

ORIGINAL ARTICLE

Latitudinal patterns in human stature and sexual stature dimorphism

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Abstract

Background: There exists substantial variation in human stature and sexual stature dimorphism that has been attributed to both genetic and environmental variables. A few studies have previously investigated possible relationships between latitude and stature, building on the idea that variation in climate can influence body size (Bergmann's rule). This change in body size can in turn have influenced sexual stature dimorphism (in accordance with Rensch's rule).

Aim: The present study investigated whether latitude is associated with variation in human mean stature and sexual stature dimorphism.

Subjects and methods: Phylogenetic and non-phylogenetic analyses were conducted on a cross-cultural sample of 124 human populations.

Results: The results indicate that both male and female mean stature increase with increasing distance from the equator. While sexual stature dimorphism also was positively related to latitude in the non-phylogenetic test, this relationship disappeared when using a phylogenetic comparative method. Evidence was also found for curved relationships between latitude and both male and female stature, as well as stature dimorphism, all indicating a maximum at around 40° from the equator.

Conclusions: The results of the present study indicate that both male and female stature are weakly associated with latitude. It is possible that these relationships are evolved responses to variation in climate. No unequivocal conclusion could be drawn regarding a possible relationship between latitude and sexual stature dimorphism.

Keywords: *Stature, dimorphism, latitude, phylogenetic comparative methods*

Introduction

In this study we investigate if Bergmann's (1847) and Rensch's (1950, 1959) rules apply simultaneously across human populations. If this is the case, we would expect that human stature, as well as sexual dimorphism in human stature, is greater in populations closer to

the equator than in populations nearer to the equator (Blanckenhorn et al. 2006). Even though both rules have been investigated separately in previous studies of human size, the present study is the first to test if both apply simultaneously.

Differences in the phenotypic expression of human stature, or standing height, between *individuals* are the results of both genetic and environmental effects. The same is probably true for differences in mean stature among *populations*. For example, it is widely accepted that some intercultural variation in mean stature is the result of genetic, i.e. evolutionary, differences (e.g. Eveleth 1975; Alexander et al. 1979; Merimee and Rimoin 1986; Holden and Mace 1999; Gustafsson and Lindenfors 2004). However, there is also evidence that the average stature in a population is affected by changes in nutrition, as well as other changes in living conditions (Steckel 1983; Eveleth and Tanner 1990).

Differences in mean stature between men and women are well documented (e.g. Eveleth 1975; Eveleth and Tanner 1990; Gustafsson and Lindenfors 2004), and can be referred to as sexual stature dimorphism, or SSD. (SSD normally represents sexual size dimorphism, but in this context the abbreviation is instead used for sexual stature dimorphism). Stature dimorphism has been observed to vary between different human populations (Wolfe and Gray 1982a, Gustafsson and Lindenfors 2004, but see Gaulin and Boster 1985), but it is still unclear what factors determine inter-population variation in SSD.

One of the proposed explanations for the evolution of genetically caused differences in SSD between populations is that different populations might have experienced varying degrees of polygyny during their evolutionary history (Alexander et al. 1979; Holden and Mace 1999). Varying degrees of male–male competition could in this scenario lead to different selection pressures for male size, and consequently cause differences in sexual size dimorphism among populations. This is the same general explanation – sexual selection – invoked to explain sexual dimorphism in animals in general (Darwin 1871). Another potential explanation, tested on human populations by Holden and Mace (1999) and by Wolfe and Gray (1982c), is that differences in size between the sexes have evolved because males and females have differed in how they have exploited natural resources during their evolutionary history (Shine 1989, but see Harvey and Bennett 1985).

It has also been suggested that global variation in SSD could be explained by non-evolutionary causes, through varying influences by the environment on individuals during their lifetimes. First, for whatever reason, it is possible that men and women are differently affected by environmental changes (e.g. Tobias 1970; Stini 1976; but see Gustafsson et al. 2007). Another possibility is that men and women can be experiencing different living conditions while living in the same population. For example, Holden and Mace (1999) present results regarding women's contribution to subsistence: SSD is lower in populations where women contribute more to subsistence.

Yet another factor that might affect mean male and female stature in a population, however, is temperature. Climate might influence both evolutionarily by selecting for genes that lead to greater or lesser stature, as well as by directly influencing the growth of an individual during its lifetime.

Numerous observations indicate that traits of organisms vary with latitude. Bergmann (1847) predicted that the body sizes of warm-blooded animal species should be affected by temperature. His ideas were later refined by Rensch (1938), who predicted that individuals of endothermic species living in colder climates should have greater body sizes than their conspecifics living in warmer climates.

The proposed logic behind this pattern, termed 'Bergmann's rule', is that larger bodies expose comparatively less surface area than smaller bodies of the same shape. This is a result of volume increasing in three dimensions while surface area only increases in two,

thus surface-to-volume ratio decreases allometrically as body size increases. A large body would therefore dissipate less heat per mass unit in a cold climate than a small sized body (Bergmann 1847).

Bergmann's rule has been tested both within and between species. This has led to results both supporting and not supporting Bergmann's rule for endotherms and, interestingly enough, for ectotherms as well (for reviews and surveys of previous studies, see Blackburn et al. 1999; Meiri and Dayan 2003; Blanckenhorn et al. 2006). These partly contradictory results make a single, simple explanation coupling body size and heat conservation less probable, and it is still not determined what causes these patterns (Blackburn et al. 1999; Ashton et al. 2000; Blanckenhorn et al. 2006). Because of this uncertainty of causality, and the close association between latitude and climate, latitude is often used instead of temperature as the independent variable in studies of Bergmann's rule. Actually, many authors prefer to define Bergmann's rule from this parameter, rather than temperature (see, e.g. Blackburn et al. 1999).

Another body size pattern that has been observed is that sexual size dimorphism often increases with increasing body size in species where males are the larger sex, while SSD often increases with decreasing body size when females are larger than males. This trend, called Rensch's rule, was first pointed out by Rensch (1950, 1959) and has since received some support in a number of comparisons within groups of closely related species (Abouheif and Fairbairn 1997). However, Rensch suggested that the trend might also apply below species level (Rensch 1959), something that has been previously tested for a small number of species, with mixed results (Wolfe and Gray 1982b, Fairbairn and Preziosi 1994; Kraushaar and Blanckenhorn 2002; Gustafsson and Lindenfors 2004; Fairbairn 1997; Young 2005).

Should a species conform to Bergmann's and Rensch's rules simultaneously, this would lead to sexual size dimorphism increasing with latitude in species where males are larger and dimorphism decreasing with latitude in species where females are the larger sex (Blanckenhorn et al. 2006).

In this study we aim to investigate if mean stature changes in relation to distance from the equator when comparing various human populations. Furthermore we aim to test whether there exists a corresponding relationship between SSD and distance from the equator.

Whether the human species conforms to Bergmann's rule has previously been tested for a number of parameters, including body weight (Roberts 1953; Hiernaux 1968a, Hiernaux and Froment 1976; Ruff 1994; Katzmárzyk and Leonard 1998), surface-to-body-mass ratio or similar (Schreider 1950; Ruff 1994; Katzmárzyk and Leonard 1998) and other variables like BMI (Katzmárzyk and Leonard 1998) and bi-iliac breadth (or hip width) (Hiernaux and Froment 1976; Ruff 1994). Bergmann's rule has received support in most of these tests.

Stature, specifically, has also previously been tested against climate or latitude in a number of tests (Roberts 1953; Hiernaux 1968a, Hiernaux and Froment 1976; Ruff 1994). Two of these contain analyses of worldwide cross-cultural samples, namely those by Roberts (1953) and Ruff (1994). Roberts (1953) found a significant correlation between mean annual temperature and stature. This relationship disappeared, however, when he controlled for body weight, which was found to be more strongly correlated with temperature than stature. Due to the state of statistical knowledge at the early date of Roberts' study, he was, however, not able to carry out a redundancy check of collinearity, which is crucial if you simultaneously want to include two such highly correlated variables as weight and stature as independent variables in the same analysis (Quinn and Keough 2002).

Ruff (1994) simultaneously tested for relationships between latitude and three body size measurements: Weight, hip width and stature. He found that the relationship between latitude and stature, as well as the between latitude and weight, were non-significant when controlling for hip width, while hip width remained significant when controlling for weight and stature. This led Ruff (1994) to argue that body breadth is the variable under climatic selection, not stature. As in the case of Roberts (1953), however, no redundancy check was carried out when simultaneously including several correlated measures of body size.

Here we repeat Ruff's and Roberts' analyses on human stature, now using a larger sample, separately investigating males and females, as well as correcting for shared ancestry using the independent contrasts method (Felsenstein 1985). Though body breadth may be climatically more relevant than stature, as suggested by, for example, Ruff (1994), we are here specifically interested in variables that may influence stature and stature dimorphism. Thus, we only analyse the possible correlation between latitude and stature, while acknowledging that the relationship may not be direct, but via selection on general body size and shape rather than stature *per se*.

A possible relationship between SSD and latitude in humans has previously been investigated by Wolfe and Gray (1982a). Their results indicate that SSD is higher at mid-latitude (between 16° and 49° north and south latitude) than closer to the equator or closer to the poles. One potential explanation for their result is that male stature is more plastic and thus more affected by environmental changes than female stature (e.g. Tobias 1970; Stini 1976). Higher standard of living of populations living in Europe (mid-latitude) might therefore not only be associated with greater stature, but also with greater SSD. However, support for male stature being more plastic than female is not unequivocal, and a recent study observing changes in SSD over time within the same population does not support this notion (Gustafsson et al. 2007). Another proposed explanation is that an inversely U-shaped relationship between latitude and SSD might be caused by two opposing selection pressures, similar to the simultaneous Bergmann and converse Bergmann clines suggested to be present in some arthropods (Blanckenhorn and Demont 2004). However, support for converse Bergmann clines have thus far only come from ectotherms (Blanckenhorn et al. 2006).

Thus, we have two separate predictions about latitude and SSD, the first being that SSD increases with increasing distance from the equator (provided that there is a positive relationship between stature and latitude), and the second that SSD should be highest at intermediate latitudes.

Methods

We analysed whether there were any associations between latitude and stature, as well as between latitude and SSD, based on a sample of human populations. The sample was the same as that used by Gustafsson and Lindenfors (2004), see Appendix I), a worldwide cross-cultural sample of human populations. As reported in Gustafsson and Lindenfors (2004), the primary literature from where this data set was collated was published throughout the 20th century. Although this means that variation due to secular change is included in the data, we could find no systematic pattern in the data indicating that sampling time would produce a strong trend in the results, but instead found that sampling time was more or less randomly scattered over the human phylogeny. Also, to limit our data

to a certain time span would be detrimental to statistical power and of dubious utility given the different rates in economic development globally during the 20th century.

As is common in this type of studies (e.g. Blackburn et al. 1999), we used distance from the equator (absolute latitude) as a proxy for temperature. This was deemed to capture the major global temperature trends sufficiently, even though the variable excludes temperature variation due to altitude, as well as other local variation. The data on latitude for the included human populations was collected from the revised version of Murdock's (1967) *Ethnographic Atlas (A Corrected Ethnographic Atlas*, Gray 1999). In cases when a population was not found in the *Corrected Ethnographic Atlas*, latitude was estimated from published maps and information in original sources, as well as the *Ethnologue* (Grimes 1992).

All analyses were performed both with ($n = 124$) and without European populations ($n = 106$), as a method of correcting for differences in standard of living. Data on mean stature and SSD was \log_{10} -transformed prior to analyses.

Both male and female stature, as well as SSD, have been shown to have phylogenetic signals (Holden and Mace 1999; Gustafsson and Lindenfors 2004), meaning that these variables are more similar in genetically more closely related populations than in genetically less closely related populations. Therefore, a method that corrects for effects arising as a consequence of shared ancestry is strongly recommended. We thus used Felsenstein's (1985) independent contrasts; a method that makes it possible to test phylogenetically independent differences (contrasts) between sister clades. However, we also tested possible linear relationships in our material with a non-phylogenetic method.

Independent contrasts analyses were carried out with the help of the computer package PDAP (Garland et al. 1993), using the same phylogeny as in Gustafsson and Lindenfors (2004) – a super-tree (see Purvis 1995 for definition) based on various genetic distance phylogenies in Cavalli-Sforza et al. (1994), (see Gustafsson and Lindenfors (2004) for details of how this human consensus/super-tree was constructed). Polytomies were handled by using zero-length branches, while all other branch lengths were set to equal length. No adjustments of branch lengths were performed since transformations did not yield any improvements in the PDAP diagnostics, as described by Garland et al. (1992). Please note that this procedure resulted in significant values in the diagnostics for the variable SSD. Thus, some caution should be taken when interpreting results involving SSD. The independent contrasts were then analysed with least-squares regressions forced through the origin (this is necessary for statistical reasons in independent contrasts analyses, see Felsenstein 1985), while the non-phylogenetic analyses were carried out using ordinary least-squares regressions.

Since a previous study by Wolfe and Gray (1982b) indicated a possible inversely U-shaped relationship between SSD and latitude, we also performed least-squares regressions with a quadratic term included in order to determine if inclusion of this term explained significant variation in the regression model (Quinn and Keough 2002). We also conducted corresponding tests for curved associations between latitude and both male and female stature.

Results

Least-squares regressions showed that female mean stature was positively associated with distance from the equator when Europeans were included ($b = 2.40 \times 10^{-4}$, adjusted $R^2 = 0.079$, $F_{1,122} = 11.51$, $p = 0.001$) but not when Europeans were excluded ($b = 9.87 \times 10^{-5}$,

adjusted $R^2 = 0.004$, $F_{1,104} = 1.467$, $p = 0.229$) (Figure 1a). Male stature, on the other hand, was positively related to latitude, both with ($b = 3.03 \times 10^{-4}$, adjusted $R^2 = 0.122$, $F_{1,122} = 18.11$, $p < 0.001$) and without Europeans ($b = 1.63 \times 10^{-4}$, adjusted $R^2 = 0.028$, $F_{1,104} = 3.978$, $p = 0.049$) (Figure 1b).

The partial significance for the quadratic term was significant for both males (Figure 1b) (with Europeans $p < 0.001$, without $p = 0.003$) and females (Figure 1a) (with Europeans $p = 0.006$, without $p = 0.044$). There is a peak in stature for both sexes at around 40° from the equator.

For females, the second degree equations were significant when including Europeans (female stature = -1.10×10^{-5} latitude² + 9.55×10^{-4} latitude + 3.17, adjusted $R^2 = 0.127$, $p < 0.001$), but not when Europeans were excluded (female stature = -8.65×10^{-6} latitude² + 6.73×10^{-4} latitude + 3.17, adjusted $R^2 = 0.034$, $p < 0.064$) (Figure 1a). For males, the second degree equations were significant whether Europeans were included (male stature = -1.49×10^{-5} latitude² + 1.27×10^{-3} latitude + 3.20, adjusted $R^2 = 0.211$, $p < 0.001$) or not (male stature = -1.27×10^{-5} latitude² + 1.01×10^{-3} latitude + 3.20, adjusted $R^2 = 0.099$, $p = 0.002$) (Figure 1b).

The phylogenetic contrast analyses of mean female stature yielded positive relationships between absolute latitude and female stature both with ($b = 4.12 \times 10^{-4}$, adjusted $R^2 = 0.082$, $F_{1,122} = 11.98$, $p = 0.001$) (Figure 2a) and without Europeans ($b = 4.22 \times 10^{-4}$, adjusted $R^2 = 0.088$, $F_{1,104} = 11.09$, $p = 0.001$) (Figure 2b).

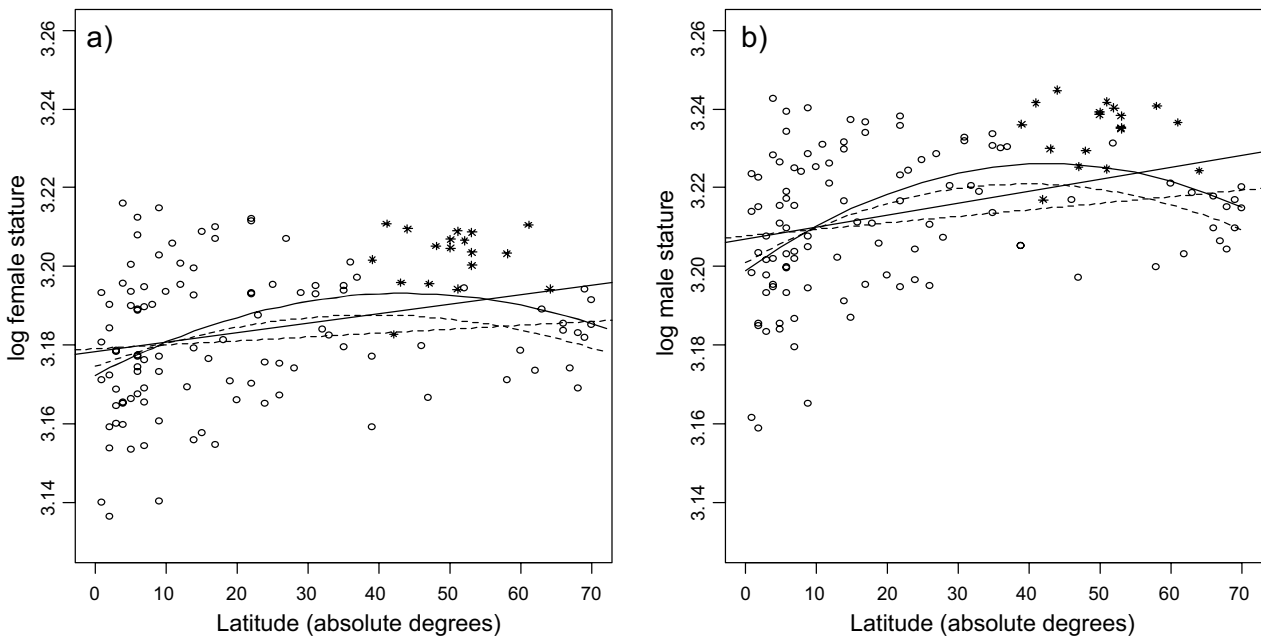


Figure 1. Least squares regressions, with (curved lines) and without (straight lines) second degree term included, of distance from the equator (in latitudinal degrees) against (a) female and (b) male stature in various human populations, both with Europeans included (solid line) and Europeans excluded (dashed line). European populations are presented as asterisks in the graphs, and non-European populations as circles. The normal least squares regressions showed that for female populations, there was a significant relationship between latitude and stature when Europeans were included, but not when Europeans were excluded, while for male populations the relationship between stature and latitude was significant both when Europeans were excluded and included. The relationship between stature and latitude was significantly better fitted to a second degree equation (curved) than a straight line, for males, both with and without Europeans, and for females, except that the second degree equations were not significant when Europeans were excluded.

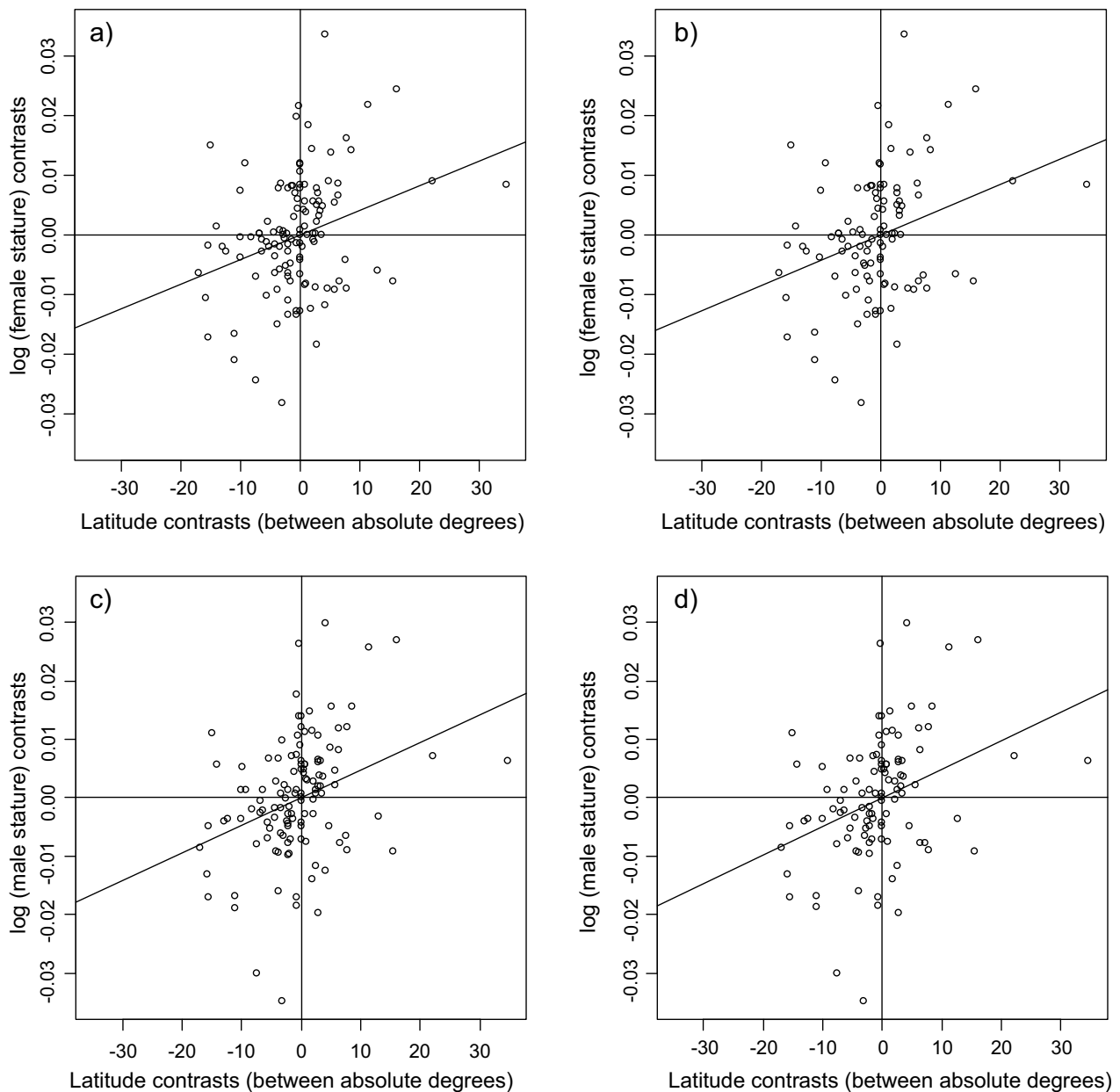


Figure 2. Least squares regression lines, forced through the origin, on standardized phylogenetic independent contrasts of latitudes and female (a and b) and male (c and d) stature for various human populations, both with (a and c) Europeans included and (b and d) Europeans excluded. The relationships between latitude and both male and female stature were significant both when Europeans were excluded and included.

When corrected for shared ancestry, there was still a positive association between latitude and male stature when Europeans were included ($b = 4.73 \times 10^{-4}$, adjusted $R^2 = 0.102$, $F_{1,122} = 14.97$, $p < 0.001$) (Figure 2c) as well as when Europeans were excluded ($b = 4.90 \times 10^{-4}$, adjusted $R^2 = 0.112$, $F_{1,104} = 14.24$, $p < 0.001$) (Figure 2d).

When SSD was tested against distance from the equator, the ordinary least-squares tests gave significantly positive relationships both with ($b = 6.29 \times 10^{-5}$, adjusted $R^2 = 0.063$, $F_{1,122} = 9.238$, $p = 0.003$) and without ($b = 6.46 \times 10^{-5}$, adjusted $R^2 = 0.052$, $F_{1,104} = 6.795$, $p = 0.010$) (Figure 3) Europeans included.

The partial significance for the quadratic term was significant for SSD (with Europeans $p < 0.001$, without $p = 0.002$). The quadratic equations for the relationships between

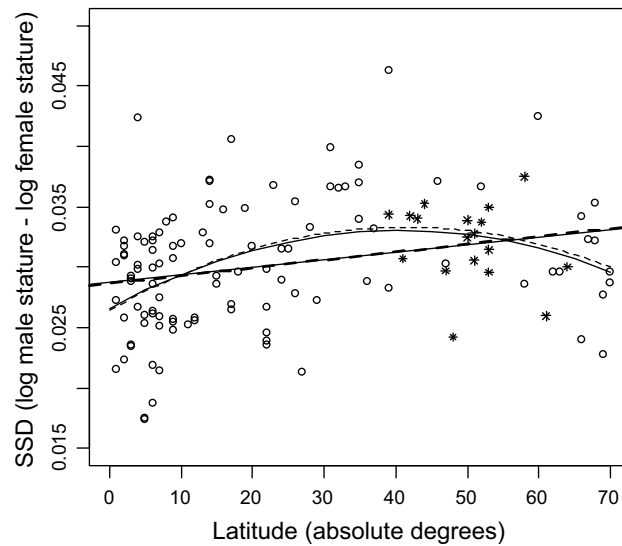


Figure 3. Least squares regressions (straight lines) without and (curved lines) with second degree term included, of distance from the equator (in latitudinal degrees) against sexual stature dimorphism (SSD) in various human populations, both with Europeans included (solid line) and Europeans excluded (dashed line, almost identical in shape to the solid line in both). European populations are presented as asterisks in the graphs, and non-European populations as circles. The relationship between SSD and latitude was significant without the second degree term included, both when Europeans were excluded and included. The relationship between SSD and latitude was, however, significantly better fitted to a second degree equation than a straight line, both when Europeans were excluded and included.

latitude and SSD were also significant, both when Europeans were included ($SSD = -3.93 \times 10^{-6} \text{ latitude}^2 + 3.19 \times 10^{-4} \text{ latitude} + 2.66 \times 10^{-2}$, adjusted $R^2 = 0.140$, $p < 0.001$) and when they were excluded ($SSD = -4.03 \times 10^{-6} \text{ latitude}^2 + 3.32 \times 10^{-4} \text{ latitude} + 2.65 \times 10^{-2}$, adjusted $R^2 = 0.130$, $p < 0.001$) (Figure 3).

When a phylogenetic method was used on the material there was no significant relationship between latitude and SSD, neither with ($b = 6.65 \times 10^{-5}$, adjusted $R^2 = 0.007$, $F_{1,122} = 1.907$, $p = 0.170$) (Figure 4a) nor without Europeans ($b = 7.40 \times 10^{-5}$, adjusted $R^2 = 0.010$, $F_{1,104} = 2.087$, $p = 0.152$) (Figure 4b).

Discussion

All but one of the tests including stature showed positive relationships between latitude and both male and female stature. The only non-significant result from these tests was obtained from the non-phylogenetic test of female stature when Europeans were excluded. Since stature has a strong phylogenetic signal (Gustafsson and Lindenfors 2004), the positive relationship from the phylogenetic test is deemed more reliable. This study hence provides strong support for the idea that human stature increases with increasing distance from the equator.

Our results on stature and latitude are therefore in line with the general consensus (Katzmárzyk and Leonard 1998; Ruff 1994; Ruff 2002) that human morphology to some extent conforms to Bergmann's rule, i.e. that populations living in colder climates have larger body sizes (Bergmann 1847, Rensch 1938). More specifically, our results are also in line with a previous study of male stature and latitude (Ruff 1994), as well as of male stature and mean temperature (Roberts 1953). Here we have confirmed a positive relationship

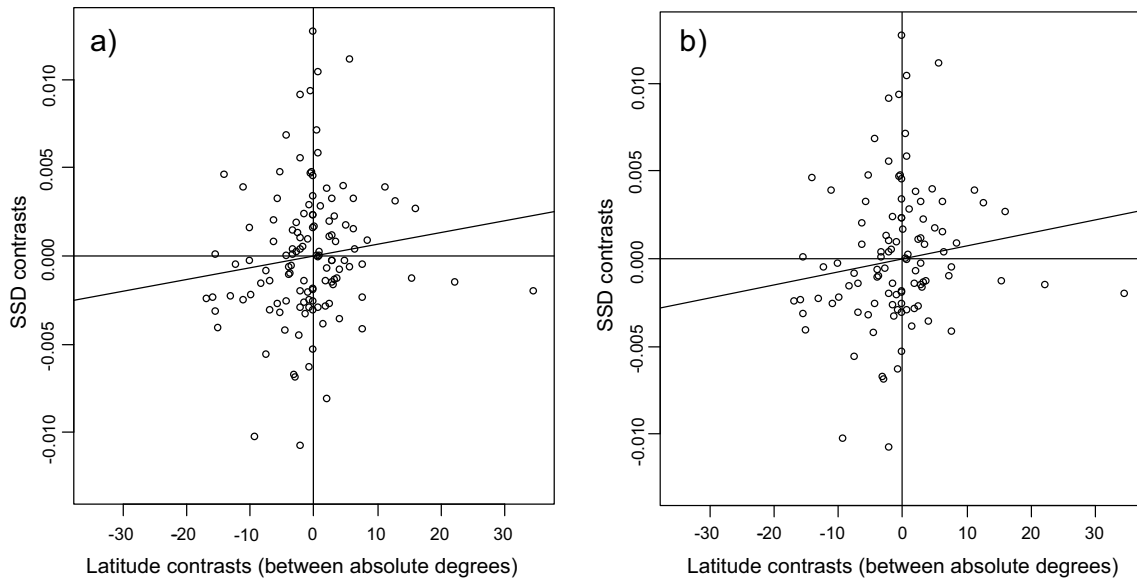


Figure 4. Least squares regression lines, forced through the origin, on standardized phylogenetic independent contrasts of latitudes and sexual stature dimorphism ($SSD = \log \text{ male stature} - \log \text{ female stature}$) for various human populations, both with (a) Europeans included and (b) Europeans excluded. The relationship between SSD and latitude across human populations was non-significant, both when Europeans were excluded and included.

between stature and latitude using a somewhat larger data-set and an updated methodology, now providing support for female stature as well. In all of our tests on human stature the coefficient of determination was low, however, unsurprisingly suggesting that other factors than latitude also are likely to contribute to variation in human stature.

One suggested explanation for the reported pattern is that the latitudinal cline in temperature that is found around the globe could have affected body size evolution in humans (Bergmann 1847, Rensch 1938; Roberts 1953). Another possibility, however, is that latitude is related to differences in nutritional standards and other aspects related to standard of living (Wolfe and Gray 1982a), as within-population studies have shown that increased standard of living in many cases leads to increasing mean stature. Both these processes can of course be in effect simultaneously.

Knowing that varying living standards might confuse a pattern caused by climate, we tried to minimize the effects of standard of living. We did this by performing all tests both with and without Europeans, because in the present sample, Europeans, as a group were likely to stand out by having a higher standard of living than the rest of the populations in the sample. Since there was a significant effect of latitude on stature also when European populations were excluded, we lean towards an explanation where at least some of the variation can be explained as effects other than standard of living.

The tests of a possible curved relationship between latitude and stature revealed that the partial significance for the quadratic term was significant for both males and females, both with and without Europeans. The second degree equations were significant in both tests on male stature, we were thus able to verify that there is indeed an inversely U-shaped relationship between latitude and male stature. There was also a curved relationship between female stature and latitude when Europeans were included, but not when excluded. Taken together, these results point towards a mild curved effect of latitude on human stature. Possibly, much of this slight peak in stature at mid-latitudes can be attributed to a higher standard of living in these areas.

The tests of SSD and latitude gave different results depending on whether phylogenetic correction for shared ancestry was used or not. When a non-phylogenetic method was used, SSD was positively related to distance from the equator, while the independent contrasts analyses did not result in any significant association between latitude and SSD. Since SSD has a clear phylogenetic signal (Holden and Mace 1999), but simultaneously broke one of the assumptions of the independent contrasts test (Garland et al. 1992), our results are hard to interpret.

Should the results from the independent contrast tests be correct, they indicate that there is no effect of latitude on SSD, and thus no support for the prediction that human SSD conforms to both Bergmann's and Rensch's rules, i.e. that SSD increases with absolute latitude. That SSD is not significantly related to latitude, while both male and female stature are, is instead in line with the results of Gustafsson et al. (2007), who suggested that variation in SSD might be independent of changes in general mean stature of a population.

On the other hand, if we should refrain from using the information from phylogenetic tests, the conclusion would instead be that there is a positive association between latitude and SSD. However, two recent studies have shown no support for Rensch's rule, neither between populations (Gustafsson and Lindenfors 2004) nor within a population as a result of changes in standard of living (Gustafsson et al. 2007). Thus, we lean towards suggesting that the results from the phylogenetic tests are the more correct.

The results from the only previous study (Wolfe and Gray 1982b) investigating a possible relationship between latitude and SSD indicated that SSD may be associated with latitude, but suggesting a more inversely U-shaped relationship, where intermediate distances from the equator give higher SSD than for populations living closer to either the equator or the poles. To investigate a possible curved relationship between SSD and latitude, we included a quadratic term in our analyses. Statistical tests indicated that this term explained significant variation in our regression models. These results corroborate an inversely U-shaped relationship between SSD and latitude. As this relationship did not disappear when European populations were excluded it is less likely that this shape is caused by differences in living standard. Interestingly, as previously mentioned, both male and female stature were also related to latitude in an inversely U-shaped way, both SSD as well as male and female stature are peaking at around 40° from the equator. These findings together are in line with the idea that dimorphism is in fact increasing with general stature. However, a previous study on the same data-set did not find that SSD was increasing with general stature (Gustafsson and Lindenfors 2004).

Even though some studies indicate that effects of Bergmann's rule leave traces in the size evolution of other animal species (Blackburn et al. 1999; Blanckenhorn et al. 2006), studies of Bergmann's rule pose special problems in the case of *Homo sapiens* because of our ability for behavioural cold protections. Through niche construction (Laland et al. 2000) we are able to alter our personal microclimate; when we find the environment to be too cold we can for example build huts, light fires, and put on warm clothes. It is therefore likely that any adaptations to the surrounding climate are less pronounced in humans than in many other mammals. See Ruff (1991, 1994) for further discussion of limitations in the applicability of Bergmann's rule in humans.

Bergmann's rule is usually interpreted in terms of body size or weight. Here, we have instead used variation in stature to assess Bergmann's rule in humans. The advantage of using stature data is that it is more easily available than many other variables. While other measures of body size may be climatically more relevant than stature (as suggested by, e.g. Ruff 1994), we have here specifically analysed latitude as a variable that may have influenced the evolution of human stature and stature dimorphism. However, we

acknowledge that the relationship may not be direct, but via selection on body size and shape rather than stature *per se*.

Conclusion

Our results indicate that both male and female stature are weakly associated with latitude. It is possible that these relationships are evolved responses to variation in climate. Regarding sexual stature dimorphism, we cannot unequivocally answer the question if Bergmann's and Rensch's rules combine so that humans are more dimorphic at higher latitudes, although it seems not to be the case. We also found that stature and SSD were related to distance from the equator in an inversely U-shaped fashion.

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Appendix I. Stature and latitude data on populations in the sample

Population in the HGHG ¹	Name in reference	Code in ACEA; and latitude ²	Male stature ³	n ⁴	Female stature	n	Reference ⁵
<i>Populations in sub-Saharan Africa</i>							
Bane	Bamum	Ae50; 6	171.5	71	163.1	58	Hiernaux 1968b
Bane	Bamileke	Ae5; 5	168.4	352	158.6	236	Hiernaux 1968b
Bantu, NE	Ganda	Ad7; 1	167.3	261	156.0	242	Hiernaux 1968b
Bantu, NE	Kikuyu	Ad4; -1	163.6	412	151.6	100	Holden and Mace 1999
Bantu, NW	Teke	Ac19; -3	159.1	200	150.7	200	Hiernaux 1968b
Bantu, NW	Duala	A12; 4	169.1	75	156.9	50	Hiernaux 1968b
Bantu, SE	Venda	Ab6; -23	167.6	168	154.0	56	Hiernaux 1968b
Bantu, SE	Durban Zulus	Ab12; -29	166.1	106	156.0	219	Eveleth and Tanner 1976
Bedik	Bassari	Ag21; 12	166.4	126	156.8	93	Hiernaux 1968b
Biaka	Binga (Cameroun)	Map; 3	152.5	478	144.5	488	Hiernaux 1968b
Biaka	Binga (Gabon)	Map; 1	157.9	53	148.3	43	Hiernaux 1968b
Biaka	Western pygmies (CAR)	Map; 4	152.7	48	145.0	43	Cavalli-Sforza 1986
Biaka	CAR Pygmies	Map; 4	152.9	427	144.3	392	Pennetti et al. 1986
Fulani	Peul du Niger	Map; 15	172.7	42	161.7	41	Hiernaux 1968b
Fulani	Peul du Sud-Cameroun	Map; 6	173.5	59	161.4	40	Hiernaux 1968b
Gur	Mossi (Donse)	Ag47; 12	167.8	49	158.6	58	Froment and Hiernaux 1984
Gur	Mossi (Kokologo)	Ag47; 12	168.9	27	158.7	119	Froment and Hiernaux 1984
Hadza	Hadza (25-54 years)	Aa9; -3	161.3	98	150.8	50	Barnicot et al. 1972
Hausa	Hausa du Niger	Cb26 (Zazzagawa); 11	170.6	143	161.0	174	Hiernaux 1968b
Hausa	Hausa du Cameroun	Cb26 (Zazzagawa); 11	168.7	40	159.2	45	Hiernaux 1968b
Ibo	Ibo orientaux	Af10; 6	165.5	68	154.5	54	Hiernaux 1968b
Khoi	Nama	Aa2; -26	162.4	73	149.7	27	Holden and Mace 1999
Kru	Kran	Af47; 6	164.9	105	154.4	95	Hiernaux 1968b
Mbuti	Ituri (E. pygmy)	Aa3; 2	144.4	71	136.0	38	Cavalli-Sforza 1986
Mbuti	Epulu	Aa3; 2	144.19	69	137.35	32	Cavalli-Sforza 1986
Mbuti	Mbuti (Congo Léopoldville)	Aa3; 2	144.0	510	137.0	382	Hiernaux 1968b
Nilotic	Turkana	Aj5; 4	173.9	40	163.3	42	Holden and Mace 1999
Nilotic	Turkana	Aj5; 4	175.19	84	165.07	67	Little and Johnson 1986
Nilotic	Maasai	Aj2; -2	171.2	88	159.9	180	Holden and Mace 1999
Nilotic	Maasai	Aj2; -2	165.9	362	152.4	333	Holden and Mace 1999
Peul	Fulakunda (Peul) du Badyar	Map; 10	168.0	100	156.1	100	Hiernaux 1968b
Pygmoid	Bunia pygmies	Map; 1	145	41	138	21	Eveleth and Tanner 1976
Pygmoid	Twa (Rwanda)	Map; -2	153	101	144.2	84	Hiernaux 1968b
San	Kung (Bochimans, Af. S.O.)	Aa1; -20	157.7	58	146.6	77	Hiernaux 1968b

Appendix I (Continued)

Population in the HGHG ¹		Name in reference	Code in ACEA; and latitude ²	Male stature ³	n ⁴	Female stature	n	Reference ⁵
Sara		Sara Madjingay	Ai22; 9	173.9	346	164	405	Crognier 1979
Volta		Ashanti	Af3; 7	164.21	48	154.74	27	Rattray 1955
Volta		Agni	Af39 (Anyi); 7	167.9	68	156.6	52	Hiermaux 1968b
Yoruba		Akufo (Yoruba)	Af6; 8	167.5	340	155	205	Eveleth and Tanner 1976
<i>Populations in Europe</i>								
Basque		Basques francais	Map; 43	169.2	219	156.4	56	Hiermaux 1968b
Basque		Basques espagnols	Map; 43	170.0	529	157.3	126	Hiermaux 1968b
Belgian		Belgium, Brussels	Map; 51	174.5	147	161.8	176	Eveleth and Tanner 1976; Hiermaux 1968b
Czechoslovakian		Tcheques	Ch3; 50	173.5	1169	161.0	2528	Hiermaux 1968b
Czechoslovakian		Czechoslovakia	Ch3; 50	172.0	—	161.0	—	Eveleth and Tanner 1976
Dutch		Hollandais du Nord	Cg1; 53	173.1	70	161.7	60	Hiermaux 1968b
Dutch		Netherlands	Cg1; 53	177.7	—	166.3	—	Eveleth and Tanner 1976
English		Great Britain	Map; 52	173.9	4707	160.9	5156	Rosenbaum et al. 1985
Finnish		Finlandais de Botnic	Map; 64	167.6	697	156.4	249	Hiermaux 1968b
French		Francais	Map; 48	169.6	60	160.4	60	Hiermaux 1968b
German		Allemands du Centre	Map; 51	167.8	450	156.4	408	Hiermaux 1968b
Greek		Greece, students	Ce7; 39	172.2	—	159.1	—	Eveleth and Tanner 1976
Hungarian		Hongrois	Ch8; 47	168.0	76	156.9	95	Hiermaux 1968b
Irish		Irish	Cg3; 53	171.9	8902	158.6	1801	Hooton et al. 1955
Italian		Italy, Naples	Ce5; 41	174.4	—	162.5	—	Eveleth and Tanner 1976
Lapp Finnish		Finnish Lapps (20–60 years)	Cg4; 68	164.1	240	152.4	248	Auger et al. 1980
Norwegian		Norvegiens	Map; 61	172.4	11 774	162.4	193	Hiermaux 1968b
Polish		Poland, Cracow	Map; 50	173.2	—	160.2	—	Eveleth and Tanner 1976
Portuguese		Portugais	Ce2; 42	164.8	200	152.3	150	Hiermaux 1968b
Russian		USSR, Moscow	Ch11; 53	171.8	—	159.8	—	Eveleth and Tanner 1976
Swedish		Suedois de Runö	Map; 58	174.1	77	159.7	75	Hiermaux 1968b
Yugoslavian		Yougoslaves	Map; 44	175.7	118	162.0	74	Hiermaux 1968b
<i>Populations in Asia</i>								
Bhutanese		Bhutan	Map; 27	169.2	44	161.1	28	Eveleth and Tanner 1976
Chukchi		Chukchi	Ec3; 66	165.08	70	152.64	82	Smirnova 1979
Druse		Druse	Cj8; 33	165.6	181	152.2	114	Shanklin and Izzeddin 1937
Iranian (E+W)		South Iranian	Ea9; 36	169.8	907	158.9	939	Ayatollahi and Carpenter 1993
Korean		South Korea (23 years)	Ed1; 35	170.1	280	156.2	49	Eveleth and Tanner 1976
Koryak		Koryak	Ec5; 62	159.6	173	149.1	133	Jochelson 1908

Appendix I (Continued)

Population in the HGHG ¹		Name in reference	Code in ACEA; and latitude ²	Male stature ³	n ⁴	Female stature	n	Reference ⁵
Kurdish		Kurds (Iraq)	Ci11; 32	166.1	597	152.7	31	Field 1952
Mongol		Khalkha-Mongols	Eb3; 46	164.83	59	151.33	49	Vlček 1965
Nenetsy		Wood Nenez	Ec4; 68	160.08	50	147.62	42	Smirnova 1979
Saudi		Saudi (Highlanders)	Map; 19	162.3	220	149.7	217	Khalid 1995
Saudi		Saudi (Lowlanders)	Map; 19	158.7	191	147.1	277	Khalid 1995
Tungus		Evenki Reindeer Herders	Ec9; 47	157.8	116	147.2	69	Leonard et al. 1994
Tungus		Tungus	Ec9; 47	156.5	52	146.5	72	Holden and Mace 1999
<i>Populations in Southeast Asia</i>								
Ami		Ami	Ia9; 22	164.6	146	155.9	94	Chen 1967
Atayal		Atayal	Ia1; 24	160.1	96	149.8	147	Chen 1967
Bunun		Bunun	Ia10; 24	157.2	96	146.2	110	Chen 1967
Javan		West Java	Ib2; -7	158.0	-	150.0	-	Eveleth and Tanner 1976
Javan		Jogjakarta	Ib2; -7	161.5	-	150.0	-	Eveleth and Tanner 1976
Khasi		Khasi (Assam)	Ei8; 26	156.66	400	146.97	325	Field 1970
Paiwan		Paiwan	Ia6; 22	156.6	127	148.0	150	Chen 1967
Philippine		Philippines (20 years)	Map; 14	164.6	36	151.1	45	Eveleth and Tanner 1976
Sea Dayak		Iban	Ib1; 2	159.7	43	148.7	41	Strickland and Ulijaszek 1993
Semai		Semang	Ej3; 5	153.3	216	142.4	97	Schebesta 1952
South Chinese		Hong Kong (Chinese, 20 years)	Map; 22	167.1	431	156.0	358	Eveleth and Tanner 1976
<i>Populations in Australia and the Pacific Islands</i>								
Australian ⁶		Aborigine	Map; -22	172.1	-	162.9	-	Eveleth and Tanner 1990
Australian		South Austr. Aborigine (Gerard and Raukkan)	Map; -35	171.2	27	156.7	21	Pretty et al. 1998
Australian		Aborigine	Map; -25	168.6	22	156.8	22	Eveleth and Tanner 1976
Australian		Yuendumu	Map; -22	173.0	26	162.7	39	Eveleth and Tanner 1976
Bougainville SE		Nasioi	Map; 6	162.1	59	150.4	63	Friedlaender 1987
Bougainville W		Nagovisi	Map; 6	159.6	109	150.3	101	Page et al. 1977
Fiji		Fiji-Melanesian	Map; -17	176.1	16	167.7	9	Eveleth and Tanner 1990
Fiji		Fiji	Map; -17	172	130	161.8	142	Eveleth and Tanner 1976
Luangua		Ontong Java	Ii5; -5	164.2	144	154.9	197	Friedlaender 1987
Malaita		Kwaio	Ig18; -9	160.3	127	149.0	114	Friedlaender 1987
Malaita		Baegu	Map; 9	161.3	126	150.3	111	Page et al. 1977
Malaita		Lau (Malaita)	Ih4; -18	162.5	76	151.8	95	Friedlaender 1987
Manus		Manus	Ig9; -2	162.9	20	151	38	Heath and Carter 1971
Manus		Manus (Pere)	Ig9; -2	164.3	19	153.4	17	Eveleth and Tanner 1990

Appendix I (Continued)

Population in the HGHG ¹		Name in reference	Code in ACEA; and latitude ²	Male stature ³	n ⁴	Female stature	n	Reference ⁵
Manus		Manus (town)	Ig9; -2	165.2	16	155.4	23	Eveleth and Tanner 1990
Samoa		Salamumumu (Western Samoa)	Ii1; -14	170.4	101	158.3	144	Eveleth and Tanner 1990
Society		Society Islands	Map; 17	171.4	85	161.1	68	Eveleth and Tanner 1976
Tokelau		Tokelau (20-54)	Ii6; -9	169.2	228	159.5	264	Prior et al. 1977
Tolai		Tolai	Map; 5	162.5	38	156.1	65	Wolstenholme and Walsh 1967
<i>Populations in New Guinea</i>								
Anga		Kukukuku (20-49 years)	Map; -7	151.2	59	142.7	99	Malcolm 1969
Awin		Awin	Map; -6	158.4	56	147.1	77	Hyndman et al. 1989
Highland E		Gadsup	Map; -6	158.28	212	148.95	55	Littlewood 1972
Highland E		Tairora	Map; 6	155.97	301	149.41	42	Littlewood 1972
Highland E		Auyana	Map; -7	153.68	260	146.31	30	Littlewood 1972
Ok		Mountain Ok	Map; -5	152.7	147	146.7	150	Eveleth and Tanner 1990
<i>Populations in North America, South America and Greenland</i>								
Arawakan		Central Arawaks	Map; -7	159.16	32	147.64	17	Gillin 1936
Aymara		Aymara (Chile, coast)	Sf2; -16	164.1	66	151.4	66	Eveleth and Tanner 1990
Aymara		Aymara (Chile, sierra)	Sf2; -16	160.0	45	149.6	69	Eveleth and Tanner 1990
Aymara		Aymara (Chile, altiplana)	Sf2; -16	163.0	70	150.0	90	Eveleth and Tanner 1990
Aymara		Aymara (Bolivia)	Sf2; -16	162.0	25	149.0	39	Eveleth and Tanner 1990
Bari		Motilon	Sb3; 9	146.2	37	138.1	37	Comas 1971
Caingang		Caingang (Rio G. do Sul, Paraná)	Sj3; -28	161.0	354	149.1	254	Neves et al. 1985
Caingang		Caingang (Palmas)	Sj3; -28	162.5	41	151.2	21	Neves et al. 1985
Caingang		Caingang (Tupa)	Sj3; -28	163.4	9	149.3	12	Neves et al. 1985
Eskimo (Alaskan)		Alaskan (20-60 years)	Map; 70	166.0	91	155.4	134	Auger et al. 1980
Eskimo (Canadian)		Copper Eskimo	Na3; 69	164.8	82	156.4	42	Jenness 1923
Eskimo (Canadian)		Labrador Inuit	Na23; 58	158.4	58	148.3	78	Holden and Mace 1999
Eskimo (Canadian)		Igloodik (Foxe Basin) 20-60 years	Na22; 70	163.5	134	152.6	114	Auger et al. 1980
Eskimo (Canadian)		Iglulik Eskimo	Na22; 70	166	20	153.7	20	Jenness 1923
Eskimo (Canadian)		Igloodik Eskimo	Na22; 70	165.8	12	157.5	12	Eveleth and Tanner 1976
Eskimo (Greenland)		Angmagsalik Inuit	Na24; 66	162.0	166	153.3	203	Holden and Mace 1999
Eskimo (Greenland)		Greenland Inuit	Na25; 69	162	500	152	400	Holden and Mace 1999
Eskimo (Greenland)		West Greenland (20-50 years)	Map; 67	160.8	45	149.3	41	Auger et al. 1980
Macushi		Macushi	Sc12; 4	156.8	42	146.3	28	Steggerda 1963
Makiritare		Maqiritare	Sc16; 3	156.0	26	146.0	24	Stinson 1990
Mapuche		Mapuche	Sg2; -39	160.4	201	144.2	25	Stinson 1990
Mapuche Araucano		Araucanian	Sg2; -39	160.38	60	150.26	86	Valenzuela et al. 1978

Appendix I (Continued)

Population in the HGHG ¹		Name in reference	Code in ACEA; and latitude ²	Male stature ³	n ⁴	Female stature	n	Reference ⁵
Mayan E		Quiche	Sa13; 15	153.8	117	143.8	83	Comas 1971
Mayan E		Maya (Guatemala)	Map; 17	156.8	42	142.8	20	Eveleth and Tanner 1976
Mayan E		Cakchiquel	Sa11; 14	155.3	72	143.2	36	Comas 1971
Na-Dene (Canadian)		Chilcotin Athapascan	Na18; 52	170.3	36	156.5	55	Birkbeck et al. 1971
Na-Dene (Canadian)		Chippewyan	Na30; 60	166.4	44	150.9	20	Holden and Mace 1999
Na-Dene (Canadian)		Dogrib	Na15; 63	165.4	60	154.5	97	Szathmary and Holt 1983
Navajo		Navaho	Nh3; 37	169.9	90	157.4	40	Hrdlička 1935
Papago		Papago	Ni2; 31	170.9	50	155.9	30	Hrdlička 1935
Pima		Pima	Ni6; 31	171.8	53	157.4	30	Hrdlička 1935
Pima		Pima	Ni6; 31	169.6	77	156.3	51	Comas 1971
Quechua		Quechua (highland)	Sf1; -13	159.9	62	148.1	58	Eveleth and Tanner 1990
Quechua		Quechua (lowland)	Sf1; -13	163.1	57	149.8	60	Eveleth and Tanner 1990
Quechua		Quechua	Sf1; -13	160.1	245	148.3	112	Comas 1971
Quechua		Quechua (Cusco, Peru)	Sf1; -13	158.8	243	146.3	85	Stinson 1990
Quechua		Quechua (Nunua, Peru)	Sf1; -13	160.0	50	148.0	50	Stinson 1990
Quechua		Quechua (Pichincha Province, Ecuador)	Sf1; -13	154.3	87	142.8	36	Stinson 1990
Trio		Trio	Map; -3	157.7	115	147.5	142	Stinson 1990
Wajana		Wajana	Map; -4	156.6	75	146.2	91	Stinson 1990
Warau		Warao	Sc1; 9	156.5	318	144.7	172	Stinson 1990
Xavante		Xavante	Sj11; -14	169.4	66	155.6	73	Stinson 1990
Yanomama		Yanomamo	Sd9; 2	153.2	316	142.3	260	Eveleth and Tanner 1976
Yanomama		Yanomama	Sd9; 2	154.8	69	144.3	70	Neves et al. 1985
Zuni		Zuni	Nh4; 35	163.5	60	151.2	32	Hrdlička 1935

¹Name used to classify the population in the *History and Geography of Human Genes* (Cavalli-Sforza et al. 1994).

²Population codes used in *A Corrected Ethnographic Atlas* (Gray 1999) and population location presented there, given in latitudinal degrees. In cases when a population was not found in the *Corrected Ethnographic Atlas*, latitude was estimated from published maps and information in original sources, as well as the *Ethnologue* (Grimes 1992). Here this is indicated by the word 'Map', followed by the latitude data. Sometimes data from more than one source is used to obtain mean stature for a population. In these cases latitude is only given for one of the sources, but applies to all.

³Mean height (cm).

⁴Sample size.

⁵References for male and female height.

⁶Thirty-nine male subjects and 23 female in Holden and Mace (1999).