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Sexual dimorphism in foot length proportionate to stature

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Abstract

Background: The preponderance of existing results suggests that, relative to stature, women have smaller feet than men. However, several investigations indicate that the relationship between foot length and stature may be curvilinear, a pattern that, due to the dimorphic nature of stature, would mask the true direction of pedal sexual dimorphism in published results.

Aim: The study aimed to determine whether proportionate foot length is sexually dimorphic and, if so, the nature of that dimorphism.

Materials and methods: Surveying genetically disparate populations (USA, Turkey, and Native North and Central American), we examined data from three previous anthropometric studies (Davis 1990, Parham et al. 1992, Özaslan et al. 2003) and foot tracings from the Steggerda Collection at the US National Museum of Health and Medicine. Analyses explored sex differences in the ratio between foot length and stature, and tested for nonlinearity.

Results: Although varying in degree across populations, proportionate to stature, female foot length is consistently smaller than male foot length.

Conclusion: Given the biomechanical challenges posed by pregnancy, smaller female proportionate foot length is somewhat surprising, as foot length affects dorsoventral stability. It is possible that the observed pattern reflects intersexual selection for small female foot size, a cue of youth and nulliparity.

Keywords: *foot length, stature, sexual dimorphism*

Introduction

The human foot, the foundation for bipedal locomotion, is a complex adaptation that evolved through extensive remodelling of the hind appendage of our arboreal primate forebears (Susman 1983). For nearly a century, scholars have examined the anthropometry of the foot and its relationship with other aspects of the body. Within the last decade, these questions have received particular attention in the fields of ergonomics and forensic science,

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the former in the service of improvements in footwear design, the latter in order to guide forensic reconstructions derived from either footprints or limb fragments. Although sex differences in foot morphology have been studied by many of these investigators, one issue that is often touched on, yet rarely examined in depth, is the possibility of sex differences not in the conformation of the foot *per se*, but rather in the size of the foot proportionate to the size of the body. Notably, in this journal, Ashizawa et al. (1997) documented that, among urban Japanese, proportionate to stature, women have smaller feet than men. This result contrasts with the earlier findings of Baba (1975) who, examining employees of a Japanese shoe manufacturer, concluded that, proportionate to stature, women have larger feet than men. The fact that two studies of the same relatively homogeneous population reached diametrically opposed conclusions regarding the direction of sexual dimorphism in foot length proportionate to stature is indicative of the extent to which this question is in need of further scrutiny. In this paper, we first review published reports that bear on the question of sex differences in foot length proportionate to stature. We then independently analyse three existing data sets, followed by an examination of previously unpublished archival material. Finding considerable evidence of patterned sexual dimorphism in proportionate foot length, we conclude by discussing the selection pressures that may have shaped this aspect of human bodies over the course of human evolution.

Work to date on proportionate foot length in women and men

Table I presents a summary of published findings on proportionate foot length in men and women of various populations. Below, we review each of the studies listed in greater detail.

Hrdlička (1935), one of the pioneers of physical anthropology, presents foot length as a percentage of stature for Pueblo Indians (Hopi, Zuni, Tewa, Tigua, Jemez, Tano, and Piro), so-called ‘Old Americans’ (US Americans of Western European/British descent), and indigenous groups of the US Southwest and Northern Mexico.[1] Female foot length is smaller proportionate to stature in the vast majority of populations, exceptions being the Navaho, in whom the two are equivalent, and the Maricopa and Southern Ute, in whom females have marginally larger feet. In a second publication (Hrdlička 1928), Hrdlička reports that African–American males have a proportionately smaller foot length than females. However, caution is in order in interpreting these results as the sample size is small ($n = 26$), of which only six are women. Elsewhere, Hrdlička (1925, p. 340) presents analysis of Quetelet’s (presumably Quetelet (1835)) Belgian data, showing that men have proportionately larger feet than women. Likewise, employing data from Martin (presumably Martin & Saller (1958) (1864–1925)), Hrdlička (1925, p. 343) summarizes proportionate foot length among Lithuanians (males slightly larger), Letts (i.e. Latvians; females slightly larger), and Badenese (i.e. Germans; males larger). However, examination of both Quetelet and Martin reveals that data on foot length and stature are presented only as means for the respective samples. This suggests that, both in these instances and elsewhere, Hrdlička calculated the foot length : stature ratio not on an individual basis, but by dividing the mean foot length by the mean stature in each sex. The ratio of averages is not necessarily equal to the average of ratios, hence this procedure potentially introduces error into the result, most notably whenever the variance in either measurement differs across the sexes. Hence, while Hrdlička’s results are interesting, caution is in order given that the mode of analysis may have been flawed.

As part of a large anthropometric study of Czech children, Klementa et al. (1973) examined approximately 60 individuals age 17–18 years (the authors note that subjects exhibiting

Table I. Summary of some published findings on foot length as a proportion of stature for men and women.

Citation	Population	*n*	Male foot length as a % of stature	Female foot length as a % of stature
Hrdlička 1935	Apache	83	14.93	14.58
Hrdlička 1935	Aztec	84	15.38	14.98
Hrdlička 1935	Cora	61	15.21	15.08
Hrdlička 1935	Maricopa	70	15.19	15.20
Hrdlička 1935	Mohave	71	15.15	14.62
Hrdlička 1935	Navaho	79	14.66	14.66
Hrdlička 1935	Otomi	75	15.45	13.73
Hrdlička 1935	Papago	80	15.07	14.83
Hrdlička 1935	Pima	83	14.99	14.83
Hrdlička 1935	Pueblos	183	14.88	14.68
Hrdlička 1935	Tarahumare	32	14.82	14.41
Hrdlička 1935	Tarasco	80	15.18	14.85
Hrdlička 1935	Southern Ute	70	15.12	15.16
Hrdlička 1935	Yuma	34	15.01	14.85
Hrdlička 1928	African–Americans	26	15.89	16.11
Hrdlička 1935	Caucasian–Americans	455	14.97	14.42
Hrdlička 1925 (after Quetelet, 1835?)	Belgians	?	15.8	15.0
Hrdlička 1925 (after Martin 1958?)	Lithuanian	?	14.6	14.4
Hrdlička 1925 (after Martin 1958?)	Letts (Latvian)	?	14.6	14.8
Hrdlička 1925 (after Martin 1958?)	Badenese (German)	?	16.0	15.5
Davis 1990 (after Todd & Lindala 1928)	African–Americans	135	14.7	14.6
Davis 1990 (after Todd & Lindala 1928)	Caucasian–Americans	136	14.3	13.5
Davis 1990 (after Davenport & Steggerda 1929)	African–Jamaicans	100	15.4	15.2
Davis 1990 (after Steggerda 1932)	Dutch	130	15.3	14.9
Robbins 1986	US age 14 and up	527	right 15.128 left 15.199	right 14.726 left 14.750
Anderson et al. 1956	US 18-year-olds	20	14.9	15.1
Davis 1990	African–American 18–26-year-olds	110	right 15.58 left 15.61	right 15.30 left 15.31
Davis 1990	Caucasian–American 18–26-year-olds	130	right 15.27 left 15.24	right 14.58 left 14.61
Giles and Vallandigham 1991	US soldiers	8012	15.346	14.926
Wunderlich and Cavanagh 2001	US soldiers	784	15.36	15.01
Barker and Scheuer 1998	Predominantly Caucasian (London)	105	right footprint: 15.222 left footprint: 15.189	right footprint: 14.853 left footprint: 14.806

pathology were dropped, but do not indicate how many individuals fit this description). Proportionate foot length is the same in males and females. Although the authors use comparable stature measurements from other studies of the same population to argue that their 17–18-year-old subjects had achieved full adult height, this claim is questionable given that, although foot growth ceases well before this age, in most populations, stature is still increasing at this point, particularly in males (Giles & Vallandigham 1991), a pattern that could skew results relevant to the question at issue here.

Seeking to provide tools for forensic investigation, Robbins (1986) collected both foot outlines and footprints from the left and right feet of 527 US subjects age 14 and over (distributions for age and ethnicity are not provided). As a proportion of stature, males are larger in both foot length and footprint than females. However, because age distributions are not provided, it is difficult to know the extent to which this finding requires qualification (see above).

Summarizing a longitudinal study of 20 US children, Anderson et al. (1956, p. 303) find that, at age 18, foot length as a percentage of stature is slightly larger in girls than in boys. However, the generalizability of these results is questionable given the small size of the sample, a problem compounded by the youthful age of the subjects.[2]

In order to inform a variety of forensic assessments, in an unpublished Master's thesis Davis (1990) compared the foot length : stature ratio in 240 African–American and Caucasian–American US college students. Results for both right and left feet are presented by sex, revealing larger proportionate foot length for both feet in males of each category compared with same-race females. Davis also presents similar figures for these two groups based on results published by Todd and Lindala (1928), as well as equivalent findings for Dutch and African–Jamaican adults based on results from Steggerda (1932) and Davenport and Steggerda (1929). However, because all of these authors provide only mean stature and mean foot length, it is evident that, at least in his use of published material, Davis commits the same error as Hrdlička, substituting the ratio of the means for the mean of the ratios. Davis presents his complete data sets in an appendix. We therefore recalculated the foot length : stature ratio using both the ratio of the means and the mean of the ratios. Comparison with Davis' figures reveals that he did indeed commit the same error in analysing his own material. However, using four significant digits, the ratio of the means calculation produces an inaccurate result for only one of the four data sets (African–American females), and, at that, overestimates the ratio by a mere 0.01%. This suggests that the use of the ratio of the means is not a fatal flaw in Davis' own analysis, and, to the extent that the distributions are similar in Hrdlička's samples, the same is likely true with regard to the latter's work as well.

In what is arguably the most extensive investigation of the topic conducted to date, in order to provide guidelines for forensic stature determination on the basis of footprints, Giles and Vallandigham (1991) analysed data on right foot length and stature collected from 8012 US soldiers. Male foot length is proportionately larger than female foot length. One limitation of the Giles and Vallandigham study is that it treats as uniform an ethnically heterogeneous sample (described as roughly representative of the US population), a procedure that precludes assessment of phenotypic differences between sets of individuals descended from once-disparate populations (Davis 1990).

Employing data collected from a second large sample of US soldiers ($n = 784$), Wunderlich and Cavanagh (2001), ergonomists interested in shoe design, find that male foot length as a proportion of stature is significantly larger than the same ratio in females. The figures presented in Table I are estimates for an individual with a height of 170 cm; the authors report that, overall, men average a foot length that is approximately 0.3% of stature longer relative to the equivalent figure for women. Like Giles and Vallandigham, the authors treat an ethnically heterogeneous sample in a uniform fashion, limiting the resolution of the results for between-population phenotypic comparisons.

Barker and Scheuer (1998) collected footprints from both feet of 105 subjects in London. Relative to stature, for both feet, female prints are proportionately smaller at a high level of significance. Because they sought to generate guidelines for stature reconstruction that would be of use to forensic investigators in the UK, the authors' sample crudely approximates the makeup of that population, namely 73% European descent, 24% Asian (presumably South Asian, though not specified), and 3% Afro-Caribbean. Unfortunately, the authors do not provide results by ethnic group, nor do they indicate whether ethnicities were equally represented among male and female subjects.

Ross and Ward (1982) studied physically fit Canadian university students ($n = 246$). Results, not included in Table I, are presented in the form of graphical representation of female z-value differences from male z-values scaled as 0.00, proportionate to stature; female foot length is depicted as approximately –0.75 under this system, i.e. proportionately smaller than male foot length.

As noted in the Introduction, Ashizawa et al. (1997) document shorter female foot length relative to stature among urban Japanese ($n = 772$); results are presented in the form of linear regressions rather than ratios, and are therefore not reproduced in Table I. Of particular interest, the authors also find the same pattern among rural Javanese ($n = 229$), a population that is both genetically removed from the former and significantly less likely to use footwear, a factor that influences foot morphology. Unfortunately for the present purposes, both samples include children as young as 6 years of age (children compose 81% of the Japanese sample; the composition of the Javanese sample is not specified). Prior to puberty dimorphism in general is limited (or even reversed – cf. Greil (1997)), and, depending on age, this applies to proportionate foot length as well (Anderson et al. 1956, Klementa et al. 1973). Caution is therefore in order in interpreting Ashizawa et al.'s results.

To summarize the discussion thus far, although methodological limitations give reason for caution in some cases, the vast majority of published results indicate that, adjusting for stature, women have shorter feet than do men. However, as discussed below, three potentially important studies call this conclusion into question.

Pursuing the goal of providing reference values for forensic reconstruction, Quamra et al. (1980) examined foot length and stature in a large sample ($n = 1015$) of members of a variety of South Asian ethnic groups in North West India. The authors generate regression equations allowing the estimation of stature from foot length, then demonstrate their accuracy using a second sample. Inspection of the regression equations reveals that, for a given foot length, men are predicted to be taller than women, and hence foot length is greater relative to stature in women than in men. While intriguing, this observation only indirectly illuminates the ratio between foot length and stature, as the two regression equations are not directly comparable to one another due to differing confidence limits.

As noted in the Introduction, Baba (1975), an ergonomist interested in providing reference values for use in shoe design, examined 1844 Japanese adults (age 18–40, mean and SD not given), measuring the right foot while weight bearing; foot length was taken as the distance between the pternion (extreme point of the heel) and the acropodion (extreme point of longest toe). Rather than providing mathematical analyses, Baba presents results in tabular form, categorizing subjects on the basis of foot length (in 4 mm inclusive intervals). Baba notes that, for a given foot length, women are shorter in stature than men, a conclusion easily verified through inspection of the author's tabular materials; rephrased in the terms used here, this is equivalent to stating that, proportionate to stature, foot length is larger in women than in men.

With the same objectives as Baba, Anil et al. (1997) examined 305 Turkish university students (age 17–25, mean and SD not given) employing the same form of measurement as Baba, and, like the latter, presenting results in tabular form on the basis of foot length. Like Baba, Anil et al. note that women of a given foot length are shorter in stature than men having the same size feet, a conclusion again supported by the tabular materials.

To summarize the investigations of Baba and Anil et al., in two seemingly well-conducted modern studies, characterized by large sample sizes, and focusing on genetically disparate populations, the opposite pattern to that which prevails in the literature appears – proportionate to stature, women have larger feet than men. More intriguing still, inspection of the data reveals a potential explanation of the discrepancy between these authors' findings and others' conclusions on the subject.

In order to more directly compare Baba's and Anil et al.'s results with those of other authors, we first calculated average foot length : stature ratios for females and males in each sample using the following procedure: Employing the grouped data presented in each of the two papers, we first selected the midpoint for each foot length category, then compared this with the reported mean stature (by sex) for individuals falling into that category. This allowed us to compute crude foot length : stature ratios for females and males in each foot length category, whereafter we calculated the average of these ratios for each sex. In Baba's Japanese data set, this leads to the conclusion that foot length is approximately 14.73% of stature in men and 14.67% of stature in women; in Anil et al.'s Turkish data set, the figures are 15.12% for men and 14.80% for women. Although these results closely resemble many of those presented in Table I, they stand in stark contrast to Baba's and Anil et al.'s correct observation that, for a given foot length, women in their respective samples are shorter than men. This raises the question as to how the overall ratios can exhibit sexual dimorphism in favour of male foot length when the examination of individual categories of subjects produces the opposite conclusion. The answer lies in the relationship between absolute stature and proportionate foot length.

Examining the figures that we had derived from Baba's and Anil et al.'s data, we inspected the foot length : stature ratios for males and females in each category of foot length, finding that, within each sex, this ratio is not constant across statures. Specifically, within each sex, as stature increases, the foot length : stature ratio grows larger. Because (a) there is sexual dimorphism in stature, and (b) the ratio between foot length and stature climbs as the latter factor increases, averaging the ratios within each sex and comparing the result across sexes produces net figures that give the impression that women have proportionately smaller feet than men when, in fact, inspection for any given foot length or stature reveals that the opposite is actually the case. Given that stature is sexually dimorphic to some degree in all populations (Holden & Mace 1999), if the same nonlinearity characterizes the foot length : stature ratio in other samples, then all of the publications discussed above will contain the same erroneous conclusion – averaging the ratios within each sex and then comparing them across sexes will lead to the wholly spurious finding that, proportionate to height, women have smaller feet than men. This possibility is plausible given that biomechanical considerations suggest that the foot length : stature ratio may indeed be nonlinear.

During walking, weight is primarily borne by two portions of the foot, namely the heel and the forward metatarsal region (Lundeen et al. 1994). While the heel is approximately plumb with the lower leg, and therefore largely bears weight statically, the forefoot is well forward of the lower leg, and hence bears weight dynamically: via the flexor tendons, the plantar flexor muscles (principally the soleus) create a moment at the ankle joint, exerting downward force on the foot (Kirby 2000). The longer the foot, the more effective these muscles can be in stabilizing the forward motion of the body. Because the leg acts as a lever, creating a countervailing moment at the ankle joint that diminishes the ability of the forefoot to stabilize forward motion, the greater the subischial height (and hence the longer the lever arm formed by the leg), the larger the force exerted by a given body mass on the forefoot. To a lesser degree, the same principle of leverage should also apply to supraischial (i.e. 'sitting') height. Accordingly, it may be that the forces exerted on the forefoot can be conceptualized as the product of body mass and the height of the centre of gravity. If correct, this thesis would predict that the relationship between foot length and stature should be curvilinear rather than linear, as a strictly linear increase in foot length with increasing stature would likely suffice to compensate for either increased body mass or increased leverage, but would likely not suffice to compensate for the product of these two factors. Such a curvilinear relationship between foot length and stature is evident in the data published by Baba and Anil et al., thus raising the possibility that this pattern is universal, but is hidden in the many publications that merely present mean ratios by sex. In order to investigate this possibility, we first analysed three existing data sets, then examined unpublished archival material.

Reanalysis of three existing data sets

Materials

As an appendix to the unpublished Master's thesis described earlier, Davis (1990, pp. 51–54) provides the complete data sets (stature and the length of both the right and left foot) upon which his conclusions were based; foot length was taken as the distance between the pternion and the acropodion for 240 African–American and Caucasian college students (males: $n = 114$, 44.7% African–American, 55.3% Caucasian; females: $n = 126$, 46.8% African–American, 53.2% Caucasian; ages unspecified).

In order to evaluate the quality of fit of US Army issue boots, Parham, Gordon, and Bensel (1992) (the source employed by Wunderlich and Cavanagh (2001)), collected a variety of anthropometric measurements from 784 soldiers (males: $n = 293$, mean age = 22.3, SD = 6.3; females: $n = 491$, mean age = 21.6, SD = 4.8), selected so as to capture the racial make-up of the US Armed Services (males: 60.7% White, 26.6% Black, 8.2% Hispanic, 3.1% Asian/Pacific Islander, 1.4% American Indian/Alaskan Native; females: 51.5% White, 39.5% Black, 6.1% Hispanic, 1.6% Asian/Pacific Islander, 1.2% American Indian/Alaskan Native) (data are not segregated by race). The authors present the data in two tables (Parham et al. 1992, pp. 204, 241) in which subjects are grouped on the basis of stature (1.9 cm increments) and foot length (0.4 cm increments).[3] To facilitate analysis, approximate values for both foot length and stature were calculated for each subject using the midpoint (arithmetic mean) values of the two endpoints for each of the foot length and stature bins.

In order to provide guidelines for the forensic reconstruction of stature on the basis of recovered body parts, Özaslan et al. (2003) collected a variety of anthropometric measurements from 311 middle class Turks residing in Istanbul (males: $n = 203$, mean age = 30.7, SD 10.35; females: $n = 108$, mean age = 35.3, SD = 9.13).

Examining data from each of the above studies independently, we first searched for nonlinear relationships between foot length and stature, then tested for sex differences (and population differences, where possible) in the ratio of foot length to stature.

Results

Reanalysis of the Davis datasets did not reveal a nonlinear relationship between foot length and stature, with no increase in the ratio as a function of stature. Using analysis of variance (ANOVA), we found a significant difference between male and female foot length : stature ratios (Male ratio = 0.154; Female ratio = 0.149), $F(1,236) = 55.807$, $P = 0.000$. The Davis data also reveal a main effect of population of origin, with African–American subjects showing larger foot length : stature ratios overall, $F(1,236) = 61.674$, $P = 0.000$. This appears to be partly driven by a two-way interaction between sex and population of origin, with Caucasians showing more pronounced sexual dimorphism than African–Americans, $F(1,236) = 10.178$, $P = 0.002$.

Analysis of the data from the Parham et al. military sample again did not reveal a nonlinear trend between foot length and stature. Using a simple ANOVA, we again found significant sexual dimorphism, with larger foot length to stature ratios for males (ratio = 0.154) compared with females (ratio = 0.151), $F(1,779) = 47.747$, $P = 0.000$.

Examining Özaslan et al.'s Turkish data yet again reveals a straightforward linear relationship between the ratio of foot length to stature and increases in the latter. Using a simple ANOVA, we again find sexual dimorphism, with males (ratio = 0.145) showing significantly larger foot length : stature ratios than females (ratio = 0.140), $F(1,309) = 66.832$, $P = 0.000$.

Discussion

Our analysis of the data collected from contemporary North Americans by Davis (1990) and Parham et al. (1992) did not reveal the curvilinear relationship between foot length and stature that we had found in Baba's (1975) Japanese data and Anil et al.'s (1997) Turkish data. Moreover, our analysis of Turkish data comparable to that of Anil et al., collected by Özaslan et al. (2003), similarly does not reveal a curvilinear relationship between these factors. Our analyses thus confirm the initial conclusions of Davis (1990) and Wunderlich and Cavanagh (2001) (who analysed the Parham et al. material), namely that, proportionate to stature, foot length is smaller in women than in men; we further generated the same result using the Özaslan et al. data. These findings call into question both the proportionately larger female foot length reported by Baba and Anil et al. and the curvilinear relationship between these factors evident in their results, a relationship which, were it to occur, could conceivably mask the true direction of dimorphism in the many other published findings reviewed earlier. Our findings provide strong preliminary grounds for concluding that proportionate foot length is smaller in women. In order to conclusively put this question to rest we sought to conduct the same analyses using materials drawn from populations that (a) are genetically disparate from those considered thus far, and (b) are characterized by limited use of structured footwear, a factor that can potentially affect both foot morphology and sexual dimorphism therein (cf. Ashizawa et al. 1997). We therefore explored the relationship between foot length and stature among Native North and Central Americans of the early part of the twentieth century.

Analysis of foot tracings from the Steggerda Collection

Materials

Between 1910 and 1940 Carnegie Institution anthropologist Morris Steggerda collected anthropometric measurements from a large number of individuals in North, Central, and South America (Sledzik 2002). Among other materials, the Steggerda Collection, now housed in the US National Museum of Health and Medicine, contains anthropometric data from members of a variety of Native American groups. After obtaining permission from the UCLA Office for the Protection of Research Subjects, one of us (R.D.L.), blind to the hypotheses at issue, examined the Steggerda Collection for files that included foot-tracings (produced when subjects were standing erect on both feet) and notations regarding age, height, and sex. This produced a sample of 460 individuals, distributed among three population groups from North and Central America. Discarding subjects who were under the age of 18 produced a total sample of 300 individuals (males: $n = 233$, mean age = 27.12,

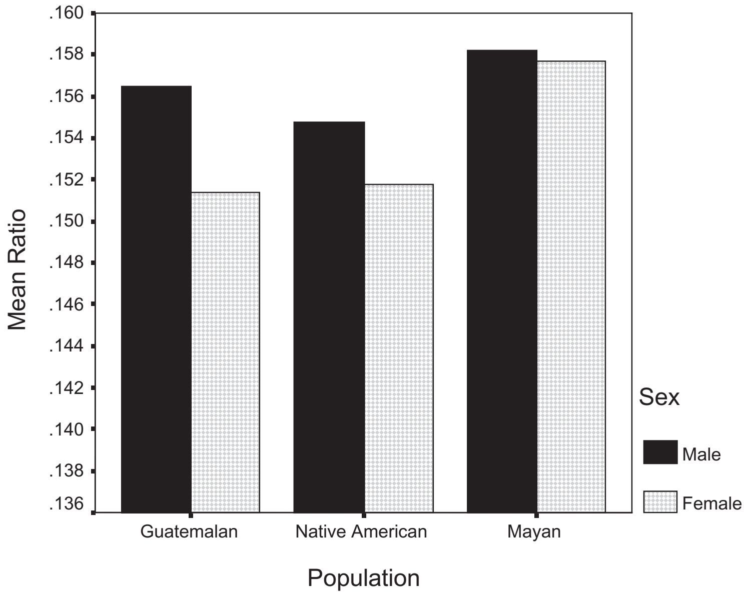

Figure 1. Foot length-to-stature ratios in three indigenous American populations.

SD = 10.38; females: $n = 67$, mean age = 30.43, SD = 14.43; 24.7% Guatemalan, 36.7% Mayan, 38.7% Native American). Using a digital calliper, R.D.L. measured foot length on the right foot as the distance between the pternion and the acropodion on each foot tracing.

Results

In analysing the Native American data we again found no nonlinear relationship between foot length and stature, as the ratio of foot length to stature neither increased nor decreased with stature. Overall, males showed significantly larger foot length : stature ratios than females (male ratio = 0.156, female ratio = 0.155), $F(1,194) = 8.101$, $P = 0.005$. Interestingly, we also found significant differences in the foot length : stature ratios between populations, $F(2,294) = 14\,872$, $P = 0.000$, although the interaction between sex and population was not significant; Figure 1 illustrates these patterns.

Discussion

Our analysis of data from 300 individuals sampled from three different Native American populations confirms our earlier findings, namely that (a) the ratio between foot length and stature does not increase as a function of the latter, and (b) women have proportionately smaller feet than men.

Pooled analysis of three data sets

Pooling the data from Davis (1999), Özaslan et al. (2003), and those derived from the Steggerda Collection, and analysing foot length : stature ratios in a univariate ANOVA, in addition to the predictable overall effect of sex (the male ratio of 0.152 being significantly

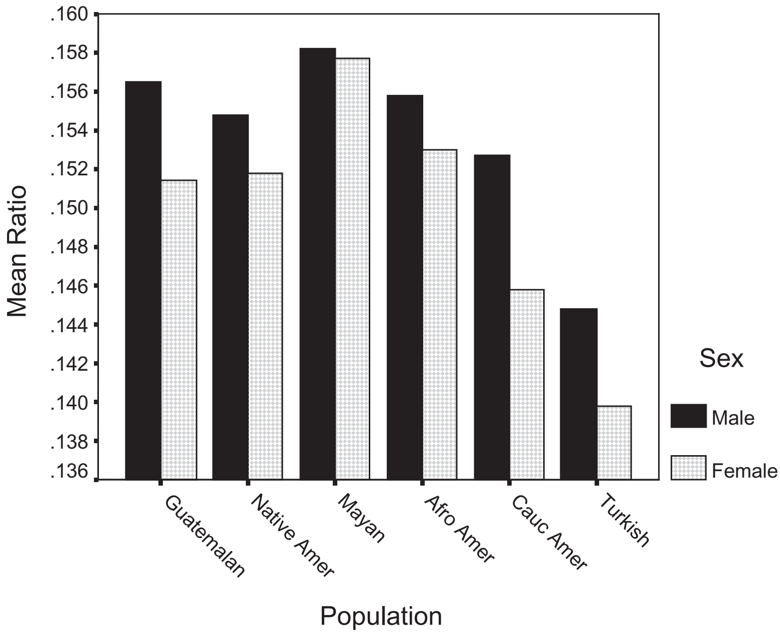

Figure 2. Foot length-to-stature ratios by sex and population.

larger than the female ratio of 0.147, $F(1,839) = 53.136$, $P = 0.000$), we also find both (a) significant differences between the overall foot length : stature ratios between populations, $F(5,839) = 184.342$, $P = 0.000$, and (b) differences in the degree of sexual dimorphism across populations, revealed by a significant Sex-by-Population two-way interaction, $F(5,839) = 5.206$, $P = 0.000$; Figure 2 illustrates these patterns.[4]

Discussion

Our analyses of genetically disparate populations reveal a clear pattern of sexual dimorphism, with women consistently having smaller feet proportionate to stature than men; in addition, we have demonstrated that the ratio between foot length and stature does not increase as a function of the latter. These findings directly contradict results presented by Baba (1975) and Anil et al. (1997), a contrast that is particularly marked in the latter case given that we drew on the same population as that examined by Anil et al. Our analyses thus allow us to dismiss the possibility, raised by data presented in the aforementioned studies, that the pattern of sexual dimorphism in proportionate foot length reported in the overwhelming majority of previous publications is spurious due to the combination of nonlinearity in the foot length : stature ratio and sexual dimorphism in stature. We therefore conclude that, while varying in degree across populations, in general, women have proportionately shorter feet than men. Given the potential utility of foot length in forensic applications (cf. Quamra et al. 1980, Robbins 1986, Davis 1990, Giles and Vallandigham 1991, Barker and Scheuer 1998, Özaslan et al. 2003), it is therefore clear that, calibrated to the local population, forensic investigators would be well-advised to take note of this aspect of sexual dimorphism.

What factors might be expected to have shaped proportionate foot length? Although it is not possible to identify all of the sources of selection pressure that have affected this attribute over the course of human evolution, interestingly, reasoning from first principles leads one to expect women to have proportionately larger, rather than smaller, feet than men. A fundamental difference between women and men is that only the former can become pregnant, a process that results in profound, if temporary, alterations in the body. Natural selection can be expected to have acted intensively on pregnant women in ancestral populations, as reproduction is the critical link in the chain of events whereby differential representation of alleles occurs in the next generation. Accidental falls substantially impact the outcome of pregnancy (Williams et al. 1990, Dahmus & Sibai 1993, Runnebaum et al. 1998), suggesting that the human female locomotor system should reflect the unique challenges that pregnancy poses for a bipedal hominid. Viewed biomechanically, the most significant aspects of pregnancy are that (a) it results in a substantial increase in body mass, and (b) '(t)his load could scarcely be placed more disadvantageously' (Fries & Hellebrandt 1943, p. 374), as the majority of the added mass is located anteriorly, while its supraischial placement results in a rise in the centre of gravity (Fries & Hellebrandt 1943). Although postural alterations partially compensate for these challenging changes (Fries & Hellebrandt 1943), pregnancy nonetheless results in a substantially increased load on the plantar flexor muscles (Foti et al. 2000). Because the force needed to regulate forward motion is in part a function of the length of the foot, natural selection could have partially compensated for the demands that pregnancy places on the locomotor system by increasing female foot length. The selective pressure favouring such an increase would have been augmented by the consequences of ligamentous laxity in the foot induced by systemic relaxin circulation during pregnancy (Block et al. 1985) – by reducing the rigidity of the foot, ligamentous laxity decreases the moment generated for a given foot length, thereby requiring a longer foot to achieve the same mechanical effect as that produced in the absence of relaxin. In sum, the biomechanical challenges posed by pregnancy might plausibly be expected to have favoured exactly the opposite pattern to the one observed, namely greater proportionate foot length in women than in men.

It is possible that natural selection compensated for the locomotor challenges of pregnancy through avenues other than changes in foot length. Congruent with the observations that (a) pregnancy results in an increase in mass and a rise in the centre of gravity, and (b) the demands placed on the foot and the plantar flexor muscles are in part a function of the length of the lever formed by the leg, proportionate to stature, subischial height is shorter in women than men (Greil 1997; see also data presented by Dangoury et al. (2002) and Rao et al. (2000); but see also Davis (1990, p. 23), Martin and Saller (1958, p. 963), and Flugel et al. (1983, cited in Pawlowski (2001))). While reduced leg length would likely have decreased female locomotor efficiency (cf. Roberts et al. 1998), these costs may have been outweighed by the benefits of increased dorsoventral stability during pregnancy. However, while these changes may well have sufficed to compensate for the biomechanical challenges posed by pregnancy, thus explaining why natural selection did not favour proportionately longer foot length in ancestral females, this does not explain why the converse pattern obtains, albeit to a modest degree, and to a variable extent across populations.[5] One intriguing possibility is that sexual dimorphism in proportionate foot length may be the product not of natural selection, but rather of sexual selection, a process that is both independent of the former and often works at odds to it.

Given the highly altricial nature of human offspring and their prolonged period of dependency (Kaplan et al. 2000), female reproductive success in ancestral human populations would have been contingent not only on surmounting the biomechanical challenges of pregnancy, but also on attracting parental investment from high-value mates.

In many primate species, males disfavour youthful, nulliparous females, a pattern explicable in terms of these individuals' low fertility and high miscarriage rates (Manson 1997). In contrast, human males generally prefer such females despite these costs. The human reversal of prevailing male primate mate selection preferences presumably derives from the fact that, unlike most other male primates, men often invest heavily in their mates and offspring for prolonged periods. A preference for youthful, nulliparous females offers human males the advantages of both (a) greater long-term returns on sustained investment and (b) reduced likelihood of prior conceptions or deliveries fathered by rival males (Symons 1979, Jones 1995, 1996). Importantly, mate selection preferences can exercise a strong selective effect on the morphology of the sex under scrutiny. For example, the neotenous facial morphology characteristic of human females is plausibly explained as the product of intersexual selection for signs of youth in females (Barber 1995, Jones 1995, Wehr et al. 2001).

Small feet may signal youthfulness for at least two reasons. First, in absolute terms, children's feet are smaller than those of adults, hence a small foot may in and of itself give the appearance of youth (Barber 1995). Moreover, because foot size increases with age (Chantelau & Gede 2002), small feet may serve as a direct sign of youth (Symons 2002). Similarly, because foot size increases with parity (Block et al. 1985; but see Bird et al. 1999), small foot size may index nulliparity (Symons 2002). Accordingly, consistent with their overarching preference for youth and nulliparity, human males may have evolved a preference for women with small feet (Barber 1995, Symons 2002). In turn, this preference may have exerted selective pressure on female morphology, causing a reduction in female foot length (Barber 1995).

Indirect support for the sexual selection hypothesis is provided by indications that small foot size may enhance women's attractiveness. Historical Chinese foot binding (Jackson 2000) can be construed as an example of the extreme cultural exaggeration of a preference for small female feet. Less dramatically, despite high rates of discomfort and injury, a large percentage of contemporary US women wear shoes that are too small for their feet (Frey et al. 1993), a pattern that (a) is not found among men, and (b) is explicable in terms of the beauty value assigned to smaller feet (Frey 2000). Directly addressing this thesis, Fessler et al. (in press) recently employed systematic methods to study the contribution of foot size to physical attractiveness in nine disparate cultures. Using identical line drawings differing only in foot size, the authors found that, in a majority of the cultures studied, including both Western and non-Western societies, small foot size enhances female attractiveness, but has no such effect on male attractiveness. Finally, returning to the results of the present investigation, the documented substantial between-population variation in the degree of sexual dimorphism in the foot length : stature ratio independent of both absolute stature and degree of dimorphism in stature, while not in itself conclusive, is nevertheless consistent with the proposition that this dimorphism reflects the somewhat capricious effects of sexual selection (cf. Miller & Todd 1993). Hence, although the available evidence does not yet suffice to definitively confirm this hypothesis, there are preliminary grounds for concluding that the pattern we have documented here, namely that women in disparate populations have smaller feet proportionate to stature than do men, may reflect a history of intersexual selection favouring reductions in female foot length.

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Notes

1. A number of the investigations cited here, particularly those which predate the Second World War, were conducted by eugenicists. While the eugenicists' agenda led to inaccuracies, distortions, and selective reporting of data in areas relevant to their objectives (Gould 1981), there is no reason to believe that it biased their assessments of foot size, stature, and related variables.
2. Giles and Vallandigham (1991, p. 1137) state that Anderson et al.'s subjects suffered from polio. However, this is incorrect – polio patients were the focus of a separate investigation reported in the same paper.
3. For the foot length : stature ratios, only 292 males are recorded. Future users of the Parham et al. data may wish to note that, as revealed by the respective sample sizes, the authors erroneously reversed the sex labels on these two tables.
4. Due to its presentation in grouped form, the Parham et al. military data could not be included in this analysis.
5. A reader of an earlier draft of this paper remarked that, if the forces placed on the forefoot are a product of both body mass and the height of the centre of gravity, because the latter is normally lower in women than in men, shorter foot length in women may reflect the lesser mechanical demands placed on the female foot. However, this reasoning overlooks the substantial changes that occur in pregnancy, a period during which natural selection can be expected to act intensively on female morphology.

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Résumé. *Arrière plan:* Les résultats actuellement disponibles indiquent de manière prépondérante que les femmes ont des pieds plus petits que ceux des hommes par rapport à la stature. Quelques recherches indiquent cependant que l'association entre longueur du pied et stature peut être de type curviligne, une modalité qui du fait du dimorphisme de la stature, pourrait masquer le véritable sens du dimorphisme sexuel du pied dans les publications

But: Déterminer si la longueur proportionnelle du pied est sexuellement dimorphique et dans l'affirmative, la nature de ce dimorphisme.

Matériels et Méthodes: Lors d'enquêtes affectant des populations génétiquement disparates (USA, Turquie et populations amérindiennes d'Amérique du Nord et Centrale) on a examiné les données de trois études anthropométriques antérieures (Davis 1990, Parham et al. 1992 et Zaslan et al. 2003) et les empreintes de pied de la collection Steggerda du US National Museum of Health and Medicine. Les analyses ont exploré les différences sexuelles du rapport longueur du pied/stature et ont éprouvé leur linéarité.

Résultats: On trouve qu'en proportion de la stature et à des degrés divers suivant les populations, la longueur du pied des femmes est plus petite que celle des hommes.

Conclusion: Dans la mesure où la longueur du pied affecte la stabilité dorsoventrale et considérant les tensions biomécaniques imposées par la grossesse, on est surpris de rencontrer une longueur du pied proportionnellement plus faible chez les femmes que chez les hommes. Il est possible que cela exprime une sélection intersexuelle en faveur d'un petit pied féminin, signe de jeunesse et de nulliparité.

Zusammenfassung. *Hintergrund:* Die Mehrzahl vorhandener Beobachtungen deutet darauf hin, dass Frauen relativ zur Körperhöhe kleinere Füße haben als Männer. Allerdings zeigen mehrere Untersuchungen, dass die Relation zwischen Fußlänge und Körperhöhe kurvilinear sein könnte, ein Muster, das aufgrund des Körperhöhendimorphismus die wirkliche Richtung des Geschlechtsdimorphismus der Füße in diesen Untersuchungen verschleiern würde.

Ziel: Ziel der Studie war aufzuklären, ob die proportionale Fußlänge geschlechtsspezifisch dimorph ist und wenn, welcher Art dieser Dimorphismus sei.
Material und Methoden: Nach Sichtung von genetisch verschiedenen Populationen (USA, Türkei und Eingeborene aus Nord- und Mittelamerika) untersuchten wir Daten aus drei vorangegangenen anthropometrischen Studien (Davies 1990, Parham et al. 1992, Ozaslan et al. 2003) und Fußabdrücke aus der Steggerda Sammlung des US Nationalmuseums für Gesundheit und Medizin. Die Analysen richteten sich auf Geschlechtsunterschiede im Verhältnis von Fußlänge und Körperhöhe und testeten diese auf Nichtlinearität.
Ergebnisse: Obgleich graduelle Unterschiede zwischen den Populationen bestehen, ist weibliche Fußlänge, relativ zur Körperhöhe, durchgehend kleiner als männliche.
Zusammenfassung: Unter dem Gesichtspunkt der biomechanischen Anforderungen in der Schwangerschaft ist die relativ kleinere Fußlänge von Frauen irgendwie überraschend, denn die Fußlänge beeinflusst die dorsoventrale Stabilität. Es ist mögliche, dass das beobachtete Muster ein Hinweis auf eine zwischen den Geschlechtern ablaufende Selektion ist in Richtung auf kleine Füße bei Frauen als Ausdruck für Jugend und Jungfräulichkeit.

Resumen. *Antecedentes:* El predominio de resultados existentes sugiere que, en relación a la estatura, las mujeres tienen pies más pequeños que los hombres. Sin embargo, varias investigaciones indican que la relación entre la longitud del pie y la estatura puede ser curvilínea, un patrón que, debido a la naturaleza dimórfica de la estatura, podría enmascarar la verdadera dirección del dimorfismo sexual del pie en los resultados publicados.
Objetivo: El estudio quería determinar si la longitud proporcional del pie es sexualmente dimórfica y, en su caso, la naturaleza de este dimorfismo.
Material y métodos: Al estudiar poblaciones genéticamente dispares (USA, Turquía y nativos Norteamericanos y Centroamericanos), examinamos datos de tres estudios antropométricos previos (Davis 1990, Parham et al. 1992, O¨zaslan et al. 2003) y las huellas de pisadas de la Colección Steggerda, en el Museo Nacional Americano de Salud y Medicina. Los análisis exploraron las diferencias sexuales en la relación existente entre la longitud del pie y la estatura, y comprobaron la no linealidad.
Resultados: Aunque con variaciones en grado entre poblaciones, proporcionalmente a la estatura, la longitud del pie femenino es consistentemente menor que la longitud del pie masculino.
Conclusión: Dados los retos biomecánicos planteados por el embarazo, una menor longitud del pie femenino es algo sorprendente, ya que la longitud del pie afecta a la estabilidad dorsoventral. Es posible que el patrón observado refleje una selección intersexual hacia un menor tamaño del pie femenino, un indicativo de juventud y nuliparidad.