AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 133:779–781 (2007)

Notes and Comments

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

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Women have lighter skin than men do across a wide range of populations, even on the unexposed skin of the upper inner arm, possibly because of sexual selection by men for lighter-skinned women. If this hypothesis is true, human skin color should become more sexually dimorphic with increasing distance from the equator, since sexual selection for lighter skin in women would be less constrained by natural selection for darker skin in both sexes. Yet when Madrigal and Kelly (2006) analyzed skin reflectance data from 53 different samples, they found that the most dimorphic human populations were actually those of medium skin color at medium latitudes.

Their finding does not necessarily falsify the sexual selection hypothesis. It may be that this sexual dimorphism cannot fully express itself in light-skinned populations at higher latitudes. Skin reflectance becomes sexually dimorphic during adolescence, when girls progressively lighten in color, and this lightening may be less effectively expressed if melanin production is already low (Frost, 2005; 57). It is perhaps significant that this sex difference seems to disappear or even reverse itself when skin reflectance is close to the physiological maximum, notably in Dutch and Belgian subjects (Leguebe, 1961; van Rijn-Tournel, 1966; Rigters-Aris, 1973). The authors of these studies attribute the absence of dimorphism to their female subjects being more likely to wear sleeveless shirts. Madrigal and Kelly (2006) cautiously attribute it to the popularity of tanning among modern European women. Yet the skin color of Spanish subjects becomes sexually dimorphic during adolescence even though young women in post-Franco Spain wear sleeveless shirts and sun themselves (Mesa, 1983).

If we eliminate samples near the maximum of skin reflectance, can we still tease out the effects, if any, of sexual selection? Doubtful. For one thing, the "ceiling effect" likely begins to manifest itself well before the limit of maximum skin reflectance. For another, there is probably too much noise in the data for such a fine-grained analysis. Skin color is less sexually dimorphic at some ages, particularly childhood (when it is absent) and adolescence (when it is still emerging), and most studies are poorly controlled for age. Madrigal and Kelly (2006) tried to minimize this problem by limiting their meta-analysis to adult men and women: "By excluding samples which worked with children and even teenagers, we feel assured that our sample will not suffer from age-related heterogeneity." Many of the papers they cite, however, apply the term "adults" or "men and women" to anyone past the age of puberty. For example, when Weiner et al. (1964) studied Black Bushmen at Bagani kraal, the "adults" were defined as those whose third molars had erupted. Leguebe (1961) studied "women" who ranged in age from 17 to 23. Banerjee (1984) examined Punjabi "mothers" and "fathers" without specifying their ages, yet many Punjabi women begin to have children in their teenage years.

Even after adolescence, age-related noise continues to muddy the data. Human skin may change more slowly during adulthood, but it does change. In particular, there is some evidence that skin color becomes less sexually dimorphic after 40, with some papers finding that women become nonsignificantly darker than men (Chamla and Démoulin, 1978; Mori and Tokuhashi, 1956; Rigters-Aris, 1973). This is a problem for any meta-analysis because relatively few skin reflectance studies exclude adults over 40 years of age.

The most serious problem with Madrigal and Kelly's meta-analysis, however, is not a methodological one. When they modeled the selection pressures on human skin color, they assumed that the only one to vary with latitude was natural selection for darker skin in both sexes. Yet sexual selection for lighter skin in women may also have varied with latitude, especially during the long period of time when all humans were hunter-gatherers. The intensity of sexual selection is determined by the operational sex ratio (i.e., the ratio of men to women among adults available for mating) and this ratio becomes more female-biased in hunter-gatherers the further away they are from the equator: first, polygyny becomes costlier for men because women cannot gather food in winter and require more food provisioning; second, more men die at a younger age because they cover longer distances while hunting. As a result, in proportion to distance from the equator, fewer men are available for mating, women compete much more for mates, and sexual selection of women intensifies. Thus, sexual selection for lighter skin in women may have varied with latitude just as natural selection for darker skin varies with latitude. The two selection pressures are confounded. Madrigal and Kelly (2006) allude to this problem when they deplore the assumption that everywhere, and to the same extent, men can pick and choose among a broad range of possible mates.

How, then, can the sexual selection hypothesis be falsified? Does it make predictions that may be proven true or false? In my opinion, there are two testable predictions:

1. If sexual selection has shaped this sexual dimorphism, men and women should differ in all of the visible skin pigments, and not simply in one of them. This prediction is borne out. Women differ from men in the two main components of skin color: melanin and hemoglo-

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Received 5 June 2006; accepted 4 December 2006.

DOI 10.1002/ajpa.20555

Published online 26 February 2007 in Wiley InterScience (www.interscience.wiley.com).

bin, i.e., women are less brown and less ruddy in complexion (Edwards and Duntley, 1939). To explain this sex difference in terms of natural selection, one must postulate two separate selection pressures.

2. If an allele lightens women's skin more than men's, and if we compare different populations with the same level of solar UV exposure (see Jablonski and Chaplin, 2000; 68), the allele should increase in frequency as we go from darker- to lighter-skinned populations. In addition, there should be more alleles that exhibit this kind of sex linkage. The reason in both cases is that the lighter-skinned populations would owe some of their loss of skin pigmentation to sexual selection for lighter-skinned women, and not simply to natural selection (either stronger selection for vitamin D synthesis or weaker selection for protection against sunburn or skin cancer). Such sex-linked alleles would thus be over-represented even if they were less effectively expressed in fair-skinned individuals. We can test this prediction by examining alleles that 1) lighten skin color and 2) appear to have been under positive selection, e.g., the "redhead" MC1R alleles, the derived SLC24A5 and SLC45A2 alleles, and possibly OCA2, MYO5A, HPS7, and TYRP1 variants (Sturm, 2006). If some or all of these alleles affect one sex more than the other, they should do so in the direction of lightening skin color more in women than in men.

On a final note, the sexual selection hypothesis does not presuppose that human skin color became sexually dimorphic solely or even mainly via the action of sexual selection. Some of its proponents argue that women's lighter skin first arose through fortuitous causes (the differing effects of male and female hormones on melanin production) and that the male mind then came to use this visible female trait, subconsciously, as a measure of hormonal status and thus childbearing potential (van den Berghe and Frost, 1986). Others believe that a lighter skin color was first part of a complex of childlike traits (smoother skin, higher-pitched voice, more pedomorphic face) that enabled women to lessen aggressiveness in men and stimulate male provisioning (Guthrie, 1970). Still others think that women first acquired a lighter skin to facilitate vitamin D synthesis and thereby ensure more calcium for pregnancy and lactation (Jablonski and Chaplin, 2000). All three of these explanations assign sexual selection a secondary, facultative role. Women's lighter skin is thought to have first evolved for other reasons and only later became a criterion that men could use for mate choice.

More importantly, regardless of the universality of this mate-choice criterion, the extent to which it actually did influence mate choice—and hence sexual selection—would have depended on the availability of mateable women and on the relative importance of other mate-choice criteria. We thus come back to one of the flaws in Madrigal and Kelly's model: the assumption that sexual selection for lighter-skinned women was equally intense in all human populations and was constrained only by natural selection for dark skin. In fact, the intensity may have varied considerably in response to a variety of local conditions.

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Human Skin-Color Sexual Dimorphism: A Test of the Sexual Selection Hypothesis. Reply to Frost (2007)

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We thank Frost (2007) for his comments. The evolution of human skin color has not received much attention in the physical anthropology literature recently, and we are glad to see it discussed.

Frost's comments focus on the following points: He proposes that sexual dimorphism might not be able to be expressed in light-skinned populations at higher latitudes. Therefore, we should not expect these populations to be more sexually dimorphic. We are aware of no data

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Received 14 December 2006; accepted 10 January 2007

DOI 10.1002/ajpa.20582

Published online 26 February 2007 in Wiley InterScience (www.interscience.wiley.com).

in support of this proposition. Indeed, the only citation provided by Frost is his own book (which our interlibrary loan office could not get for this reply to be published timely, as the book is not held by any library in the State of Florida system or the Library of Congress). However, even if it were true that light-skin populations might not be able to express sexual dimorphism, the other human populations should follow a correlation with latitude of increasing dimorphism with increasing distance from the equator. Moreover, Frost only mentions the Dutch and Belgian subjects, in which females are darker than males in support of his point. He fails to mention the other populations in which this is also the case, all of which are listed in our Table 1. Most of these populations are not particularly light skinned, and some of them are very dark. Lastly, the proposition that the effects of sexual selection in high latitude populations is present but not detectable is untestable, and therefore out of the range of a scientific paper.

We included in our sample of 53 studies, three that according to Frost should not have been included because of the age of the subjects. Any researcher who does a meta-analysis of existing data must make difficult decisions about which studies to include. In this particular case, the main issue was to increase sample size to improve statistical power. To argue that three out of 53 papers should not have been included (one because the subjects had erupted third molars) misses the point about statistical power. As we clearly acknowledged in the paper, meta-analyses are done with less than perfect data. In addition, we note that any osteology textbook will define the adult human dental formula as one which includes the third molar because the eruption of this tooth is one which is considered as a marker of adulthood.

The hypothesis which we tested did not consider that sexual selection might vary crossculturally. Indeed it did not. We state:

> 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.

Therefore, we tested the hypothesis as proposed by authors other than Frost, who state that the preference is universal, and who did not consider that there might be crosscultural differences in such preference. We hope that Frost will be able to test that the intensity of sexual selection "varied considerably in response to a variety of local conditions." But this is something that we did not attempt to do because it is not part of the hypothesis as stated by Aoki (2002) and Ihara and Aoki (1999). We note that it would have been helpful for further studies if Frost had provided citations in support of his assertion that polygyny becomes costlier for men in societies far away from the equator.

The sexual selection hypothesis does not presuppose that human skin color became dimorphic solely or mainly via the action of sexual selection. Different views of the hypothesis "...assign sexual selection a secondary, facultative role." Indeed, the aim of our paper was not to look at what might have initially caused sexual dimorphism but to examine one explanation of what brought it to its current levels.

Frost then sets an agenda for possible further research, proposing two predictions. We applaud this endeavor and hope to see further peer-reviewed research on the matter.

In conclusion, a careful reading of our paper demonstrates that we tested one specific proposal, namely one which does not consider crosscultural differences in sexual selection. In addition, the purpose of our paper was not to examine the origin of human skin color sexual dimorphism. We hope that Frost or others will attempt to do so in the future, and look forward to seeing those results.

Although our data set is typical of that of meta-analyses, namely, collected by different authors with different guidelines, we believe that it is better to explore ideas and different views with the data that are available rather than not exploring or investigating simply because the data are not perfect. In addition, we worked with actual skin reflectance data which can be quantified and subjected to statistical analysis, as opposed to qualitative data on stated sexual preferences.

According to Frost, it is doubtful that we can "still tease out the effects, if any, of sexual selection," whether because data on skin reflectance were collected in people of different ages, or because sexual selection is more acute if the subjects evolved in hunter-gatherer societies far away from the equator. We do not subscribe to a view of science that claims that something (the sexual selection hypothesis) should be accepted as valid even if it cannot be tested. On the contrary, we focused on a specific proposal (not Frost's proposal) which could be tested. We did not incorporate variables which were not measured in our subjects (such as the operational sex ratio in cold-weather hunters and gatherers) because the data were not available.

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