AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 132:470–482 (2007)

Human Skin-Color Sexual Dimorphism: A Test of the Sexual Selection Hypothesis

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KEY WORDS solar radiation; skin color; vitamin D

ABSTRACT Applied to skin color, the sexual selection hypothesis proposes that male preference for light-skinned females explains the presence of light skin in areas of low solar radiation. According to this proposal, in areas of high solar radiation, natural selection for dark skin overrides the universal preference of males for light females. But in areas in which natural selection ceases to act, sexual selection becomes more important, and causes human populations to become light-skinned, and females to be lighter than males. The sexual selection hypothesis proposes that human sexual dimorphism of skin color should be positively correlated with distance from the equator. We tested the prediction that sexual dimorphism should increase with increasing latitude, using adult-only data sets derived from measurements with standard reflectance spectrophotometric devices. Our analysis failed to support the prediction of a positive correlation between increasing distance from the equator and increased sexual dimorphism. We found no evidence in support of the sexual selection hypothesis. Am J Phys Anthropol 132:470–482, 2007. ©2006 Wiley-Liss, Inc.

Human skin color, its distribution, and evolution have been of interest to biological anthropologists for many generations. Anthropologists have been interested in skin color for purposes which have changed through time. This change reflects the discipline's switch in interest on human variation from a classificatory racial perspective to one that seeks to explain human variation in terms of evolutionary forces. Thus, the literature demonstrates a change from using skin color to categorize humans into races, to explaining the distribution of skin color in an evolutionary perspective (Washburn, 1951).

Three reviews on human skin color provide an exhaustive history of evolutionary explanations for human skin color variation (Byard, 1981; Jablonski, 2004; Jablonski and Chaplin, 2000). Only the hypotheses which have more supportive evidence, or which were discussed at greater length in the recent literature, are mentioned here. Otherwise, the reader is directed to these sources.

All the major evolutionary proposals to explain skin color variation involve, in one way or another, the effect of ultraviolet (UV) radiation on human skin (for dissenting voices, see Morison, 1995; Wasserman, 1965). Dark skin color was proposed as adaptive in areas of high solar radiation because it protects from sunburn (which might injure sweat glands, thus disrupting thermoregulation), skin cancer, and malignant melanoma (Daniels et al., 1972; Harrison, 1973; Quevedo et al., 1975, 1985, 1995; Rees, 2003; Roberts, 1977), or from photodestruction of folate, which is correlated with neural tube defects (Barsh, 2003; Branda and Eaton, 1978; Byard, 1981; Jablonski, 2004; Jablonski and Chaplin, 2000).

More controversial have been the evolutionary explanations for light skin color in areas of low solar radiation. After Loomis (1967) revived an earlier proposal (Murray, 1934) that suggested that light skin was adaptive in such regions because it allowed individuals to produce adequate amounts of cholecalciferol (otherwise known as vitamin D_3; Webb and Holick, 1988), the so-called vitamin D hypothesis became virtually universally accepted (Daniels et al., 1972; Harrison, 1973; Rees, 2003). Although the proposal by Loomis (1967) that dark skin was adaptive to prevent overproduction of cholecalciferol was quickly falsified (Holick, 1987; Holick et al., 1987; Webb and Holick, 1988), the vitamin D hypothesis gained much acceptance (Frisancho, 1993). However, Robins (1991) presented a strong challenge to the vitamin D hypothesis. He argued, among other things, that rickets (caused by low levels of cholecalciferol in children) was a disease associated with urbanization and industrialization in Europe, and could not have acted as a selective force in human evolution. Robins (1991) pointed to the lack of paleopathological evidence for preindustrial rickets, and to the culture-specific context of osteomalacia, or low vitamin D production, in adults who are kept away from sunlight. According to Robins (1991), a very small amount of sun exposure is necessary for cholecalciferol production, even by dark skin. Following Robins (1991), the vitamin D hypothesis lost acceptance, but subsequently gained back some (though not universal) support (Barsh, 2003). Although Jablonski (2004) and Jablonski and Chaplin (2000) argued that production of vitamin D is the main evolutionary explanation for the origin of light skin in areas of solar radiation, others, such as Aoki (2002), were less convinced, still pointing to the lack of paleopathological evidence of rickets (Webb and Holick, 1988), and the abundant dietary

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Received 14 June 2005; accepted 22 February 2006.

DOI 10.1002/ajpa.20453

adaptations of humans living in such areas to acquire the component. Recently, evidence for strong natural selection for light skin in Europeans, presumably to facilitate vitamin D production, was reported by Lamason et al. (2005).

It is within this context that sexual selection for light skin was proposed to account for the evolution of light skin in high latitudes and for human skin color sexual dimorphism. Although Byard (1981) observed that there is no clear pattern to human skin color sexual dimorphism, this was challenged by many data sets collected throughout the world: most researchers reported that adult females are lighter than adult males (Correnti et al., 1964; Frost, 1996; Kalla, 1973; Leguebe, 1983; Robins, 1991; Relethford et al., 1983; Roh et al., 2001; Tobias, 1974; Towne and Hulse, 1990).

Darwin himself was aware of this sexual dimorphism, and discussed it in Chapters 19 and 20 of *The Descent of Man*. After Darwin (1936), other researchers proposed various hypotheses to explain the virtually universal sexual dimorphism of human skin color. According to Garn et al. (1956), sex differences in skin color can be attributed to influences of hormones on melanocyte activity, with estrogens and androgens especially thought to affect pigmentation. Edwards and Duntley (1939), Lasker (1954), Harrison and Owen (1964), Smith and Mitchell (1973), and Kahlon (1976) attributed the difference to differential exposure to sunlight (with females receiving less cross-culturally). Smith and Mitchell (1973) and Edwards and Duntley (1939) also cited richer blood flow to the skin's surface in males. Harvey and Lord (1978) accounted for the sexual dimorphism they observed among the Ainu by differences in clothing habits, a factor also cited by Harrison and Salzano (1966). According to Frost (1988), the universality of the human skin color sexual dimorphism negates the possibility that such dimorphism results from culturally specific gender roles and occupations. Jablonski and Chaplin (2000) proposed that human females tend to be lighter than males because the former have higher calcium needs during pregnancy and lactation, and a lighter skin allows them to produce more vitamin D. This initial cause for lighter skin color in females was later enhanced by male preference for light skin color in their partners (Jablonski and Chaplin, 2000).

Van den Bergh and Frost (1986) proposed that sexual selection alone is responsible for human skin color sexual dimorphism. They undertook an analysis of cultural data taken from the Human Relations Area Files (HRAF; www.yale.edu/hraf/) in an attempt to uncover a cross-cultural male preference for light-skinned females, which they found. This, according to van den Bergh and Frost (1986), supports the notion that sexual selection has led to sexual dimorphism of skin color because males universally favor light-skinned females. Based on HRAF data, van den Bergh and Frost (1986) suggested that postpubescent skin color is a secondary sex characteristic, implying a linkage between light pigmentation and fecundability in women. Men, then, would select light-skinned women for their perceived greater fecundity. Very little work has focused on female choice of males, although Aoki (2002) noted that the preference for light skin is more strongly expressed in males than in females. Frost (1994) showed that female preferences for male skin color changed with their menstrual cycle, and were therefore not stable.

Based on van den Bergh and Frost (1986) and on the refutation of the vitamin D hypothesis (Robin, 1991), Aoki (2002) and Ihara and Aoki (1999) argued that sexual selection, and not the need for greater production of cholecalciferol, led to increasing lightness of skin with increasing latitude. Natural selection and sexual selection work in tandem in this model, with the natural adaptive effect of dark skin color in low latitudes being overridden by sexual selection as latitude increases. Simply put, Aoki (2002) and Ihara and Aoki (1999) proposed that there is a universal preference on the side of males for females with lighter skin color. In the absence of natural selection for dark skin, sexual selection would be strongest in areas of low solar radiation. This proposal explains not only the presence of light skin in areas of low solar radiation, but also human skin color sexual dimorphism. From this point on, we refer to this hypothesis as the sexual selection hypothesis.

The sexual selection hypothesis is testable. According to it, in low latitudes, the powerful force of natural selection for dark skin should override sexual selection to a greater degree than it would as latitude increases. The result of this should be a reduced amount of variation in skin color between the sexes, i.e., lower sexual dimorphism. As latitude increases, skin color sexual dimorphism should increase as well, with sexual selection overriding the force of natural selection as dark skin becomes less adaptive. In this paper, we investigate whether a trend of increasing sexual dimorphism with increasing latitude, such as the one suggested by the sexual selection model, exists in humans. Instead of relying on stated preferences, we look at the actual distribution of human sexual dimorphism, and test if it can be statistically correlated to latitude.

MATERIALS AND METHODS

We used data collected with either an Evans Electric limited (EEL) spectrophotometer or photovolt reflectometer. Although regression equations to convert data collected with either machine into measures compatible with data collected with the other machine were proposed (Garrard et al., 1967; Lees and Byard, 1978; Lees et al., 1979), they are impractical because they require data measured in more filters than are usually available. Thus, we must consider the data obtained by different filters with both machines separately. Many of the papers in which the EEL machine was utilized did not use the same filters, and after separating results from the published data by filter, we determined that only at wavelengths of 425 mμ (601 filter = blue), 545 mμ (605 filter = green), and 685 mμ (609 filter = red) did we have at least 20 reflectance values to conduct our tests. Data collected with all other EEL filters were not used (Correnti et al., 1964). Unfortunately, we had smaller numbers of reflectance values from the published data using all three Photovolt tristimuli, and not enough papers to work with the red, blue, and green Photovolt filters. We did not utilize more recent papers, which used yet other machines, as there are not enough data to do quantitative tests with them (Park and Lee, 2005; Parra et al., 2004; Shriver and Parra, 2000; Roh et al., 2001; Wu et al., 2001).

To be considered for this paper, published data had to be taken at the inner face of the upper arm from adult (18 years or more) males and females within a certain population. Data on pregnant women were not included in our analysis, as pregnancy affects the skin color of women (Garn et al., 1956). One paper with adult male and female data was excluded because the numerical data were inconsistent with their description in the text (Harrison et al., 1969). Studies which focused on nonrandom members of a group, such as specific families or twins, were not considered (Clark et al., 1981; Kalla, 1972; Rebato et al., 1999; Walsh and Price, 1963); nor were those with very small sample sizes of adults (Greksa, 1998a,b) or whose males and females came from different populations (Tiwari, 1963). We excluded papers which either did not provide the age range of subjects but only the mean (Sunderland, 1979, 1967), or which did not discuss subjects' ages at all (Kalla, 1969; Roberts et al., 1986; Sunderland et al., 1973).

The decision to exclude children and infants was based on a summary by Robins (1991) of a large cross-cultural data set which showed that skin pigmentation changes with age in a nonlinear manner, and that this change is not uniform across populations. Moreover, since skin-color changes do not appear to be the same for males and females through life, a study of sexual dimorphism is difficult unless the samples are age-controlled. Furthermore, a close examination of samples reported in the literature reveals that some authors grouped children and adults, whereas others separated these age categories. Therefore, we did not want to include in our analysis papers which only included children, those which included both children and adults, and those which measured only adults, as these samples are not comparable. By excluding samples which worked with children and even teenagers, we feel assured that our sample will not suffer from age-related heterogeneity. Indeed, Byard (1981, p. 132) noted that the fact that samples of different age composition have been compared has contributed to a "confusing picture of sex differences in pigmentation" (see also Kalla 1973, 1974). We acknowledge that we are relying on other authors' statements that their subjects are adults, and that our decision to exclude children and teenagers caused us to discard a good number of papers (e.g., Byard and Lees, 1982; Carbonnel and Olivier, 1966; Chamla and Demoulin, 1978; Clark et al., 1981; Conway and Baker, 1972; Greksa, 1998a,b; Harrison and Owen, 1964; Harrison and Salzano, 1966; Harrison et al., 1967; Harvey and Lord, 1978; Hulse, 1967, 1973; Kalla, 1973; Kalla and Tiwari, 1970; Lasker, 1954; Ojikutu, 1974; Omoto, 1968; Park and Lee, 2005; Relethford et al., 1985; Rebato et al., 1993; Smith and Mitchell, 1973; Sunderland and Coope, 1973; Sunderland and Woolley, 1982; Walsh, 1963; Wasserman and Heyl, 1968; Weiner et al., 1963). Our sample is smaller than that used by Relethford (1997, 2000) because he used male-only data sets, and we excluded papers which only reported data on one gender or which pooled male and female data (Büchi, 1957/1958; Caro, 1980; Das and Mukherjee, 1963; Ducros et al., 1975; Eriksson et al., 1980; Garrard et al., 1967; Harrison and Owen, 1964; Hiernaux, 1976, 1977; Jaswal, 1979; Ojikutu, 1965; Rebato et al., 1993; Rigters-Aris, 1973b; Spurgeon et al., 1984; Tiwari, 1963 (Indian data); Walsh, 1963; Wienker, 1979; Williams-Blangero and Blangero, 1991). The sample is also smaller than that collected by Jablonski (2004) and Jablonski and Chaplin (2000), who did not have an age or gender restriction in their data.

In addition to data taken from the literature, we used unpublished data collected by Madrigal et al. (2004) among Afro- and East-Indian derived groups on the Atlantic coast of Costa Rica. Common procedures were followed, taking three readings with each filter from the upper underarm of adult subjects with a portable Photovolt spectrophotometer (Model 577) after cleaning the area with a wet cloth. The three readings were then averaged for a final reading per subject. The machine was standardized before each subject was measured, according to the manufacturer's instructions. All data were taken by one researcher (L.M.) in an effort to remove interobserver error from the data. Three tristimulus filters were used: tri-blue, tri-green, and tri-amber, which sample the visible wavelength at 450 mμ, 550 mμ, and 600 mμ, respectively.

Latitude coordinates for place of origin of the samples were obtained from various Internet sites (see Internet Sites, following Literature Cited, below), in order to establish a measure of the level of solar radiation under which the population evolved. For migrant populations, we estimated their place of origin to the best of our knowledge, utilizing historical information regarding the migration of each one. Although it is to be expected that some of these migrant groups might be lighter than they would be in their place of origin (e.g., British Sikhs) because they are exposed to less solar radiation, this should not impact their level of sexual dimorphism, which was proposed by Aoki (2002) and Ihara and Aoki (1999) to have evolved by sexual selection, and not to be the result of exposure to the sun. Nonetheless, we wished to determine if the pattern of sexual dimorphism of migrant groups differed from that of nonmigrants, so we tested with a nonparametric Wilcoxon test whether the female-male differences between migrants and nonmigrants differed significantly.

Latitude was coded as a continual variable, with the equator counting as "0" and positive numbers assigned to both Southern and Northern latitudes. From now on, we refer to this variable as "absolute latitude." Relethford (1997) showed that if skin color is regressed on latitude, the 0 point or intercept for both hemispheres should be the equator, but that the slope of both hemispheres should be different, to account for the darker skin of people from the Southern Hemisphere. Unfortunately, given our small sample size, we are not in a position to separate our data by Northern and Southern hemispheres. However, the observations of Relethford (1997) were considered in the choice of statistical correlation performed.

Sexual dimorphism was measured by taking the difference between female − male (F-MD) skin color mean reflectance measures by filter. We acknowledge that there might be error involved in the computation of this difference, as we are relying on data collected by numerous other investigators. However, all other metastudies on human skin color relied on similar sets of published data. Moreover, Lees et al. (1978) noted that inter- and intraobserver errors when measuring skin reflectance are not significant.

Since the sexual selection hypothesis attempts to explain why human females are lighter than males, data in which males were lighter than females were excluded from the analysis. We correlated absolute latitude and F-MD with a nonparametric Spearman test. A nonparametric test was used because of our small sample size, and because Relethford (1997) showed the relationship between latitude and skin-color reflectance not to be the same for both hemispheres. We performed the correlation analysis separately for each wavelength, instead of limiting our analysis to a single one.

In addition, for each wavelength, we transformed F-MD into z-scores. Given that z-scores have a mean of zero and a standard deviation of one, we can look at all of them as one single data set, even if they are transformations of data obtained with different filters. For populations in which more than one F-MD was available, one was randomly chosen so that each sample was represented by one z-score only. Finally, we correlated these z-scores with latitude, using a parametric Pearson test, as the sample size is not small when all z-scores are considered together. To find out if areas of low solar radiation have more pro-

TABLE 1. Populations in which males are lighter than females

Sample	mμ	Source	Region
Perú Mestizo	450, 440, 600	Frisancho et al., 1981	South America
Bagani Kraal	685	Weiner et al., 1964	Sub-Saharan Africa
Belgium	425, 545, 685	Van Rijn-Tournel, 1966	Europe
Belgium	425, 545, 685	Leguebe, 1961	Europe
Beswick	425, 545, 685	Abbie, 1975	Australia
Dutch	685	Rigters-Aris, 1973a	Europe
Guipúzcoa (Basques)	425	Rebato, 1987	Europe
Haast's Bluff	685	Abbie, 1975	Australia
Holy Island	425, 545, 685	Cartwright, 1975	Europe
Kalumburu	685	Abbie, 1975	Australia
Nyaturu	545	Weiner, 1971	Sub-Saharan Africa
Punjab	425, 545, 685	Banerjee, 1984	India
Sandawe	425	Weiner, 1971	Sub-Saharan Africa
Viscaya (Basques)	425	Rebato, 1987	Europe
Yalata	545	Abbie, 1975	Australia

TABLE 2. Descriptive statistics and normality test of female-male differences in mean skin reflectance

mμ	n	Mean	SD	Minimum	Maximum	Shapiro-Wilks W	*P*
425	19	1.02	0.97	0.10	3.25	0.833705	0.0037
450	9	4.40	5.29	0.64	17.37	0.712145	0.0020
545	19	1.76	1.53	0.25	4.86	0.823939	0.0026
550	9	4.26	4.83	1.4	16.58	0.618987	0.0002
600	12	3.15	3.28	0.6	13.13	0.586034	0.0001
685	32	2.55	2.02	0.04	8.9	0.871682	0.0013

nounced skin-color sexual dimorphism, we determined which populations had an F-MD z-score $\geq$1.96, the cutoff point between the acceptance and rejection regions of the normal distribution (Sokal and Rohlf, 1981). All statistical analyses were done with SAS 9.1.

RESULTS

The Appendix shows the 53 samples which met the age requirements for males and females for the 425, 450, 545, 550, 600, and 685 wavelengths. The population designation for each sample reported by the authors was retained here. If a paper reported several samples from a single region/country, the separate samples were used in this analysis, as some samples were separated by a large geographical area (e.g., Australia and South Africa). If a paper reported adult data broken down by age categories, a mean reflectance was computed to include the various categories, and this is noted in the Appendix. Thirty-five samples were measured with three filters, 17 with one filter, and one with two filters. The specific breakdown by filter is: 27 for 425, 26 for 545, 41 for 685, 10 for 450, 10 for 550, and 13 for 600 mμ. The latter three wavelengths were measured with the Photovolt reflectometer, which was used in fewer studies than the EEL spectrophotometer.

Table 1 shows the populations in which males were lighter than females. In total, 15 populations had this pattern of sexual dimorphism for at least one filter, and six groups had lighter males for three filters. Six samples came from Europe, six from sub-Saharan Africa, four from Australia, and from India, and one was of Peruvian Mestizos. Although Leguebe (1961) and Van Rijn-Tournel (1966) noted that their female Belgian subjects were more likely to wear sleeveless shirts than were males, most other authors did not explain the presence of lighter males in their sample. Evidently, we are not in a position to discuss these groups' cultural habits. However, given that 6 of 15 groups are from post-1960s Europe, it is tempting to venture that perhaps these females were actively trying to become more tanned, an activity that became fashionable after the 1960s. The groups shown in Table 1 are not considered in the following analysis, and as a result, the samples sizes will decrease accordingly.

Table 2 shows the descriptive statistics of F-MD in mean skin reflectance. Sample sizes for the EEL filters are satisfactory, with 19 for 425 and 545, and 32 for 685 mμ. For the Photovolt filters, however, the sample sizes are very small, with 9 for 450 and 550, and 12 for 600. The normality of the distribution of differences was tested with a Shapiro-Wilks test, which rejected the null hypothesis of normality for all filters.

To test if migrant and nonmigrant samples had a significantly different pattern of sexual dimorphism, we performed a Wilcoxon nonparametric two-sample test. Because of the small number of migrant groups, we could only use EEL data. We determined that the migrant and nonmigrant groups did not differ significantly for any of the three EEL filters (mμ = 425, $z = -0.33$, $P = 0.73$; mμ = 545, $z = 0.0664$, $P = 0.94$; mμ = 685, $z = -0.8954$, $P = 0.37$). Therefore, we can conclude that migrant groups do not have significantly different patterns of sexual dimorphism than do nonmigrants. All samples are considered together for the remaining of the paper, regardless of migrant status.

The results of the nonparametric Spearman correlation between absolute latitude and F-MD are shown in Table 3. Out of six statistical tests, only two achieved significance, and both indicated a conflicting direction to the relationship between skin-color sexual dimorphism and latitude. Whereas 425 mμ suggests that sexual dimorphism increases with distance from the equator (in support of the sexual selection hypothesis), 600 mμ suggests that sexual dimorphism decreases with distance from the equator (contradicting the sexual selection hypothesis). A plot between latitude and F-MD for both filters is shown in Figures 1 and 2.

TABLE 3. Correlation between latitude and F-MD

mμ	n	r_s	*P*
425	19	0.46816	0.04
450	9	−0.27603	0.47
545	19	0.38384	0.10
550	9	−0.24152	0.53
600	12	−0.70346	0.01
685	32	−0.00899	0.96

r_s = Spearman correlation coefficient.

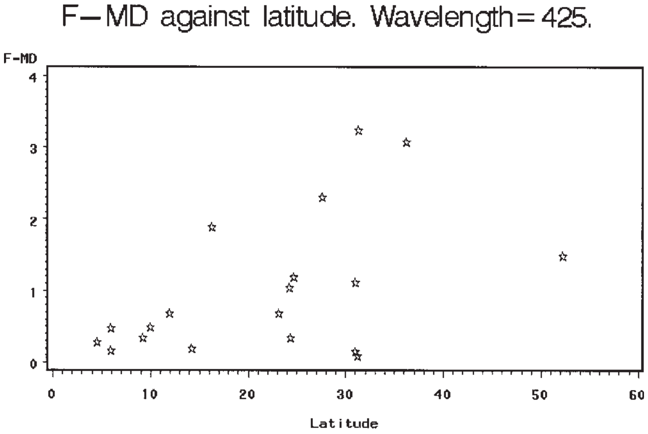

Fig. 1. Female-male differences against latitude. Wavelength = 425.

In order to use all samples in a single test, and thus increase our statistical power, we transformed F-MD into z-scores for each mμ. After randomly choosing one z-score per sample, the total sample size was 46. With this sample, we computed a Pearson correlation between z-score and latitude. The sexual selection hypothesis predicts that with increasing latitude, there should be an increasing positive z-score. However, the null hypothesis of no correlation between latitude and z-scores was accepted, with a correlation coefficient of 0.08989 and a *P*-value of 0.5525. Therefore, when we looked at one measure of male-female sexual dimorphism per population, standardized to a mean of 0 and a standard deviation of 1, we found no correlation between increased sexual dimorphism and latitude, thus finding no support for the sexual selection hypothesis. A plot of these two variables is shown in Figure 3.

Finally, in order to determine if the most sexually dimorphic populations were found in areas of low solar radiation, we examined which groups had an F-MD z-score ≥1.96, the usual cutoff point to decide if a z-score is statistically significantly different from the usual 95% acceptance region. Against the predictions of the sexual selection hypothesis, five populations which did not inhabit and did not evolve in areas of low solar radiation were beyond the cutoff point. One of the three groups was of the Indo-Costa Ricans, who descend from East Indian indentured servants and who inhabit the Atlantic coast of Costa Rica (z-scores of 2.90, 2.55, and 2. 47 for 600, 550, and 450 mμ, respectively). The other four groups are from Iran (z = 3.05 for 685 mμ), the Jirel from Nepal (z = 2.2 and z = 2.4 for 545 and 685, respectively), the Kurdish (z = 2.20 and z = 2.04 for 425 and 545, respectively), and Yemen (z = 2.3 and z = 2.23 for 425 and 545, respectively). India, Costa Rica, Yemen, Nepal, and the Middle East are hardly areas of low solar radiation.

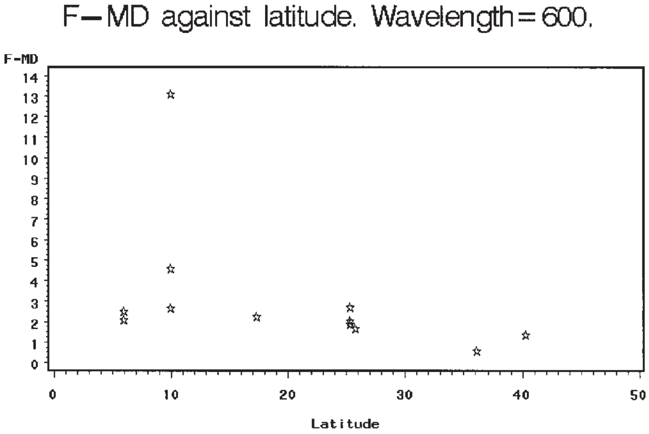

Fig. 2. Female-male differences against latitude. Wavelength = 600.

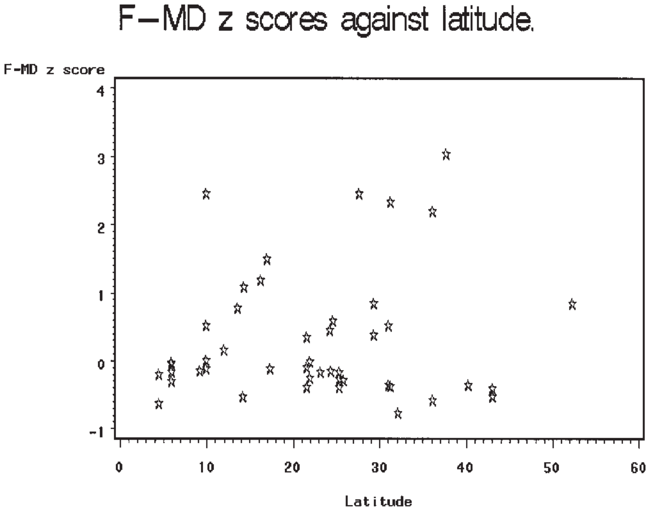

Fig. 3. Female-male differences z-scores against latitude.

DISCUSSION

In this paper, we addressed evolutionary explanations for the virtually universal sexual dimorphism of human skin color whereby females are lighter than are males. Specifically, we tested the hypothesis that skin-color sexual dimorphism should increase with increasing distance from the equator. According to Aoki (2002) and Ihara and Aoki (1999), the results of sexual selection for lighter-skin color females is strongest in areas of low solar radiation, where there is little natural selection for dark skin.

It is unfortunate that few skin-color quantitative genetics studies are available besides Byard (1981). This type of research could elucidate the response of skin-color sexual dimorphism to selection. In her review, Byard (1981) noted that although some studies indicate high heritability of skin color, there are many interactions which make any further statement impossible. For example, she noted that correlations between relatives suggest an X-linked-type of expression of the trait, a maternal effect, or even very low correlations among relatives. In the absence of further quantitative genetics studies on skin color, we note that two papers looked at the quantitative genetics of other human sexually dimorphic traits: stature (Rogers and Mukherjee, 1992) and several anthropometric traits

(Commuzzie et al., 1993). Rogers and Mukherjee (1992) showed that the mean height of both genders responds more quickly to sexual selection for tall males than does sexual dimorphism for height. For this reason, sexual dimorphism can only track environmental changes very slowly, and should not be well-adapted to environmental conditions. Moreover, since sexual selection for tall males is posited to occur in polygamous societies, and since (according to Rogers and Mukherjee, 1992) societies change their preferred type of marriages frequently, the sexual selection pressure for tall males would not be constant enough to have a significant effect on stature sexual dimorphism. If skin-color sexual dimorphism behaved in the same manner as stature, then we would not expect skin-color dimorphism to respond to sexual selection. However, the scenario proposed by Rogers and Mukherjee (1992) is different from that posited by the skin-color sexual selection hypothesis. Whereas the former proposes that there is sexual selection for tall males only, the latter proposes sexual selection for light-skinned females but natural selection for dark skin in both sexes. Moreover, whereas the sexual selection pressure for tall males is not constant but changes with preferred marriage type, the sexual selection pressure for light-skinned females is presumably constant and universal (Aoki, 2002).

In contrast with Rogers and Mukherjee (1992), Commuzzie et al. (1993) found significant genotype-sex interaction in several human sexually dimorphic anthropometric traits. Their results show that the genotypes affecting these phenotypes express themselves differently with regard to the sex of the individual. Therefore, under natural or sexual selection, the traits would respond differently in each sex. If skin-color sexual dimorphism behaved in the same manner as these anthropometric traits, then we would expect skin-color dimorphism to respond to sexual selection. It would be useful to perform similar quantitative genetics studies with human skin-color sexual dimorphism to determine if, in the presence of natural and/or sexual selection, skin color is expressed differently in the sexes as in some anthropometrics traits (Commuzzie et al., 1993), or not, as in stature (Rogers and Mukherjee, 1992).

In their proposal of the skin-color sexual dimorphism hypothesis, Aoki (2002) and Ihara and Aoki (1999) argued against an unquestionable acceptance of the vitamin D hypothesis, and attempted to explain the presence of light skin in high latitudes. They based themselves on the suggestion by van den Berghe and Frost (1986) that cross-culturally, human males prefer light-skinned females. According to the latter authors, males perceive light females to be more attractive, because light skin is a signal of fecundability. In contrast, Ihara and Aoki (1999) proposed that light skin is always maladaptive, and that preference for light skin is arbitrary. Hunter (2002) noted that the definition of beauty as light skin in her African and Mexican American subjects is a lingering effect of European colonization and slavery.

Van den Berghe and Frost (1986) acknowledged that the HRAF results showing a preference for light skin in females could be due to the fact that the data were collected by Western males who preferred light-skinned females. Although the HRAF data might be limited, Frost (1988) and van den Berghe and Frost (1986) worked with what cross-cultural data were available on the issue of male-female skin-color preferences.

Instead of working with preferences, we wished to test the hypothesis that human sexual dimorphism increases with increasing latitudes, as a result of decreased natural selection for dark skin and the presumably universal preference for light-skinned females.

A possible confounding variable in our data was migration and the formation of new populations. However, we determined that the migrant samples were not significantly different from nonmigrant groups in their F-MD.

We were limited in our data analysis by small sample sizes, particularly with Photovolt data. When we correlated the level of F-MD with latitude, we found two significant correlations in opposite directions, and four nonsignificant correlations. When we transformed F-MD into z-scores per wavelength, and randomly chose one per sample, we again did not find any correlation between increasing sexual dimorphism and latitude.

If sexual selection does not explain human skin-color dimorphism, then what does? After reviewing the literature, it seems to us that gender-specific roles are unlikely to explain the virtual universality of lighter human females than human males. We suggest that a hormonal basis to such a difference, as proposed by Garn et al. (1956), might be a more fruitful line of research. After all, it is well-established that hormonal changes during puberty and pregnancy affect skin color.

The sexual selection hypothesis has broadened the theoretical discussion on human skin-color evolution in general, and sexual dimorphism in particular, from a purely naturally selective perspective to one that incorporates sexual selection. Perhaps the discussion needs to be broadened even more, to include nonadaptationist explanations for the pattern of human pigmentation, as suggested by Quevedo et al. (1985).

Independently from our results, we find it difficult to explain the emphasis placed on male choice of females and the absence of female choice in the sexual selection hypothesis. The evidence that women are willing and frequently able to engage in extramarital affairs is very strong, and suggests that they engage in mate choice, even if their husbands have been chosen for them. Unfortunately, that human females are ascribed virtually absent or totally passive roles in narratives of human evolution is not new (Falk, 1997; Hrdy, 1993; Zihlman, 1997).

CONCLUSIONS

We tested the hypothesis that human sexual dimorphism of skin color should be positively correlated with distance from the equator, a proposal generated by the sexual selection hypothesis. We found no support for that proposition. Before this paper was written, the sexual selection hypothesis was based on stated male-preference data in a number of human groups. Here, we focused on the actual pattern of sexual dimorphism. We report that the distribution of human sexual dimorphism in relation to latitude is not that which is predicted by the sexual selection hypothesis. According to that hypothesis, in areas of low solar radiation, there should be greater sexual dimorphism, because sexual selection for lighter females is not counterbalanced by natural selection for dark skin. Our data analysis does not support this prediction.

INTERNET SITES

http://www.bcca.org/misc/qiblih/latlong_oc.html
http://www.infoplease.com/ipa/A0001769.html

http://www.cia.gov/cia/publications/factbook/appendix/appendix-f.html
http://www.mapsofworld.com/lat_long/index.html

ACKNOWLEDGMENTS

We thank the following individuals: E. Amador, J. Avery, G. Barbujani, R. Frisancho, D. Himmelgreen, J. Relethford, and C. Wienker. Also, we thank our Afro- and Indo-Limonense groups, who welcomed us with open arms. Finally, we are deeply indebted to the University of South Florida Library's interlibrary loan staff, who were able to get us virtually every single paper in our Literature Cited. Because of their excellent service, L.M. now has most of the literature in PDF format, and will be happy to share it with other researchers.

Appendix. Mean reflectance values for males and females

Wavelength	Sample	Female mean	Male mean	Absolute latitude	Source
Data sorted by population					
685	Algiers (mean of 30–57 years)	58.04	58.0	32.2	Chamla and Demoulin, 1978
550	Afro-Limonenses	25.15	19.57	17.3	Madrigal et al., 2004
600	Afro-Limonenses	25.23	22.94	17.3	Madrigal et al., 2004
450	Afro-Limonenses	23.99	18.94	17.3	Madrigal et al., 2004
600	Afro-South Carolina	16.6	14.5	6.0	Pollitzer et al., 1970b
425	Aymara (20–29 years)	16.9	15.0	16.27	Greksa, 1991
545	Aymara (20–29 years)	25.8	23.0	16.27	Greksa, 1991
685	Aymara (20–29 years)	53.5	49.9	16.27	Greksa, 1991
685	Bagani Kraal	22.22	22.6	22.0	Weiner et al., 1964
450	Bahamas	5.93	5.29	6.0	Mazess, 1967
550	Bahamas	10.6	8.57	6.0	Mazess, 1967
600	Bahamas	13.12	10.61	6.0	Mazess, 1967
425	Belgians	36.5	37.7	50.833	Leguebe, 1961
545	Belgians	44.6	44.8	50.833	Leguebe, 1961
685	Belgians	65.9	67.3	50.833	Leguebe, 1961
425	Belgians	38.18	39.12	50.5	van Rijn-Tournel, 1966
545	Belgians	43.15	43.8	50.5	van Rijn-Tournel, 1966
685	Belgians	63.65	64.51	50.5	van Rijn-Tournel, 1966
425	Beswick	10.1	10.8	14.34	Abbie, 1975
545	Beswick	11.1	12.1	14.34	Abbie, 1975
685	Beswick	23.2	24.8	14.34	Abbie, 1975
685	Black Bushmen	29.36	28.15	22.0	Weiner et al., 1964
425	British Sikh	23.34	23.18	31.0	Roberts and Kahlon, 1976
545	British Sikh	30.46	29.62	31.0	Roberts and Kahlon, 1976
685	British Sikh	54.94	53.96	31.0	Roberts and Kahlon, 1976
425	Bushmen	13.7	12.65	24.3	Tobias, 1961
545	Bushmen	19.03	18.11	24.3	Tobias, 1961
685	Bushmen	43.62	42.54	24.3	Tobias, 1961
450	Chamizal	14.29	12.7	25.3	Relethford and Lees, 1981
550	Chamizal	23.47	21.22	25.3	Relethford and Lees, 1981
600	Chamizal	28.84	26.09	25.3	Relethford and Lees, 1981
425	Chope	7.7	7.34	24.42	Weninger, 1969
685	Chope	21.1	17.81	24.42	Weninger, 1969
450	Indo-Limonenses	35.61	18.24	10.0	Madrigal et al., 2004
550	Indo-Limonenses	35.14	18.56	10.0	Madrigal et al., 2004
600	Indo-Limonenses	34.89	21.76	10.0	Madrigal et al., 2004
685	Dogons (Mali)	36.7	31.4	17.0	Huizinga, 1965
685	Dutch	66.7	68.9	52.3	Rigters-Aris, 1973a
425	Europeans	34.3	32.8	52.3	Barnicot, 1958
545	Europeans	40.5	37.9	52.3	Barnicot, 1958
685	Europeans	63.1	61.5	52.3	Barnicot, 1958
425	Fali (Cameroon; mean of adults, 21+ years)	7.65	7.3	9.19	Rigters-Aris, 1973c
545	Fali (Cameroon; mean of adults, 21+ years)	8.25	7.2	9.19	Rigters-Aris, 1973c
685	Fali (Cameroon; mean of adults, 21+ years)	20.8	19.4	9.19	Rigters-Aris, 1973c
600	Florida Seminoles	29.4	27.7	25.8	Pollitzer et al., 1970c
685	Ghanzi	44.59	43.01	21.6	Weiner et al., 1964
425	Guipúzcoa (Basques)	29.2	29.96	43.0	Rebato, 1987
545	Guipúzcoa (Basques)	40.92	39.56	43.0	Rebato, 1987
685	Guipúzcoa (Basques)	66.38	65.53	43.0	Rebato, 1987
425	Haast's Bluff	10.9	10.2	23.22	Abbie, 1975
545	Haast's Bluff	13.0	12.1	23.22	Abbie, 1975
685	Haast's Bluff	26.6	26.7	23.22	Abbie, 1975
685	Habbanites	56.65	52.32	14.35	Hulse, 1969
425	Holy Island	34.06	34.07	55.0	Cartwright, 1975
545	Holy Island	39.55	39.83	55.0	Cartwright, 1975
685	Holy Island	62.29	63.35	55.0	Cartwright, 1975
685	Iran	60.1	51.2	37.7	Mehrai and Sunderland, 1990

(continued)

Appendix. (Continued)

Wavelength	Sample	Female mean	Male mean	Absolute latitude	Source
425	Jirel	20.5	18.18	27.633	Williams-Blangero and Blangero, 1992
545	Jirel	31.43	26.59	27.633	Williams-Blangero and Blangero, 1992
685	Jirel	56.64	49.12	27.633	Williams-Blangero and Blangero, 1992
425	Kalumburu	10.4	10.2	14.25	Abbie, 1975
545	Kalumburu	11.0	10.7	14.25	Abbie, 1975
685	Kalumburu	20.4	20.7	14.25	Abbie, 1975
685	Karkar	33.24	30.78	6.0	Harvey, 1985
425	Karkar	10.1	9.62	6.0	Harvey, 1985
545	Karkar	15.02	13.81	6.0	Harvey, 1985
425	Kurdish	24.19	21.11	36.2	Lourie, 1973
545	Kurdish	33.73	29.19	36.2	Lourie, 1973
685	Kurdish	60.02	54.89	36.2	Lourie, 1973
685	Lone Tree	43.1	40.48	21.6	Weiner et al., 1964
425	Lufa	9.31	9.14	6.0	Harvey, 1985
545	Lufa	13.79	13.29	6.0	Harvey, 1985
685	Lufa	31.58	30.83	6.0	Harvey, 1985
425	Maningrida	9.4	8.7	12.0	Abbie, 1975
545	Maningrida	10.1	9.5	12.0	Abbie, 1975
685	Maningrida	21.1	19.1	12.0	Abbie, 1975
685	Mazua Kraal	22.05	20.29	22.0	Weiner et al., 1964
450	Minita	13.6	12.43	25.3	Relethford and Lees, 1981
550	Minita	22.89	20.94	25.3	Relethford and Lees, 1981
600	Minita	27.84	25.75	25.3	Relethford and Lees, 1981
685	Namaquanland	48.13	45.45	29.3	Weiner et al., 1964
450	New York	31.0	29.5	40.29	Little and Sprangel, 1980
550	New York	41.5	39.8	40.29	Little and Sprangel, 1980
600	New York	47.7	46.3	40.29	Little and Sprangel, 1980
425	Nyaturu (mean of middle-aged and old subjects)	8.05	7.75	4.54	Weiner, 1971
545	Nyaturu (mean of middle-aged and old subjects)	9.85	9.9	4.54	Weiner, 1971
685	Nyaturu (mean of middle-aged and old subjects)	25.3	24.05	4.54	Weiner, 1971
600	Oklamma Seminoles	32.4	31.8	36.1	Pollitzer et al., 1970a
600	Peru Mestizos	33.6	36.8	6.0	Frisancho et al., 1981
550	Peru Mestizos	26.5	29.5	6.0	Frisancho et al., 1981
450	Peru Mestizos	15.5	18.8	6.0	Frisancho et al., 1981
425	Punjab	17.94	18.81	30.5	Banerjee, 1984
545	Punjab	26.15	27.02	30.5	Banerjee, 1984
685	Punjab	53.64	54.52	30.5	Banerjee, 1984
450	Rural Nuñoa	19.4	12.5	10.0	Conway and Baker, 1972
550	Rural Nuñoa	22.2	20.8	10.0	Conway and Baker, 1972
600	Rural Nuñoa	27.8	25.1	10.0	Conway and Baker, 1972
450	Saltillo	14.08	12.52	25.3	Relethford and Lees, 1981
550	Saltillo	23.25	21.05	25.3	Relethford and Lees, 1981
600	Saltillo	28.38	26.45	25.3	Relethford and Lees, 1981
425	Sandawe (mean of middle-aged and old subjects)	8.95	9.15	4.54	Weiner, 1971
545	Sandawe (mean of middle-aged and old subjects)	11.3	11.05	4.54	Weiner, 1971
685	Sandawe (mean of middle-aged and old subjects)	28.3	27.95	4.54	Weiner, 1971
685	Sara de Ndila (adults)	26.5	22.9	13.57	Hiernaux, 1972
425	Sikh	22.36	21.23	31.0	Kahlon, 1976
545	Sikh	29.88	27.77	31.0	Kahlon, 1976
685	Sikh	55.52	53.2	31.0	Kahlon, 1976
425	South African Negroes	16.5	15.3	24.65	Robins, 1972[1]
545	South African Negroes	20.6	18.2	24.65	Robins, 1972[1]
685	South African Negroes	44.3	41.7	24.65	Robins, 1972[1]
685	Takashwani	43.86	42.98	21.6	Weiner et al., 1964
450	Urban Nuñoa	16.8	12.9	10.0	Conway and Baker, 1972
550	Urban Nuñoa	26.3	21.6	10.0	Conway and Baker, 1972
600	Urban Nuñoa	31.3	26.7	10.0	Conway and Baker, 1972
425	Viscaya (Basques)	28.95	29.98	43.0	Rebato, 1987
545	Viscaya (Basques)	39.88	39.57	43.0	Rebato, 1987
685	Viscaya (Basques)	65.78	65.25	43.0	Rebato, 1987
685	Warmbad	45.62	41.86	29.3	Weiner et al., 1964
425	Yalata	10.4	10.3	31.29	Abbie, 1975
545	Yalata	11.8	12.0	31.29	Abbie, 1975
685	Yalata	26.2	25.2	31.29	Abbie, 1975
425	Yemen	21.61	18.36	31.3	Lourie, 1973
545	Yemen	31.36	26.5	15.0	Lourie, 1973
685	Yemen	56.94	53.15	15.0	Lourie, 1973

(continued)

Appendix. (Continued)

Wavelength	Sample	Female mean	Male mean	Absolute latitude	Source
425	Yoruba	8.5	8.0	10.0	Barnicot, 1958
545	Yoruba	11.1	10.1	10.0	Barnicot, 1958
685	Yoruba	26.1	23.6	10.0	Barnicot, 1958
Data sorted by wavelength					
425	Aymara (20–29 years)	16.9	15.0	16.27	Greksa, 1991
425	Belgians	36.5	37.7	50.833	Legúebe, 1961
425	Belgians	38.18	39.12	50.5	van Rijn-Tournel, 1966
425	Beswick	10.1	10.8	14.34	Abbie, 1975
425	British Sikh	23.34	23.18	31.0	Roberts and Kahlon, 1976
425	Bushmen	13.7	12.65	24.3	Tobias, 1961
425	Chope	7.7	7.34	24.42	Weninger, 1969
425	Europeans	34.3	32.8	52.3	Barnicot, 1958
425	Fali (Cameroon; mean of adults, 21+ years)	7.65	7.3	9.19	Rigters-Aris, 1973c
425	Guipúzcoa (Basques)	29.2	29.96	43.0	Rebato, 1987
425	Haast's Bluff	10.9	10.2	23.22	Abbie, 1975
425	Holy Island	34.06	34.07	55.0	Cartwright, 1975
425	Jirel	20.5	18.18	27.633	Williams-Blangero and Blangero, 1992
425	Kalumburu	10.4	10.2	14.25	Abbie, 1975
425	Karkar	10.1	9.62	6.0	Harvey, 1985
425	Kurdish	24.19	21.11	36.2	Lourie, 1973
425	Lufa	9.31	9.14	6.0	Harvey, 1985
425	Maningrida	9.4	8.7	12.0	Abbie, 1975
425	Nyaturu (mean of middle-aged and old subjects)	8.05	7.75	4.54	Weiner, 1971
425	Punjab	17.94	18.81	30.5	Banerjee, 1984
425	Sandawe (mean of middle-aged and old subjects)	8.95	9.15	4.54	Weiner, 1971
425	Sikh	22.36	21.23	31.0	Kahlon, 1976
425	South African Negroes	16.5	15.3	24.65	Robins, 1972[1]
425	Viscaya (Basques)	28.95	29.98	43.0	Rebato, 1987
425	Yalata	10.4	10.3	31.29	Abbie, 1975
425	Yemen	21.61	18.36	31.3	Lourie, 1973
425	Yoruba	8.5	8.0	10.0	Barnicot, 1958
450	Afro-Limonenses	23.99	18.94	17.3	Madrigal et al., 2004
450	Bahamas	5.93	5.29	6.0	Mazess, 1967
450	Chamizal	14.29	12.7	25.3	Relethford et al., 1981
450	Indo-Limonenses	35.61	18.24	10.0	Madrigal et al., 2004
450	Minita	13.6	12.43	25.3	Relethford and Lees, 1981
450	New York	31.0	29.5	40.29	Little and Sprangel, 1980
450	Peru Mestizos	15.5	18.8	6.0	Frisancho et al., 1981
450	Rural Nuñoa	19.4	12.5	10.0	Conway and Baker, 1972
450	Saltillo	14.08	12.52	25.3	Relethford and Lees, 1981
450	Urban Nuñoa	16.8	12.9	10.0	Conway and Baker, 1972
545	Aymara (20–29 years)	25.8	23.0	16.27	Greksa, 1991
545	Belgians	44.6	44.8	50.833	Leguebe, 1961
545	Belgians	43.15	43.8	50.5	van Rijn-Tournel, 1966
545	Beswick	11.1	12.1	14.34	Abbie, 1975
545	British Sikh	30.46	29.62	31.0	Roberts and Kahlon, 1976
545	Bushmen	19.03	18.11	24.3	Tobias, 1961
545	Europeans	40.5	37.9	52.3	Barnicot, 1958
545	Fali (Cameroon; mean of adults, 21+ years)	8.25	7.2	9.19	Rigters-Aris, 1973c
545	Guipúzcoa (Basques)	40.92	39.56	43.0	Rebato, 1987
545	Haast's Bluff	13.0	12.1	23.22	Abbie, 1975
545	Holy Island	39.55	39.83	55.0	Cartwright, 1975
545	Jirel	31.43	26.59	27.633	Williams-Blangero and Blangero, 1992
545	Kalumburu	11.0	10.7	14.25	Abbie, 1975
545	Karkar	15.02	13.81	6.0	Harvey, 1985
545	Kurdish	33.73	29.19	36.2	Lourie, 1973
545	Lufa	13.79	13.29	6.0	Harvey, 1985
545	Maningrida	10.1	9.5	12.0	Abbie, 1975
545	Nyaturu (mean of middle-aged and old subjects)	9.85	9.9	4.54	Weiner, 1971
545	Punjab	26.15	27.02	30.5	Banerjee, 1984
545	Sandawe (mean of middle-aged and old subjects)	11.3	11.05	4.54	Weiner, 1971
545	Sikh	29.88	27.77	31.0	Kahlon, 1976
545	South African Negroes	20.6	18.2	24.65	Robins, 1972[1]
545	Viscaya (Basques)	39.88	39.57	43.0	Rebato, 1987
545	Yalata	11.8	12.0	31.29	Abbie, 1975
545	Yemen	31.36	26.5	15.0	Lourie, 1973
545	Yoruba	11.1	10.1	10.0	Barnicot, 1958

(continued)

Appendix. (Continued)

Wavelength	Sample	Female mean	Male mean	Absolute latitude	Source
550	Afro-Limonenses	25.15	19.57	17.3	Madrigal et al., 2004
550	Bahamas	10.6	8.57	6.0	Mazess, 1967
550	Chamizal	23.47	21.22	25.3	Relethford and Lees, 1981
550	Indo-Limonenses	35.14	18.56	10.0	Madrigal et al., 2004
550	Minita	22.89	20.94	25.3	Relethford and Less, 1981
550	New York	41.5	39.8	40.29	Little and Sprangel, 1980
550	Peru Mestizos	26.5	29.5	6.0	Frisancho et al., 1981
550	Rural Nuñoa	22.2	20.8	10.0	Conway and Baker, 1972
550	Saltillo	23.25	21.05	25.3	Relethford and Lees, 1981
550	Urban Nuñoa	26.3	21.6	10.0	Conway and Baker, 1972
600	Afro-Limonenses	25.23	22.94	17.3	Madrigal et al., 2004
600	Afro-South Carolina	16.6	14.5	6.0	Pollitzer et al., 1970b
600	Bahamas	13.12	10.61	6.0	Mazess, 1967
600	Chamizal	28.84	26.09	25.3	Relethford and Lees, 1981
600	Indo-Limonenses	34.89	21.76	10.0	Madrigal et al., 2004
600	Florida Seminoles	29.4	27.7	25.8	Pollitzer et al., 1970c
600	Minita	27.84	25.75	25.3	Relethford and Lees, 1981
600	New York	47.7	46.3	40.29	Little and Sprangel, 1980
600	Oklamma Seminoles	32.4	31.8	36.1	Pollitzer et al., 1970a
600	Peru Mestizos	33.6	36.8	6.0	Frisancho et al., 1981
600	Rural Nuñoa	27.8	25.1	10.0	Conway and Baker, 1972
600	Saltillo	28.38	26.45	25.3	Relethford and Lees, 1981
600	Urban Nuñoa	31.3	26.7	10.0	Conway and Baker, 1972
685	Algiers (mean of 30–57 years)	58.04	58.0	32.2	Chamla and Demoulin, 1978
685	Aymara (20–29 years)	53.5	49.9	16.27	Greksa, 1991
685	Bagani Kraal	22.22	22.6	22.0	Weiner et al., 1964
685	Belgians	65.9	67.3	50.833	Leguebe, 1961
685	Belgians	63.65	64.51	50.5	van Rijn-Toumel, 1966
685	Beswick	23.2	24.8	14.34	Abbie, 1975
685	Black Bushmen	29.36	28.15	22.0	Weiner et al., 1964
685	British Sikh	54.94	53.96	31.0	Roberts and Kahlon, 1976
685	Bushmen	43.62	42.54	24.3	Tobias, 1961
685	Chope	21.1	17.81	24.42	Weninger, 1969
685	Dogons (Mali)	36.7	31.4	17.0	Huizinga, 1965
685	Dutch	66.7	68.9	52.3	Rigters-Aris, 1973a
685	Europeans	63.1	61.5	52.3	Barnicot, 1958
685	Fali (Cameroon: mean of adults, 21+ years)	20.8	19.4	9.19	Rigters-Aris, 1973c
685	Ghanzi	44.59	43.01	21.6	Weiner et al., 1964
685	Guipúzcoa (Basques)	66.38	65.53	43.0	Rebato, 1987
685	Haast's Bluff	26.6	26.7	23.22	Abbie, 1975
685	Habbanltes	56.65	52.32	14.35	Hulse, 1969
685	Holy Island	62.29	63.35	55.0	Cartwright, 1975
685	Iran	60.1	51.2	37.7	Mehrai and Sunderland, 1990
685	Jirel	56.64	49.12	27.633	Williams-Blangero and Blangero, 1992
685	Kalumburu	20.4	20.7	14.25	Abbie, 1975
685	Karkar	33.24	30.78	6.0	Harvey, 1985
685	Kurdish	60.02	54.89	36.2	Lourie, 1973
685	Lone Tree	43.1	40.48	21.6	Weiner et al., 1964
685	Lufa	31.58	30.83	6.0	Harvey, 1985
685	Maningrida	21.1	19.1	12.0	Abbie, 1975
685	Mazua Kraal	22.05	20.29	22.0	Weiner et al., 1964
685	Namaquanland	48.13	45.45	29.3	Weiner et al., 1964
685	Nyaturu (mean of middle-aged and old subjects)	25.3	24.05	4.54	Weiner, 1971
685	Punjab	53.64	54.52	30.5	Banerjee, 1984
685	Sandawe (mean of middle-aged and old subjects)	28.3	27.95	4.54	Weiner, 1971
685	Sara de Ndila (adults)	26.5	22.9	13.57	Hiernaux, 1972
685	Sikh	55.52	53.2	31.0	Kahlon, 1976
685	South African Negroes	44.3	41.7	24.65	Robins, 1972[1]
685	Takashwani	43.86	42.98	21.6	Weiner et al., 1964
685	Viscaya (Basques)	65.78	65.25	43.0	Rebato, 1987
685	Warmbad	45.62	41.86	29.3	Weiner et al., 1964
685	Yalata	26.2	25.2	31.29	Abbie, 1975
685	Yemen	56.94	53.15	15.0	Lourie, 1973
685	Yoruba	26.1	23.6	10.0	Barnicot, 1958

[1] Data taken from Robins (1991).

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