



A naked ape would have fewer parasites

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Unusually among the mammals, humans lack an outer layer of protective fur or hair. We propose the hypothesis that humans evolved hairlessness to reduce parasite loads, especially ectoparasites that may carry disease. We suggest that hairlessness is maintained by these naturally selected benefits and by sexual selection operating on both sexes. Hairlessness is made possible in humans owing to their unique abilities to regulate their environment via fire, shelter and clothing. Clothes and shelters allow a more flexible response to the external environment than a permanent layer of fur and can be changed or cleaned if infested with parasites. Naked molerats, another hairless and non-aquatic mammal species, also inhabit environments in which ectoparasite transmission is expected to be high, but in which temperatures are closely regulated. Our hypothesis explains features of human hairlessnesssuch as the marked sex difference in body hair, and its retention in the pubic regions—that are not explained by other theories.

Keywords: human hairlessness; parasites; sexual selection; naked apes

1. INTRODUCTION

Humans are unique among the monkeys and apes in lacking a dense layer of hair covering their bodies. More generally, hairlessness is rare in the mammals. Of the *ca.* 5000 extant mammals, the only other effectively hairless species are elephants, rhinoceroses, hippopotamuses, walruses, pigs, whales and naked mole-rats, and at least four of these species are aquatic or semi-aquatic.

Hairlessness, then, demands some sort of explanation in evolutionary terms, and especially so as, in humans at least, hairlessness is not without its costs. Humans are more exposed to the sun, may suffer greater heat loss when the ambient temperature is low (Newman 1970; Amaral 1996) and, with the exception of the naked molerats, differ from the other hairless mammals in not having a thick or toughened hide for protection.

What, then, accounts for our relatively naked state? Before proceeding we must clarify our use of the term 'hairless' as applied to humans. Humans are not literally hairless, having about the density of hair follicles expected of an ape of our body size (Schwartz & Rosenblum 1981).

What distinguishes human body hair is that it is very fine and short, making it, effectively, invisible. We use 'hairless' with respect to humans, then, to mean that they lack a dense layer of thick fur.

2. THE BODY-COOLING HYPOTHESIS

The best-known hypothesis to explain human hairlessness is that it evolved to promote cooling of the body. In a series of papers beginning in 1984, Wheeler argued that the loss of body hair occurred when bipedal hominids moved to open savannah environments. According to Wheeler (1984), animals living on the hot savannah would suffer from excess exposure to the sun. Bipedality may have evolved in part to reduce exposure, meaning that upright hominids could forage for longer in the open sun than comparably sized quadrupeds (Wheeler 1991). Later, Wheeler (1992) suggested that the combination of an upright posture and lack of hair made it easier to radiate heat back into the environment or to lose heat by convective cooling from the wind. But these thermoregulatory advantages of nakedness are limited. Wheeler (1992) acknowledges that naked skin increases the rates of both energy gain and loss during periods of too much or too little heat, respectively. This might mean that naked skin is actually a worse solution when the entire day is taken into account: more heat must be dissipated from daytime exposure and, at night time, more heat is lost (Amaral 1996).

3. THE AQUATIC-APE HYPOTHESIS

Another idea is that between 6 and 8 Myr ago, the ancestors to the hominids had a 1 or 2 million year phase of aquatic or semi-aquatic existence (Morgan 1997). Morgan's view (1997) is that hairlessness and high levels of body fat evolved in these ancestors for the same reasons as in other aquatic mammals, viz., that fur is not an effective thermal layer under water. This theory then supposes that the aquatic adaptations were retained as ancestral characters throughout at least 5 million years of subsequent hominid evolution in predominantly terrestrial habitats.

Although human fossil remains are often found near bodies of water (Foley 1987), evidence for an aquatic phase of proto-hominid existence as yet eludes palaeontologists. Morgan's theory (1997) also fails to explain why features supposedly adaptive to an aquatic lifestyle should have been retained despite several millions of years of subsequent evolutionary change in other features of hominids. In a similar vein, the body-cooling hypothesis does not directly explain why hairlessness has been retained despite human populations having occupied colder regions of the Earth for perhaps 100 000 years, and possibly for up to 800 000 years for their Homo erectus and later Homo forbearers (Arsuaga 2002). The amount of body hair can change rapidly in evolutionary time as seen from comparing mammoths with extant savannah-dwelling and relatively hairless elephants, or domestic pigs and some dog breeds with their closely related and hairy wild cousins. Among modern humans there is variation in the degree of body hair, suggesting substantial genetic variance for this trait. Finally, neither the aquatic ape nor the body-cooling hypotheses has a ready explanation for the marked difference in body hair between males and females.

4. HAIRLESSNESS AS AN ADAPTATION TO REDUCE PARASITE LOADS

It is desirable to seek explanations for human hairlessness that link its origin and continued maintenance to advantages that arose and operated throughout hominid evolution, and differentially so between the sexes. We propose here the view that hominid cultural adaptations made it possible for hairlessness to evolve in humans as an adaptation to reduce parasite loads, especially ectoparasite loads. We suggest that hairlessness is maintained by its naturally selected advantages in reducing disease, and by sexually selected effects arising from mate choice for hairless partners. This mechanism could have worked either alone or in concert with other factors that might have favoured hairlessness.

Elements of our hypothesis have existed at least since the time of Darwin, although he was convinced that no naturally selected advantage could be adduced for the lack of body hair in humans. Instead, noting that 'in all parts of the world women are less hairy than men', Darwin argued 'we may reasonably suspect that this character has been gained through sexual selection' (Darwin 1888, p. 600). Darwin considered the idea—attributed to a Mr Belt (Naturalist in Nicaragua 1874, p. 209, cited in Darwin 1888)—that within the tropics human hairlessness provides a naturally selected advantage for freeing oneself of 'the multitude of ticks (acari) and other parasites' (Darwin 1888, p. 57). He even noted that 'as some confirmation of Mr Belt's view, I may quote the following passage from Sir W. Denison (Varieties of vice-regal life, vol. i, 1870, p. 440): "it is said to be a practice with the Australians, when the vermin get troublesome, to singe themselves" (Darwin leaves unspecified to which Australians Sir William refers). But he dismissed Belt's idea as unlikely because 'none of the many quadrupeds inhabiting the tropics have ... acquired any specialised means of relief'.

We suggest, based upon information and ideas not available to Darwin, that the ectoparasite hypothesis is, in concert with sexual selection, the most plausible explanation for hairlessness in humans. There would not have been any real understanding in the late nineteenth century of the important role that pathogens play in natural selection. Ectoparasites exact a large toll on the fitness of furry or feathered animals (Lehmann 1993). Fleas and ticks affect animals directly by biting and causing local irritation, and indirectly by carrying a variety of infectious including viral—diseases. Animals have specialized muscles for twitching their skin, long tails to swat at flies and many other anti-parasite morphological and behavioural adaptations (Hart 1997). The colourful feathers and displays of many bird species may be metabolically costly advertisements to prospective mates of their lack of parasites (Hamilton & Zuk 1982; Read 1987). Features of beak size and shape in some birds may be adaptations to removing parasites from feathers (Clayton 1991). Primates devote substantial amounts of time to grooming, increasingly so as group size increases, most of which is to remove ectoparasites (Dunbar 1991). When humans suffer ectoparasite infection it is largely confined to the head and pubic hair. This may be because it is easier to remove ectoparasites from hairless regions, or that ectoparasites are less attracted to hairless skin, or both.

What features of early hominid evolution make hairlessness a plausible response to the toll exacted by parasites? Humans most likely evolved in Africa (Ingman et al. 2000) where biting flies and other ectoparasites are found in abundance. Early humans probably lived in close quarters in hunter-gatherer social groups in which rates of ectoparasite transmission were high. Precisely when humans or their hominid ancestors evolved hairlessness must remain a matter of speculation. What we can say is that having fire and the intelligence to produce clothes and shelter, early humans (and possibly even earlier hominids-H. erectus may have had fire) were well equipped to evolve hairlessness as a means of reducing ectoparasite loads, while avoiding the costs of exposure to sun, cold and rain. Ectoparasites can and do infest clothing, but clothes, unlike fur, can be changed and cleaned. Infections that do occur on hairless skin can be more easily cleaned than when fur is present. We suggest, then, that a set of cultural adaptations unique to humans made hairlessness a flexible and advantageous naturally selected adaptation.

By contrast, we do not suggest that the ectoparasite hypothesis explains other mammalian hairlessness, with the possible exception of the naked mole-rat. Naked molerats inhabit arid regions of Kenya, Ethiopia and Somalia, where they live underground in large social colonies, rarely coming above ground (Sherman 2002). Ectoparasite transmission is expected to be high in these colonies, but their climate tends to be regulated within narrow bounds, making hairlessness feasible for a species that does not produce clothes or fire. Like humans, they are effectively hairless—having been described as resembling 'overcooked sausages with buck teeth' (Sherman 2002, p. 793)—and like humans they lack a thick and protective hide.

Sir Ronald Fisher, one of the founders of modern genetically based Darwinian thinking, emphasized that sexual selection typically relies upon a trait having a naturally selected advantage to begin the process of its exaggeration (Fisher 1930). The ectoparasite hypothesis provides this advantage: initial naturally selected evolution towards reduced amounts of body hair may then have been reinforced by Fisherian or other forms of sexual selection as hairlessness—by virtue of advertising reduced ectoparasite loads—became a desirable trait in a mate. Unusually among sexually selected traits, reduced body hair would be desirable in both sexes. Greater loss of body hair in females plausibly follows from the conventionally stronger sexual selection from male versus female mate choice in humans. Common use of depilatory agents testifies to the continuing attractions of hairlessness, especially in human females.

The retention of hair on the face, head, and pubic regions may also be linked to sexual selection. Head hair may have naturally selected advantages—such as reducing exposure to the sun—that permitted further elaboration by sexual selection. Darwin noted—and contemporary practises attest to—the important role of facial and head hair in attraction and mate choice. The retention of pubic hair poses a challenge for the ectoparasite hypothesis, as it provides a warm and humid environment favourable to ectoparasites—and indeed many specialize on these regions. An interesting possibility is that pubic areas may, owing to their warmth and humidity, be especially conducive

to pheromonal signalling between the sexes. In support of this idea, the density of sweat glands in pubic regions is high (Stoddart 1990).

Our hypothesis can be tested. We might expect less body hair among human groups whose evolutionary history has been in regions of the Earth with higher ectoparasite concentrations. Ectoparasite loads should, in general, be greater on the hairy parts of our bodies, as anecdotal evidence would already seem to suggest. We should find that apes suffer from higher ectoparasite loads despite having the ability to remove them with their hands. We might also expect that attacks by biting flies are not particularly well defended against by fur-the biting fly simply evolving adaptations to circumvent it.

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