

## European hair and eye color A case of frequency-dependent sexual selection?

Peter Frost

*c/o Dr. D.I. Perrett, School of Psychology, University of St. Andrews, St. Mary's College, South St., St. Andrews,  
Fife, KY169JA, UK*

Initial receipt 14 June 2004; final revision received 7 July 2005

---

### Abstract

Human hair and eye color is unusually diverse in northern and eastern Europe. The many alleles involved (at least seven for hair color) and their independent origin over a short span of evolutionary time indicate some kind of selection. Sexual selection is particularly indicated because it is known to favor color traits and color polymorphisms. In addition, hair and eye color is most diverse in what used to be, when first peopled by hunter-gatherers, a unique ecozone of low-latitude continental tundra. This type of environment skews the operational sex ratio (OSR) of hunter-gatherers toward a male shortage in two ways: (1) men have to hunt highly mobile and spatially concentrated herbivores over longer distances, with no alternate food sources in case of failure, the result being more deaths among young men; (2) women have fewer opportunities for food gathering and thus require more male provisioning, the result being less polygyny. These two factors combine to leave more women than men unmated at any one time. Such an OSR imbalance would have increased the pressures of sexual selection on early European women, one possible outcome being an unusual complex of color traits: hair- and eye-color diversity and, possibly, extreme skin depigmentation.

© 2006 Elsevier Inc. All rights reserved.

*Keywords:* Gender roles; Monogamy; Pigmentation; Polygyny; Sexual selection; Upper Paleolithic

---

---

*E-mail address:* peter\_frost61z@globetrotter.net.

## 1. Introduction

Human hair and eye color is unusually diverse in a geographic area centered on the East Baltic and covering northern and eastern Europe (Figs. 1 and 2). Within this area, eyes are not only brown but also blue, gray, hazel, or green, while hair is not only black but also brown, flaxen, golden, or red (Beals & Hoijer, 1965, pp. 212–214). As one moves outward from this area, color diversity declines markedly with eyes becoming uniformly brown and hair uniformly black.

Is this diversity due to chance? In particular, could it reflect founder effects during the re peopling of glaciated Europe 15,000 to 10,000 years ago? When a founder group breaks off from its parent population, such “sampling” may indeed increase the frequency of a variant hair- or eye-color allele. It is less probable that two alleles of the same gene would become

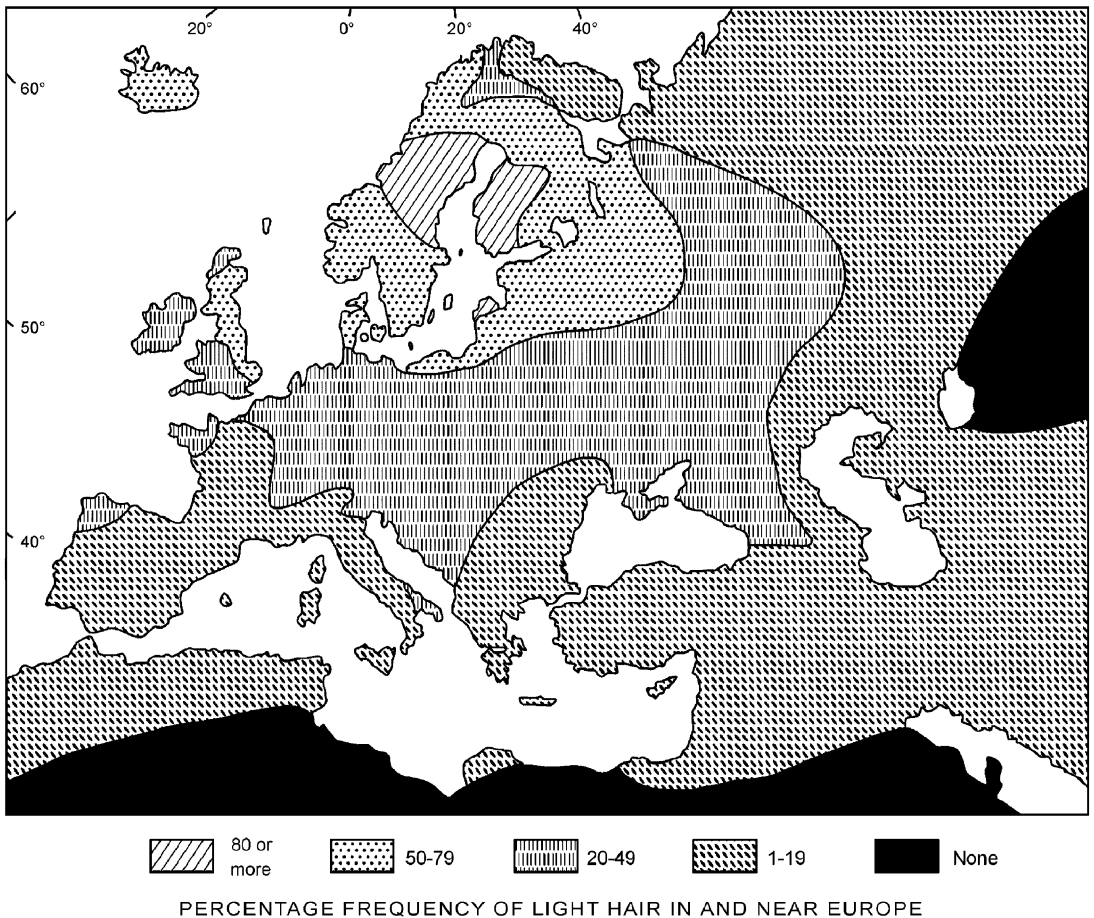


Fig. 1. Hair-color diversity in and near Europe (after Beals & Hoijer, 1965, p. 214). (Reprinted with permission from Beals et al., “An Introduction to Anthropology,” 3rd ed. Published by Allyn and Bacon, Boston, MA. Copyright © 1965 by Pearson Education.)

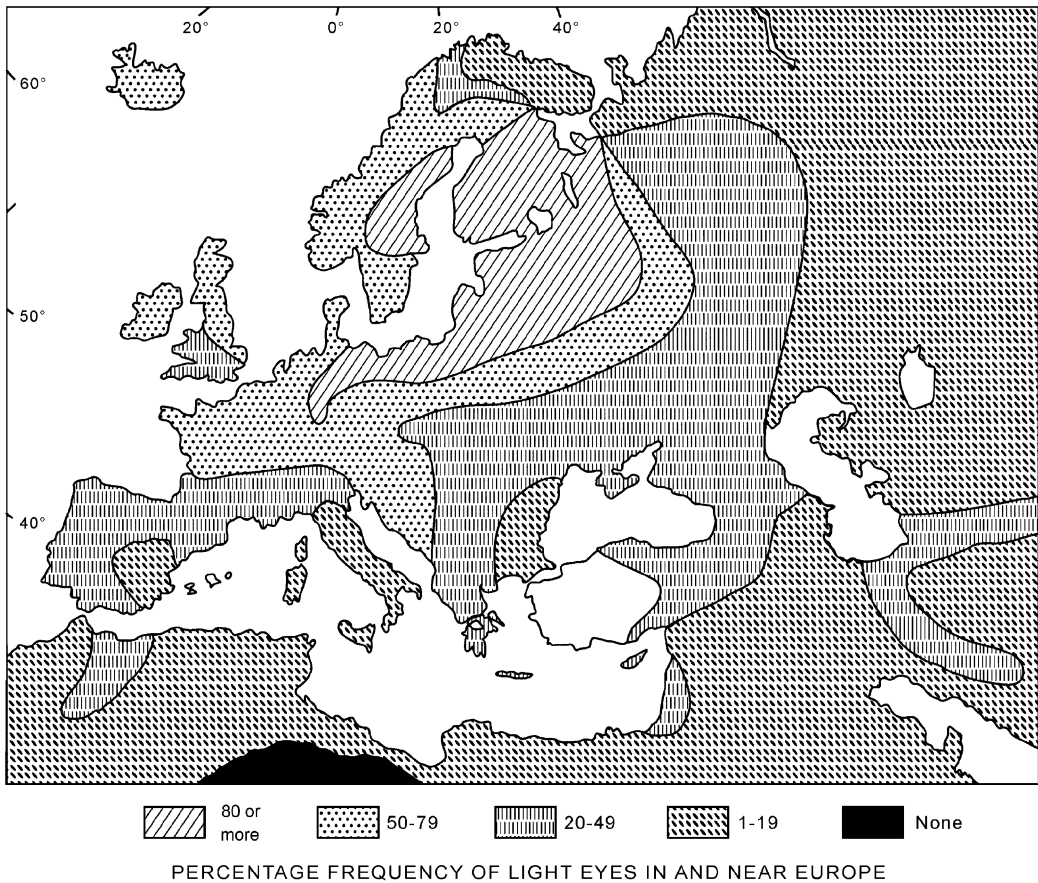


Fig. 2. Eye-color diversity in and near Europe (after [Beals & Hoijer, 1965](#), p. 213). (Reprinted with permission from Beals et al., “An Introduction to Anthropology,” 3rd ed. Published by Allyn and Bacon, Boston, MA. Copyright © 1965 by Pearson Education.)

more frequent, and this probability would decline exponentially with each additional allele. Yet the hair-color gene, *MC1R*, has at least seven phenotypically distinct alleles that exist only in Europe ([Box et al., 1997](#); [Harding et al., 2000](#); [Rana et al., 1999](#)). Furthermore, eye-color diversity results from another set of alleles at a locus that is at best weakly linked to hair color ([Eiberg & Mohr, 1987](#)).

Is this diversity due to relaxation of selection and a resulting accumulation of variant alleles? [Harding et al. \(2000\)](#) have investigated this evolutionary scenario and found that the time to the most recent common ancestral hair color would be about a million years, with the redhead alleles alone being approximately 80,000 years old. [Templeton \(2002\)](#) has come to a similar conclusion: If the cause were relaxation of selection, the current level of hair-color diversity would have taken 850,000 years to develop. Yet modern humans have been in Europe for approximately 35,000 years.

Is this diversity due to admixture with older European populations, notably the Neanderthals? Recently, human mtDNA has been retrieved from skeletal material on both sides of the transition from Neanderthals to modern humans: No genetic continuity is discernible between the late Neanderthals and the early modern Europeans (Caramelli et al., 2003). In addition, the mtDNA and dental traits of Neanderthals are no more similar to those of present-day Europeans than they are to those of any other modern human population (Krings et al., 1990; Ovchinnikov et al., 2000; Tyrrell & Chamberlain, 1998). Neanderthal admixture seems to have been minor, if not negligible, and could hardly account for the high proportion of Europeans who deviate from the species norm of black hair and brown eyes.

Is this diversity due, then, to some selective force, either natural or sexual selection? The first kind of selection is unlikely. As a rule, highly visible color traits are not adaptations to the natural environment, which typically favors an unobtrusive, cryptic coloration as a means to evade predators. It has been suggested that a lighter colored iris may offer more visual acuity in dim light, such as in the misty maritime environments of northwestern Europe (Short, 1975). Eye color, however, is polymorphic over a much larger area of Europe, most of which is typically continental in climate. It is also unclear why selection for visual acuity would have favored more variability in eye color as opposed to a simple reduction in eye pigment.

The alternative, sexual selection, has already been advanced to explain Europe's hair- and eye-color diversity (Cavalli-Sforza et al., 1994, p. 266). This kind of selection is known to favor colorful traits, but there is little consensus on the reasons why. It may be that bright colors stimulate sexual attraction in the brain through (1) mate-assessment algorithms that interpret pigment production as a sign of health and, hence, mate quality; (2) sex-recognition algorithms that pick out sex-specific color stimuli and respond open-endedly with stronger responses to more intense colors; and (3) general monitoring algorithms that respond to highly visible stimuli and indirectly alert other systems, including those related to sexual attraction (Farr, 1980; Hamilton & Zuk, 1982; Kirkpatrick, 1987; Manning, 1979, pp. 66–75). The opposite sex may exploit all three algorithm types by intensifying its color stimuli until functional constraints intervene or until the cost of easier detection by predators exceeds the benefit of stronger sexual attraction (Endler, 1980; Endler, 1991).

Under certain conditions, sexual selection may also diversify color traits within a single population. When an individual is faced with potential mates of equal value, it will tend to select the one that "stands out from the crowd," that is, that has the rarest color morph. The selection is frequency-dependent, declining in strength as the rare morph becomes more common and tending toward an equilibrium that maximizes color diversity. This rare-color advantage has been studied mainly in fruit flies and guppies but has also been reported in a parasitic wasp, in red flour beetles, in ladybugs, and in leafroller moths (Anderson, 1969; Brooks, 2002; Farr, 1980; Grant et al., 1974; Hughes et al., 1999; Muggleton, 1979; Simchuk, 2001; Sinnock, 1970). There are also a number of bird species that exhibit color polymorphisms for which the mode of selection remains unclear (Lank, 2002). Whatever the cause, color polymorphisms are relatively uncommon. They are often hindered by two evolutionary constraints: (1) high predation pressure, this being

a constraint on color traits in general and (2) the presence of related species within the same geographic range, apparently because too much intraspecific variability interferes with species recognition and leads to hybridization (Endler, 1980).

Many evolutionary biologists dislike the concept of rare-color advantage. There is no gain in fitness from sexual attraction to unusual colors; therefore natural selection should eliminate such nonadaptive behavior. Yet it is difficult to see how, just as it is difficult to see how we can counter the many subterfuges that advertisers use to attract our notice. There are good adaptive reasons for paying attention when an eye-catching object enters our field of view, and it is impossible to disable this response in advance for sexual attraction, given that the nature of the object (animate/inanimate, conspecific/nonconspecific, male/female) is determined at a later stage of mental processing. At that stage, the increased attention could be reversed or given a negative meaning. But there would be a cost: not only in additional processing time but also in overcorrection and undercorrection—like a spam-filter that fails to screen out all unwanted e-mails while blocking some legitimate ones. The cost may be justified if attraction to rare-color morphs leads to hybridization or if the color itself is somehow maladaptive. Otherwise, the benefit will not justify the cost.

Rare-color advantage has been reported in humans. Thelen (1983) presented three series of slides showing blonde and brunette females and asked male participants to select the one from each series that they would most prefer to marry. The first series showed 6 brunettes, the second 1 brunette and 5 blondes, and the third 1 brunette and 11 blondes. For the same brunette, preference increased significantly from the first to the third series, that is, in proportion to the rarity of her hair color. The same effect was observed, albeit to a lesser extent, when the study was repeated with male photos and female participants. These findings have some support from other studies. Schweder (1994) found that women tended to change their hair color and hair form to a type that was less common in the general population. Riedl (1990) found that men tended to prefer female faces that diverge from the norm. Finally, Ellis (1928, pp. 182–183) noted less preference for blonde women in England than in France, which he ascribed to the higher prevalence of blondness among the English.

Rare-color advantage may have caused hair and eye color to diversify in ancestral humans, there being neither of the evolutionary constraints mentioned above, that is, high predation pressure or likelihood of hybridization. Outside Africa, there were only two potential predators: wolves and bears, the latter being uncommon and the former only an occasional threat to recent hunter-gatherers (Hoffecker, 2002, pp. 238, 240). Hybridization was just as nonproblematic. All other *Homo* populations had been reduced to extinction or relic status by 30,000 BP.

It is less clear, though, why hair and eye color diversified in Europe and not elsewhere. Rare-color advantage is a special case of sexual selection, and the intensity of sexual selection normally varies with the operational sex ratio (OSR; the ratio of unmated males to unmated females). The usual pattern is too many males competing for too few females (pregnancy and early infant care exclude some females from mating at any one time). But why would there have been more competition for women in northern and eastern Europe? If anything, there should have been more in sub-Saharan Africa or Papua New Guinea, where a high incidence of polygyny leaves fewer women unmated.

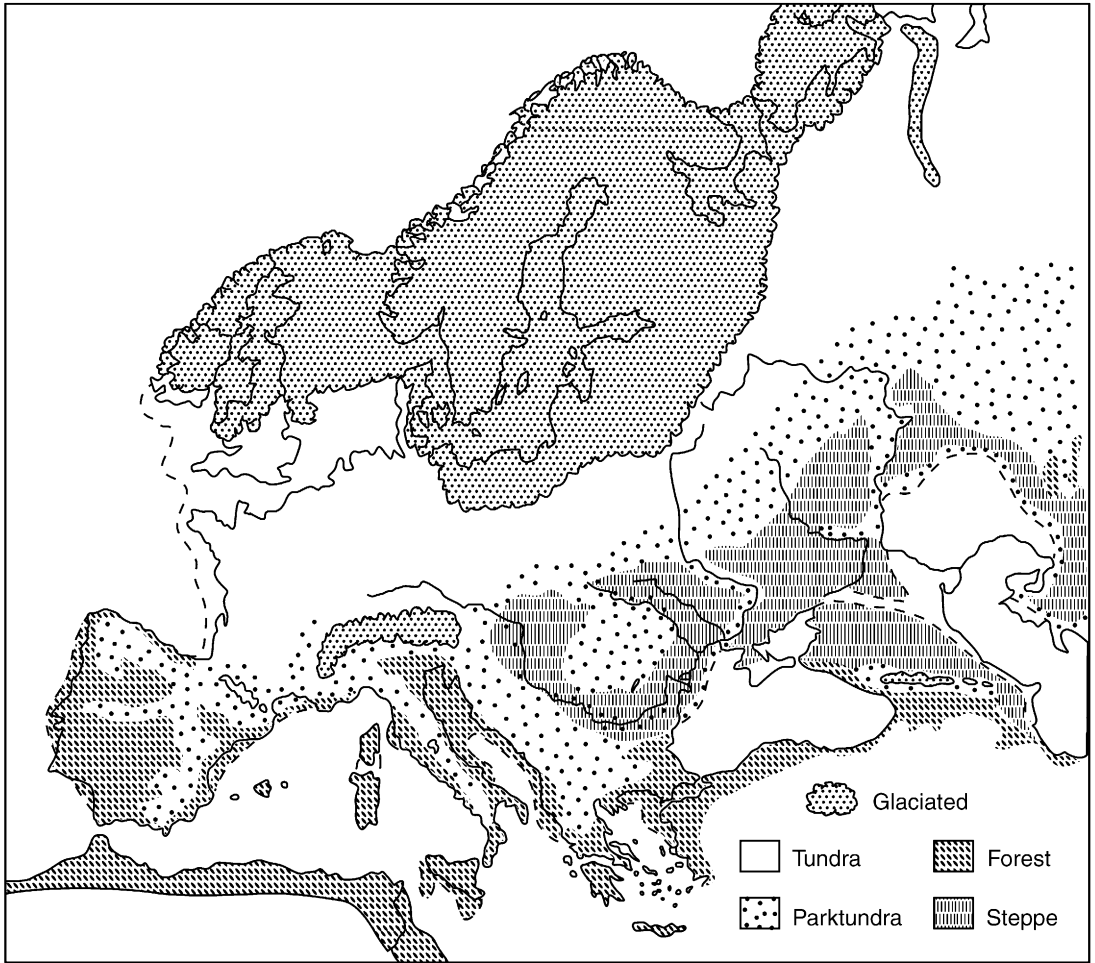


Fig. 3. Major vegetation zones in Europe approximately 18,000 BP (after Mellars, 1985, p. 275, reprinted with permission from Elsevier).

I will argue here that the usual pattern of too many males and too few females was reversed among ancestral Europeans, specifically among the highly mobile groups that once inhabited the continental tundra of ice-age Europe. This environment exposed men to a higher risk of hunting mortality while limiting their ability to provide for more than one wife. With fewer men altogether and even fewer polygynous ones, women had to compete for a limited supply of potential husbands. There was thus sexual selection, but it acted primarily on women—not on men.

## 2. The Eurasian tundra belt: low-latitude west and high-latitude east

As modern humans spread out of Africa during the Upper Paleolithic, they entered new environments, including one that no longer exists. Loess-steppe covered the plains of

northern and eastern Europe during successive ice ages and interglacials until 10,000 years ago (Fig. 3). Quite unlike today's northern barrens, it combined Arctic tundra with fertile loess soil and low latitudes, the Eurasian tundra belt having been pushed far to the south by the Scandinavian icecap. Long intense sunlight favored a lush growth of mosses, lichens, grasses, and low shrubs with grazing herds of mammoths, reindeer, bison, and horses. Despite high bioproductivity, Europe's tundra plains posed several adaptive challenges. Winter temperatures averaged  $-20$  to  $-30^{\circ}\text{C}$ , with little natural protection. Wood for fuel or shelter was scarce. Finally, almost all consumable biomass was in the form of large herds of migrating herbivores (Hoffecker, 2002, pp. 21–26, 32–34).

South of  $60^{\circ}\text{N}$ , the Eurasian tundra belt lay entirely within Europe. East of the Urals, it narrowed and ran further north across Asia and into Beringia. Colder and drier with proportionately less fertile loess, this eastern end had a lower carrying capacity for herbivores (Goebel, 1999; Hoffecker, 2002, p. 22).

### 3. Continental Arctic tundra: consequences of human adaptation

#### 3.1. *Less food gathering=increased female dependence on male provisioning*

In adapting to Arctic tundra, modern humans had to change their sexual division of labor, which normally allocated food gathering to women and hunting to men. Women now processed meat provided by men and did tasks unrelated to food procurement, such as garment making and shelter building. Men procured almost all of the food (Hoffecker, 2002, p. 8).

We can see this task reallocation by comparing recent hunter-gatherers from the Tropics to the Arctic. Near the equator, women procure about half of the family food supply by gathering berries, fruits, roots, grubs, eggs, and other sessile items, these tasks being more compatible than hunting with the demands of pregnancy, breast feeding, and infant transport (Kelly, 1955, pp. 268–269). Away from the equator, the cold season lengthens and gatherable food becomes harder to find, declining from 40% to 55% of the family food supply in hunter-gatherers below  $40^{\circ}\text{N}$  to less than 10% above  $60^{\circ}\text{N}$  (Martin, 1974, pp. 16–18). The end point of this trend is Arctic tundra. Among the Caribou Inuit, female food gathering is limited to eggs (during 2 weeks in summer), raw gadfly larvae, the root of a plant species, and some berries (Birket-Smith, 1929, p. 133).

On this north–south continuum, ice-age European hunter-gatherers were much closer to the 'Arctic' end, with most of their food being procured through hunting. Dickson (1990, p. 180) summarizes the evidence: the abundance of game animals in Europe during the late Pleistocene; the volume of animal bone at archeological sites like Solutré, Moldova, Predmosti, and Dolni Vestonice; the large amount of usable meat on late Pleistocene game animals; and the lack of wear on Upper Paleolithic dentition, indicating a grit-free, carnivorous diet (Butzer, 1964, p. 374; Dahlberg & Carbonell, 1961). In addition, biochemical analysis of human remains from a British Upper Paleolithic site reveals a diet high in animal protein, principally from aurochs and red deer (Richards et al., 2000). At Czech, Russian, and British Upper Paleolithic sites, similar analyses reveal a diet high in protein from terrestrial herbivores, waterfowl, and fish

(Richards et al., 2001). None of this means that food gathering was absent, only that it was less important. Indeed, a Czech site has yielded evidence of fleshy taproots from charred plant remains (Mason et al., 1994). The remains date, however, to approximately 26,000 BP, when forest-steppe predominated, and the investigators concluded that such foods were limited to southern and central Europe.

### 3.2. *Increased female dependence on male provisioning=constraints on polygyny*

As males assume more responsibility for food procurement, polygyny becomes more difficult. In his review of Inuit mating systems, Kjellström (1973, p. 118) concludes, “Since the duty of being a provider was more onerous for the man who had two or more wives, this meant that as a rule it was only the really able and skilful hunters and fishers who could manage this double duty.” Hodge (1959[1905], p. 809) concurs: “monogamy is prevalent, as the support of several wives is possible only for the expert hunter.” This pattern also prevailed among the Chukchi of northeastern Siberia: “The Chukchees commonly live in monogamy; it is only exceptionally that they have two wives” (Nordenskiöld, 1882, p. 504). According to the earliest ethnography of the Sami of northern Scandinavia, “Neither is it Lawful for them to Marry more than one Wife at a time, or to be divorced from her. Polygamy and Divorces..., are Things unknown to the Laplanders, both whilst they were Pagans, and since” (Scheffer, 1704, p. 296).

These observations are supported by genetic data. The ratio of Y to X chromosome variability rises markedly as one goes from long-established tropical populations (sub-Saharan Africans, New Guineans, and Aboriginal Australians) to other populations (Europeans, Asians, and Amerindians), indicating that the latter have had a higher proportion of men contributing to the gene pool (Dupanloup et al., 2003; see also Scozzari et al., 1997; Torroni et al., 1990). More work is needed to determine whether this trend peaks in recent Arctic hunter-gatherers.

### 3.3. *Longer hunting distances=higher death rate among young men*

As hunter-gatherers adapt to less tropical environments, men have to cover more terrain while hunting, partly because they need to hunt more (to offset the decline in food gathering) and partly because the game animals themselves roam over a larger territory, the land supporting less vegetation at colder temperatures (Kelly, 1955, pp. 128–132). Hunting distance peaks in the continental Arctic, where almost all potential food is in the form of wide-ranging and highly mobile herds (Hoffecker, 2002, p. 8). It then decreases further north in the extreme Arctic, where hunters cover shorter distances in pursuit of solitary game, fish, and seals (Kelly, 1955, p. 129).

As hunting distance lengthens, more young men die from starvation, accidents, or exposure. Among the Chukchi of the 18th to early 20th centuries, men died young because they followed reindeer over the tundra with a minimum of possessions; in contrast, men lived longer among the Nenets because herd dogs confined the semidomesticated reindeer to nearby pastures (Krupnik, 1985). Arctic populations that still hunted wild game thus had



highly skewed sex ratios. Among 19th century Labrador Inuit, only 57 males remained for every 100 females in the 15+ age bracket because of hunting deaths from drowning or exposure (Scheffel, 1984). Among Inuit, in general, “the preponderance of adult women is generally explained by the higher death rate among men due to the natural hazards of hunting” (Weyer, 1932, pp. 135–136).

Some evidence points to long hunting distances and high male mortality on the tundra plains of Upper Paleolithic Europe. Many central Russian sites contain large quantities of black flint from sources at least 130–150 km away and other raw materials from sources up to 650 km away (Hoffecker, 2002, pp. 184–185, 248). Human remains from Upper Paleolithic Europe were once thought to be mainly males (Binford, 1968; Harrold, 1980; Vallois, 1961), but reanalysis with improved sexing criteria has found that females predominate, suggesting either that many men died under conditions unsuited for burial, such as hunting accidents, or that male burials were less conducive to preservation, such as in aboveground coffins (Mallegni & Fabbri, 1995). The Maszycka Cave in Poland has provided the only ‘snapshot’ of a single extended family from the Upper Paleolithic: the remains of three men, five women, and eight children, all apparently killed and partially eaten (Kozłowski & Sachse-Kozłowska, 1995).

#### 3.4. *Constraints on polygyny+higher death rate among young men=skewed OSR*

With less polygyny and more young men dying, the OSR is skewed toward a male shortage. Many women lose reproductive time, even among non-Arctic hunter-gatherers with less skewed OSRs. Among the !Kung, about 75% of all women lose some reproductive time while waiting between partners, and 10–20% lose 5 to 15 years. “A relative scarcity of husbands, then, is a regular and expected part of the !Kung marriage system” (Howell, 1979, pp. 247–250). One might expect that this female surplus would encourage more men to take second wives, but “having two families simultaneously is difficult to manage, both economically (in providing for a large number of dependents) and socially (in avoiding the conflicts and irritations of polygamous marriages)” (Howell, 1979, p. 272). Each additional wife, with her offspring, decreases the ratio of food-providing adults to food-consuming children (Howell, 1979, pp. 53–54).

These constraints on polygyny peak in Arctic tundra environments, where women have few opportunities for food gathering. Parallel to this trend, death rates among young men peak in the continental Arctic. OSRs should therefore be most skewed among hunter-gatherers (or rather hunters) living on continental Arctic tundra. Today, this environment is a shadow of its former self, both in the size of its migrating herds and in the extent of its land mass, essentially the northern fringes of mainland Eurasia and North America. Most of its indigenous peoples—low-Arctic Inuit, Chukchi, Yukaghir, Tungus, Nenets, and Sami (Lapps)—rely on a mix of maritime fishing and inland hunting; thus, their OSR characteristics are, at best, indicative of Upper Paleolithic conditions. Nonetheless, if we look at the Labrador Inuit of the 19th century, a very lopsided sex ratio appears at all reproductive ages, with many women, especially widows, shut out of the marriage market entirely (Scheffel, 1984). In the Siberian Arctic east of the Taymyr Peninsula, in the 18th to early 20th centuries, women outnumbered men at all reproductive ages because the men still followed reindeer on

foot and suffered proportionately higher death rates. (Krupnik, 1985). OSR skewing seems to have occurred even further west, where reindeer were already semidomesticated in historic times. Sami of 18th to 19th century Finland had female-biased OSRs, although the same was true among the mainly agricultural Finns (Lummaa et al., 1998). Indeed, female-biased OSRs prevailed in most preindustrial European societies, reflecting perhaps the key importance of paternal investment and also cultural constraints on polygyny that predated Christianity (Seccombe, 1992, pp. 184–190; Sherman, 1922, Vol. II, p. 475; Tacitus, 1970, 18; Vatin, 1970, p. 201).

North of the continental Arctic, in the extreme Arctic, OSRs were more evenly balanced and sometimes had a male surplus (Schrire & Steiger, 1974). First, male mortality was lower. Men hunted dispersed marine animals and thus avoided the ‘feast or famine’ dilemma that occurred when hunting spatially concentrated terrestrial herbivores. Second, female mortality was higher, specifically female infanticide. In the extreme Arctic, parents viewed the prospects for a daughter as problematic. She would have trouble finding a husband locally (the low carrying capacity of the land limited the local group’s size), and thus she would probably marry into another group and not support her parents later on, either directly or through her future husband (Balikci, 1967; Riches, 1974; Smith & Smith, 1994). At lower latitudes, where the land had a higher carrying capacity, female infanticide occurred much less often, apparently because bigger and closer groups allowed women to marry locally and provide their parents with ‘son-in-law payback’ (Riches, 1974; Schrire & Steiger, 1974).

#### **4. Peopling of the Eurasian tundra belt**

Modern humans penetrated the Eurasian tundra belt no earlier than 35,000 years ago, at first in its most southerly and resource-rich portion—southwestern France (Mellars, 1985). This ‘beachhead’ was dissected by valleys that offered wild fruits, grains, tubers, salmon, and non-Arctic game, as well as migrating reindeer in the fall and winter (Blades, 1999a, 1999b; Mellars, 1985). The reindeer may have drawn humans out of the sheltered valleys, briefly at first, and then for longer periods, as hunting bands adapted to the new niche. Eventually, some bands left the valleys to hunt year-round on the surrounding tundra plains. The initial founder group may have been small, as suggested by the very low genetic variability of northern Europeans today (Reich et al., 2001). There then seems to have been rapid growth (perhaps reflected in the spread of the Gravettian culture) with the front of the demographic expansion spreading eastward into the Central Russian Plain and ultimately reaching Siberia and Beringia by the end of the last interglacial approximately 25,000 BP (Goebel, 1999; Pitulko et al., 2004; Soffer, 1985, p. 238; Soffer et al., 1993).

Thus, when the last ice age began, a single human population occupied a corridor stretching from Europe to Beringia. This inference is supported by several lines of evidence. A Y chromosome study has found that all North Eurasian peoples descend from a common ancestral population dated to about 15,000 BP (Stepanov & Puzyrev, 2000; see also Armour et al., 1996; Santos et al., 1999; Zerjal et al., 1997). The language families of northern Eurasia, particularly Uralic and Yukaghir and more generally Uralic-Yukaghir, Eskimo-Aleut, Chukotko-Kamchatkan, and Altaic, share deep structural affinities that point to a common

origin and not simply to word borrowing (Cavalli-Sforza et al., 1994, pp. 97–99; Fortescue, 1998; Rogers, 1986). Archeological evidence (characteristic lithic technology, grave goods with red ocher, and sites with small shallow basins) also suggests a common cultural tradition throughout Europe and Siberia 20,000 to 15,000 years ago (Goebel, 1999; Haynes, 1980, 1982). Finally, dental and cranial remains from Mal'ta (23,000–20,000 BP) in southern Siberia indicate strong affinities with Upper Paleolithic Europeans (Alexeyev & Gokhman, 1994; Goebel, 1999).

This Eurasian population would have broken up at the glacial maximum (20,000–15,000 BP). East–west gene flow was severely constricted by the merging of the Feno-Scandian and Ural icecaps and by the formation of large glacial lakes along the Ob (Rogers, 1986; Crawford et al., 1997). At the same time, both sides of this ice-age barrier saw sharp declines in human population (Goebel, 1999; Hahn, 1987). After the glacial maximum, cultural and biological unity continued to disintegrate as part of a trend toward higher population densities, regional diversification, and probably more restricted breeding units (Formicola & Giannecchini, 1999).

As gene flow declined between the two ends of the Eurasian tundra belt, selection pressures would have become more localized. Sexual selection, in particular, would have varied in intensity with regional OSR differences. This may explain why hair- and eye-color diversity arose in Europe but not in Asia—where hair is uniformly black and eyes uniformly brown. The eastern end of the Eurasian tundra belt differed from the western end in two OSR-relevant ways. First, its narrower width constrained herbivore mobility, thus shortening hunting distances and reducing hunting deaths among young men. Male mortality would have further decreased after the glacial maximum: An absence of base camps in the archeological record suggests that residential units were dispersing to exploit a variety of resources with shorter hunting distances (Goebel, 1999, p. 223). Second, the eastern Eurasian tundra had higher latitudes, lower carrying capacity, and a more dispersed human population, thus providing the same environmental conditions that in more recent times have led to female infanticide in the extreme Arctic. These two factors, shorter hunting distances and increased female infanticide, would have resulted in a more balanced OSR and, consequently, less sexual selection to diversify hair and eye color.

Such diversification would have begun in western Eurasia no earlier than 20,000 BP, given the uniform black hair and brown eyes of populations east of the ice-age barrier in eastern Eurasia. If the beginning of human history marks the latest end date, we are left with a maximum timeframe of 14,000 years. This is fast evolutionary change for human pigmentation, which elsewhere has responded more slowly to selection by the natural environment. A full range of environments, from the Arctic to the Tropics, has not caused the Amerindians to differentiate in hair, eye, or skin color, despite their being in the Americas for approximately 15,000 years.

## **5. Diversification of European hair color**

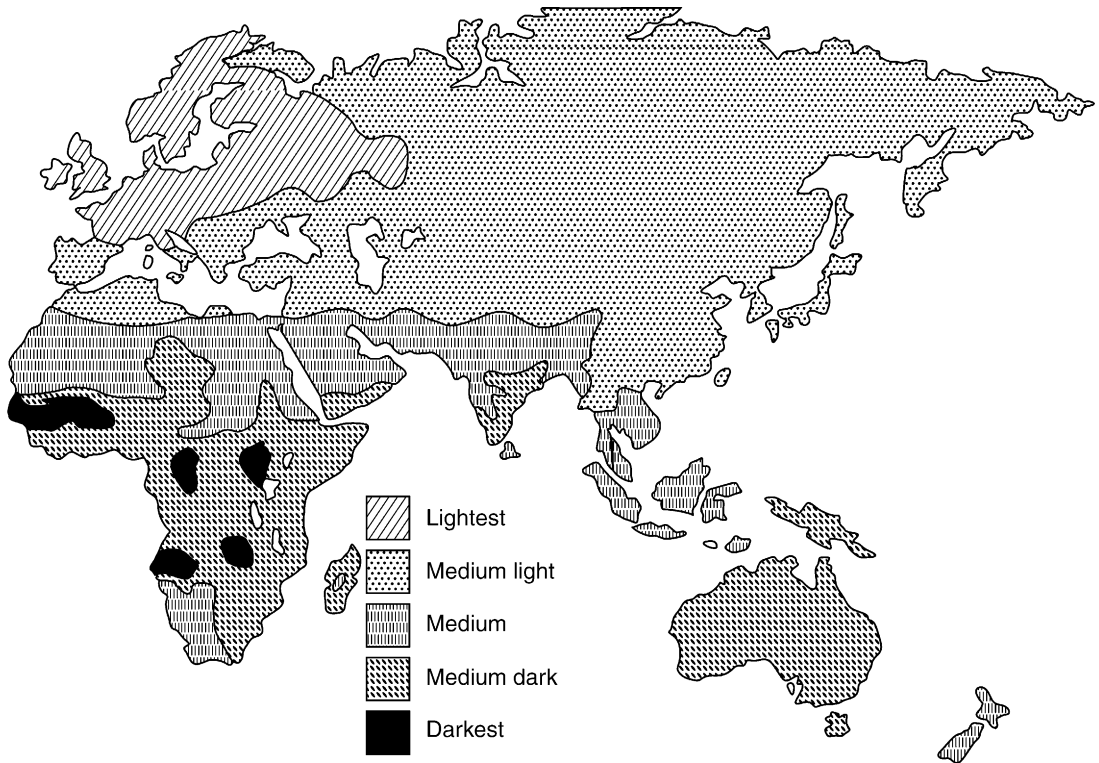
The MC1R gene determines hair color by controlling the production of eumelanin (brown and black pigments) and pheomelanin (red and yellow pigments). It is unusually polymorphic in humans, both in its high number of alleles and in its high ratio of nonsynonymous (phenotypically distinct) to synonymous (phenotypically identical) alleles (Box et al., 1997;

Flanagan et al., 2000; Harding et al., 2000; Rana et al., 1999; Rees, 2000). Whereas most genes have more synonymous alleles than nonsynonymous ones, the reverse is true for human MC1R (Rana et al., 1999).

Nonsynonymous MC1R alleles are distributed differently in European and non-European populations: 11 in Europeans, 5 in Asians, and 1 in Africans (Harding et al., 2000, p. 1355). Furthermore, the Asian alleles differ little in their phenotypic effects. Harding et al. (2000) attribute the high MC1R diversity of Europeans to relaxed selection for dark skin outside the tropical zone. This would account for the redhead alleles, which are linked to skin depigmentation, but not for the other alleles. Relaxed selection also fails to explain the low MC1R diversity of non-tropical Asians. Nonetheless, Harding et al. (2000) advance three arguments for relaxed selection, rather than positive selection, to explain the high MC1R diversity of Europeans. The first argument is that relaxed selection has produced a comparable level of diversity at the  $\beta$ -globin locus. Yet  $\beta$ -globin variants clearly have selective value, as indicated by heterozygote advantage and the short time span (less than 5000 years) over which the  $\beta$ -globin polymorphism has evolved (Cavalli-Sforza et al., 1994, pp. 149–152). The second argument is that the ratio of nonsynonymous to synonymous alleles is only 10 to 3 in Eurasia and thus comparable to the ratio of 10 nonsynonymous to 6 synonymous MC1R substitutions that separate humans from chimpanzees. The data in table 1 of their article, however, indicate a ratio of 12 to 3 (2 redhead alleles are excluded because they came from a study that specifically looked for them). In any case, the 10 to 6 ratio separating humans from chimpanzees is hardly a benchmark for neutral selection: Ratios greater than 1 are normally deemed to be evidence of positive selection, and such selection has acted on MC1R in some primate lineages (Mundy & Kelly, 2003). Finally, the third argument against positive selection is that MC1R diversity does not depart significantly from the Hardy-Weinberg equilibrium, there being neither excess homozygotes nor excess heterozygotes. No such departure, however, would be expected, inasmuch as MC1R heterozygotes exhibit partial effects (Flanagan et al., 2000; Rees, 2000).

## 6. Discussion

One might object that sexual selection could not have diversified European hair and eye color because there is no sexual dimorphism in these traits. Had women been selected for a diversity of hair and eye colors, they would now be more diverse in this respect than men are. It should be noted, however, that both hair and eye colors are, at best, weakly sex-linked; hence, selection acting on women should have affected men and women equally until sex-linked alleles had arisen through chance mutations. The original alleles (i.e., the non-sex-linked ones) could then have been selected out, but only if men were somehow disadvantaged by the novel hair and eye colors. For most animals, the disadvantage is an increased risk of predation, which will reduce highly visible colors in the sex that does not need them. For early Europeans, such a disadvantage would have been slight. Even wolves were more likely to be prey than predators (Hoffecker, 2002, pp. 180–183, 225, 241–242).



DISTRIBUTION OF SKIN COLOR IN AFRICA AND EURASIA

Fig. 4. Skin-color depigmentation in Eurasia approximately 500 BP (after [Brace, 1973](#), p. 344, reprinted with permission from Wiley).

This being said, some hair and eye colors seem to be sex linked. Blond hair darkens with age more slowly in women than in men ([Olivier, 1960](#), p. 74). Furthermore, prenatal exposure to estrogen, as indicated by digit ratio, appears to be higher in individuals with blond hair or non-brown eyes ([Mather et al., unpublished](#)). If a sex difference does indeed exist in these novel hair and eye colors, it seems to be expressed only right after puberty. It was notably absent in the 18-to-38 year olds studied by [Mather et al. \(unpublished\)](#).

Besides diversifying European hair and eye color, sexual selection may have accentuated existing sexual dimorphisms. Several studies have found wider hips, narrower waists, and thicker deposition of subcutaneous fat in women of European descent than in women of other origins ([Hrdlička, 1898](#); [Meredith & Spurgeon, 1980](#); [Nelson & Nelson, 1986](#)). Even before birth, Euro-American fetuses show significantly more sexual dimorphism than do African-American fetuses ([Choi & Trotter, 1970](#)). The proximal cause may be lower androgen production than in women of sub-Saharan African descent ([Falkner et al., 1999](#)) and higher estrogen production and lower fecal excretion of estrogen than in women of north/east Asian descent ([Adlercreutz et al., 1994](#); [Coker et al., 1997](#); [Key et al., 1990](#); [Taioli et al., 1996](#); [Wang et al., 1991](#)). Prenatal exposure to estrogen, as indicated by digit ratio, may also be higher in European women, albeit with much interpopulation variation ([Manning et al., 2000](#);

Manning, J. T. (2003). Personal communication). This variation may reflect a maternal-age effect: digit ratio is higher in Catholic countries like Poland and Spain, where mothers generally bear children in their 20s, than in Germany and Finland, where more mothers bear children in their 30s (Manning et al., 2000).

Sexual selection may have also lightened European skin color. The extreme depigmentation of northern and eastern Europeans deviates markedly from the much weaker north–south gradient in skin color of other human populations (the latter gradient may reflect selection pressures to maintain a critical level of vitamin D synthesis). Yet the geographic extent of this extreme depigmentation does not coincide with a specific pattern of solar radiation: Skies are generally overcast over coastal northwestern Europe and become clearer and typically continental further east. It does coincide, however, with the area where hair and eye color has diversified (Fig. 4). Aside from red hair, the color of the hair and eyes is not genetically linked to skin color (Flanagan et al., 2000; Sturm et al., 2001). It seems, therefore, that a common selective force has acted simultaneously on skin, hair, and eye color within this geographic area while being absent at similar latitudes in northern Asia and North America (Frost, 1994a; Manning et al., 2004).

If this common selective force were sexual selection, it could have lightened European skin color by acting on an existing sexual dimorphism. Men and women differ in complexion because of differing amounts of melanin and cutaneous blood flow; in short, women are fairer, men browner and ruddier (Edwards & Duntley, 1939; Frost, 1988; Frost, 2005; Hulse, 1967; Jablonski & Chaplin, 2000). The size of this sex difference is still debated, largely because most studies are poorly controlled for age (girls lighten only after puberty and immediately before are actually darker than boys). Investigators also try to exclude tanning by measuring under the arm, where there is less subcutaneous fat and probably less dimorphism in skin color, given that the lightness of a woman's skin correlates with the thickness of her subcutaneous fat (Mazess, 1967). In any event, sexual selection may have targeted this sex difference, as suggested by a cross-cultural male preference for lighter complexioned women and, conversely, by some evidence of a female preference for darker complexioned men (Aoki, 2002; Feinman & Gill, 1978; Frost, 1988; Frost, 1994b; Frost, 2005; Van den Berghe & Frost, 1986).

Among ancestral Europeans, such selection, even if acting only on women, would have lightened the complexions of both sexes because most skin-color genes are not sex linked. Nonetheless, some of these genes are; thus, there should have been some selective pressure to make European skin color more sexually dimorphic. Yet skin color actually seems to be less sexually dimorphic in light-skinned populations (Relethford et al., 1985). The reason may be a ceiling effect. As ancestral Europeans approached the phenotypic limit of maximum skin depigmentation, further lightening would have become harder to achieve for women than for men, with the result that sexual selection, although acting primarily on women, lightened men more.

In conclusion, sexual selection may have acted on all three color traits in northern and eastern Europe, with hair and eye color being diversified and skin color lightened. This hypothesis is consistent with the narrow timeframe for the evolution of these traits, their geographic distribution, and the large number of alleles involved.

## Acknowledgments

I wish to thank Dr. John Thomas Manning, who independently came to similar conclusions as I did, despite his approaching the question from a different academic perspective and drawing on a different body of evidence. This ‘repeatability of conclusions’ is further support for the arguments presented here.

## References

- Adlercreutz, H., Gorbach, S. L., Goldin, B. R., Woods, M. N., Dwyer, J. T., & Hämäläinen, E. (1994). Estrogen metabolism and excretion in Oriental and Caucasian Women. *Journal of the National Cancer Institute*, *86*, 1076–1082.
- Alexeyev, V. P., & Gokhman, I. I. (1994). Skeletal remains of infants from a burial on the Mal'ta Upper Paleolithic site. *Homo*, *45*, 119–126.
- Anderson, W. W. (1969). Polymorphism resulting from the mating advantage of rare male genotypes. *Proceedings of the National Academy of Sciences of the United States of America*, *64*, 190–197.
- Aoki, K. (2002). Sexual selection as a cause of human skin colour variation: Darwin's hypothesis revisited. *Annals of Human Biology*, *29*, 589–608.
- Armour, J. A. L., Anttinen, T., May, C. A., Vega, E. E., Sajantila, A., Kidd, J. R., Kidd, K. K., Bertranpetit, J., Paabo, S., & Jeffreys, A. J. (1996). Minisatellite diversity supports a recent African origin for modern humans. *Nature Genetics*, *13*, 154–160.
- Balikci, A. (1967). Female infanticide on the Arctic coast. *Man*, *2*, 615–625.
- Beals, R. L., & Hoijer, H. (1965). *An introduction to anthropology* (3rd ed.). New York: Macmillan.
- Binford, S. R. (1968). A structural comparison of disposal of the dead in the Mousterian and the Upper Paleolithic. *Southwestern Journal of Anthropology*, *24*, 139–151.
- Birket-Smith, K. (1929). The Caribou Eskimos. Material and social life and their cultural position. In K. Rasmussen (Ed.), *Report of the 5th Thule expedition* (vol. 5, pp. 1921–1924). Copenhagen: Nordisk Forlag.
- Blades, B. S. (1999a). Aurignacian settlement patterns in the Vézère valley. *Current Anthropology*, *40*, 712–719.
- Blades, B. S. (1999b). Aurignacian lithic economy and early modern human mobility: New perspectives from classic sites in the Vézère valley of France. *Journal of Human Evolution*, *37*, 91–120.
- Box, N. F., Wyeth, J. R., O'Gorman, L. E., Martin, N. G., & Sturm, R. A. (1997). Characterization of melanocyte stimulating hormone receptor variant alleles in twins with red hair. *Human Molecular Genetics*, *6*, 1891–1897.
- Brace, C. L. (1973). A nonracial approach towards the understanding of human diversity. In C. L. Brace, & J. Metress (Eds.), *Man in evolutionary perspective* (pp. 341–363). New York: Wiley.
- Brooks, R. (2002). Variation in female mate choice within guppy populations: Population divergence, multiple ornaments and the maintenance of polymorphism. *Genetica*, *116*, 343–358.
- Butzer, K. W. (1964). *Environment and archaeology*. Chicago: Aldine.
- Caramelli, D., Laluez-Fox, C., Vernesi, C., Lari, M., Casoli, A., Mallegni, F., Chiarelli, B., Dupanloup, I., Bertranpetit, J., Barbujani, G., & Bertorelle, G. (2003). Evidence for a genetic discontinuity between Neanderthals and 24,000-year-old anatomically modern Europeans. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 6593–6597.
- Cavalli-Sforza, L. L., Menozzi, P., & Piazza, A. (1994). *The history and geography of human genes*. Princeton: Princeton University Press.
- Choi, S. C., & Trotter, M. A. (1970). Statistical study of the multivariate structure and race–sex differences of American White and Negro fetal skeletons. *American Journal of Physical Anthropology*, *33*, 307–312.
- Coker, A. L., Crane, M. M., Sticca, R. P., & Sepkovic, D. W. (1997). Re: Ethnic differences in estrogen metabolism in healthy women. *Journal of the National Cancer Institute*, *89*, 89–90.

- Crawford, M. H., Williams, J. T., & Duggirala, R. (1997). Genetic structure of the indigenous populations of Siberia. *American Journal of Physical Anthropology*, *104*, 177–192.
- Dahlberg, A. A., & Carbonell, V. M. (1961). The dentition of the Magdalenian female from Cap Blanc, France. *Man*, *61*, 49–50.
- Dickson, D. B. (1990). *The dawn of belief. Religion in the upper Paleolithic of Southwestern Europe*. Tucson: University of Arizona Press.
- Dupanloup, I., Pereira, L., Bertorelle, G., Calafell, F., Prata, M. J., Amorim, A., & Barbujani, G. (2003). A recent shift from polygyny to monogamy in humans is suggested by the analysis of worldwide Y-chromosome diversity. *Journal of Molecular Evolution*, *57*, 85–97.
- Edwards, E. A., & Duntley, S. Q. (1939). The pigments and color of living human skin. *American Journal of Anatomy*, *65*, 1–33.
- Eiberg, H., & Mohr, J. (1987). Major genes of eye color and hair color linked to LU and SE. *Clinical Genetics*, *31*, 186–191.
- Ellis, H. (1928). Studies in the psychology of sex. *Sexual selection in man* (vol. IV). Philadelphia: F.A. Davis Company.
- Endler, J. A. (1980). Natural selection on color patterns in *Poecilia reticulata*. *Evolution*, *34*, 76–91.
- Endler, J. A. (1991). Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. *Vision Research*, *31*, 587–608.
- Falkner, B., Sherif, K., Sumner, A., & Kushner, H. (1999). Hyperinsulinism and sex hormones in young adult African Americans. *Metabolism, Clinical and Experimental*, *48*, 107–112.
- Farr, J. A. (1980). Social behavior patterns as determinants of reproductive success in the guppy *Poecilia reticulata* Peters (Pisces: Poeciliidae). *Behaviour*, *74*, 38–91.
- Feinman, S., & Gill, G. W. (1978). Sex differences in physical attractiveness preferences. *Journal of Social Psychology*, *105*, 43–52.
- Flanagan, N., Healy, E., Ray, A., Philips, S., Todd, C., Jackson, I. J., Birch-Machin, M. A., & Rees, J. L. (2000). Pleiotropic effects of the melanocortin 1 receptor (MC1R) gene on human pigmentation. *Human Molecular Genetics*, *9*, 2531–2537.
- Formicola, V., & Gianecchini, M. (1999). Evolutionary trends of stature in upper Paleolithic and Mesolithic Europe. *Journal of Human Evolution*, *36*, 319–333.
- Fortescue, M. D. (1998). *Language relations across Bering strait. Reappraising the archaeological and linguistic evidence*. London: Cassell.
- Frost, P. (1988). Human skin color: A possible relationship between its sexual dimorphism and its social perception. *Perspectives in Biology and Medicine*, *32*, 38–58.
- Frost, P. (1994a). Geographic distribution of human skin colour: A selective compromise between natural selection and sexual selection? *Human Evolution*, *9*, 141–153.
- Frost, P. (1994b). Preference for darker faces in photographs at different phases of the menstrual cycle: Preliminary assessment of evidence for a hormonal relationship. *Perceptual and Motor Skills*, *79*, 507–514.
- Frost, P. (2005). *Fair women, dark men. The forgotten roots of color prejudice*. Christchurch, New Zealand: Cybereditions.
- Goebel, T. (1999). Pleistocene human colonization of Siberia and peopling of the Americas: An ecological approach. *Evolutionary Anthropology*, *8*, 208–227.
- Grant, B., Snyder, A., & Glessner, S. F. (1974). Frequency-dependent mate selection in *Mormoniella vitripennis*. *Evolution*, *28*, 259–264.
- Hahn, J. (1987). Aurignacian and Gravettian settlement patterns in Central Europe. In O. Soffer (Ed.), *The Pleistocene old world* (pp. 251–261). New York: Plenum.
- Hamilton, W. D., & Zuk, M. (1982). Heritable true fitness and bright birds: A role for parasites? *Science*, *218*, 384–386.
- Harding, R. M., Healy, E., Ray, A. J., Ellis, N. S., Flanagan, N., Todd, C., Dixon, C., Sajantila, A., Jackson, I. J., Birch-Machin, M. A., & Rees, J. L. (2000). Evidence for variable selective pressures at MC1R. *American Journal of Human Genetics*, *66*, 1351–1361.



- Harrold, F. B. (1980). A comparative analysis of Eurasian Paleolithic burials. *World Archaeology*, *12*, 195–211.
- Haynes, C. V. (1980). The Clovis culture. *Canadian Journal of Anthropology*, *1*, 115–121.
- Haynes, C. V. (1982). Were Clovis progenitors in Beringia? In D. M. Hopkins (Ed.), *Paleoecology of Beringia* (pp. 383–398). New York: Academic Press.
- Hodge, F. W. ([1905]1959). *Handbook of American Indians north of Mexico*. Part 1. New York: Pageant.
- Hoffecker, J. F. (2002). *Desolate landscapes. Ice-age settlement in Eastern Europe*. New Brunswick: Rutgers University Press.
- Howell, N. (1979). *Demography of the Dobe !Kung*. New York: Academic Press.
- Hrdlička, A. (1898). Physical differences between white and colored children. *American Anthropologist*, *11*, 347–350.
- Hughes, K. A., Du, L., Rodd, F. H., & Reznick, D. N. (1999). Familiarity leads to female mate preference for novel males in the guppy, *Poecilia reticulata*. *Animal Behaviour*, *58*, 907–916.
- Hulse, F. S. (1967). Selection for skin color among the Japanese. *American Journal of Physical Anthropology*, *27*, 143–156.
- Jablonski, N. G., & Chaplin, G. (2000). The evolution of human skin coloration. *Journal of Human Evolution*, *39*, 57–106.
- Kelly, R. L. (1955). *The foraging spectrum. Diversity in hunter-gatherer lifeways*. Washington: Smithsonian Institution Press.
- Key, T. J. A., Chen, J., Wang, D. Y., Pike, M. C., & Boreham, J. (1990). Sex hormones in women in rural China and in Britain. *British Journal of Cancer*, *62*, 631–636.
- Kirkpatrick, M. (1987). Sexual selection by female choice in polygynous animals. *Annual Review of Ecology and Systematics*, *18*, 43–70.
- Kjellström, R. (1973). *Eskimo marriage. An account of traditional Eskimo courtship and marriage*. Lund: Nordiska Museets Handlingar 80.
- Kozłowski, S. K., & Sachse-Kozłowska, E. (1995). Magdalenian family from the Maszycka Cave. *Jahrbuch der Römisch Germanischen Zentral Museums Mainz*, *40*, 115–205.
- Krings, M., Geisert, H., Schmitz, R. W., Krainitzki, H., & Pääbo, S. (1999). DNA sequence of the mitochondrial hypervariable region II from the Neanderthal type specimen. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 5581–5585.
- Krupnik, I. I. (1985). The male–female ratio in certain traditional populations of the Siberian Arctic. *Inuit Studies*, *9*, 115–140.
- Lank, D. B. (2002). Diverse processes maintain plumage polymorphisms in birds. *Journal of Avian Biology*, *33*, 327–330.
- Lummaa, V., Merila, J., & Kause, A. (1998). Adaptive sex ratio variation in pre-industrial human (*Homo sapiens*) populations? *Proceedings of the Royal Society of London. Series B*, *265*, 563–568.
- Mallegni, F., & Fabbri, P. F. (1995). The human skeletal remains from the Upper Paleolithic burials found in Romito Cave (Papasidero, Cosenza, Italy). *Bulletin et Mémoires de la Société d'Anthropologie de Paris, n.s.*, *7*, 99–137.
- Manning, A. (1979). *An introduction to animal behaviour*. London: Edward Arnold.
- Manning, J. T., Barley, L., Lewis-Jones, I., Walton, J., Trivers, R. L., Thornhill, R., Singh, D., Rhode, P., Bereckzei, T., Henzi, P., Soler, M., & Sved, A. (2000). The 2nd to 4th digit ratio, sexual dimorphism, population differences and reproductive success: Evidence for sexually antagonistic genes. *Evolution and Human Behavior*, *21*, 163–183.
- Manning, J. T., Bundred, P. E., & Mather, F. M. (2004). Second to fourth digit ratio, sexual selection, and skin colour. *Evolution and Human Behavior*, *25*, 38–50.
- Martin, M. K. (1974). *The foraging adaptation—Uniformity or diversity?* Addison-Wesley Module in anthropology 56. Reading, Mass: Addison-Wesley.
- Mason, S. L. R., Hather, J. G., & Hillman, G. C. (1994). Preliminary investigation of the plant macro-remains from Dolní Věstonice II, and its implications for the role of plant foods in Palaeolithic and Mesolithic Europe. *Antiquity*, *68*, 48–57.

- Mather, F., Manning, J. T., Bundred, P. E. (unpublished). 2nd to 4th digit ratio, hair and eye colour in Caucasians: Evidence for blond hair as a correlate of high prenatal oestrogen.
- Mazess, R. B. (1967). Skin color in Bahamian Negroes. *Human Biology*, 39, 145–154.
- Mellars, P. A. (1985). The ecological basis of social complexity in the Upper Paleolithic of Southwestern France. In T. D. Price, & J. A. Brown (Eds.), *Prehistoric hunter-gatherers. The emergence of cultural complexity* (pp. 271–297). Orlando: Academic Press.
- Meredith, H. V., & Spurgeon, J. H. (1980). Somatic comparisons at age 9 years for South Carolina White Girls and girls of other ethnic groups. *Human Biology*, 52, 401–411.
- Muggleton, J. (1979). Non-random mating in wild populations of polymorphic *Adalia Bipunctata*. *Heredity*, 42, 57–65.
- Mundy, N. I., & Kelly, J. (2003). Evolution of a pigmentation gene, the melanocortin-1 receptor, in primates. *American Journal of Physical Anthropology*, 121, 67–80.
- Nelson, J. K., & Nelson, K. R. (1986). Skinfold profiles of Black and White boys and girls ages 11–13. *Human Biology*, 58, 379–390.
- Nordenskiöld, A. E. (1882). *The voyage of the Vega round Asia and Europe, with a historical review of previous journeys along the north coast of the old world*. New York: Macmillan & Co.
- Olivier, G. (1960). *Pratique anthropologique*. Paris: Vigot Frères.
- Ovchinnikov, I. V., Götherström, A., Romanova, G. P., Kharitonov, V. M., Lidén, K., & Goodwin, W. (2000). Molecular analysis of Neanderthal DNA from the Northern Caucasus. *Nature*, 404, 490–493.
- Pitulko, V. V., Nikolsky, P. A., Girya, E. Y., Basilyan, A. E., Tumskey, V. E., Koulakov, S. A., Astakhov, S. N., Pavlova, E. Y., & Anisimov, M. A. (2004). The Yana RHS site: Humans in the Arctic before the last glacial maximum. *Science*, 303, 52–56.
- Rana, B. K., Hewett-Emmett, D., Jin, L., Chang, B. H. -J., Sambuughin, N., Lin, M., Watkins, S., Bamshad, M., Jorde, L. B., Ramsay, M., Jenkins, T., & Li, W. -H. (1999). High polymorphism at the human melanocortin 1 receptor locus. *Genetics*, 151, 1547–1557.
- Riches, D. (1974). The Netsilik Eskimo: A special case of selective female infanticide. *Ethnology*, 13, 351–361.
- Rees, J. L. (2000). The melanocortin 1 receptor (MC1R): More than just red hair. *Pigment Cell Research*, 13, 135–140.
- Relethford, J. H., Lees, F. C., & Byard, P. J. (1985). Sex and age variation in the skin color of Irish children. *Current Anthropology*, 26, 396–397.
- Reich, D. E., Cargill, M., Bolk, S., Ireland, J., Sabeti, P. C., Richter, D. J., Lavery, T., Kouyoumjian, R., Farhadian, S. F., Ward, R., & Lander, E. S. (2001). Linkage disequilibrium in the human genome. *Nature*, 411, 199–204.
- Richards, M. P., Hedges, R. E. M., Jacobi, R., Current, A., & Stringer, C. (2000). Gough's cave and sun hole cave human stable isotope values indicate a high animal protein diet in the British Upper Paleolithic. *Journal of Archaeological Science*, 27, 1–3.
- Richards, M. P., Pettitt, P. B., Stiner, M. C., & Trinkaus, E. (2001). Stable isotope evidence for increasing dietary breadth in the European Mid-Upper Paleolithic. *Proceedings of the National Academy of Sciences of the United States of America*, 98, 6528–6532.
- Riedl, B. I. M. (1990). Morphological and metrical characteristics of the male and female Leitmotif in mate-selection and its impact on the selection of the spouse. *Homo*, 41, 72–85.
- Rogers, R. A. (1986). Language, human subspeciation, and ice age barriers in Northern Siberia. *Canadian Journal of Anthropology*, 5, 11–22.
- Santos, F. R., Pandya, A., Tyler-Smith, C., Pena, S. D. J., Schanfield, M., Leonard, W. R., Osipova, L., Crawford, M. H., & Mitchell, R. J. (1999). The Central Siberian origin for Native American Y chromosomes. *American Journal of Human Genetics*, 64, 619–628.
- Scheffel, D. (1984). From polygyny to cousin marriage? Acculturation and marriage in 19th century Labrador Inuit society. *Inuit Studies*, 8, 61–75.
- Scheffer, J. (1704). *The history of Lapland: Containing a geographical description, and a natural history of that country; with an account of the inhabitants, their original, religion, customs, habits, marriages, conjurations, employments, etc.* London: Tho. Newborough & R. Parker.

- Schrire, C., & Steiger, W. L. (1974). A matter of life and death: An investigation into the practice of female infanticide in the Arctic. *Man*, 9, 161–184.
- Schweder, B. I. M. (1994). The impact of the face on long-term human relationships. *Homo*, 45, 74–93.
- Scozzari, R., Cruciani, F., Malaspina, P., Santolamazza, P., Ciminelli, B. M., Torroni, A., Modiano, D., Wallace, D. C., Kidd, K. K., Olckers, A., Moral, P., Terrenato, L., Akar, N., Qamar, R., Mansoor, A., Mehdi, S. Q., Meloni, G., Vona, G., Cole, D. E. C., Cai, W. W., & Novelletto, A. (1997). Differential structuring of human populations for homologous X and Y microsatellite loci. *American Journal of Human Genetics*, 61, 719–733.
- Secombe, W. (1992). *A millennium of family change*. London: Verso.
- Sherman, C. P. (1922). *Roman law in the modern world*. New Haven: New Haven Law Book Co.
- Short, G. B. (1975). Iris pigmentation and photopic visual acuity: A preliminary study. *American Journal of Physical Anthropology*, 43, 425–434.
- Simchuk, A. P. (2001). Frequency-dependent sexual selection in a natural population of oak leafroller moth (*Tortrix viridana* L.). *Tsitologiya i Genetika*, 35, 25–29.
- Sinnock, P. (1970). Frequency dependence and mating behavior in *Tribolium castaneum*. *American Naturalist*, 104, 469–476.
- Smith, E. A., & Smith, S. A. (1994). Inuit sex-ratio variation. *Current Anthropology*, 35, 595–624.
- Soffer, O. (1985). Patterns of intensification as seen from the Upper Paleolithic of the Central Russian Plain. In T. D. Price, & J. A. Brown (Eds.), *Prehistoric hunter-gatherers. The emergence of cultural complexity* (pp. 235–269). Orlando: Academic Press.
- Soffer, O., Vandiver, P., Klima, B., & Svoboda, J. (1993). The pyrotechnology of performance art: Moravian venuses and wolverines. In H. Knecht, A. Pike-Tay, & R. White (Eds.), *Before Lascaux. The complex record of the early upper Paleolithic* (pp. 259–275). Boca Raton: CRC Press.
- Stepanov, V. A., & Puzyrev, V. P. (2000). Evolution of Y-chromosome haplotypes in populations of North Eurasia. *American Journal of Human Genetics*, 67, 220.
- Sturm, R. A., Teasdale, R. D., & Box, N. F. (2001). Human pigmentation genes: Identification, structure and consequences of polymorphic variation. *Gene*, 277, 49–62.
- Tacitus, C. (1970). *Germania* Transl. by M. Hutton. Loeb Classical Library. Cambridge: Harvard University Press.
- Taioli, E., Garte, S. J., Trachman, J., Garbers, S., Sepkovic, D. W., Osborne, M. P., Mehl, S., & Bradlow, H. L. (1996). Ethnic differences in estrogen metabolism in healthy women. *Journal of the National Cancer Institute*, 88, 617.
- Templeton, A. R. (2002). Out of Africa again and again. *Nature*, 416, 45–51.
- Thelen, T. H. (1983). Minority type human mate preference. *Social Biology*, 30, 162–180.
- Torroni, A., Semino, O., Scozzari, R., Sirugo, G., Spedini, G., Abbas, N., Fellous, M., et al. (1990). Y-chromosome DNA polymorphisms in human populations: Differences between Caucasoids and Africans detected by 49a and 49f probes. *Annals of Human Genetics*, 54, 287–296.
- Tyrrell, A. J., & Chamberlain, A. T. (1998). Non-metric trait evidence for modern human affinities and the distinctiveness of Neanderthals. *Journal of Human Evolution*, 34, 549–554.
- Vallois, H. V. (1961). The social life of early man: The evidence of skeletons. *Viking Fund Publications in Anthropology*, 31, 214–235.
- Van den Berghe, P. L., & Frost, P. (1986). Skin color preference, sexual dimorphism and sexual selection: A case of gene-culture co-evolution? *Ethnic and Racial Studies*, 9, 87–113.
- Vatin, C. (1970). *Recherches sur le mariage et la condition de la femme mariée à l'époque hellénistique*. Paris: Éditions E. de Boccard.
- Wang, D. Y., Key, T. J. A., Pike, M. C., Boreham, J., & Chen, J. (1991). Serum hormone levels in British and rural Chinese females. *Breast Cancer Research and Treatment*, 18, S41–S45.
- Weyer, E. M. (1932). *The Eskimos. Their environment and folkways*. New Haven, CT: Yale University Press.
- Zerjal, T., Dashnyam, B., Pandya, A., Kayser, M., Roewer, L., Santos, F. R., Scheifenhövel, W., Fretwell, N., Jobling, M. A., Harihara, S., Shimizu, K., Semjiddma, D., Sajantila, A., Salo, P., Crawford, M. H., Ginter, E. K., Evgrafov, O. V., & Tyler-Smith, C. (1997). Genetic relationships of Asians and Northern Europeans, revealed by Y-chromosomal DNA analysis. *American Journal of Human Genetics*, 60, 1174–1183.