Human size evolution: no evolutionary allometric relationship between male and female stature

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Abstract

In many animal groups, sexual size dimorphism tends to be more pronounced in species with large body size. Similarly, in a previous cross-cultural analysis, male and female stature in humans were shown to be positively allometrically related, indicating a similar relationship where populations with larger stature were more dimorphic. In this study, we re-examine the hypothesis of an allometric relationship between the sexes using phylogenetic methodology. First, however, we tested whether there exist phylogenetic signals in male and female stature. Data on mean stature from 124 human populations was gathered from the literature. A phylogenetic test showed that male and female stature were significantly associated with phylogeny. These results indicate that comparative methods that to some degree incorporate genetic relatedness between populations are crucial when analyzing human size evolution in a cross-cultural context. Further, neither non-phylogenetic nor phylogenetic analyses revealed any allometric relationship between male and female stature. Thus, we found no support for the idea that sexual dimorphism increases with increasing stature in humans.
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Introduction

In the animal kingdom, adult males and females often differ in size. In most animal groups, females are usually the larger sex, though in mammals and birds males are most often larger — a pattern that can be attributed to sexual selection through male-male competition in these two groups (Darwin, 1871).

Sexual size dimorphism (SSD) varies considerably between different animal species and taxa. This variation among species appears to follow a general allometric pattern between SSD and

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body size in related species. In taxa in which males is the larger sex, SSD tends to increase with body size (hyperallometry), i.e. larger species have relatively larger sexual size dimorphism, while SSD decreases with body size in species where females are larger (hypoallometry). This trend was first pointed out by Rensch (1950, 1959) and is hence called Rensch's rule.

Rensch's rule, however, contains no statement on what causes the phenomenon. Instead, a number of functional hypotheses have been proposed to explain the pattern, comprehensively summarized and evaluated in a review by Fairbairn (1997). One potential explanation is that female size changes when larger male size is being selected for as a result of a genetic correlation between the sexes concerning size-controlling genes (Maynard Smith, 1978; Lande, 1980, 1987; Lande and Arnold, 1983). That a genetic correlation for size-controlling genes is likely to exist in humans is indicated by a high degree of covariance between the sexes in stature (Rogers and Mukherjee, 1992; but see Rice, 1984; Roldan and Gomendio, 1999). Theoretical work shows that this effect is only expected initially, however, as natural selection is expected to reverse the process and eventually return female body size to its natural selection optimum (Lande, 1980; Reeve and Fairbairn, 2001).

Another potential explanation for Rensch's rule is what Fairbairn (1997) terms correlational selection; when male size increases because of sexual selection, larger female size will be selected for as well due to effects of the larger size of the males. In mammals this selection can come about, for example, because of increased demands for giving birth to and nursing larger male offspring (e.g. Lindenfors, 2002).

Even though Rensch's rule has been widely accepted and is supported by a number of studies in different animal groups, there are also several contradicting results (Abouheif and Fairbairn, 1997, and references cited therein). Particularly primates is a well-studied group and several non-phylogenetic analyses support the notion that primates conform to Rensch's rule (e.g. Ralls, 1976; Clutton-Brock et al., 1977; Leutenegger, 1978; Leutenegger and Cheverud, 1982; Gaulin and Sailer, 1984; Reiss, 1986), with the exception

of strepserhines (Kappeler, 1990), and with a weaker trend for platyrrhines (Ford, 1994). Since much of the size variation among species can be explained by shared ancestry, however, a comparative method that takes phylogeny into account is necessary (Brooks and McLennan, 1991; Harvey and Pagel, 1991).

Phylogenetic analyses of primate SSD do not show clear-cut results in favour of either the presence or absence of Rensch's rule, however. Lindenfors and Tullberg (1998) found no significant allometric relationship between male and female size, while an allometric relationship was found in studies by Cheverud et al. (1986), Abouheif and Fairbairn (1997), Plavcan and van Schaik (1997) and Smith and Cheverud (2002).

These discrepant results can possibly be explained as an effect of different sample sizes, however. For example, as both theoretical work (Maynard Smith, 1978; Lande, 1980, 1987; Lande and Arnold, 1983) and empirical evidence (Lindenfors and Tullberg, 1998) indicate that sexual selection on male body size induces a correlated response in female body size, it should follow that co-variation between body size and body size dimorphism should be found only in comparisons between clades differing in degree of sexual selection, while comparisons within clades sharing a common mating system should show no such co-variation. Thus, by excluding species randomly in the phylogeny, hence excluding many species within clades sharing a common mating system, one excludes the exact variation that would diffuse the evidence for the presence of Rensch's rule. Note that this problem would not only occur if sexual selection is the mechanism behind Rensch's rule, but should apply equally to any cause behind Rensch's rule that contains a phylogenetic component.

Most studies in support of Rensch's rule have been carried out on an interspecific level. However, Rensch claimed that the rule also should apply to "subspecies of a species" (Rensch, 1959, p. 159), thus implying that it ought to be possible to also trace effects of Rensch's rule in comparisons between populations.

Human SSD is most commonly measured as the male to female stature (height) ratio. In every

population of human adults ever studied, mean stature in males has been greater than in females (Eveleth, 1975). The average SSD in a cross-cultural sample has previously been reported to be approximately 1.07 (Gaulin and Boster, 1985). Different human populations vary somewhat in SSD, however. For example, in a population with a relatively high SSD, like the Mountain Ok (Eveleth and Tanner, 1990), the SSD will be about 8 percent higher than in a population with low SSD, like Assyrians (Field, 1952). If differences in human SSD are consistent with Rensch's rule, then populations with above average mean stature should be more likely to display a high SSD.

To test this, Wolfe and Gray (1982) collected and compared mean heights of men and women in various human populations and found support for an allometric relationship between male and female stature, thus indicating that Rensch's rule applies also to interpopulation comparisons on stature dimorphism. Their conclusion was later criticised by Gaulin and Boster (1985), who claimed that the feeble support for allometry found by Wolfe and Gray (1982) was an artefact of too small sample sizes for some of the populations.

Instead, Gaulin and Boster (1985) argued that cross-cultural differences in SSD are mainly a function of within-population sample size, and that the degree of dimorphism in humans actually is very consistent. However, variation in SSD between populations is clearly present in the sample used in the present study (Appendix I). Further, in e.g. the examples mentioned above of populations with large differences between recorded SSD − Mountain Ok and Assyrians − sample size is over 100 subjects per sex.

None of the two above mentioned studies on human sexual stature allometry used a comparative phylogenetic method, however, or any other method appropriate to correct for errors arising as a consequence of populations sharing a common ancestry. In a previous study on human SSD, though not testing for the presence of Rensch's rule, Holden and Mace (1999) found that sexual stature dimorphism showed a highly significant association with phylogeny, thus suggesting that there should be phylogenetic signals in both male

and female stature. If human populations have more similar body sizes the more genetically related they are, comparative methods that to some degree incorporate genetic relatedness between populations are a necessity when analyzing human size evolution in a cross-cultural context.
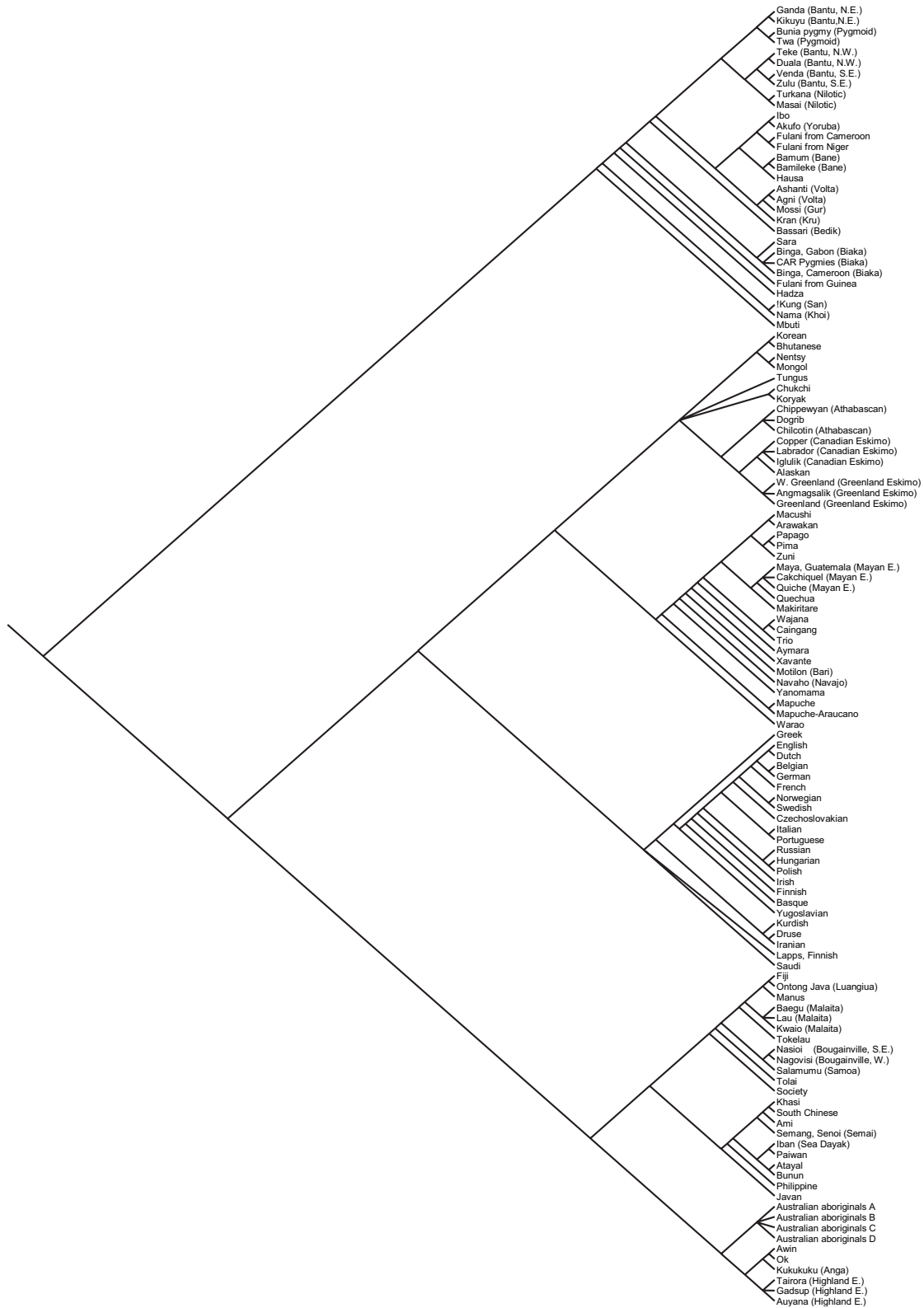
Here, we investigate the presence of phylogenetic signals in male and female stature, and test the possibility of an allometric relationship between male and female stature in humans using both non-phylogenetic and phylogenetic approaches.

Materials and methods

Data on male and female mean stature were collected from a variety of published sources (Appendix I) for 124 of the populations included in Cavalli-Sforza et al. (1994). Data from different sources were considered as belonging to the same ethnic group if they had the same name and location, if a matching synonymous name could be found in Grimes (1992), or could otherwise be deduced to be the same from e.g. Murdock (1967).

Populations with data on fewer than 14 individuals of each sex were excluded. In a few cases, though, data was included for sources lacking information on number of subjects, however, provided that the source was considered reliable. No specific year or period of data recording was preferred to the other, but most of the recordings were from the latter part of the 20th century. When more than one source, or year of recording, was used for a population, means from the different sources were weighted with respect to the number of subjects in each source, while sources lacking information on number of subjects were given equal weighting. Only sources with data on both male and female stature were used. Since only measurements of adult stature were desired, data on individuals under 19 years of age were excluded when age distributions were given. All continuous variables were log_{10}-transformed prior to analysis.

The phylogeny used (Fig. 1), was constructed by combining the various phylogenies in Cavalli-Sforza et al. (1994) that were based on genetic

Ganda (Bantu, N.E.)
Kikuyu (Bantu,N.E.)
Bunia pygmy (Pygmoid)
Twa (Pygmoid)
Teke (Bantu, N.W.)
Duala (Bantu, N.W.)
Venda (Bantu, S.E.)
Zulu (Bantu, S.E.)
Turkana (Nilotic)
Masai (Nilotic)
Ibo
Akufo (Yoruba)
Fulani from Cameroon
Fulani from Niger
Bamum (Bane)
Bamileke (Bane)
Hausa
Ashanti (Volta)
Agni (Volta)
Mossi (Gur)
Kran (Kru)
Bassari (Bedik)
Sara
Binga, Gabon (Biaka)
CAR Pygmies (Biaka)
Binga, Cameroon (Biaka)
Fulani from Guinea
Hadza
!Kung (San)
Nama (Khoi)
Mbuti
Korean
Bhutanese
Nentsy
Mongol
Tungus
Chukchi
Koryak
Chippewyan (Athabascan)
Dogrib
Chilcotin (Athabascan)
Copper (Canadian Eskimo)
Labrador (Canadian Eskimo)
Iglulik (Canadian Eskimo)
Alaskan
W. Greenland (Greenland Eskimo)
Angmagsalik (Greenland Eskimo)
Greenland (Greenland Eskimo)
Macushi
Arawakan
Papago
Pima
Zuni
Maya, Guatemala (Mayan E.)
Cakchiquel (Mayan E.)
Quiche (Mayan E.)
Quechua
Makiritare
Wajana
Caingang
Trio
Aymara
Xavante
Motilon (Bari)
Navaho (Navajo)
Yanomama
Mapuche
Mapuche-Araucano
Warao
Greek
English
Dutch
Belgian
German
French
Norwegian
Swedish
Czechoslovakian
Italian
Portuguese
Russian
Hungarian
Polish
Irish
Finnish
Basque
Yugoslavian
Kurdish
Druse
Iranian
Lapps, Finnish
Saudi
Fiji
Ontong Java (Luangiua)
Manus
Baegu (Malaita)
Lau (Malaita)
Kwaio (Malaita)
Tokelau
Nasioi   (Bougainville, S.E.)
Nagovisi (Bougainville, W.)
Salamumu (Samoa)
Tolai
Society
Khasi
South Chinese
Ami
Semang, Senoi (Semai)
Iban (Sea Dayak)
Paiwan
Atayal
Bunun
Philippine
Javan
Australian aboriginals A
Australian aboriginals B
Australian aboriginals C
Australian aboriginals D
Awin
Ok
Kukukuku (Anga)
Tairora (Highland E.)
Gadsup (Highland E.)
Auyana (Highland E.)

distances calculated on the basis of allele frequencies (or actually, frequencies of polymorphic, genetic markers, like blood groups or proteins). When a population appeared in contradicting phylogenies, a "super-tree" method (Purvis, 1995) was used to determine a composite tree. In cases where such a composite tree could not be constructed because of conflicting information (e.g. many populations in North Africa and India), the population, or cluster of populations, was excluded.

To avoid great differences in nutritional standard one could choose not to include populations from industrialized countries (e.g. Holden and Mace, 1999). For this reason, all analyses in this study were carried out both including and excluding Europeans. Though excluding Europeans does not necessarily mean that all variation resulting from different living conditions disappears (see below), analyses both including and excluding Europeans at least checks for one possible source of error.

The test for phylogenetic signal suggested by Blomberg et al. (2003) was used in order to determine whether there were phylogenetic signals in male and female stature. In these analyses, we used the computer package PDAP (Garland et al., 1993), and set the number of randomizations to 1001. Since the tests showed that there were significant phylogenetic signals (see below) we proceeded to analyse the data with phylogenetic methods.

An independent contrasts analysis (Felsenstein, 1985), as implemented in the computer package PDAP (Garland et al., 1993), was used to determine whether sexual dimorphism increases with increasing stature in humans. Polytomies were handled by using zero-length branches, while all other branch lengths were set to equal length. No adjustments of branch-lengths were needed, since diagnostics as described by Garland et al. (1992) revealed no significant trends in the data. Major axis regressions were used for the statistical analyses concerning the possible presence of allometry, rather than ordinary least-squares regressions, as there was no a priori reason to assume any variable (male or female height) as dependent or independent.

Results

Mean SSD in the whole sample, analyzing tip values directly, was 1.072 both when including and excluding Europeans. An average calculated incorporating phylogenetic information as suggested by Garland et al. (1993) gave a mean of 1.069, both with and without Europeans.

Major axis regressions on population data directly, without taking phylogeny into account, showed a strong correlation between male and female stature data (Europeans included: Male Stature = 1.030·Female Stature−0.066, $p < 0.001$; $R^2 = 0.921$, n = 124; Europeans excluded: Male Stature = 1.016·Female Stature−0.021, $p < 0.001$; $R^2 = 0.907$, n = 106) (Fig. 2). Neither of these slopes were significantly different from a slope of 1 (Europeans included: $p = 0.125$; Europeans excluded: $p = 0.300$) (Fig. 2).

A test for phylogenetic signal, however, as described by Blomberg et al. (2003), revealed the necessity for phylogenetic analyses as there were strong phylogenetic signals in both male and female stature. Male stature was significantly associated with the phylogeny, both when including ($p < 0.001$) and excluding Europeans ($p < 0.001$), as was female stature, both including ($p < 0.001$) and excluding Europeans ($p < 0.001$).

Phylogenetic independent contrasts analysis on the whole data-set showed that male and female size evolution are significantly correlated (b = 1.042, $p < 0.001$, $R^2 = 0.879$, n = 123). Also, the major axis regression showed that there is no significant allometric relationship between general stature and sexual dimorphism in stature in that the regression slope was significantly indistinguishable from a slope of 1 ($p = 0.228$) (Fig. 3a). Repeating the analysis without Europeans gave

Fig. 1. Phylogeny of human populations constructed from information in Cavalli-Sforza et al. (1994). Names in brackets indicate population names used by Cavalli-Sforza et al. for clarification in cases where another name has been used in the present study to represent a population.
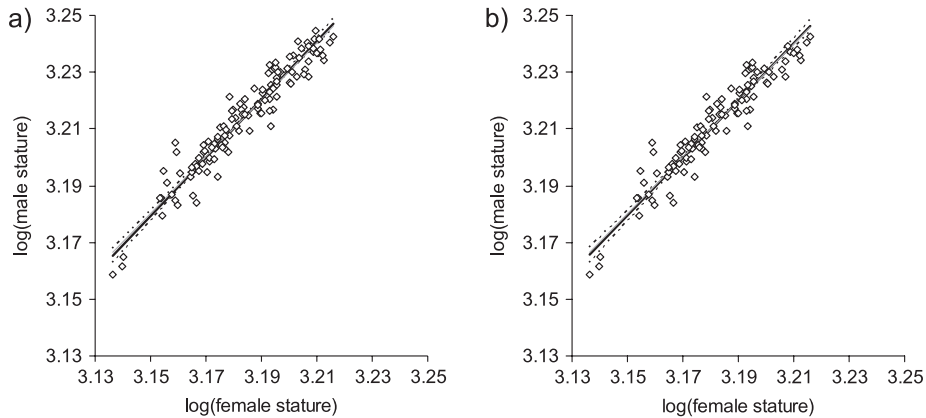
Fig. 2. Major axis regression lines (thick black lines) on male and female stature with a) Europeans included, and, b) Europeans excluded. The slopes are not significantly different from slopes of 1 in that the 95% confidence intervals (dotted lines) include slopes of 1 (grey lines). Thus, the relationship between male and female stature in humans does not deviate significantly from isometry.

similar results; male and female stature were significantly correlated (b = 1.042, p < 0.001, R^2 = 0.881, n = 105) and the slope was not significantly different from a slope of 1 (p = 0.268) (Fig. 3b).

Discussion

In this study we show that the relationship between average male and female stature in human populations follow a pattern that is not significantly different from isometry. Hence, the level of sexual dimorphism cannot be seen as a function of stature. Furthermore, we show that there are clear phylogenetic signals in the data on human stature, indicating that comparative methods taking genetic ancestry into account are a necessity when analyzing human size evolution.

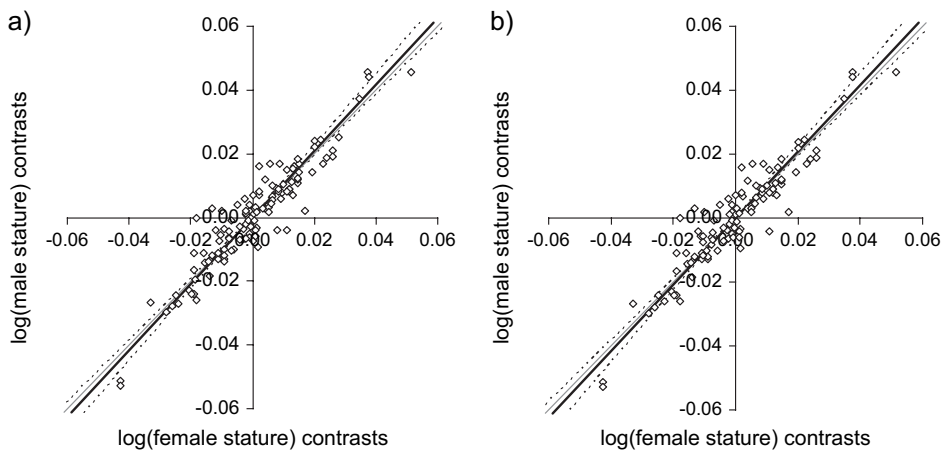Since there was no support for the hypothesis that sexual stature dimorphism increases with

Fig. 3. Major axis regression lines through the origin (thick black lines) on male and female stature contrasts with a) Europeans included, and, b) Europeans excluded. The slopes are not significantly different from slopes of 1 in that the 95% confidence intervals (dotted lines) include slopes of 1 (grey lines). Thus, the relationship between male and female stature in humans does not deviate significantly from isometry.

increased stature in our human cross-cultural sample, neither when using a phylogenetic nor a non-phylogenetic method, no support for Rensch's rule could be found. This was not the expected result based on a previous study on human SSD (Wolfe and Gray, 1982; but see Gaulin and Boster, 1985). The reason that our non-phylogenetic result differs from theirs may be due to slightly different methods (e.g. major axis regressions in favour of ordinary least-squares regressions) and a revised data-set. Our results from using non-phylogenetic analyses were also confirmed using phylogenetic independent contrasts (Felsenstein, 1985). This is a more appropriate method since it corrects for similarity due to shared ancestry.

Correcting for shared ancestry is necessary due to the strong phylogenetic signals in the data reported here, but also because there is a large heritable component in human stature, as shown both by studying genetic covariances directly (Rogers and Mukherjee, 1992; but see Rice, 1984; Roldan and Gomendio, 1999). Thus, comparative methods that to some degree incorporate genetic relatedness between populations are crucial when analyzing human size evolution.

Phylogenetic comparative analyses used in within-species studies – as in this case of human populations – pose a special problem, however. Populations cannot be seen as absolute entities where no genes are transferred. Therefore, a bifurcating tree does not give a complete picture of the evolutionary history of populations within a species. Felsenstein (2002) has initiated the development of a new comparative method to analyse contrasts within species, using migration matrices rather than phylogenetic trees. The basic idea of the method seems very promising, and it might prove useful for future studies.

As there is no *a priori* reason to suspect that the causal factors behind the presence of Rensch's rule on the intraspecific level differs from those responsible on an interspecific level, comparisons of our results with those on primates in general are also meaningful. However, previous phylogenetic studies on sexual size dimorphism in this group have mainly found support for the presence of Rensch's rule (Cheverud et al., 1986; Abouheif and

Fairbairn, 1997; Plavcan and van Schaik, 1997; Smith and Cheverud, 2002; but see Lindenfors and Tullberg, 1998). The discrepant results on primates, however, may be explained by differences in sample size (see above).

Average SSD as obtained in the present study, both using phylogenetic and non-phylogenetic approaches, confirmed the previous estimate of 1.07 reported by Gaulin and Boster (1985). Our results show that the variation around this average is not a function of population differences in mean stature. Probable causes of the differences in SSD are instead specific selection factors, e.g. differences in marriage systems (Alexander et al., 1979; but see Gray and Wolfe, 1980; Gaulin and Boster, 1992; Holden and Mace, 1999), social stratification (Gaulin and Boster, 1992), or sexual division of labour (Holden and Mace, 1999).

Further, Gray and Wolfe (1980) and Wolfe and Gray (1982) have tested whether varying nutritional standards can explain differences in SSD. Many intrapopulation longitudinal studies over many years have shown that increased standard of living leads to an increase in stature and that low nutritional standard and health-care conditions, conversely, can cause the mean stature of a population to decrease (e.g. Ganguly, 1979; Steckel, 1983; Eveleth and Tanner, 1990). It has been suggested that men are more sensitive to such nutritional deficits than women (e.g. Greulich, 1951; Stini, 1969; Tobias, 1970), but empirical support for this hypothesis has not been entirely unequivocal (Hall, 1978). If true, however, one would expect a lower SSD in populations with substandard nutritional level. The existence of such differences in male and female reaction norms under varying standards of living is an empirical question, though, warranting further research.

The close relationship between phylogeny and male and female stature might also be an artefact of a relationship between stature and climate, due to the fact that populations living close to each other have high probabilities of being both genetically similar and sharing the same climatic conditions. Bergmann's rule (Bergmann, 1847) which predicts that body size should be inversely correlated with temperature, has previously received some empirical support in studies on human populations

(e.g. Roberts, 1953; Ruff, 1994; Katzmarzyk and Leonard, 1998). However, a quick view of population data on stature makes us sceptical concerning a possible relationship between climate and stature. For example, male average stature in the tallest and shortest populations ever recorded (to our knowledge) – Nuer (184.88 cm: Hiernaux, 1968a) and Mbuti (144.1 cm: average calculated in the present study) – were both recorded in central Africa, not very far from each other. Furthermore, the various populations of Inuits included in the present study – who live on extremely northern latitudes – do not have correspondingly high average statures. Also, a previous study by Holden

and Mace (1999), testing for the strength of association between body stature dimorphism and phylogeny as well as geography found a significantly stronger signal from phylogeny as compared to geographic proximity.

Acknowledgements

Appendix I

Height data on populations in the sample

Population in the H.G.H.G.[1]	Name in reference	Male height[2]	n[3]	Female height[2]	n[3]	Reference[4]
Populations in sub-Saharan Africa						
Bane	Bamum	171.5	71	163.1	58	Hiernaux, 1968b
Bane	Bamileke	168.4	352	158.6	236	Hiernaux, 1968b
Bantu, N.E.	Ganda	167.3	261	156.0	242	Hiernaux, 1968b
Bantu, N.E.	Kikuyu	163.6	412	151.6	100	Holden and Mace, 1999
Bantu, N.W.	Teke	159.1	200	150.7	200	Hiernaux, 1968b
Bantu, N.W.	Duala	169.1	75	156.9	50	Hiernaux, 1968b
Bantu, S.E.	Venda	167.6	168	154.0	56	Hiernaux, 1968b
Bantu, S.E.	Durban Zulus	166.1	106	156.0	219	Eveleth and Tanner, 1976
Bedik	Bassari	166.4	126	156.8	93	Hiernaux, 1968b
Biaka	Binga (Cameroun)	152.5	478	144.5	488	Hiernaux, 1968b
Biaka	Binga (Gabon)	157.9	53	148.3	43	Hiernaux, 1968b
Biaka	Western pyg. CAR	152.7	48	145.0	43	Cavalli-Sforza, 1986
Biaka	CAR Pymies	152.9	427	144.3	392	Pennetti et al., 1986
Fulani	Peul du Niger	172.7	42	161.7	41	Hiernaux, 1968b
Fulani	Peul du Sud-Cameroun	173.5	59	161.4	40	Hiernaux, 1968b
Gur	Mossi (Donse)	167.8	49	158.6	58	Froment and Hiernaux, 1984
Gur	Mossi (Kokologo)	168.9	27	158.7	119	Froment and Hiernaux, 1984
Hadza	Hadza (25–54 yr)	161.3	98	150.8	50	Barnicot et al., 1972
Hausa	Hausa du Niger	170.6	143	161.0	174	Hiernaux, 1968b
Hausa	Hausa du Cameroun	168.7	40	159.2	45	Hiernaux, 1968b
Ibo	Ibo orientaux	165.5	68	154.5	54	Hiernaux, 1968b
Khoi	Nama	162.4	73	149.7	27	Holden and Mace, 1999
Kru	Kran	164.9	105	154.4	95	Hiernaux, 1968b
Mbuti	Ituri (E. pygmy)	144.4	71	136.0	38	Cavalli-Sforza, 1986
Mbuti	Epulu	144.19	69	137.35	32	Cavalli-Sforza, 1986
Mbuti	Mbuti (Congo Léopoldville)	144.0	510	137.0	382	Hiernaux, 1968b
Nilotic	Turkana	173.9	40	163.3	42	Holden and Mace, 1999
Nilotic	Turkana	175.19	84	165.07	67	Little and Johnson, 1986
Nilotic	Maasai	171.2	88	159.9	180	Holden and Mace, 1999
Nilotic	Maasai	165.9	362	152.4	333	Holden and Mace, 1999

Appendix (*continued*)

Population in the H.G.H.G.[1]	Name in reference	Male height[2]	n[3]	Female height[2]	n[3]	Reference[4]
Peul	Fulakunda (Peul) du Badyar	168.0	100	156.1	100	Hiernaux, 1968b
Pygmoid	Bunia pygmies	145	41	138	21	Eveleth and Tanner, 1976
Pygmoid	Twa (Rwanda)	153	101	144.2	84	Hiernaux, 1968b
San	Kung (Bochimans, Af. S.O.)	157.7	58	146.6	77	Hiernaux, 1968b
Sara	Sara Madjingay	173.9	346	164	405	Crognier, 1979
Volta	Ashanti	164.21	48	154.74	27	Rattray, 1955
Volta	Agni	167.9	68	156.6	52	Hiernaux, 1968b
Yoruba	Akufo(Yoruba)	167.5	340	155	205	Eveleth and Tanner, 1976
	Populations in Europe					
Basque	Basques francais	169.2	219	156.4	56	Hiernaux, 1968b
Basque	Basques espagnols	170.0	529	157.3	126	Hiernaux, 1968b
Belgian	Belgium, Brussels	174. 5	147	161.8	176	Eveleth and Tanner, 1976 or Hiernaux, 1968b
Czechoslovakian	Tcheques	173.5	1169	161.0	2528	Hiernaux, 1968b
Czechoslovakian	Czechoslovakia	172.0	—	161.0	—	Eveleth and Tanner, 1976
Dutch	Hollandais du Nord	173.1	70	161.7	60	Hiernaux, 1968b
Dutch	Netherlands	177.7	—	166.3	—	Eveleth and Tanner, 1976
English	Great Britain	173.9	4707	160.9	5156	Rosenbaum et al., 1985
Finnish	Finlandais de Botnic	167.6	697	156.4	249	Hiernaux, 1968b
French	Francais	169.6	60	160.4	60	Hiernaux, 1968b
German	Allemands du Centre	167.8	450	156.4	408	in Hiernaux, 1968b
Greek	Greece, students	172.2	—	159.1	—	Eveleth and Tanner, 1976
Hungarian	Hongrois	168.0	76	156.9	95	Hiernaux, 1968b
Irish	Irish	171.9	8902	158.6	1801	Hooton et al., 1955
Italian	Italy, Naples	174.4	—	162.5	—	Eveleth and Tanner, 1976
Lapp Finnish	Finnish Lapps (20-60 yrs)	164.1	240	152.4	248	Auger et al., 1980
Norwegian	Norvegiens	172.4	11774	162.4	193	Hiernaux, 1968b
Polish	Poland, Cracow	173.2	—	160.2	—	Eveleth and Tanner, 1976
Portuguese	Portugais	164.8	200	152.3	150	Hiernaux, 1968b
Russian	USSR, Moscow	171.8	—	159.8	—	Eveleth and Tanner, 1976
Swedish	Suedois de Runö	174.1	77	159.7	75	Hiernaux, 1968b
Yugoslavian	Yougoslaves	175.7	118	162.0	74	Hiernaux, 1968a,b
	Populations in Asia					
Assyrians[5]	Assyrians	170.52	106	152.34	137	Field, 1952
Bhutanese	Bhutan	169.2	44	161.1	28	Eveleth and Tanner, 1976
Chukchi	Chukchi	165.08	70	152.64	82	Smirnova, 1979
Druse	Druse	165.6	181	152.2	114	Shanklin and Izzeddin, 1937
Iranian (E + W)	South Iranian	169.8	907	158.9	939	Ayatollahi and Carpenter, 1993
Korean	South Korea (23 yr)	170.1	280	156.2	49	Eveleth and Tanner, 1976
Koryak	Koryak	159.6	173	149.1	133	Jochelson, 1908
Kurdish	Kurds (Iraq)	166.1	597	152.7	31	Field, 1952
Mongol	Khalkha-Mongols	164.83	59	151.33	49	Vlček, 1965
Nentsy	Wood Nenetz	160.08	50	147.62	42	Smirnova, 1979
Saudi	Saudi (Highlanders)	162.3	220	149.7	217	Khalid, 1995
Saudi	Saudi (Lowlanders)	158. 7	191	147.1	277	Khalid, 1995
Tungus	Evenki Reindeer Herders	157.8	116	147.2	69	Leonard et al.,1994
Tungus	Tungus	156.5	52	146.5	72	Holden and Mace, 1999
	Populations in Southeast Asia					
Ami	Ami	164.6	146	155.9	94	Chen, 1967
Atayal	Atayal	160.1	96	149.8	147	Chen, 1967
Bunun	Bunun	157.2	96	146.2	110	Chen, 1967

Appendix (*continued*)

Population in the H.G.H.G.[1]	Name in reference	Male height[2]	n[3]	Female height[2]	n[3]	Reference[4]
Javan	West Java	158.0	–	150.0	–	Eveleth and Tanner, 1976
Javan	Jogjakarta	161.5	–	150.0	–	Eveleth and Tanner, 1976
Khasi	Khasi, Assam	156.66	400	146.97	325	Field, 1970
Paiwan	Paiwan	156.6	127	148.0	150	Chen, 1967
Philippine	Philippines (20yr)	164.6	36	151.1	45	Eveleth and Tanner, 1976
Sea Dayak	Iban	159.7	43	148.7	41	Strickland and Ulijaszek, 1993
Semai	Semang	153.3	216	142.4	97	Schebesta, 1952
South Chinese	Hong Kong (Chinese, 20 yr)	167.1	431	156.0	358	Eveleth and Tanner, 1976
Populations in Australia and the Pacific Islands						
Australian[6]	Aborigine	172.1	–	162.9	–	Eveleth and Tanner, 1990
Australian	South Austr. Aborigine (Gerard and Raukkan)	171.2	27	156.7	21	Pretty et al., 1998
Australian	Aborigine	168.6	22	156.8	22	Eveleth and Tanner, 1976
Australian	Yuendumu	173.0	26	162.7	39	Eveleth and Tanner, 1976
Bougainville S.E.	Nasioi	162.1	59	150.4	63	Friedlaender, 1987
Bougainville W.	Nagovisi	159.6	109	150.3	101	Page et al., 1977
Fiji	Fiji-Melanesian	176.1	16	167.7	9	Eveleth and Tanner, 1990
Fiji	Fiji	172	130	161.8	142	Eveleth and Tanner, 1976
Luangiua	Ontong Java	164.2	144	154.9	197	Friedlaender, 1987
Malaita	Kwaio	160.3	127	149.0	114	Friedlaender, 1987
Malaita	Baegu	161.3	126	150.3	111	Page et al., 1977
Malaita	Lau (Malaita)	162.5	76	151.8	95	Friedlaender, 1987
Manus	Manus	162.9	20	151	38	Heath and Carter, 1971
Manus	Manus (Pere)	164.3	19	153.4	17	Eveleth and Tanner, 1990
Manus	Manus (town)	165.2	16	155.4	23	Eveleth and Tanner, 1990
Samoa	Salamumu, Western Samoa	170.4	101	158.3	144	Eveleth and Tanner, 1990
Society	Society Islands	171.4	85	161.1	68	Eveleth and Tanner, 1976
Tokelau	Tokelau (20–54)	169.2	228	159.5	264	Prior et al., 1977
Tolai	Tolai	162.5	38	156.1	65	Wolstenholme and Walsh, 1967
Populations in New Guinea						
Anga	Kukukuku (20–49 yr)	151.2	59	142.7	99	Malcolm,1969
Awin	Awin	158.4	56	147.1	77	Hyndman et al., 1989
Highland E.	Gadsup	158.28	212	148.95	55	Littlewood, 1972
Highland E.	Tairora	155.97	301	149.41	42	Littlewood, 1972
Highland E.	Auyana	153.68	260	146.31	30	Littlewood, 1972
Ok	Mountain Ok	152.7	147	146.7	150	Eveleth and Tanner, 1990
Populations in North America, South America and Greenland						
Arawakan	Central Arawaks	159.16	32	147.64	17	Gillin, 1936
Aymara	Aymara (Chile coast)	164.1	66	151.4	66	Eveleth and Tanner, 1990
Aymara	Aymara (Chile sierra)	160.0	45	149.6	69	Eveleth and Tanner, 1990
Aymara	Aymara (Chile altiplana)	163.0	70	150.0	90	Eveleth and Tanner, 1990
Aymara	Aymara (Bolivia)	162.0	25	149.0	39	Eveleth and Tanner, 1990
Bari	Motilon	146.2	37	138.1	37	Comas, 1971
Caingang	Caingang Rio G. do Sul + Paraná	161.0	354	149.1	254	Neves et al., 1985
Caingang	Caingang Palmas	162.5	41	151.2	21	Neves et al., 1985
Caingang	Caingang Tupa	163.4	9	149.3	12	Neves et al., 1985
Eskimo (Alaskan)	Alaskan (20–60 yrs)	166.0	91	155.4	134	Auger et al., 1980
Eskimo (Canadian)	Copper Eskimo	164.8	82	156.4	42	Jenness, 1923
Eskimo (Canadian)	Labrador Inuit	158.4	58	148.3	78	Holden and Mace, 1999
Eskimo (Canadian)	Igloolik (Foxe Basin) 20–60 yrs	163.5	134	152.6	114	Auger et al., 1980

Appendix (*continued*)

Population in the H.G.H.G.[1]	Name in reference	Male height[2]	n[3]	Female height[2]	n[3]	Reference[4]
Eskimo (Canadian)	Iglulik Eskimo	166	20	153.7	20	Jenness, 1923
Eskimo (Canadian)	Igloolik Eskimo	165.8	12	157.5	12	Eveleth and Tanner, 1976
Eskimo (Greenland)	Angmagsalik Inuit	162.0	166	153.3	203	Holden and Mace, 1999
Eskimo (Greenland)	Greenland Inuit	162	500	152	400	Holden and Mace, 1999
Eskimo (Greenland)	West Greenland (20–50yr)	160.8	45	149.3	41	Auger et al., 1980
Macushi	Macushi	156.8	42	146.3	28	Steggerda, 1963
Makiritare	Maquiritare	156.0	26	146.0	24	Stinson, 1990
Mapuche	Mapuche	160.4	201	144.2	25	Stinson, 1990
Mapuche Araucano	Araucanian	160.38	60	150.26	86	Valenzuela et al., 1978
Mayan E.	Quiche	153.8	117	143.8	83	Comas, 1971
Mayan E.	Maya guatemala	156.8	42	142.8	20	Eveleth and Tanner, 1976
Mayan E.	Cakchiquel	155.3	72	143.2	36	Comas, 1971
Na-Dene (canadian)	Chilcotin Athapascan	170.3	36	156.5	55	Birkbeck et al., 1971
Na-Dene (canadian)	Chippewyan	166.4	44	150.9	20	Holden and Mace, 1999
Na-Dene (canadian)	Dogrib	165.4	60	154.5	97	Szathmary and Holt, 1983
Navajo	Navaho	169.9	90	157.4	40	Hrdlička, 1935
Papago	Pápago	170.9	50	155.9	30	Hrdlička, 1935
Pima	Pima	171.8	53	157.4	30	Hrdlička, 1935
Pima	Pima	169.6	77	156.3	51	Comas, 1971
Quechua	Quechua highland	159.9	62	148.1	58	Eveleth and Tanner, 1990
Quechua	Quechua lowland	163.1	57	149.8	60	Eveleth and Tanner, 1990
Quechua	Quechua	160.1	245	148.3	112	Comas, 1971
Quechua	Quechua Cusco, Peru	158.8	243	146.3	85	Stinson, 1990
Quechua	Quechua Nunoa, Peru	160.0	50	148.0	50	Stinson, 1990
Quechua	Quechua Pichincha Province, Ecuador	154.3	87	142.8	36	Stinson, 1990
Trio	Trio	157.7	115	147.5	142	Stinson, 1990
Wajana	Wajana	156.6	75	146.2	91	Stinson, 1990
Warau	Warao	156.5	318	144.7	172	Stinson, 1990
Xavante	Xavante	169.4	66	155.6	73	Stinson, 1990
Yanomama	Yanomamo	153.2	316	142.3	260	Eveleth and Tanner, 1976
Yanomama	Yanomama	154.8	69	144.3	70	Neves et al., 1985
Zuni	Zuni	163.5	60	151.2	32	Hrdlička, 1935

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

[2] Mean height (cm).

[3] Sample size.

[4] References for male and female height.

[5] Assyrians were not included in the analyses but are referred to in the text.

[6] 39 male subjects and 23 female in Holden and Mace (1999).

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