MATHEMATICAL MODELING OF FLUCTUATIONS IN HUMAN HEIGHT: THE ROLE OF GENDER EQUALITY AND EQUITABLE MATE SELECTION

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Abstract

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The rapid increase in European height during the mid to late nineteenth century has yet to be fully explained. Improved nutrition and decreased pathogen exposure can account for some, but not all of the observed increase in average height for particular European countries during this period. A new model is proposed that incorporates evolved psychological preferences for taller mates in addition to effects of improved nutrition and sanitation. In humans, height correlates positively with social status, economic well-being and reproductive success, and the preference for height in human mate selection shows key hallmarks of an evolved psychological trait that arose through sexual selection. However, cultural practices can sometimes override evolved psychological traits.

I argue that practices such as arranged marriages and political disenfranchisement of women, which were common in Europe until late 19th century, suppressed the effect of sexual selection for height. However, as European cultures became more socially progressive, sexual equality increased, allowing innate mate selection preferences to be expressed more fully. I use a cultural historical analysis and population genetics modeling to show that, in three European countries, average height increased rapidly after cultural changes that led to greater freedom in female mate selection, and that the rate and degree of height increase fits well what would be expected from a sexual selection process.

Sweden and Portugal are used as case studies to test the relationship between gender equality and the expression of sexual selection for height. Archival records of population heights and distributions were collected from previous studies, military registries, government censuses and statistical records.

Using estimates of the heritability of and sexual selection for height, a population genetics model was created to explore the rapid evolution in height. This paper expands upon previous quantitative genetics models of population height increases by factoring in cultural changes that affected the expression of an evolved mate preference for height. A non-linear difference equation model was generated which included sexual selection pressures, heritability statistics, and quantified measures of gender equality. For each of the countries examined, my model yields estimates of average population height increases that closely fit observed height changes.

Results suggest that changes in cultural norms in the late 19th century in Sweden and Portugal unmasked an innate mate selection preference for height. Increased freedom of mate selection led to a period of average population height increase that is attributable in part to sexual selection. This new model of changes in human height, by incorporating psychological and cultural factors, more accurately accounts for the changes in European height during this era than do previous accounts based on improved nutrition and health alone.

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I WOULD LIKE TO THANK MY COMMITTEE FOR THERE REVISIONS AND SUPPORT AND SPECIAL THANKS TO MY WONDERFUL WIFE JESSICA FOR ALL OF HER SUPPORT AND LOVE. LAST BUT NOT LEAST, THE PUGS, LUCY AND MOJO FOR THEIR MANY HOURS OF PUG THERAPY.

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Introduction

> "For my own part I conclude that of all the causes which have led to the differences in external appearances between the races of man, and to a certain extent between man and the lower animals, sexual selection has been by far the most efficient"
> Charles Darwin, Descent of Man and Selection in Relation to Sex, 1871

Psychological research has extensively explored the female preference for taller mates (Norm, 1996). Studies ranging from simple surveys and questionnaires (Hensley, 1994) to observations of dating service records (Pawlowski & Koziel, 2002) and results from speed dating sessions (Kurzbanand & Weeden, 2005), have found that women prefer men who are taller than themselves.

Several explanations have been proposed for this female preference for height. Taller males have been found to have higher immunocompetency (Saino, Moller & Bolzern, 1995; Silventoinen, Lahelma, & Rahkonen, 1999), be perceived as more dominant (Barber, 1994), more powerful and of higher status (Bielicki & Charzewski, 1983), are considered more honest and trustworthy (Melamed, 1992), receive better educations (Silventoinen & Lahelma, 2000) and are in general more attractive mates (Geary, 2004). More generally, the sexually dimorphic characteristic of height provides an important, unalterable visual cue for "good genes" (Hume & Montgomerie, 2001) and the evolutionary quality of a potential mate (Barber, 1994). These theoretical benefits of taller mates have been found to influence actual mating behaviors of women (Rhodes, Simmons, & Peters, 2005).

During the mid to late nineteenth century many European populations experienced a rapid increase in the mean heights of the population (Eveleth & Tanner, 1990; Komlos, 1994). Over the years there have been numerous hypotheses proposed by economists, psychologists, sociologists, geneticists, biologists and anthropologists to explain this phenomenon. Many of these hypotheses have contended that improvements in standards of living can account for the observed increases in height. However, for most European populations the rapid increases in population height began prior to the introduction of these advances, so improved standards of living cannot be the complete explanation. This thesis proposes that sexual selection also contributed to the rapid increase in heights observed in certain countries during the 19th and 20th centuries. Specifically, social changes that granted women greater freedom in selecting mates unmasked the expression of an ancient, evolved preference for taller mates, leading to positive selection for height that drove an overall increase in average population height.

Fluctuations in European height by population: Sweden

Sweden was one of the first European nations to experience an increase in population mean height and is now one of the tallest populations on earth. Throughout the middle Ages and into the industrial revolution Swedish heights remained relatively stable, with two exceptions as noted in the discussion (Gustafsson, Werdelin, Tullberg, & Lindenfors, 2007). However, starting in the mid 1800’s there was a drastic increase in height (Figure 1). In 1840 the male population mean height was recorded at 167.6 cm and by 1965 the mean height had climbed to 179.3 cm (Garcia, 2007; Sandberg & Steckel, 1987)

Figure 1. Swedish male, female and mean heights 1840-1979.

Fluctuations in European Height by Population: Portugal

Similarly, historical records indicate that Portugal's population mean height began a steady upward trajectory starting around 1900 (Padez, 2002; Padez & Johnston, 1999). In 1904 the mean height in Portugal was recorded at 157.7 cm and by 1998 the average height had climbed to 167.46 cm, an increase of 9.76 cm.

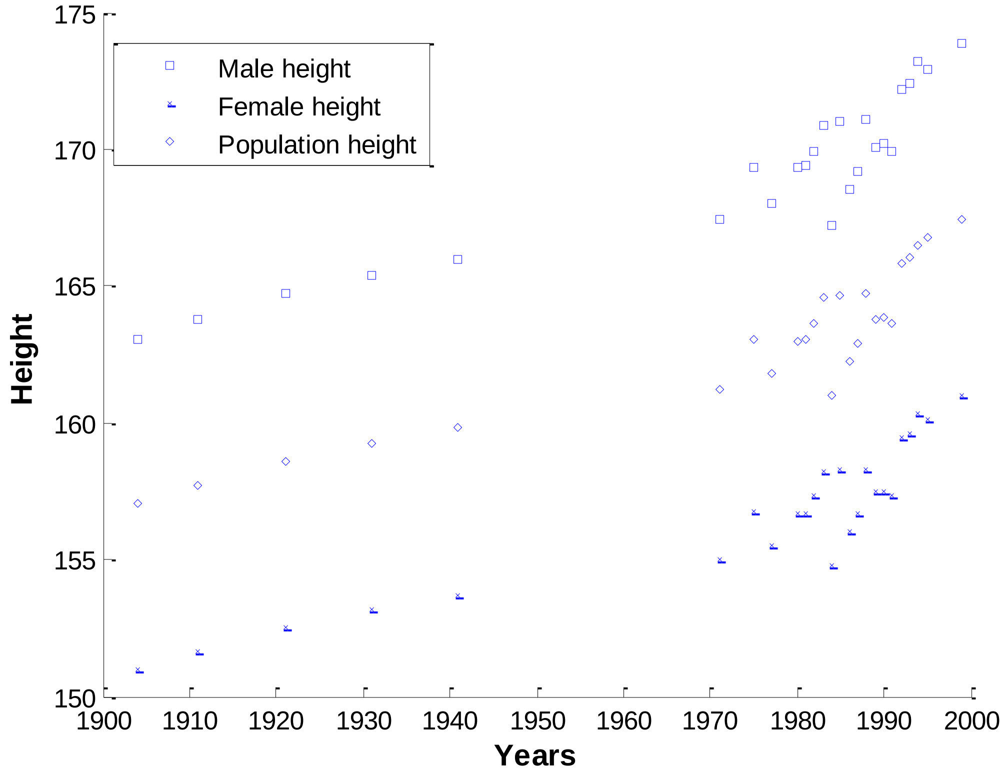

Figure 2. Portugal mean male, female and population height 1904-2000.

General Trends in European Height

There was a steady upward trend in mean heights across Europe beginning in the mid to late nineteenth century (Jorden, 1999), and this trend, although the rate of increase has slowed, continues to be observed today (Rosenbaum, 1988). In addition to Sweden and Portugal, archival records have been used to analyze the European populations of Great Britain (Cole, 2000; Floud & Harris, 1997; Floud & Wachter, 1982), Turkey (Ozer, 2008), Finland (Silventoinen, Kaprio, Lahelma, & Koskenvuo, 2000), Spain (Onland-Moret et al., 2005), and Poland (Bielicki & Szklarska, 1999).

Proposed Theories for Changes in European Height

The upward trend in height in Europe in the past 150 years has been attributed to accessibility to general improvements in the standard of living including public health infrastructure, nutrition, pathogen exposure and even education and socio-economic status (Burstrom, Macassa, Oberg, Bernhardt, & Smedman, 2005; Fogel et al., 1983; Haines, 2004; Kuh, Power, & Rodgers, 1991; Padez, 1999; Padez, 2002; Peck & Lundberg, 1995; Steckel, 1995; Tanner, 1992). These causes will be referred to in this paper as environmental causes to distinguish them from population genetic changes that may have also influenced height. However, all of these environmental causes affect height through their effects on biology, especially development. The evidence for each of these proposed causes is examined below.

Improvements in general standard of living. Perhaps the strongest of these environmental arguments was made based on observations of Mayan immigrant populations (Bogin, Smith, Orden, Silva, & Loucky, 2002). The axiological measurements of a population of Guatemalan refugees and their children living in America were observed for a period of twenty years. It was observed that the first generation of immigrant children was significantly taller than their non-immigrant counterparts. Since the increase occurred in a single generation it was hypothesized that it was a result of the higher standard of living experienced in America. However, they also noted that the mean height of the second generation was still significantly lower than their American and European counterparts.

Adoption studies have also been used to evaluate the effect of environmental influence on height. Infants who are institutionalized for long periods of time can develop significant lags in their heights and that if the infants were adopted before or during a particular critical point of development (approximately 18 months) they could catch up to their adopted counterparts' adult height (Ijzendoorn, Marinus, Bakermans-Kranenburg, Marian, Juffer, & Femmie, 2007) . This study provides support for the idea that the environment during early postnatal development has a powerful influence on the adult height that is achieved.

Sanitation and running water. Strong correlations between the implementation of public health projects and increases in European mean heights also support a causal relationship between postnatal environment and adult height (Fogel, Engerman, & Trussel, 1982). Implementation of water and sanitation systems in developing countries has been correlated with increases in adult height (Esrey & Habicht, 1986). In one of these analyses British children that were raised in homes without accessibility to hot tap water were found to be an average of 4 cm. shorter than their counterparts (Kuh & Wadsworth, 1989).

Nutrition. Nutritional accessibility has been argued to be a critical determinant of height (Malina, 1979). Nutritional deficiencies during early childhood development were found to have a detrimental effect on adult height (Schmidt, Jorgensen, & Michaelsen, 1995; Luo & Karlber, 2000). Correlation studies have examined the relationship between the increase in Japanese height following World War II and milk consumption by children. It was observed that the introduction of milk distribution programs was correlated with a sudden increase in Japanese height (Takahashi, 1984).

Pathogen exposure. The sudden increase in European heights has also been attributed to the decrease in exposure to pathogens (Beard & Blaser, 2002). It is known that pathogen exposure in early development can have a detrimental effect on the expression of the genetic height potential (Dowd, Zajacova, & Aiello, 2009). For example, British children who had suffered from four or more bouts of pneumonia or bronchitis were found to be an average of a full inch shorter than those who had not had a history of infection (Tanner, 1962). While public health generally improved throughout Europe during the 19th century, pathogen exposure may have increased during this period due to increased population densities and travel. Therefore it is difficult to predict how this particular environmental modifier of height would have changed overall adult height.

Other observed correlations. Variations between socio-economic groups in cross-cultural studies have found differences based on education levels (Cavelaars et al., 2000). Historical reviews of the economic well-being of European nations during the industrialization of Europe have attempted to correlate changes in height with changes in real income and economic developments (Fogel et al., 1982). As early as the seventeenth century it was observed that nutrition and sanitation played a critical role in an individual's height (Tanner, 1981). London boys employed full time in factory labor during the late eighteenth century and first half of the ninetieth century were found to be of shorter stature than their non-employed counterparts (Floud & Wachter, 1982).

Improvements in Sanitation and Nutrition by Population: Sweden

In the last 40 years of the nineteenth century Sweden made significant advances in public health and sanitation. The first set of advances pertained to piped water and fresh water supplies. In 1861 the first piped water was introduced to Stockholm and by 1896 nearly half the population of the city had accessibility to clean water (Burstrom et al., 2005). In 1874 the first sanitation ordinance was established to insure the sanitary removal of wastewater.

The second set of advances pertained to sewage and waste treatment. In 1894 there were only 40 premises that had private water closets (precursors to the modern septic tank). This number increased to 1,506 premises in 1904 and by 1909 the first waste water treatment facility was built and most urban areas had waste removal services (Burstrom et al., 2005).

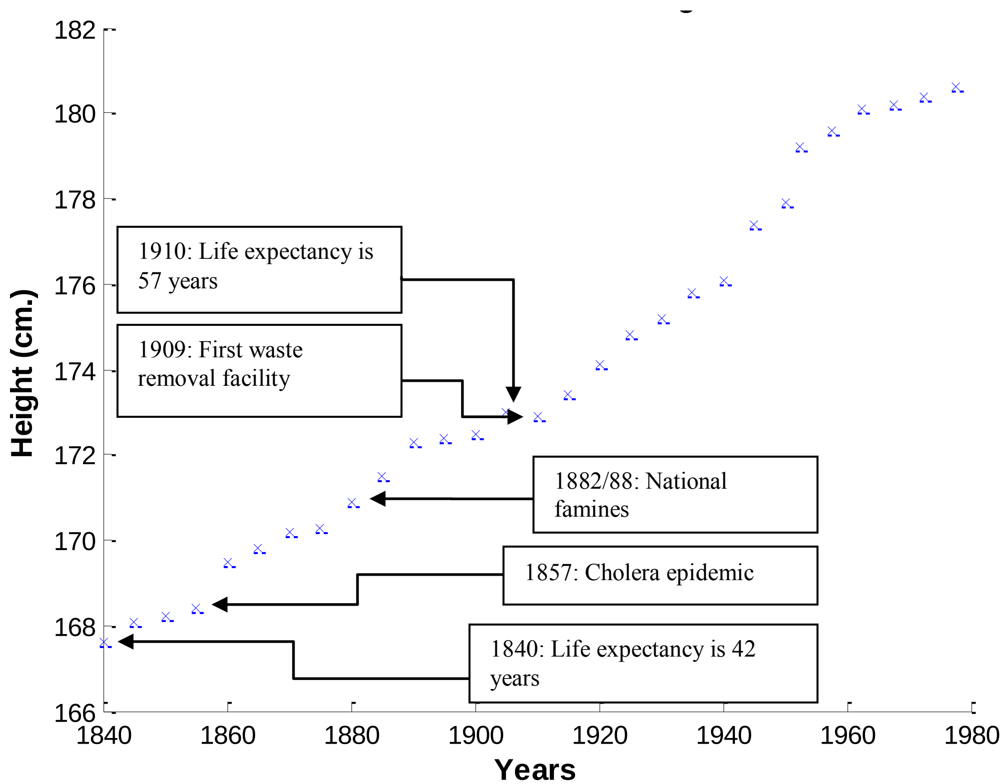

Figure 3. Swedish changes in standard of living from 1840-1980 compared with increases in mean male height through time.

In addition to advances in accessibility to clean water and sewage there was an increase in availability in medical services as well. In 1850 there were only 400 physicians on record in the whole of Sweden. However by 1880 there were 555 and by 1900 there were over 1,100 (Porter, 1994).

Improvements in Sanitation and Nutrition by Population: Portugal

In contrast to the early development of sanitation and water systems in Sweden, Portugal did not begin developing sewage or piped water systems until the 1960's. Since the 1960's there has been a rapid development in sanitation and water systems.

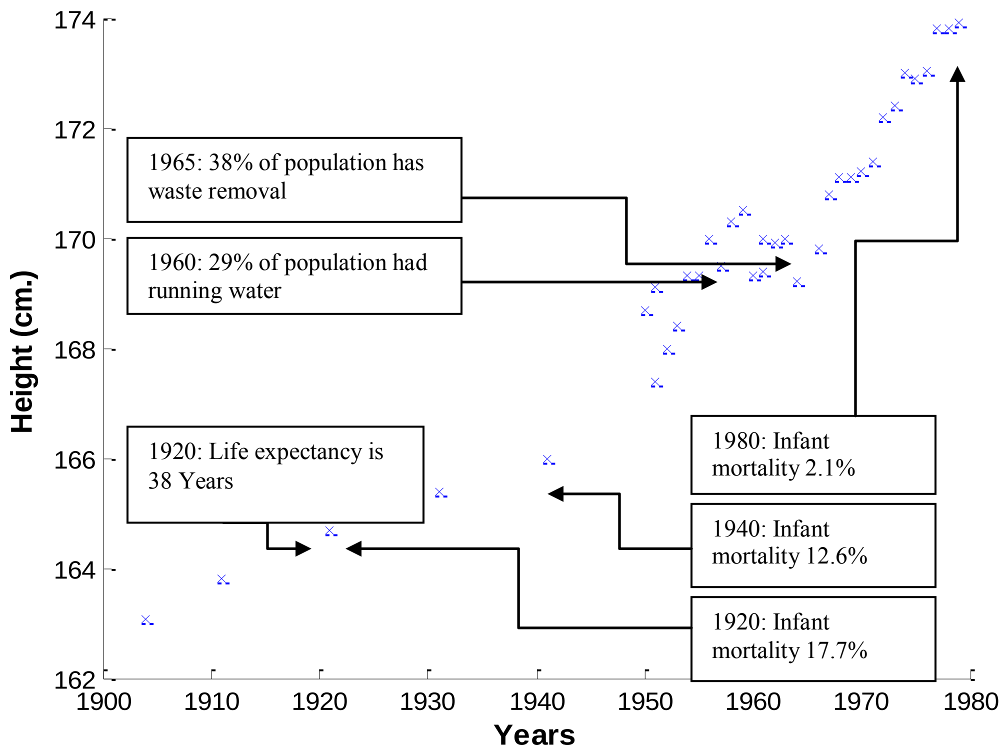

Figure 4. Portugal changes in standard of living from 1900-1980 compared with increases in mean male height.

In the late 1960's only 28.9% of the population had running water, 38.3% had accessibility to sewage facilities and only 18.6% had showers or bathtubs (Padez, 2002). By the end of the 1990's there had been a drastic reversal in accessibility with 86.8% of the population having running water, 90.7% having modern sewage facilities and 81.8% having indoor bathtubs or showers (Padez, 2007).

Shortcomings of Environmental Theories of Height Increase

Despite the significant evidence supporting the claim that environmental causes such as pathogen exposure limit the expression of the mean height of the population, there is insufficient support for the argument that environmental changes alone account for the phenotypic changes observed in each population's height (Xu, 2006). While nutritional deficiencies and pathogen exposure may inhibit the expression of genetic height potentials it cannot alter the genetic potential height. That is to say, nutritional deficiencies do not alter the genes that influence height, just the expression of those genes.

The advantages of less pathogen exposure in the population are not a selection upon any particular trait; an individual who is above or below the mean height receives the same advantages as everyone else in the population, prohibiting a genetic shift from occurring. If it was the case that greater pathogen exposure was occurring in individuals who were shorter than the mean height or that nutritional improvements were only occurring in isolated pockets, leading to a few taller individuals, then the genetic "target" height of the population could change.

Additionally, if population-wide environmental changes like sanitation and water accessibility were the driving force behind the increase in European height then we would not expect to observe changes in average population height until their introduction. In both populations, the rapid increase in height began prior to widespread introduction of public health improvements.

Perhaps the best argument against the hypothesis of improved sanitation playing the pivotal role in European height increases is the case of Portugal. In Portugal, from 1904 to 1996 the average increase in male height was 8.99 cm. (Padez & Johnston, 1999). Unlike other European nations Portugal did not experience a sudden accessibility to sanitation and cleaner environments in the early 1900's. It was not until the 1960's that 40% of the nation had accessibility to sewage systems, and still less than 30% of the population had running water (Padez, 2002).

This lag in accessibility to sanitation provides a unique opportunity to examine the influence of sanitation and living conditions on height. Despite this delay in public health improvements a drastic increase in the average height within the population is observed. Beginning in 1904, the mean height of Portuguese men began a steady upward climb. In 1904 the mean male population height was 163.2 and by 1960 it had increased to 166.5 (Padez, 2002). Nearly 40% of the total change in average population height in Portugal had occurred prior to the introduction of improved sanitation. If the increase in height was attributable to accessibility to sanitation, lack of exposure to pathogens or increases in standards of living, then an increase in height would not be expected until the 1960's at the earliest. Instead the upward trend occurs some six decades earlier, and nearly half of the total increase in Portuguese height to date occurred prior to implementation of those public health improvements.

In addition to these discrepancies between public health advances and changes in Portuguese population heights, the economics and historical literature reveal what is known as the antebellum puzzle (Margo & Steckel, 1983), first observed in America and then in several other European nations during the first half of the nineteenth century (~1800-1850's). American heights drastically decreased despite the substantial increase in real income, public infrastructure and general social development (Haines, Craig, & Weiss, 2003; Komlos, 1998). While public works projects were improving health, sanitation standards, and real wages, mean population heights experienced significant downward trends.

A paradox similar to the antebellum puzzle can be found in Poland following World War II. Following decades of rapid increases in mean height, the Polish population experienced a short-term reversal whereby their mean height stopped increasing and for a short span decreased. Although post war reconstruction provided many new infrastructure improvements in sanitation and nutrition, heights trended downward. In light of these conflicts alternatives to the strictly environmental argument need to be examined.

Evolution of Mate Preferences

The evolution of preferences for specific traits in mating partners through sexual selection is one of the most active areas of research and theory in evolutionary psychology. Sexual selection, a term introduced by Darwin, refers to the selection of traits in one sex by members of the other sex. The most common example of sexual selection is peacocks. Females choose males with large decorative feathers, so over the generations the feathers of males became larger. Sexual selection is distinguished from natural selection, in which aspects of the environment, not members of the other sex, select for specific traits. As the epigraph of this thesis implies, sexual selection is believed to be responsible for many remarkable traits of animals. Sexual selection is likely to be especially important in shaping psychological traits such as preferences since mating often requires social communication and decision making, which are psychological functions.

In many species females are more discriminating than males in selecting mating partners, arguably because their reproductive physiology is more costly than that of men and because of the limited number of potential offspring. Women who preferred useful traits in males reproduced more successfully or had offspring that survived at a higher rate than those who didn't. Theoretically the children of such women inherited the same preferences, until these preferences spread throughout the population. There have been a host of observed evolved sexual selection preferences by women including preferences for economic resources (Waynforth & Dunbar, 1995), higher social status (Davis, 1990), somewhat older men (Buss, 1993), good health and physical appearance (Buunk, Pieternel, Detlef, & Kenrick, 2002) and similarity (Wilson, Cousins, & Fink, 2006). There is evidence that each of these traits conferred reproductive advantages for offspring.

From an evolutionary perspective the preference for taller men makes sense. Male height is an unalterable signal of potential contributions to offspring. Height is a signal that a mate is more able to provide not only accessibility to resources but better immune-response genes (Manning, 1995; Pawlowski, 2000). Taller men have been found to be perceived more positively in social groups (Bielicki & Charzewski, 1983), receive better educations (Schumacher & Knussman, 1979) and subsequently have more opportunities to provide for offspring. This potential social and personal contribution to offspring is a powerful incentive for mate selection (Buss, 1993).

From a genetic perspective height is an important signal of good genes (Gangestad & Simpson, 2000). Taller men have been found to live longer than their shorter counter parts (Kemkes & Grottenthaler, 2005). This powerful combination of social and genetic advantages for the children of taller men provides a strong basis for expecting positive sexual selection pressure for height in humans. Sexual selection for height has been well documented in a host of cultures (Pierce, 1996). This female preference for taller mates can also be observed across a range of cultures (Buss, 1989) further supporting the hypothesis that it is an evolved psychological trait. This preference has ramifications in the quality and quantity of mates a male might have as well. Taller men are found to have “prettier girlfriends” (Feingold, 1982), as defined by feminine characteristics such as desirable hip-to-waist ratios and skin quality. Taller men also have more long term and short term mates (Rhodes et al., 2005) and have sex at earlier ages and later into life (Buss & Schmitt, 1993). Women’s preference for tall mates also increases during the follicular phase of the menstrual cycle, when the probability of conception is greatest, which also argues for the adaptive origin of this preference (Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004; Pawlowski & Jasienska, 2005). Finally, infidelity studies have found that when a woman cheats she is more likely to do so with a mate who is taller than her current partner (Gangestad & Thornhill, 1997).

Consistent with the theory of sexual selection for height, taller men have been found to have more offspring than shorter men (Pawlowski, Dunbar, & Lipowicz, 2000). There is also evidence that taller men are more likely to have long term mating partners and to have more partners than shorter men (Nettle, 2002). This reproductive success provides evidence of a directional selection pressure for male height (Mueller & Mazur, 2001).

There have been some important limitations observed for the male height preference. First, the height preference is dimorphic with women preferring men who are taller in relationship to themselves at a ratio of 1.08 (Fink, Neave, Brewer, & Pawlowski, 2007; Pawlowski, 2003). Secondly, the preference for height is limited to heights that are within the norms of the population (Salka et al., 2008). Extreme male height, relative to the population and to the female has been found to have a detrimental effect on female mate selection (Hensley, 1994). Another limitation to the effect of female preference for taller men on the evolution of population height is the freedom that women have to choose the men they mate with. But that freedom is likely to have changed considerably across the history of the human species. Greater freedom in female mate selection should result in more selection for height and greater increases in population height. The next section describes changes in women's freedom of mate selection in recent recorded history, and how they might relate to changes in average population height.

Gender Relations and Equality Indexes

Multiple indexes have been created in an effort to empirically measure gender equality across cultures, demographic regions and through time (Apodaca, 1998). The gender equality measures are expected to correlate strongly with mate selection freedom so they are used as an indirect index of mate selection freedom. The most common gender equality indexes are described below.

GEM/GDI. In 1995 the United Nations Human Development report introduced, alongside the Human Development Index (HDI), the Gender-related Development Index (GDI) and the Gender Empowerment Measure (GEM; United Nations Development Programme , 1995). The index has continued to be used as a measure of global trends in gender equality ever since (United Nations Development Programme, 2008).

The GDI was developed as a means of noting the differences in achievement in relative well being between men and women and uses such variables as adjusted incomes, education levels and health. The primary focus of the GEM is the measurement of the economic and political power of women by nation. The GEM includes variables such as parliamentary control, adjusted income, and share of managerial roles and ratio of professional and technical careers.

There have been some methodological complaints waged against the GEM and GDI, mainly that the indexes are less about measuring the differences between genders and more to do with adjusting or penalizing a nation's HDI rating for gender inequality (Bardhan, 1999; Dijkstra, 2002). Subsequent adjustments and alternative indexes have been proposed.

SIGE. One alternative proposed is the Standardized Index of Gender Equality (SIGE; Dijkstra, 2002). Many of the same variables are used to create this index (education access, life expectancy, labor market activity, share in government and share in professional careers). However, the way the variables are inputted are not dependent upon the HDI or biased by general improvements in standards of living.

The SIGE creates an average ratio of each of the ratios observed in each of the five variables and provides the opportunity for the additional constructs to be added or for estimates to be taken even if a particular constructs data is not available. For example, for some populations estimates of literacy rates or relative income are either not available or irrelevant and the SIGE enables these constructs to be eliminated.

GEI. The Gender Equality Index (GEI) was modeled after the consumer price index (CPI; Harvey, Blakely, & Tepperman, 1990). Using seven variables (unemployment rates, labor force participation, earnings, community college enrolment, university enrolment, occupational segregation and part time employment), a weighted average of the ratio of differences between men and women is calculated.

SIGI. The Social Institutions and Gender Index (SIGI) is a gender equality index created by the Organization for Economic Co-Operation and Development (OECD, 2009). Unlike other indexes the SIGI creates a composite that includes variables related to social institutions that influence gender equality such as family code, physical integrity, son preference, civil liberties and ownership rights. The most noticeable difference between the SIGI and other indexes is the inclusion of social institutions and norms, for example the family code variable addresses the average age of marriage, inheritance rights and family influence in mate selection.

There are overlapping themes in these different indexes, as summarized in Table 1. In particular, most use similar measures of gender equality including equitable representation in education (primary through professional academia), politics and economic activity (labor force participation, wage distributions, private ownership and employment). Not surprisingly, the different indexes yield similar ratings for different countries. For example, Sweden, Finland and Denmark receive the highest ratings regardless of which index is used (Dijkstra, 2002; United Nations Development Programme, 2008).

Table 1

Variables included in each index

	GEM/GDI	GEI	SIGI	SIGE
Economic Variables	Earned Income	-Employment Ratio -Labor Participation -Earned Income -Occupation Segregation	-Ownership Rights Access to Property/ Banking	-Share in Professional Careers -Share in Technical Careers
Education Variables	-Adult Literacy - Combined enrollment	University Enrollment		-Literacy Rates -Education Enrollment Rates
Political Variables	Parliament Seats			Parliament Seats
Health Variables	Life Expectancy		Physical Integrity (violence and genital mutilation)	Life Expectancy
Social Variables			-Family Code -Civil Liberties	

Background of Gender Equality by Nation: Sweden

Sweden has a distinct and well-outlined history of gender equality as measured by advances in education, economics and legal standing. Significant advances in education began as early as 1842 when laws requiring compulsory education for both boys and girls were passed. By 1853 women were allowed to teach at universities and an overwhelming percentage of women, as compared to other nations at that time period, began attending institutions of higher education.

During the last half of the 1800's recognition of the need for gender equality in economics and law were being argued in social and political arenas throughout Sweden. These economics debates led to advances which included women receiving equal inheritance rights under the law in 1845 and by 1874 married women had achieved the right to control their own income and banking. More equal employment opportunities were guaranteed by law and in 1859 limited government and civil service positions were opened to women.

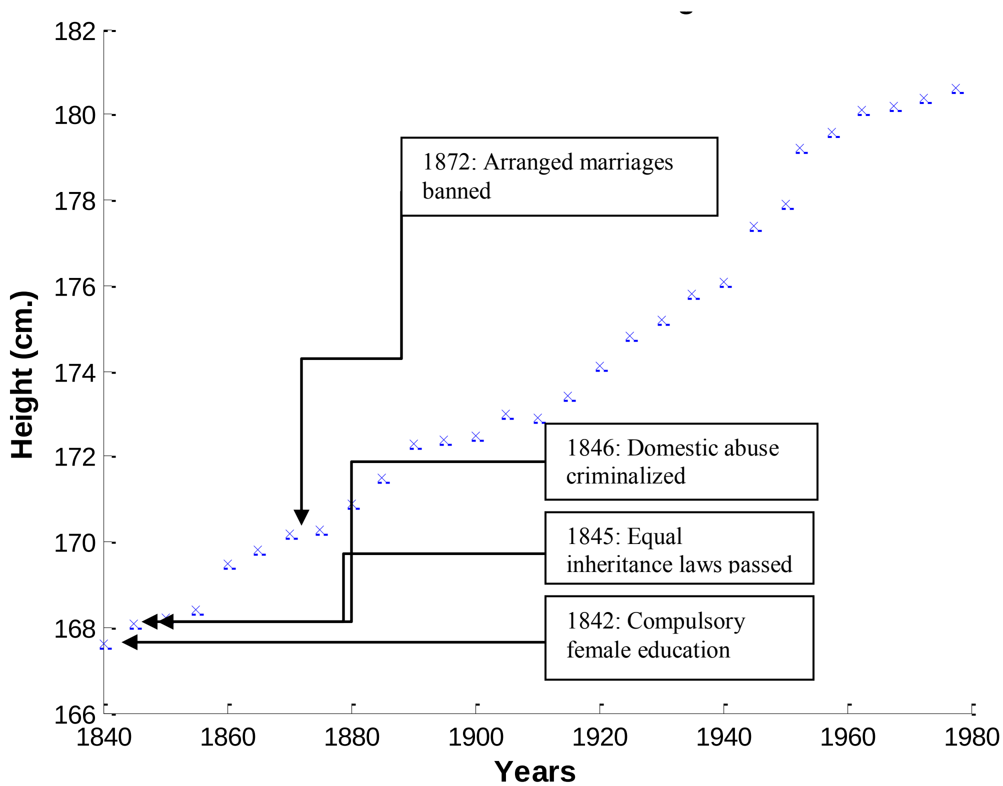

Figure 5. Selected changes in gender equality is Sweden from 1840-1980.

The legal recognition and protection of women's' rights began being expressed in 1858 when full legal majority was recognized for women. In 1864 laws prohibiting husbands from physically striking their wives were enacted to curb domestic violence and guarantee a women's safety at home. Perhaps one of the most significant legal changes, with direct implications to the model of human height evolution, is that in 1872 arranged marriages were officially outlawed in Sweden. Although there were long-standing social pressures pushing towards political gender equality it was not until 1919 when, after public outcry, municipal suffrage was achieved and 1921 when full national suffrage was enacted.

Background of Gender Equality by Nation: Portugal

The turbulent political environments that punctuated the first quarter of the 1900's and the fact that a dictatorship maintained control for over 40 years impede examination of critical points in Portugal's history of gender equality. Unlike Sweden, there is not a clear history of public influence or public sentiment in regards to gender equality. However, what can be observed is the pre and post dictatorship eras (1900-1920's and 1976-present) and the social and political actions implemented.

In 1910 Portugal underwent a republican revolution that overthrew the previous monarch. Gender equality and female suffrage immediately became relevant issues for the new government and legal protections for women were introduced for the first time including legal equality in marriage, "civil" marriages, and the legalization of divorce.

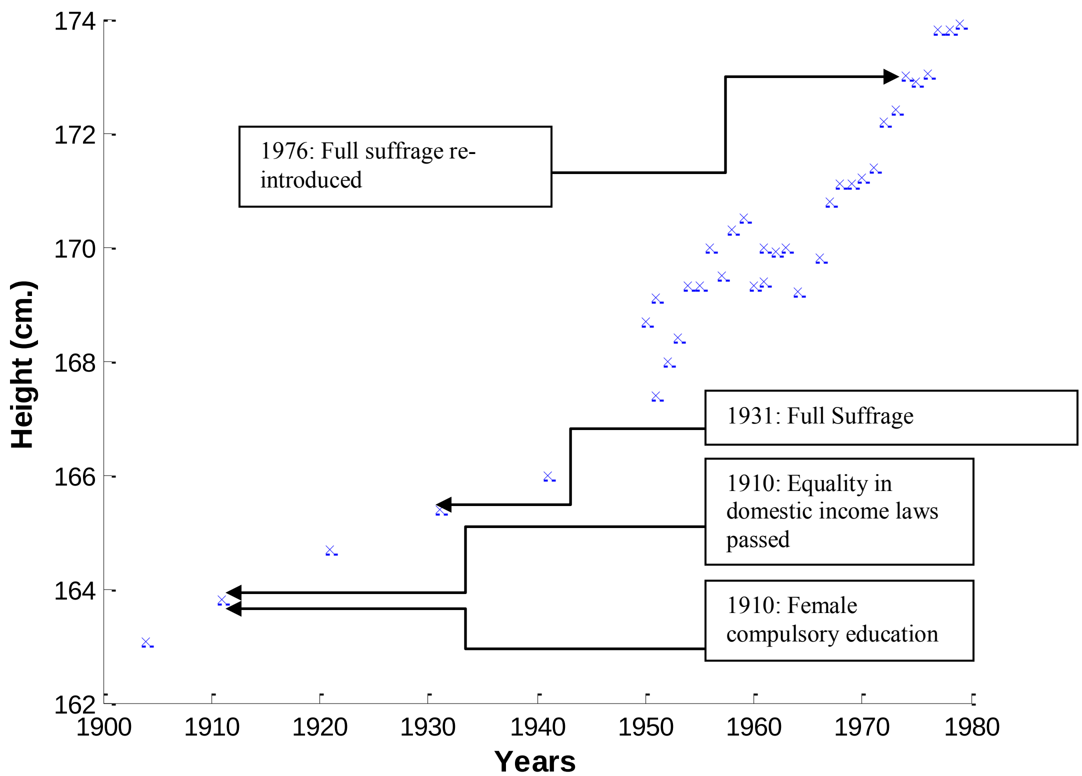

Figure 6. Selected changes in gender equality is Portugal from 1900-1980.

Further reforms were passed and in 1931 women received the right to vote, extended in 1934, and the right to a public education.

In 1926 Portugal experienced a military coup establishing the Ditadura Nacional, or “the national dictatorship”. In 1933 Salazar Novo seized power and began reversing many of the gender reforms passed just years before. This reversal in the legal recognition of gender equality may not provide an accurate or conclusive model for the prediction of the expression of mate selection for this time period in Portugal because the actions were not representative of the popular sentiment or the result of public action.

Portugal remained a dictatorship until 1974 when the Carnation Revolution introduced sweeping political reforms and a more democratic government. Immediately following the revolution the issue of gender equality reemerged and in 1976 women received full legal equality including in matters of inheritance, voting and education.

The observable public concern for gender equality pre- and post- dictatorship suggests that some level of public conception of gender equality remained despite the legal and social stagnation resulting from the dictatorship.

Heritability and Genetics of Height

Heritability (often denoted as h^2), in the most general definition, is a term used to address the rate of transmission of a trait to offspring. There are three general concepts that are often addressed with the single word of heritability; biometric heritability, broad sense heritability and narrow sense heritability (Jacquard, 1983). Biometric heritability is the slope of the regression line of offspring calculated on measurements of the parents' means and is one of the oldest metrics used to estimate similarity. Broad sense heritability attempts to separate the causes of similarity, generally genetic and environmental. Monozygotic and dizygotic twin studies are a common tool used to estimate broad sense heritability. As an extension of broad sense heritability, narrow sense heritability investigates the contribution of individual genes and the additive effects of each gene.

Techniques in the measurement of heritability. There are multiple techniques available to examine the heritability of height ranging from twin and longitudinal studies (Silventoinen, Kaprio, Lahemla, & Viken, 2003) to genome-wide linkage analysis (Benyamin et al., 2008; Hischhorn et al., 2001) and molecular analysis (Visscher et al., 2006). Recent efforts to identify the specific genetic loci responsible for variation in human heights have yielded a total of 44 genes, with predictions indicating a strong probability of finding potentially hundreds more (Weedon & Frayling, 2008). Current genetic meta-reviews have found height to have a high heritability across cultures (most estimates ranging from .80-.94) and to be consistent across measurement techniques (Perola, Sammalisto, Hiekkalinna, Martin, & Visscher, 2007; Silventoinen et. al., 2003).

Changes in estimates of heritability of height through time. There is strong evidence that both broad and narrow sense heritability of height has increased over the past century (Silventoinen et al., 2000). Using the same definitions and tools of biometric heritability it is observed that the heritability of height has increased through time from around an h=.5 to h=.89 (Pearson & Lee, 1903; Tambs, et al., 1992). This increase in heritability is not surprising given the extreme selection pressures for height and the increasing homogeneity of environmental factors.

Mathematical and Quantitative Genetics Models

The genetic basis for height variation has been of particular interest to mathematicians and life scientists for well over a century. As early as 1889 (Galton, 1889) the heritability of height, especially human height, had become an important subject in mathematical modeling. Utilizing the vast collections of statistical data from a host of cultures, great efforts were made to create models that represented the genetic variations of human height and their distributions across cultures and time.

Prior to the molecular genetics revolution, mathematical representations and models of heritability were powerful tools used to measure genetic traits. Utilizing quantitative and qualitative heritability models, life scientists could make predictions about physiological differences and population characteristics within current and future populations.

Quantitative genetics. Phenotypic traits that are under the control of multiple genotypic influences are referred to as quantitative traits. For most genetically based variation there is not a single gene responsible but rather an interaction of a number of genes. When there is a single gene or a couple of genes that are responsible for a trait, simple probabilities can be used to make predictions about the characteristics of the potential outcomes in offspring. However, once there are a large number of genes interacting it gets more difficult. For those traits that have multiple alleles involved in determining a phenotypic characteristic, quantitative genetics models were created. Quantitative genetics models allow for examination of physiological traits that are the result of a host of unknown genes. Through the examination of quantitative genetics models complex traits such as eye color, body symmetry and height can be analyzed.

Difference equation modeling. A common approach to making predictions of population changes over time is what is known as difference equations. Difference equations are recursive functions that use the solution at a previous time step to update the solution through time. Recursive functions are particularly pertinent in population modeling because each generation is a product of the previous population. If the original population trait of interest is known then mathematical computations of the variables and interactions of variables can be used to predict the subsequent population's trait characteristics. For example, when examining population densities, the density of population at time x_{t+1} is dependent upon the density of the population at time x_t.

In addition to their use in the biological sciences difference equations have been utilized in psychology to predict the outcomes of complex interactions and behavioral states (Guastello, 2001). Relationship models have been constructed that utilize the recursive nature of interpersonal relationships and make predictions of marriage relationship outcomes (Gottman, Swanson, & Swanson, 2002). For example, Sprott (2004) used a nonlinear differential equation to examine the behavior of "love" in a relationship given different behaviors for "Romeo" and "Juliet" and when a third party was introduced. Similarly, emotional states such as happiness have been modeled and the oscillatory and chaotic behaviors predicted have been compared to the emotional responses observed under a variety of situations (Sprott, 2005).

In addition to individual or personal interactions, recursive models have been expounded upon to make models that predict everything from population densities (Guckenheimer, Oster, & Ipaktchi, 1977) and extinction rates (Foley, 1994) to a host of questions relating to the evolution of a species (Hofbauer & Sigmund, 2003).

Directional selection model. When selection forces continuously favor a value of a phenotypic trait that is different than the mean, it is said that the trait is under directional selection pressure (Mueller & Mazur, 2001). Models of directional selection operate under the assumption that either natural or sexual selection is occurring within the breeding population and that this selection favors a particular phenotypic trait. It should come as no surprise, given the two fundamental requirements of evolution, selection and heritability, that the variables of these quantitative genetics models incorporate these tenets. One of the most foundational and eloquent models of directional selection on a population's mean expression of a quantitative trait is elaborated as (Roughgarden, 1979)

$$X_{T+1}=X_T+h(X_{W,T}-X_T)$$

Where X_T is the starting mean, X_{T+1} is the new mean for a quantitative trait in the next generation after selection, h is the heritability factor, $(X_{W,T}-X_T)$ is the new mean value of the trait after selection, minus the previous mean of the population, or more simply put, the selection pressure exhibited on a particular trait within the population.

Hypotheses

Hypothesis 1: Changes in Swedish and Portuguese male mean height can be mathematically modeled using the known heritability of height, observed selection pressures and quantified by estimates of ratios of gender equality through time.

Hypothesis 2: The mathematical models will project a new population height and general behavior similar to those observed in each population.

Method

Participants

Archival records of height were obtained from previously published studies that exploited sources such as military conscription data, passport applications and medical survey records. Large data sets and measurements of population demographics have been created over the years and are available in journal publications across multiple disciplines.

Records of mean heights in Sweden come from a host of sources including military conscript service records (Sandberg & Steckel, 1997), passport application records (Gustafsson et. al., 2007) and household survey reports performed by the European Community Household Panel (Garcia & Quintana-Domeque, 2007; See Appendix A for year, male, female and population heights). Records of Portuguese mean heights were obtained from medical examinations (Padez & Johnson, 1999) and from military records (Padez, 2002; Sobral, 1990; See Appendix B for year, male, female and population heights).

Instruments

Directional selection on population means. This study utilized a modified version of Roughgarden's recursive population dynamics function that explores changes in genetic variation within the population through time:

$$X_{T+1}=X_T+h(X_{W,T}-X_T)\text{(Roughgarden, 1979).}$$

Heritability. As noted earlier, the heritability of height has been observed to have increased over the past century. Current cross-cultural measurements of the heritability of height are calculated as: Sweden (.91), Portugal (.90; Silventoinen et al., 2003). A linear approximation of the changes in heritability over time was created using the h=.5 observed in 1903 (Pearson & Lee, 1903) and current estimates resulting in the function: h(t)=.0037t-6.5411

Sexual selection pressure. Using meta-analysis of the preferences for taller men by women and for shorter women by men (Pierce, 1996), the effect size for the male preference (.36) is subtracted from the female preference (.41) to create the final population effect size (.05) and directional selection pressure for height.

Gender equality index. Multiple values of gender equality were used to create linear approximations of changes through time. Since the SIGE provides for the use of available archival data such as education obtainment ratios, income ratios and property obtainment ratios, this index will be used to create historical estimates of potential expression of female selection. Relevant population demographic information such as income discrepancies, legal representation, education obtainment, legal land and property ownership and political participation are included.

Procedure

Using the known heritability, sexual selection pressures and historical measurements of gender equality, a model was constructed that represents the changes in the mean heights of both the Portuguese (1900-1979) and Swedish (1840-1979) populations. The model was run using the software package Matlab. Using each population's initial twenty years of mean height values, the model was run and the numerical solutions as well as the general behavior of the systems were compared to the observed historical population dynamics. Assessment of the predicted versus actual height as well as the behavior of the curve as it changes through time was analyzed.

The Model

$$X_{t+20}=X_t+\{h(t)(FQ(t)-M)(1.08P(X_t)- P(X_t)\}\ X_t$$

X_{t+20}: The mean height in the next generation in 20 years

X_t: The mean height of the population at time t in years

h: The functions for heritability of height through time for Sweden was $h(t)=.0027777t-4.555555$ and $h(t)=.00408t-7.17$ for Portugal.

(FQ(t)-M): A function representing the directional selection pressure exhibited by males (M) and females (F) with female selection being quantified by the function Q(t). Q(t) is

a function that represents the changes in gender equality or the percentage of female preference that can be expressed at any time.

Q(t) Sweden (1849-1980): Using the SIGE estimate of gender equality of .888 in 1849 and .99 in 1979 the following function was generated; Q (t)=.0006438t-.28762.

Q(t) Portugal (1900-2000): Using the SIGE estimate of gender equality of .87 in 1900 and .99 in 2000 the following function was generated; Q (t)=.000643t-.28762.

$P(X_t)$: a function that represents the probability of finding a mate whose height is greater than the population mean at time t. As X_n gets further from X_0 the harder it is to find a mate who is taller than the population mean. To find the probability of selecting a mate who's height is greater than the population mean I will use the transformed distribution z such that

$$Z=(X_t-X_o)/sd\ (X)$$

Where X_t is the population mean height at time t, X_0 is the population mean averaged over time (see Appendix C and D for Swedish and Portuguese heights through time) and sd is the standard deviation. This provided the probability of being able to find a mate who is above the mean at any time. To account for the female preference for male height in relation to self, $P(X_t)$ is then subtracted from the area of distribution representing the cross section of the population 1.08 above the mean at time t.

There are two general assumptions that must be met. The first is that there are no new genes being introduced to the genome. Random mutation and migration represent the most common challenges to this assumption. Given the relatively short period of time in question and the fact that the changes can be observed in multiple cultures it is not likely that there were any new alleles introduced. Furthermore, for both populations, migration was limited by government intervention and immigration was minimal for most of their histories.

The second major assumption is that there are a limited number of possible phenotypic expressions of the quantitative trait of height and that these expressions are normally distributed. Research indicates that this assumption is valid.

Results

To quantify the success of the model and generate an R^2 like value of the proportion of explained variance the final predicted population height generated from the model was divided by the total observed change in the population.

Sweden

Between the years of 1820 and 1980 Sweden's mean population height increased 13.1 centimeters from 160.81 to 173.9. The model predicted a final mean population height of 171.2 or a total change of 10.39 centimeters equivalent to 79.4% of the total change.

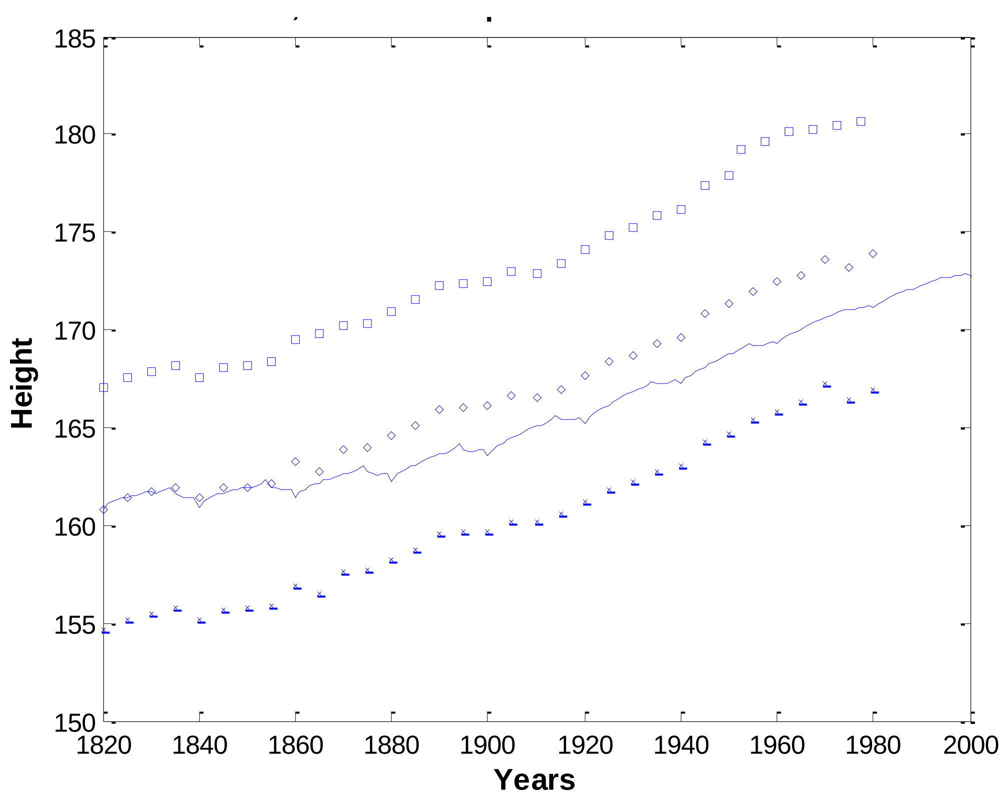

Figure 7. Mean male, female and population height data with model predictions.

Portugal

Between the years of 1900 and 2000 Portugal's mean population height increased 10.36 cm from 157.1 cm to 167.46 cm. The model predicted a final mean population height of 163.8 cm or a total change of 6.7 cm equivalent to 64.67% of the total change.

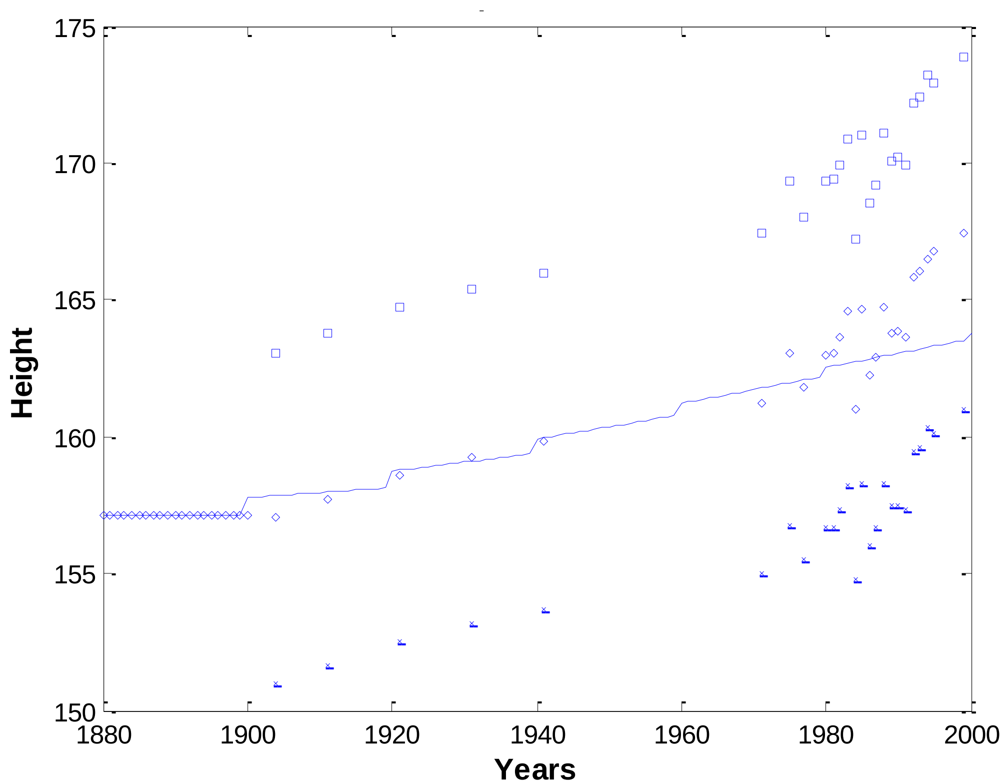

*Figure 8.*Mean male, female and population heights data with model predictions.

Critical Point

As Q, the parameter representing the expression of mate selection is varied; we see that for some values the average height decreases while for others the average height increases. At the threshold value of Q (Q(t)=.8841141) the population height does not change. This result makes a testable prediction about changes in population height as gender equality varies. Figure 9 demonstrates the behavior of the model over 2000 years with different constant values of Q(t).

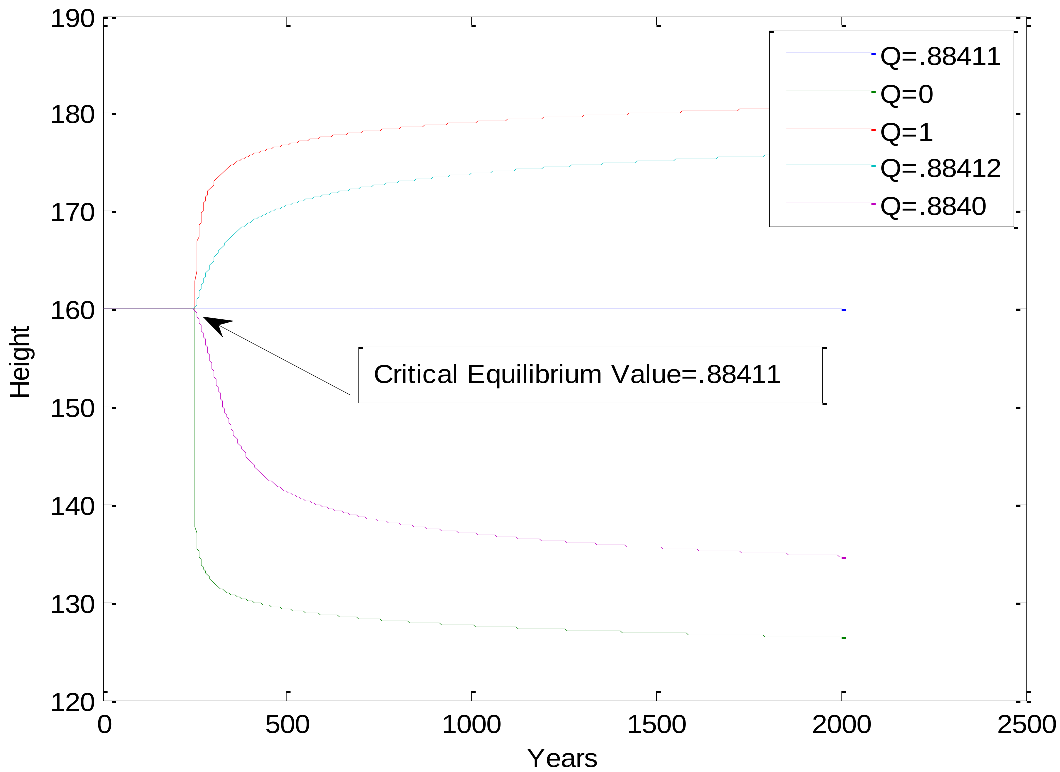

Figure 9. General behavior around the critical point of .88411. Values above the critical value result in increases in population height whereas values below the critical point result in decreases in population heights.

This critical point arises as a result of the male and female selection variables. Female selection for taller males is greater than male selection for shorter females. As long as female selection remains above the critical value, mean height will increase. However, if female mate selection is inhibited beyond this critical point then population heights will trend negative. The magnitude of deviation from this value sets the rate of change the population will experience.

Discussion

Results suggest that cultural changes in Sweden and Portugal unmasked an innate female mate selection preference for height. According to this theory, increased freedom of mate selection led to a period of average population height increase that is attributable to this sexual selection mechanism. This new population genetics model accounts for observed changes in average height in Sweden and Portugal during this era more accurately than do previous accounts based on improved nutrition and health alone. While the model does not perfectly predict the final observed heights for each population, what can be observed is that social changes that influenced the expression of gender equality influenced the observed increases in European height.

Changes that influence the expression of sexual selection and mate selection have significant implications in explaining fluctuations in height. From the model a critical value emerged such that if gender equality is inhibited beyond a particular point then the trend in population height will decrease over time.

Limitations

The most critical assumption in this model is that the measures used to quantify gender equality are accurate measures of expression of female mate selection. While there is evidence that each of the variables used for the measures of gender equality do play an important role in the potential expression of mate selection it is difficult to concretely state that any one indicator used is itself sufficient in measuring mate selection. Given that not all of the available measures of gender equality are adequately available in the archival records there may be discrepancies between the estimates generated with limited archival data and historical reality.

Unfortunately, given the relatively new interest in mathematical modeling, there are few methods of quantifying results that have been developed. This lack of universal quantification impedes the ability to fully address the accuracy of a model. What can be said about accuracy and significance of this model is that at no point are the predicted values of the model greater than a single standard deviation of height. While this is a qualitative measure, it does provide the assurance that if a method of quantification were available it would rely upon the standard error of the measurement in relationship to the expected deviations. Since at no point do the deviations observed between the model and the data exceed a single standard deviation it would be unlikely to quantify the findings of the model as statistically insignificant.

Future Additions to the Model

Public health and sanitation and well as nutrition are known to play a role in the target heights achieved by a population. While this model performs well at predicting the final height of a population after selection it is not a perfect representation of the observed changes and an additional variable that represented the changes in population health may result in more accurate predictions. Unfortunately there is limited literature that has conclusively established the effect size or proportion of explained variance in height as a function of public health improvements. There is some evidence that improvements in public health can account for some of the observed population changes and it is possible to utilize this argument to form a more accurate model of changes in height.

An additional consideration for future improvements to the model is rather than utilizing a difference equation, generate the model as a differential equation. All of the variables used in this model can be used in a differential equation. The use of a differential would allow for improvements such as a graded generational cycle rather than a 20 years reproductive cycle, the inclusion of population gender ratios and a generally more fluid model predicted line of accent.

Furthermore, this model assumed a 20 year breeding cycle and does not account for differences in age of fecundity. An improved model might include efforts to represent a cohort of ages with variations in age of reproduction. There is evidence that taller males tend to reproduce at younger ages and the modeling of this trend may result in a more accurate prediction.

Other Populations

One of the benefits of utilizing a generalized directional selection model is that it can be used in for any population that has available population height data. All of the variables used by this model are either available from the population data sets themselves (means, standard deviations and starting heights) or are observed to be constant across cultures (male and female selection pressures). The subject of human height fluctuations, whether upward or downward trends, has been researched in multiple cultures resulting in many population data sets available for analysis including but not limited to; Japan (Kimura, 2005), Spain (Onland-Moret et. al., 2005), Turkey (Ozer, 2008), Czechoslovakia (Vignerva, Brabec, & Blaha, 2006), Great Britain (Floud & Harris, 1997; Floud & Wachter, 1982), Finland (Silventoinen et al., 2000), Poland (Bielicki & Szklarska, 1999) and Brazil (Castilho & Lahr, 2001).

Historical Applications

If this model is correct, and societal changes that altered the expression of female mate selection influenced fluctuations in human height then it may be possible to go back into historical eras and assess fluctuations in gender equality as a function of height. It may be possible that anthropological and archeological questions pertaining to the social structure of historical epochs can be addressed by reviewing trends in population heights at the time.

For example, in Sweden it is observed that during the 13th and 18th centuries Swedish population heights took significant downward turns (see Appendix C for Swedish heights through time). These significant downward trajectories in population heights may be the result of social changes that were occurring in Sweden at the time. A similar pattern of oscillations in population heights has been observed in Portugal (see Appendix D for Portuguese heights through time). There are two general eras of increases and decreases in population heights. From around 200 B.C. till around the 10th century Portuguese heights were decreasing (Figure 9). This trend was quickly reversed and for only two centuries population heights increased before beginning to decrease again.

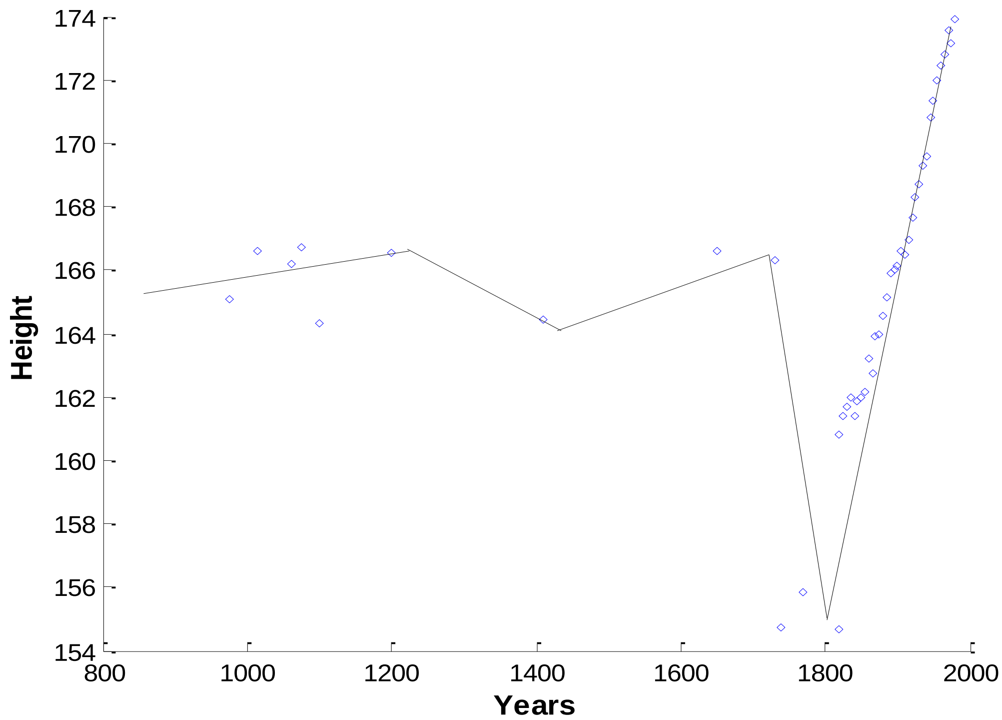

Figure 10. Historical trends in population heights in Sweden and approximate trends from year 800-2000.

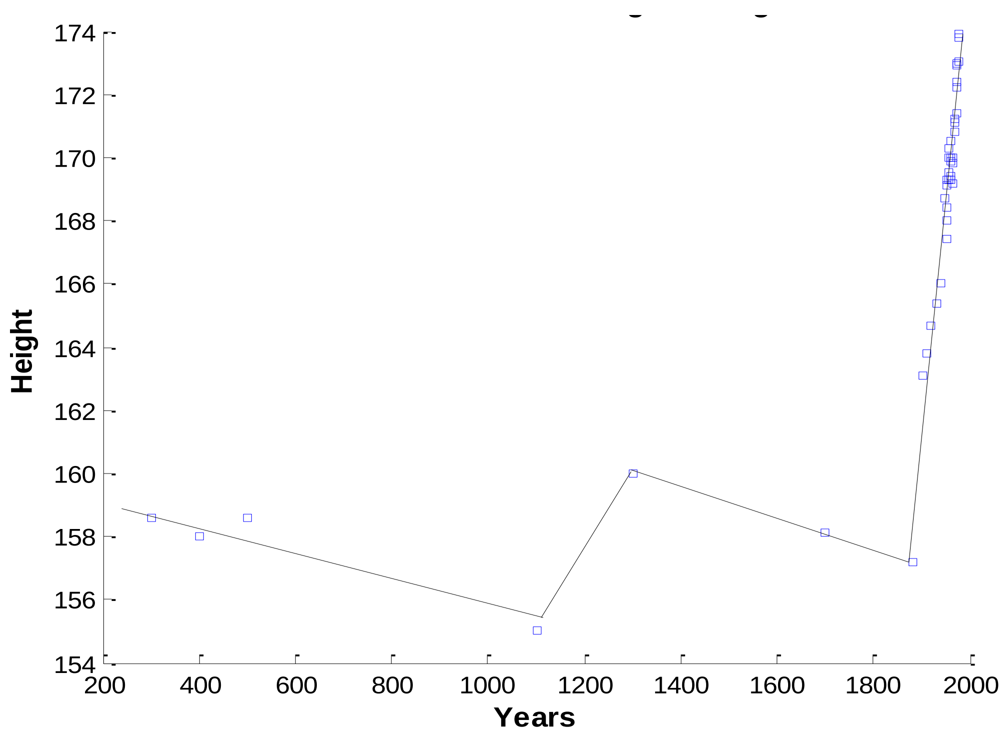

Figure 11. Historical trends in population heights in Portugal and approximate trends from 200-2000.

Other Traits

Height is not the only trait selected for by males or by females (Barkow, Cosmides, & Tooby, 1992). It should come as no surprise that there are multiple physical and behavioral characteristics that contribute to variations in mate selection and mating opportunities. Most of these evolved mate selection preferences are for traits that indicate an ability to acquire resources or provide for offspring such as displays of wealth and education level. Further exploration and modeling of mate selection behavior and preferences may provide insight into historical social changes. Given that historical changes in a physiological trait such as height may have been the result of changes in gender equality and expression of mate selection it would be reasonable to expect similar traits that experience intense mate selection also increased in the population during this time. It may not be coincidence that as gender equality increased, European history observed the first robber barons, private millionaires and an explosion of university enrollment and construction. It may be possible to generate similar models that utilize the known proportion of explained variance in mate selection for different traits to predict and compare social behavior through time.

Modeling in Psychology

In psychology it is often the case that a behavioral or social trait cannot be accurately predicted by a single variable. Given the known complexity of human behavior, psychology has utilized a host of statistical methods to identify critical variables, their proportion of explained variance, and the interactions generated by each variable. While there is no doubt as to the invaluable contribution statistical methodologies such as regression and principle component analysis have made to the understanding of complex behavioral traits, these methods fail to provide the same capabilities of predictions of changes through time that are utilized in other mathematical techniques.

Mathematical modeling enables researchers to take the available data and statistics that have been gathered and to make predictions as to the behavior of an individual, group of or population through time. By assimilating the available literature and statistical analysis that has been done, stochastic models can be generated to predict changes and rates of change in social and individual behavior through time.

The Potential for Rapid Evolution

In classical Darwinian evolution, changes in allele frequencies occur over great spans of time and while there is no doubt as to the slow steady change of allele frequencies it may also be possible that allele frequencies in a population can change rapidly if placed under intense enough selection pressure. Sexual selection can be extreme. Temperature changes can result in migrations of forests or the formation of deserts over centuries of time, sexual selection, and the social variables that influence sexual selection, can manipulate the next generations allele frequencies with great efficacy.

Social changes can affect the expression of mate selection. Arranged marriages are a draconian example. However, general social norms and behaviors associated with mate selection and mating behavior can affect the expression of mate selection. If sexual selection posses the ability to rapidly alter a population's allele distribution, then human cultural changes that influence sexual selection could lead to shifts in allele frequencies much more rapidly than classical Darwinian evolution theorizes.

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Appendix A: Sweden Male, Female and Population Height

Year	Male	Female	Population
1820	167	154.63	160.815
1825	167.6	155.18	161.39
1830	167.9	155.46	161.68
1835	168.2	155.74	161.97
1840	167.6	155.18	161.39
1845	168.1	155.65	161.875
1850	168.2	155.74	161.97
1855	168.4	155.92	162.16
1860	169.5	156.94	163.22
1865	169	156.48	162.74
1870	170.2	157.59	163.895
1875	170.3	157.68	163.99
1880	170.9	158.24	164.57
1885	171.5	158.79	165.145
1890	172.3	159.54	165.92
1895	172.4	159.63	166.015
1900	172.5	159.72	166.11
1905	173	160.18	166.59
1910	172.9	160.09	166.495

1915	173.4	160.55	166.975
1920	174.1	161.2	167.65
1925	174.8	161.85	168.325
1930	175.2	162.22	168.71
1935	175.8	162.773	169.28
1940	176.1	163.05	169.575
1945	177.4	164.26	170.83
1950	177.9	164.72	171.31
1955	178.6	165.37	171.985
1960	179.1	165.83	172.465
1965	179.3	166.3	172.8
1970	179.9	167.2	173.55
1975	179.9	166.4	173.15
1980	180.9	166.9	173.9

Appendix B: Portugal Male, Female and Population Height

year	male	female	population
1904	163.08	151	157.04
1911	163.8	151.67	157.735
1921	164.7	152.5	158.6

1931	165.4	153.15	159.275
1941	166	153.7	159.85
1971	167.4	155	161.2
1975	169.3	156.76	163.03
1977	168	155.55	161.775
1980	169.3	156.7	163
1981	169.4	156.7	163.05
1982	169.9	157.31	163.605
1983	170.9	158.24	164.57
1984	167.2	154.81	161.005
1985	171	158.33	164.665
1986	168.5	156.01	162.255
1987	169.2	156.66	162.93
1988	171.1	158.3	164.7
1989	170.1	157.5	163.8
1990	170.2	157.5	163.85
1991	169.9	157.31	163.605
1992	172.2	159.44	165.82
1993	172.4	159.62	166.01
1994	173.2	160.37	166.785
1995	172.9	160.09	166.495
1999	173.9	161.02	167.46

Appendix C: Sweden Population Heights Through Time

Year	Male	Female	Population
975	170.3	159.9	165.1
1015	173.6	159.6	166.6
1060	171.5	160.9	166.2
1075	170.9	159.1	165
1075	172.5	161.5	167
1075	174.6	162.8	168.7
1100	168.2	156.4	162.3
1200	173	161.7	167.35
1200	171.2	160.4	165.8
1215	172.7	162.5	167.6
1400	171.3	157.5	164.4
1415	169.9	157.7	163.8
1418	172.2	160.4	166.3
1418	173.8	161.2	167.5
1650	169.6	163.6	166.6

Appendix D: Portugal Population Heights Through Time

Year	Male	Female	Population
5060 B.C.	153.2	148	150.6
2800 B.C.	157	144.4	150.7
400 A.D.	163.4	153.8	158.6
600 A.D.	163.3	152.7	158
1400 A.D.	165	155	160
1700 A.D.	162.9	153.2	158.1
1880 A.D.	162	152.5	157.2
1920 A.D.	162.9	153.1	158
1990 A.D.	167.9	157.7	162.8