 165 cm and above 192.5 cm, and for women bins below 150 cm and above 177.5 cm were collapsed. A significant curvilinear effect was found for men (with the optimum at a height of 177 cm) and a negative effect for women (Table S11.3).

Table S11.4: Mixed model Poisson parameter estimates (± *SE*) and *p*-values (based on *Z*-value) for the effect of the average height (standardized) and height^2 of the sibling pair, sex of the individual and their interactions on the number of children (*N* = 7,044). A random intercept was included for sibling pair.

	Parameter estimates (± *SE*)	***p*-value**
Intercept	0.93 (± 0.014)	<.001
Sex (ref. cat=male)	0.054 (± 0.019)	.004
Pair height	-0.025 (± 0.014)	.066
Pair height^2	-0.035 (± 0.011)	.002
Sex * Pair height	-0.035 (± 0.018)	.052
Sex * Pair height^2	0.046 (± 0.015)	.003
Random effect	**Parameter estimates (± *SD*)**	
Sibling pair	0.025 (± 0.16)	

Table S11.5: Mixed model Poisson parameter estimates (± *SE*) and *p*-values (based on *Z*-value) for the effect of the height (standardized) and height^2 of both individuals from the sibling pair, sex of the individual and their interactions on the number of children (*N* = 7,044). A random intercept was included for sibling pair.

	Parameter estimates (± *SE*)	***p*-value**
Intercept	0.94 (± 0.014)	<.001
Sex (ref. cat=male)	0.045 (± 0.018)	.014
Height	-0.019 (± 0.012)	.105
Height^2	-0.037 (± 0.008)	<.001
Sex * Height	-0.035 (± 0.016)	.023
Sex * Height^2	0.043 (± 0.011)	<.001
Random effect	**Parameter estimates (± *SD*)**	
Sibling pair	0.024 (± 0.16)	

Table S11.6: Mixed model Poisson parameter estimates (± SE) and p-values (based on Z-value) for the effect of the average height (standardized) and height^2 of the sibling pair, sex of the individual and their interactions on the number of children in opposite-sex[a] sibling pairs (N = 3,346). A random intercept was included for sibling pair.

	Parameter estimates (± *SE*)	***p*-value**
Intercept	0.95 (± 0.019)	<.001
Sex (ref. cat=male)	0.023 (± 0.026)	.37
Pair height	-0.029 (± 0.019)	.13
Pair height ^{2}	-0.048 (± 0.016)	.003
Sex * Pair height	-0.021 (± 0.025)	.41
Sex * Pair height^2	0.061 (± 0.021)	.004
Random effect	**Parameter estimates (± *SD*)**	
Sibling pair	0.024 (± 0.15)	

[a] Estimates were very similar when including same-sex sibling pairs (see main text, Table 11.1, and Table S11.4). No significant three-way interaction was found between sex and type of sibling pair (same-sex versus opposite sex) and the average height of the sibling pair (p = .41) nor the squared average height (p = .31). Thus, the effect of height was not specific to opposite-sex sibling pairs, nor could they be attributed to the inclusion of same-sex sibling pairs.

Table S11.7: Mixed model Poisson parameter estimates (± SE) and p-values (based on Z-value) for the effect of an individual's height (standardized) and height^2, sibling sex, and their interactions on the number of children by the sibling[a], while controlling for the sex of the individual (N = 7,044). Because we had data available from 3,522 pairs of siblings, a random intercept was included for sibling pair (see main text).

	Parameter estimates (± *SE*)	***p*-value**
Intercept	0.82 (± 0.039)	<.001
Sex (ref. cat=male)	0.021 (± 0.015)	.160
Sibling sex (ref. cat=male)	0.064 (± 0.018)	<.001
Height	-0.0067 (± 0.025)	.791
Height ^{2}	-0.012 (± 0.017)	.019
Sex sibling * Height	-0.012 (± 0.015)	.454
Sex sibling * Height^2	0.024 (± 0.010)	.017
Random effect	**Parameter estimates (± *SD*)**	
Sibling pair	0.025 (± 0.16)	

[a] Rather than analysing the effect of height on reproductive success within sibling pairs, a different approach to examine intralocus sexual conflict over height would be to examine what the effect of an individual's height is on the reproductive success of the sibling of that individual. This approach is more similar to that of Garver-Apgar et al. (2011), who showed that physically and hormonally masculine men and women rated their brothers as more attractive than their sisters. In line with this study, we predict that the height of an individual predicts the reproductive success of a sister differently than the reproductive success of a brother. Thus, a significant effect of an interaction between an individual's height and the sex of the sibling on the reproductive of that sibling is expected.

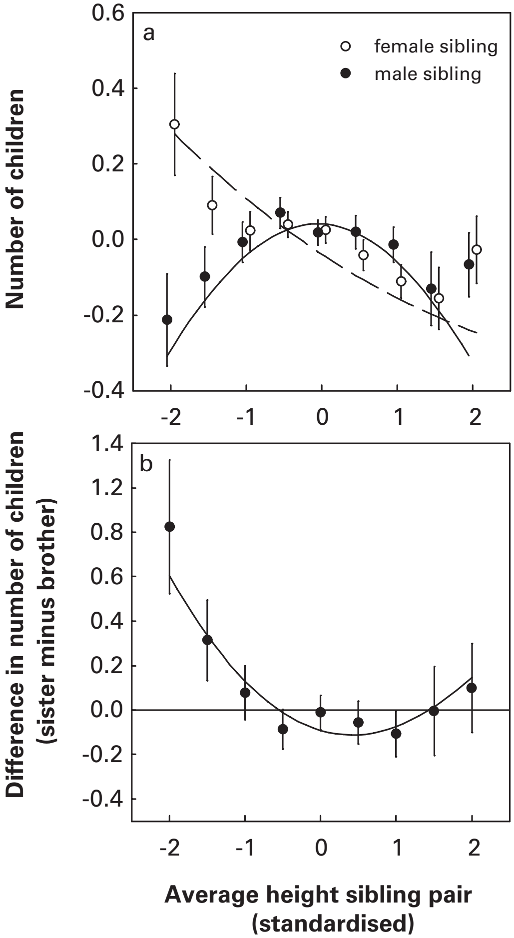

Figure S11.2: The effect of the average height of the sibling pair (average over heights standardised per sex) on (a) the number of children (*mean ± SE*) through the brother (closed circle and solid line) and the sister (open circle and dashed line; predictions based on estimates Table S11.4) and (b) the difference in reproductive success (pooled *SE* from (a)) between sisters and brothers (minus the overall average difference in number of children between the sexes – see text). Height was divided in bins of 0.5. Bins ≤-2 and ≥2 were pooled.

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Dutch summary

Samenvatting

Aan een rechtop lopend dier als de mens is lichaamslengte misschien wel het meest opvallende kenmerk. De variatie in lengte is enorm: de gemiddelde man uit Nederland is met zijn 185 cm bijzonder veel langer dan een gemiddelde Efe jager-verzamelaar uit Congo met zijn 150 cm. Maar ook binnen een populatie bestaan dergelijke grote verschillen: de 5% kleinste en 5% langste Nederlanders verschillen ongeveer 30 cm. In dit proefschrift behandel ik de vraag of er natuurlijke selectie plaatsvindt op deze variatie in lichaamslengte (**Hoofdstuk 1**). Meer specifiek geformuleerd: hangt lichaamslengte samen met eigenschappen die helpen bij het overleven en reproduceren, en derhalve bij het voorplantingssucces. Een belangrijk onderdeel van natuurlijke selectie is de zogeheten seksuele selectie. Te onderscheiden vallen de intra-seksuele selectie (wie overheerst tussen de seksegenoten?), en de inter-seksuele selectie (wie weet de andere sekse over te halen?). Of, bondiger: de strijd om het andere geslacht door kracht of door charme.

LICHAAMSLENGTE EN INTRA-SEKSUELE SELECTIE

'Een groot man' of 'een man van statuur' kan in de Nederlandse taal wijzen op een lange man, maar ook op een man van zeker belang of iemand die een grootse prestatie heeft geleverd. Soortgelijke associatieve verbanden zijn te vinden in veel andere talen. De samentrekking van lichaamslengte en de betekenis van bekwaamheid komt waarschijnlijk voort uit het feit dat langere mensen gedurende de menselijke geschiedenis een hogere status hadden. Ook in de hedendaagse maatschappij bestaat een duidelijke relatie tussen lichaamslengte en sociale status: langere individuen zijn vaker leiders, zijn vaker hoog opgeleid, hebben een hoger inkomen en hebben vaker banen met aanzien.

Ook in dit proefschrift blijkt dat de effecten van lengte op status substantieel kunnen zijn. In **Hoofdstuk 2** toon ik aan dat scheidsrechters gemiddeld 4 cm langer zijn dan hun assistenten in het professionele voetbal. Een ander voorbeeld betreft Amerikaanse presidenten, die gemiddeld 7 cm langer zijn dan de gemiddelde Amerikaanse mannelijke bevolking (**Hoofdstuk 3**); slechts 5 van 43 presidenten zijn kleiner dan het gemiddelde. Niet alleen de gekozen presidenten, maar ook de verliezende kandidaten zijn 7 cm langer dan de gemiddelde bevolking, wat suggereert dat lang zijn bijna onontbeerlijk is voor het Amerikaanse presidentschap, de baan met wellicht het hoogste aanzien in de wereld (**Hoofdstuk 3**).

Waarom zijn scheidsrechters langer dan hun assistenten en presidenten langer dan de gemiddelde Amerikaanse man? Meer algemeen, waarom bestaat er een relatie tussen lengte en status? Verschillende redenen voor deze relatie kunnen worden aangegeven, zoals de relatie tussen de lengte en de bezittingen van de ouders (waarbij de assumptie is dat rijkere ouders de middelen bezitten om hun kinderen zowel goed te kunnen laten groeien, als van goede status te kunnen voorzien), de positieve relatie tussen lengte en cognitieve capaciteit, en de positieve relatie tussen lengte en gezondheid. Al deze verklaringen gaan ervan uit dat de relatie tussen statuur en status een consequentie is van een derde onderliggende variabele. In dit proefschrift hypothetiseer ik echter dat lengte ook een directe invloed heeft op het behalen van hogere status, door middel van het overwicht dat langere individuen hebben tijdens sociale interacties. Deze hypothese is gebaseerd op bevindingen uit het dierenrijk waar grotere dieren door hun fysieke overwicht ten opzichte van kleinere dieren een grotere beschikking tot middelen alsook tot het andere geslacht hebben. Ondanks het feit dat fysiek geweld in aanzienlijke mate gereguleerd is in de hedendaagse maatschappij, veronderstel ik dat fysiek overwicht van langere mensen toch nog een invloed heeft tijdens confrontaties.

De eerste vorm van bewijs voor deze hypothese komt uit een steekproef van professionele scheidsrechters (**Hoofdstuk 2**). Mocht lengte een bepalende factor zijn in de interacties met het zelfde geslacht, dan zouden langere scheidsrechters mogelijkerwijs minder moeite hebben met het in het gareel houden van de spelers tijdens voetbalwedstrijden dan kleinere scheidsrechters. Dit blijkt het geval. Wanneer slechts de overtredingen gericht op andere spelers werden beschouwd (ergo, uitsluitend fysieke overtredingen en geen gevallen als ‘hands’ of buitenspel), dan bleken er minder van deze overtredingen te zijn tijdens wedstrijden geleid door langere scheidsrechters dan in wedstrijden geleid door kortere scheidsrechters. Wellicht mede doordat langere scheidsrechters de spelers op het veld beter onder controle hielden, werden ze vaker toegewezen aan belangrijke wedstrijden.

Alhoewel deze bevindingen suggestief zijn voor het feit dat langere mensen inderdaad een overwicht hebben tijdens sociale interacties, is de confrontatie tussen spelers en scheidsrechter uitzonderlijk in de zin dat scheidsrechters sowieso overwicht demonstreren vanuit hun rol. In **Hoofdstuk 3** onderzocht ik derhalve confrontaties zonder deze limitatie: de Amerikaanse presidentsverkiezingen. Zou in deze steekproef van toch al lange mannen (zie boven) lengte er nog toe doen bij het winnen van het presidentschap? Ja, alhoewel langere presidentskandidaten geen significant hogere kans hadden om de verkiezingen te winnen, kwam de lengte van de kandidaten wel overeen met het aantal stemmen dat werd verkregen. De kandidaat die langer was verkreeg vaker het overgrote deel, en het lengteverschil tussen de kandidaten was evenredig met het verschil in uitgebrachte stemmen voor beide. Meer dan 15% van de variatie in stemmen was gerelateerd aan het lengteverschil tussen de kandidaten. Resumeert men de percepties van experts, zoals historici en politicologen, over alle ooit regerende presidenten, dan blijkt dat de langere presidenten vaak als 'groots' worden afgeschilderd, terwijl kleinere vaak als presidentiële mislukkingen worden geschetst. Ook werden langere presidenten gepercipieerd als betere leiders en in het bezit van grotere communicatieve vaardigheden dan kleinere presidenten. Dergelijke percepties geassocieerd met lengte hebben mogelijk bijgedragen aan de verhoogde populariteit van langere presidentskandidaten.

Hoofdstuk 4 beschrijft of lengte er ook toe doet in meer alledaagse confrontaties tussen mensen. Drie observatiestudies en een experiment komen aan de orde. De eerste observatiestudie betrof het passeren van een smalle doorgang door voetgangers. De doorgang was dermate smal, dat slechts één persoon tegelijkertijd kon passeren. Het nemen of geven van voorrang bij gelijktijdige aankomst bij de doorgang werd geobserveerd en genoteerd. Alleen confrontaties van het gelijke geslacht werden in aanmerking genomen. Bij zowel mannen als vrouwen bleek dat personen die voorrang namen langer waren dan de personen die voorrang (moesten) verlenen.

Een tweede observatiestudie betrof de reacties van voetgangers in een drukke winkelstraat op tegemoetkomende onderzoeksassistenten van variabele lengte (telkens slechts één onderzoeksassistent). Voetgangers weken vaker uit voor de lange dan voor de kleine onderzoeksassistenten, ongeacht het geslacht van voetganger of onderzoeksassistent. Niet alleen weken de voetgangers vaker uit, ook waren zij minder geneigd fysiek contact te hebben met de langere assistenten.

Uit de derde observatiestudie bleek dat lichaamslengte ook gerelateerd was aan de afstand die individuen nemen ten opzichte van anderen. Onderzoeksassistenten werden zo gepositioneerd dat ze gedeeltelijke een druk bewandeld pad blokkeerden voor andere voetgangers. Degenen die het pad trachtte te bewandelen hadden een keuze: of het eigen pad zoveel mogelijk blijven bewandelen waardoor de onderzoeksassistent rakelings gepasseerd werd, of afwijken van het pad en de onderzoeker op een ruime afstand passeren. Wanneer een persoon van het zelfde geslacht het pad gedeeltelijke blokkeerde, waren langere voetgangers meer dan kleinere voetgangers geneigd om hun pad te blijven volgen en de onderzoeker dicht te naderen. Het tegengestelde effect vond overigens plaats wanneer een individu van het andere geslacht het pad blokkeerde.

Uit drie observatiestudies bleek aldus dat langere individuen overwicht hadden in kortstondige confrontaties, waarbij "winnen" of "verliezen" een gering tijdsverschil opleverde. Om te onderzoeken of een dergelijk met lengte geassocieerd overwicht ook stand zou houden in een langer durende interactie, waarbij bovendien een meer indrukwekkende beloning op het spel stond, werd het volgende experiment opgezet: biologiestudenten werd individueel gevraagd een taak uit te voeren, namelijk het aanbrengen van rangorde in een opsomming van objecten die van belang kunnen zijn bij het overleven in een koude omgeving. De taak werd vervolgens herhaald door willekeurig samengestelde paren (waarbij beide individuen van hetzelfde geslacht waren). Een beloning van 50 euro werd in het vooruitzicht gesteld voor het paar dat de rangorde van een expert het meest wist te benaderen. Bij het komen tot overeenstemming over een rangorde werd staand overlegd. De mate van overwicht in dit experiment werd uiteindelijk afgemeten aan de mate van overeenstemming van de individuele en de gezamenlijke rangordening. Wederom voorspelde lichaamslengte het overwicht tijdens de onderhandelingen: langere mannen en vrouwen weken minder van hun aanvankelijke rangordening af dan kleinere mannen en vrouwen (althans in situaties waar de individuen sterk van elkaar verschilden in aanvankelijke individuele scores).

Samenvattend: **Hoofdstuk 2**, **3** en **4** laten duidelijk zien dat lichaamslengte een rol speelt in de intra-seksuele competitie. Deze bevindingen sluiten nauw aan bij studies betreffende de prominente rol die lichaamsgrootte speelt in dominantie bij vele diersoorten, en die grotere dieren een betere sociale positie oplevert. Het grotere overwicht van langere individuen tijdens confrontaties draagt mogelijk ook bij aan de positieve relatie tussen lengte en sociale status. In het volgende gedeelte van dit proefschrift behandel ik de rol van lengte in het tweede aspect van seksuele selectie, namelijk de inter-seksuele selectie, ofwel de strijd om het andere geslacht door charme.

LICHAAMSLENGTE EN INTER-SEKSUELE SELECTIE

Lengte is vaak het object van onderzoek geweest in partnervoorkeurstudies, en uit deze studies blijkt dat over het algemeen langere mannen en vrouwen van gemiddelde lengte het meest aantrekkelijk worden gevonden. Door specifieker de voorkeuren voor partnerlengte te onderzoeken, blijken er verschillende voorkeursregels te kunnen worden geabstraheerd: i) langere individuen prefereren langere partners, ii) mannen en vrouwen prefereren een partner zodanig dat de man langer is dan de vrouw in het paar, iii) mannen en vrouwen prefereren grote verschillen in lengte tussen partners te mijden, en iv) langere vrouwen en kleinere mannen geven de voorkeur aan kleinere lengteverschillen tussen henzelf en hun partner, waar kortere vrouwen en langere mannen de voorkeur geven aan grotere lengteverschillen.

Door middel van een meer gedetailleerde vraagstelling van lengtevoorkeuren in **Hoofdstuk 5** en **6**, was ik in staat om de bovenstaande voorkeursregels verder te nuanceren en nadere patronen te ontdekken. Gevraagd naar de minimaal verlangde lengte van de partner, antwoordden vrouwen, maar niet mannen, per se in een koppel te willen belanden waarin de man langer is dan de vrouw. Ook waren vrouwen strikter in hun voorkeuren voor lengte dan mannen, en gaven vrouwen gemiddeld genomen aan een kleiner bereik van lengte van mannen te prefereren dan mannen bij vrouwen prefereren. Vrouwen gaven verder de voorkeur aan een ruimschoots langere man, terwijl mannen juist de voorkeur gaven aan een slechts weinig kortere vrouw. Er ontstond dus een conflict tussen mannen en vrouwen over het optimale lengteverschil binnen een koppel. Dit conflict vond ook zijn weerslag in de tevredenheid met in werkelijkheid gevonden partnerlengteverschillen. Uit de antwoorden van de participanten die een partner hadden, bleek namelijk dat vrouwen met een 23 cm langere partner het meeste tevreden waren over dit lengteverschil, terwijl mannen juist het meeste tevreden waren wanneer hun partner 8 cm kleiner was.

In aansluiting op de aldus gevonden voorkeursregels voor partnerlengte werd in **Hoofdstuk 6** nagegaan of deze voorkeuren ook tot uiting kwamen in de keuzes in een steekproef van speed-daters. In het speed-dating worden groepen alleenstaande mannen en vrouwen in de gelegenheid gesteld om kort met elkander te interacteren. Alle mannen hebben mini-dates van drie minuten met alle aanwezige vrouwen, waarna allen individueel en discreet op een formulier aangeven of ze de recentelijk ontmoete persoon nog eens willen zien (er wordt ‘Ja’ aangevinkt op een formulier). In het geval dat twee individuen voor elkaar 'Ja' aangeven, worden email adressen uitgewisseld (via de organisator van het speed-daten), waarna een meer traditionele afspraak kan worden georganiseerd.

Hoe goed voorspellen individuele voorkeuren voor partnerlengte de keuzes gemaakt tijdens het speed-daten? Alhoewel mannen en vrouwen meer geneigd waren om 'Ja' te zeggen tegen speed-daters die overeenkwamen met de lengtevoorkeuren, hadden ook de speed-daters die langer of korter waren dan de geprefereerde lengte een substantiële kans dat 'Ja' tegen hen gezegd werd. Ergo, partnervoorkeuren voorspellen keuze maar vele niet geheel geprefereerde individuen werden ook gekozen. Er zijn verscheidene redenen aan te wijzen waarom de gekozen partnereigenschappen tijdens het speed-daten verschillen van eerder aangegeven geprefereerde eigenschappen. Geprefereerde potentiële partners kunnen bijvoorbeeld simpelweg ontbreken tijdens het speed-daten. Verder speelt mee dat het aantal eigenschappen en voorkeuren waarmee rekening gehouden dient te worden zo groot is, dat het onwaarschijnlijk is dat aan alle voorkeuren voldaan kan worden. Zelfs nadat een geprefereerde partner gekozen is, kunnen rivalen de paarvorming dwarsbomen. Ook kan een keuze simpelweg niet geapprecieerd worden door de gekozene. Eerder werd bijvoorbeeld genoemd dat vrouwen een groter lengteverschil tussen partners prefereren dan mannen doen, en dit kwam ook tot uiting in de keuze tijdens het speed-daten: vrouwen waren het meest geneigd om 'Ja' te zeggen tegen een man die 25 cm langer was dan de vrouw, waar mannen het meest geneigd waren om 'Ja' te zeggen tegen een vrouw die 8 cm korter was. De ontstane koppels in het speed-daten (de gevallen waar beide individuen 'Ja' zeiden) waren het meest waarschijnlijk bij een lengteverschil van 18 cm. Het seksueel conflict in partnervoorkeuren en keuze met betrekking tot lichaamslengte resulteert dus in koppels die door beide seksen niet geheel naar wens zijn.

Ook uit **Hoofdstuk 7** blijkt dat partnervoorkeuren voor lengte lang niet altijd volledig gehonoreerd worden. In een steekproef van Britse ouders werd nagegaan of partnervoorkeuren voor lengte ook tot uiting kwamen in daadwerkelijk tot stand gekomen koppels. De bovengenoemde partnervoorkeuren waren allen aanwezig in de koppels: i) langere individuen hadden vaak langere partners, ii) de man was vaker langer dan de vrouw dan op basis van kans verwacht mocht worden, iii) grote lengteverschillen waarbij de man substantieel langer was dan de vrouw kwamen ook minder vaak voor dan op basis van kans verwacht mocht worden, en iv) langere vrouwen en kleinere mannen hadden gemiddelde genomen kleinere partnerverschillen dan kortere vrouwen en langere mannen. Alhoewel alle partnervoorkeuren tot uiting kwamen in de koppels, waren er ook veel koppels waarin de voorkeuren geschonden werden. Wederom bleek dat partnervoorkeuren niet altijd gerealiseerd worden.

In conclusie, lichaamslengte hangt samen met zowel intra-seksuele (**Hoofdstuk 2-4**) als inter-seksuele selectie (**Hoofdstuk 5-7**), suggererende dat de lengte van een individu van invloed is op het bemachtigen van een partner. Niet alleen is het verkrijgen van een partner van belang voor het voorplantingssucces van een dier, ook zijn de gezondheid en de overlevingskansen van het dier en zijn nakomelingen cruciaal voor dit succes. Lichaamslengte blijkt ook samen te hangen met deze aspecten van natuurlijke selectie.

LICHAAMSLENGTE, GEZONDHEID EN OVERLEVING

Lange mannen en vrouwen van gemiddelde lengte blijken het meest gezond. Ook hangt lichaamslengte samen met levensduur, en blijken zowel langere mannen als langere vrouwen ouder te worden dan kortere individuen. Deze gegevens spelen mogelijkerwijs een rol bij de overleving van het nageslacht. In deze these presenteer ik twee voorbeelden van de relatie tussen lichaamslengte en het welzijn van de kinderen. **Hoofdstuk 8** beschrijft het grotere risico op een noodkeizersnede die kleinere vrouwen hebben ten opzichte van langere vrouwen. Dus, kleinere vrouwen zijn in dit opzicht in het nadeel wat betreft de daad van reproduceren. Niet alleen de maternale lichaamslengte had een voorspellende waarde voor problemen bij de geboorte, ook de lengte van de partner deed er toe. Hoe groter de lengteverschillen tussen de moeder en de vader van de nieuwgeborene, des te groter de kans dat de baby via een keizersnede ter wereld kwam. De geboorte van een kind via een noodkeizersnede heeft vaak nadelige gevolgen op de gezondheid in het latere leven van de pasgeborene.

Ook uit **Hoofdstuk 9** blijkt dat het negatieve effect van kleinere maternale lichaamslengte niet beperkt blijft tot de bevalling, maar zich doorzet tot in de overleving van de kinderen. In bijna alle onderzochte non-Westerse populaties, krijgen langere moeders kinderen met een hogere overlevingskans dan kleinere moeders. Zelfs in de bestudeerde Westerse populatie bleek dit het geval (**Hoofdstuk 9**). Samenvattend: lichaamslengte hangt ook samen met de gezondheid en overlevingskansen van een individu en het nageslacht van dat individu, wat waarschijnlijk zijn weerslag vindt in het voortplantingssucces.

DE RELATIE TUSSEN LICHAAMSLENGTE EN REPRODUCTIEF SUCCES

Omdat lichaamslengte samenhangt met vele evolutionair relevante variabelen is natuurlijke selectie op deze eigenschap dan ook waarschijnlijk. Mannelijke lichaamslengte is positief gerelateerd aan gezondheid, status en inkomen (**Hoofdstuk 2-4**), en ook hebben langere mannen een voordeel bij het aantrekken van de andere sekse (**Hoofdstuk 5** en **6**). Op basis van deze associaties, kan dus worden verondersteld dat langere mannen meer reproductief succes hebben dan kleinere mannen. Voor vrouwelijke lichaamslengte geldt een gecompliceerder verhaal. Uit eerder onderzoek blijkt dat kleinere vrouwen eerder vruchtbaar zijn, wat hun voorplantingssucces mogelijk positief beïnvloedt. Daarentegen hebben kleinere vrouwen een grotere kans op problemen bij geboortes (**Hoofdstuk 8**) en kindersterfte (**Hoofdstuk 9**). Als gewenste partner lijken vrouwen van gemiddelde lengte het meeste succes te hebben (**Hoofdstuk 5** en **6**), en ook qua gezondheid is gemiddelde lengte optimaal. Er is dan ook geen eenduidige voorspelling te maken over hoe reproductief succes samenhangt met vrouwelijke lichaamslengte.

Vrouwelijke lichaamslengte en reproductief succes

Gebruik makende van een grote steekproef vrouwen uit Wisconsin (VS) kon ik vaststellen dat kleinere vrouwen een hoger reproductief succes hadden dan langere vrouwen (**Hoofdstuk 9**). Kleinere vrouwen hadden een groter aantal kinderen ondanks de hogere kindersterfte dat deze vrouwen ervoeren. Een literatuurstudie bevestigde de negatieve relatie tussen lengte en reproductief succes in Westerse populaties. De selectiedrukken op lichaamslengte in niet-Westerse samenlevingen waren zeer variabel van aard. Een gedeelte van de variatie in deze resultaten heeft vermoedelijk te maken met de relatie tussen lichaamslengte en kindersterfte in de eerste jaren na de geboorte. In populaties met hoge kindersterfte lijken langere vrouwen in het voordeel ten opzichte van kleinere vrouwen, vanwege de hogere kansen op overleven van de kinderen van langere vrouwen.

De bevinding dat kleinere vrouwen hoger reproductief succes behalen is mogelijk te verklaren uit de “afweging” binnen een lichaam om te “kiezen” tussen groei, herstel, of reproductie. Energie kan slechts éénmalig geïnvesteerd worden en energie gestoken in één aspect van het dier gaat ten koste van een ander aspect van het dier. Deze gedachtegang maakt deel uit van de zogenaamde “life history theory”. De omgeving bepaalt in hoge mate in welk aspect geïnvesteerd wordt, en dergelijke afwegingen kunnen grote consequenties hebben, ook voor lichaamslengte. Bij kleine vrouwen komt de niet in groei geïnvesteerde energie kennelijk vrij ten bate van reproductie, en zo zijn zij in staat om eerder te beginnen met reproduceren. En inderdaad beginnen kleinere vrouwen eerder met reproduceren dan langere vrouwen. Eerder onderzoek heeft aangetoond dat de leeftijd waarop het eerste kind geboren wordt een sterke invloed heeft op het uiteindelijke reproductieve succes. Het verhoogde reproductieve succes van kleinere vrouwen wordt dus mogelijk verklaard doordat er geïnvesteerd is in reproductie ten koste van groei. De omgeving is overigens niet de enige bepalende factor in dit verband. Dat kleinere vrouwen op jongere leeftijd reproduceren heeft ook een genetische basis: die vrouwen die op jonge leeftijd hun eerste kind krijgen, blijken genetisch te zijn aangelegd om kleiner van stuk te zijn. Samenvattend, de selectie op vroege aanvang van reproductie lijkt kleinere vrouwen een reproductief voordeel op te leveren.

Mannelijke lichaamslengte en reproductief succes

De in **Hoofdstuk 9** al genoemde Wisconsin steekproef kon ik ook gebruiken om af te leiden dat mannen van gemiddelde lengte het grootste aantal kinderen hadden (**Hoofdstuk 10**). Dit was mede te verklaren doordat mannen van gemiddelde lengte op jongere leeftijd trouwden en hun eerste kind kregen, dan kleinere en langere mannen. Wederom bevestigde een literatuurstudie dit curvilineaire effect van lengte op reproductief succes bij mannen in Westerse populaties. De relatie tussen lengte en het aantal kinderen was wederom variabel in niet-Westerse maatschappijen. De redenen voor deze variatie is vooralsnog onduidelijk, alhoewel de eerdergenoemde afwegingen tussen het investeren in groei, herstel en reproductie een mogelijke rol spelen.

Het verhoogde reproductieve succes van mannen van gemiddelde lengte ten opzichte van langere mannen is opvallend te noemen. Immers, mannelijke lichaamslengte hangt positief samen met evolutionair relevante variabelen als gezondheid, inkomen en aantrekkelijkheid. De 'kwaliteit' van de partner speelt hierbij misschien een verklarende rol. Uit **Hoofdstuk 5** en **6** blijkt dat kleinere vrouwen voorkeur geven aan mannen van gemiddelde lengte, en dat lange mannen lange vrouwen prefereren. Gegeven deze voorkeuren is het dan ook niet verbazingwekkend dat lange mannen het minst waarschijnlijk zijn om een kleine vrouw als partner te hebben (**Hoofdstuk 1, 6** en **7**). Het verlaagde reproductief succes van lange mannen ten opzichte van mannen van gemiddelde lengte wordt mogelijk verklaard door het feit dat de laatste vaker gepaard zijn met kleinere vrouwen, die meer kinderen voortbrengen. Ergo, de lengte van de partner is mogelijk een bepalende factor in het reproductieve succes van mannen.

Intralocus seksueel conflict

Gezien de verschillende selectiedrukken op mannelijke en op vrouwelijke lichaamslengte dringt zich de vraag op of er mogelijk sprake is van een intralocus seksueel conflict. Een dergelijk conflict ontstaat wanneer, met betrekking tot het reproductieve succes, de expressie van een eigenschap voordelig voor de ene, maar nadelig voor de andere sekse is. Wijde heupen hebben is bijvoorbeeld voordelig voor het reproductieve succes van vrouwen, maar nadelig voor dat van mannen. Gelijkerwijze is kleine lichaamslengte voordelig voor het reproductieve succes van vrouwen, maar nadelig voor dat van mannen. Aangezien langere ouders zowel langere zonen als langere dochters krijgen en kleinere ouders zowel kleinere zonen als kleinere dochters, zouden families van kleineren potentieel meer reproductief succes behalen via de vrouwen in die families dan via de mannen. Voor gemiddelde lengte families zou het tegenovergestelde gelden. Dit is inderdaad wat ik heb aangetoond in **Hoofdstuk 11.** Er heerst dus een intralocus seksueel conflict over menselijke lichaamslengte dat het reproductieve succes beïnvloedt.

In conclusie, er bestaat, zo blijkt uit dit proefschrift, *natuurlijke selectie op lichaamslengte in hedendaagse menselijke populaties*.

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