

REVIEW

Evolution of nakedness in *Homo sapiens*

M. J. Rantala

Department of Biology, Section of Ecology, University of Turku, Turku, Finland

Keywords

ectoparasites; hairlessness; human; naked ape; nudity; parasites; sexual selection.

CorrespondenceMarkus J. Rantala, Department of Biology, Section of Ecology, University of Turku, FIN-20014, Turku, Finland.
Email: marrant@cc.jyu.fi

Received 23 November 2006; accepted 28 November 2006

doi:10.1111/j.1469-7998.2007.00295.x

Abstract

Homo sapiens L. is the only existing primate species lacking in functionally effective thermally insulating fur. As all other primates have considerable hair covering, it has always been accepted that our ancestors must once have had a respectable amount of body hair. Unfortunately, fossils cannot help us when it comes to differences in skin and hair. Recent DNA analysis, however, has given us some idea of when and where the great denudation took place. A number of hypotheses have been proposed to account for this feature, but none of these has gained general acceptance. In this paper, I present these hypotheses in the light of current empirical evidence and discussion.

Introduction

Humans have been described as the naked ape, and this nakedness undoubtedly constitutes one of the most striking differences in appearance between humans and other apes (Morris, 1967). Actually, humans are not hairless; in fact, they do not differ significantly in the number and density of hair follicles from their nearest primate relatives. Most of these hairs, however, are relatively miniscule, and certainly neither protect the skin nor provide appreciable thermal insulation (Kushlan, 1985). This 'naked skin' makes humans more vulnerable to UV radiation and to both high and low temperatures (Amaral, 1996). Furthermore, fur would protect humans from wounds, sores and insect bites, which may cause serious inflammations. A hairy individual also looks larger, which confers an advantage especially in sexual selection and in defence against predators. Thus, nakedness causes many clear costs for the naked ape. What caused one species of ape to become naked? This problem has puzzled experts for a long time, and many speculative theories have been put forward. In this paper, I discuss and evaluate these theories.

The cooling device hypothesis

Perhaps the most commonly held explanation for the evolution of the nakedness in humans is that it evolved as a cooling device (e.g. Morris, 1967; Leakey & Lewin, 1977; Mount, 1979; Ebling, 1985). It has commonly been thought that by abandoning the shady forest, the hunting ape exposed himself to much higher temperatures than those to which he had previously adapted. Thus, it has been assumed

that the hunting ape took off his hairy coat to avoid becoming overheated in the hot savannah (Morris, 1967).

Unfortunately, this hypothesis does not bear closer scrutiny. When we compare the thermal budgets of haired and naked hominids (Wheeler, 1992*b*), we can easily see that a naked skin is a disadvantage with regard to the circadian integral over both day time (it receives more solar energy, requiring dissipation) and night-time (it requires more endogenous heat production) (Amaral, 1996). Exposure of the naked skin to the air certainly increases the chances of heat loss, but at the same time it also increases heat gain and risks damage from the sun's rays. Thus, it increases perspiration, leading to dehydration; this in turn may be detrimental in a dry savannah environment. A haired hominid in an open hot environment should actually increase its insulation rather than decrease it. This is precisely the trend followed by savannah monkeys, which have a dense hair-coat and are better insulated than forest primates (Mahoney, 1980).

The hunting hypothesis

The hunting hypothesis (Brace, 1966; Campbell, 1966; Morris, 1967; Ardrey, 1976; Brace & Montagu, 1977) held the field for some time, and was believed to explain many things about human physiology. The problem with hairlessness was why one savannah primate needed to go naked while all other species in the same habitat retained their fur. This was explained on the grounds that vegetarian primates do not need to move very fast; a carnivorous primate, on the other hand, would get hot while chasing its prey, and losing its hair would enable it to cool down (Campbell, 1966).

Morris (1967) considered such hairlessness necessary because hunting chases were activities for which early man was otherwise physically poorly adapted.

This diurnal hunter hypothesis, however, is also based on an incorrect idea of hairlessness as a cooling factor. A further weakness in the theory is the sexual dimorphism in *Homo sapiens* with respect to body hair. It was the male who was the hunter and allegedly became overheated in the chase across the hot savannah, but it was the female who became the most hairless (Morgan, 1990).

The bipedality hypothesis

The bipedality hypothesis put forth by Wheeler (1984) argued that the reduction of body hair was made possible by the lower direct solar radiation fluxes incident upon a bipedal mammal, which also explains the absence of this characteristic among savannah quadrupeds. During the last two decades, Wheeler has published a series of papers on the thermoregulatory advantages of hominid bipedalism combined with a naked skin and a larger body size (Wheeler, 1985, 1990, 1991*a,b*, 1992*a,b*, 1993, 1994, 1996).

Although Wheeler's experiments and calculations demonstrate the thermoregulatory advantages of bipedalism over quadrupedalism and the advantages of increased body size in hot savannah environments, the results do not indicate that the initial step in the denudation process occurred in open hot environments, or that bipedality preceded body-hair reduction (Amaral, 1996). Furthermore, his estimates of the percentage of total body surface area exposed to direct solar radiation (Wheeler, 1992*b*) merely demonstrate the advantage of bipedalism in relation to quadrupedalism. Unfortunately, Wheeler has not tackled the crucial point: a haired biped might have an advantage with regard to thermal stress from direct solar radiation (Amaral, 1996).

The allometry hypothesis

The term allometry refers to the fact that as species become larger in the course of evolution, not all organs of their bodies increase in the same ratio as their overall body size and mass (Schwartz & Rosenblum, 1981). Allometric analysis shows that a primate that is twice the size of another primate does not have twice as many hairs to cover the increased surface of its body. In a small primate like the marmoset, the hairs grow very close together, but the larger the primate, the fewer hairs it has per unit of body surface (Schwartz & Rosenblum, 1981).

The allometric theory proposes that as the first hominids descended from apes and apes are larger than monkeys, the hominids would have had sparser hair and been less well protected against the direct heat of the sun than small savannah species like baboons and patas monkeys (Schwartz & Rosenblum, 1981). It has therefore been argued that hominids had to evolve an alternative system of keeping cool, that is, perspiration; this system ultimately became so effective that they were able to dispense with body hair almost entirely (Schwartz & Rosenblum, 1981).

Unfortunately, the allometric theory ignores the fact that a covering of hair is a multi-functional mammalian asset; it would not become redundant merely because one function (heat regulation) was being otherwise catered for (Morgan, 1990). Furthermore, a reduced density of hairs per square centimetre does not necessarily entail decreased coverage. For example gorillas, the largest of the great apes, are larger than humans and their hairs are farther apart, but they are certainly not more naked. The mountain gorilla *Gorilla gorilla beringei* has a particularly deep and luxurious fur coat. Thus, if a hominid had needed a better shield against the sun's rays on the hot savannah, its body hairs would have grown longer rather than shorter (Amaral, 1996).

The clothing hypothesis

It has been suggested that clothing made hairlessness inconsequential and that hair reduction provided no intrinsic advantage (Westermarck, 1894; Glass, 1966). Among living human populations, however, those that are most dependent upon clothing are also those that have retained the greatest amount of body hair, while those populations that wear little or no clothing are precisely the ones that retain a minimum of body hair (Brace, 1966). On the other hand, why would a hairy animal have begun to use clothes in the first place, if it already had an insulative coat of body hair? Recent DNA analysis by Rogers, Iltis & Wooding (2004), based on a number of silent mutations at the melanocortin I receptor locus that affects the colour of skin and hair, suggests that humans have been hairless savannah dwellers for at least 1.2 million years. The oldest sewn clothing found, on the other hand, is only about 20 000 years old (Klein, 1999), while the oldest hide-scrapings found are about 300 000 years old (Toth & Schick, 1993). Thus, all the evidence so far suggests that humans were naked long before they started to wear clothes.

The vestimentary hypothesis

The vestimentary hypothesis by Kushlan (1980, 1985) proposes that hair reduction in humans evolved concurrently with a developing intellectual capacity that permitted the use of artificial insulation. Functional hairlessness permitted the elaboration of whole-body evaporation, but with the sacrifice of the heat retention function of typical pelage. The latter need was met by clothing, which required a capacity for fabrication and for cultural transmission, and may have developed early in hominid evolution (Kushlan, 1985). However, this theory too is based on the mistaken idea of hairlessness as a cooling factor.

Neoteny hypothesis

Neoteny is the retention of juvenile physical characteristics in the adult individual; it is a subject studied in the field of developmental biology. It has been suggested that humans are a juvenilized form of ape (Gould, 1977). Humans are said to be characterized by a general retardation of pace of

development, so that they mature more slowly than other primates and live longer. This involves retaining some of the characteristics of the juvenile or even foetal ape into adult life. The examples most often cited when comparing humans with apes are the flatter face, the rapid pre-natal rate of brain growth persisting for some time after birth and the hairlessness characteristic of a foetal ape. The hypothesis suggests that a prolonged period of rapid brain growth was advantageous to the species, and that certain other characteristics were retained as part of the neotenic package. One of these was nakedness, described as 'the embryonic distribution of body hair' (Gould, 1977).

If the hairlessness of the foetal ape was being retained into adulthood by a process of neoteny, one would expect the human body to retain this characteristic throughout its whole development from embryo to adult. However, this is not the case. When the human foetus is 6 months old, it becomes completely covered with a coat of fine hair known as lanugo. Normally, this hair is shed long before birth; occasionally, a baby is born still wearing its woolly coat, only to lose it within the first days after birth (Morgan, 1982).

Another weakness of the theory is that while some characteristics may be retained as part of a neotenic package, this only applies to characteristics that are either benign or neutral in their effect on fitness to survive. No one claims that all foetal characteristics are retained in a neotenic species. For example, a human foetus and a human baby both have very short bandy legs, but natural selection ensures that this feature is not retained in adult life (Morgan, 1990). Furthermore, the neoteny theory does not tell us anything about the value of nudity as a new character that helped the naked ape to survive better in his hostile environment (Morris, 1967).

Carrion-eating hypothesis

Some of the messiest eaters in the animal kingdom are the vultures and condors, which feed on carrion and have naked necks. It has been suggested that because man is another messy eater, it would somehow be helpful if he were also naked (Stephensson, 1972). This argument is invalidated by the fact that, at least in human males, one of the hairiest areas surrounds the mouth. (And men who wear beards tend to 'dribble' into them.) (Stephensson, 1972)

Sex-related hypothesis

Compared with a fur-covered surface, hairless skin is much more sensitive to environmental stimuli, particularly to temperature changes, touch and pain. It has therefore been suggested that increased sensitivity to touch in humans has been particularly useful to us in a social sense, permitting more intense mutually pleasant contacts between man and woman and between woman and child (Stephensson, 1972). It may also be significant that in other mammals, the least hairy areas are generally in the area of most intimate contact between mother and offspring, in the region of the teats. As

human society depends upon the specific 'bonding' of pairs of individuals, anything adding to the pleasure of contact may have conferred a biological advantage (Stephensson, 1972).

The weakness of the theory is that it does not explain why hair was also shed from areas not associated with intimate contact (e.g. from the back). Furthermore, we do have some hair left, particularly in 'intimate' areas and on the male chest. On the other hand, none of the other monogamous animals have taken this step: why should man be an exception? After all, there is no evidence that sensitivity to touch is significantly worse in the case of hairy animals.

Aquatic ape hypothesis

The aquatic ape hypothesis, put forth by Hardy (1960), assumes that hominids were forced by interspecies competition from an arboreal life to feeding on the seashore, hunting for food – for example, shellfish and sea-urchins, and thus gradually becoming more adapted to swimming. In time, hominids became increasingly aquatic, moving further and further out from the shore. Humans therefore lost their long, shaggy coat of fur, which is typical of primates but not of marine animals. This streamlining improved our smooth passage through the water (Hardy, 1960). The aquatic ape theory was subsequently elaborated by Morgan (1972, 1982, 1985, 1990), Morris (1977, 1994), Cuanne (1980), La Lumiere (1981), Ellis (1986), Verhaegen (1985, 1987) and Evans (1992).

The nakedness of some aquatic mammals, such as whales, manatees and dolphins, has been cited as evidence to support the hypothesis that man may have an aquatic ancestor (e.g. Hardy, 1960). Nakedness is naturally advantageous to these aquatic mammals because it reduces drag and buoyancy (Wheeler, 1985). Once insulating fur is removed, however, excessive heat loss is an even greater problem than for terrestrial species, as water has a higher thermal conductivity than air (Wheeler, 1985). Most of the diverse mammalian groups that have adopted an aquatic mode of life have therefore retained a dense covering of body hair (Sokolov, 1962; Wheeler, 1985).

Most of the aquatic mammals that have lost their hair have large and fusiform bodies with small appendages; large animals possess low thermal conductances, while small appendages minimize the area of skin in contact with water (Wheeler, 1985). Furthermore, heat loss from the extremities is restricted among these mammals by vascular adaptation, such as heat-exchanging rates at the base of the flippers (Scholander & Schevill, 1955). Neither of these properties, however, applies to early hominids; it is therefore difficult to reconcile the hairless condition of humans with an aquatic existence (Wheeler, 1985). A naked mammal of the shape and size of the early hominids – or modern humans – would have found maintaining a high body temperature in the sea energetically very expensive. Even those species of comparable body mass that inhabit warm tropical freshwater bodies have retained a thick coat (Wheeler, 1985). There is, furthermore, no fossil evidence to support the aquatic ape

hypothesis, although human fossil remains are often found near bodies of water (Foley, 1987). It is not very realistic to claim that humans have ever lived such a totally aquatic life as those marine mammals that have shed their fur. It is more likely that our ancestors lived on the shore and caught their food offshore by wading and diving. Humans would naturally have returned to the beach to sleep, and would have spent most of their time ashore. At night, insulating fur would have been an advantage.

Adaptation-against-ectoparasites hypothesis

The parasite argument was first presented by Belt (1874), but was later rejected by Darwin (1888) and was forgotten for a century. According to Belt, a naked primate would be less liable to harbour ticks and other noxious parasites, which, in the tropics, may constitute a serious danger to health (Darwin, 1888). According to Darwin (1888), the weakness of Belt's hypothesis is that it does not explain why the human species in particular lost its hair: ectoparasites are a problem for all primates, not for humans alone. A modern version of the parasite hypothesis was presented but simultaneously rejected by Morris (1967). Yet another version has subsequently been elaborated by Rantala (1999); according to this hypothesis, the explanation may lie in the unique ecology of hominids.

As a consequence of change in the structure of human society towards a group-hunting primate, humans started to occupy the fixed 'home bases'. The earliest evidence of a home base dates to the beginning of the Pleistocene (roughly 1.8 million years ago) in Tanzania (Leakey, 1971; Johanson & Blake, 1996), where remains of *Homo habilis* have also been recovered (Johansson *et al.*, 1987). It has been postulated that, at the same time, a set of new adaptive strategies, including toolmaking, transport of food and materials, eating of meat and sharing of food, was attained (e.g. Tobias, 2003). This change to a group-hunting primate was beneficial to many ectoparasite species (Rantala, 1999). Humans, for instance, became the only one out of the 193 species of monkeys and apes to harbour fleas, as fleas can only complete their life cycle if their host animal lives in a permanently inhabited den or lair (Morris, 1994). Lairs and dens also provided greater opportunities for many other ectoparasites to thrive and breed (Rantala, 1999).

As the ectoparasite burden on hominids increased, having fewer parasites may have become more important for survival than a warm fur coat. Natural selection may have started to favour shorter-haired and less parasite-ridden individuals, leading to the naked ape of today (Rantala, 1999). Selection pressure towards nudity may have been enforced by the many lethal diseases that are carried by blood-sucking ectoparasites. For example an outbreak of typhus, various forms of spotted fever, bubonic plague or any similar pandemic could have wiped out an entire fur-bearing segment of the human population (Olson, 1966).

Recently, Rogers *et al.* (2004) calculated on the basis of the number of silent mutations in African versions of the

MC1R gene (which produces darker skin) that humans became naked about 1.2 million years ago in Africa; this is consistent with the hypothesis that denudation took place during the period when humans started to occupy the fixed 'home bases' (Johanson & Blake, 1996) that were so beneficial to many ectoparasite species (Rantala, 1999). It furthermore suggests that *H. sapiens* was not the first 'naked ape'. This finding contrasts sharply with previous visual representations depicting human evolution, which represent *H. sapiens* as the only naked primate in our evolutionary line.

In general, women are less hairy than men and hairy women are less attractive to men (Darwin, 1871). Women tend to spend more time at the home base, thus being more susceptible to ectoparasites. If this preference goes back to hominids, we can expect 'hairless' women to have had more reproductive success than hairy ones, and to have produced both sons and daughters with less hair (Rantala, 1999). The resulting reduced parasite load in the offspring may also have been a selective advantage, causing males to start to prefer more naked females (Rantala, 1999); ultimately, this would lead through a process of run-away selection to the almost totally naked ape of today (see Fisher, 1930; Kokko *et al.*, 2002). The continuing attractiveness of hairlessness is supported by the findings of an American study (Tiggemann & Lewis, 2004), in which a vast majority (98%) of women reported that they regularly remove their leg and underarm hair; they attributed this to motives of femininity and attractiveness.

Interestingly, although men prefer naked women as mates, there is some evidence that women prefer males with a hairy trunk (chest) (Dixson *et al.*, 2003). It is important to note that thicker hair on the male trunk and beard is androgen dependent (Leshin & Wilson, 1981), and may be explained by a handicap effect of sexual signalling (Zahavi, 1975) or by the hypothesis of an immunocompetence handicap (Folstad & Karter, 1992); this would explain the lesser hairiness of women and their sexual attraction towards hairy men.

The best support for the ectoparasite hypothesis comes from medical science: traditionally, one of the most effective ways to get rid of ectoparasites such as lice has been to cut the hair shorter (see e.g. Bailey & Procriv, 2000). The parasite hypothesis is also consistent with findings among certain animal species that indicate that animals with a short coat or none have a lower ectoparasite load than those with long hair (e.g. Hassanloo *et al.*, 1995). It is also easier to remove troublesome parasites from naked skin, easing the task that, today, still occupies a great deal of time among the hairier primates (see e.g. Dunbar, 1991; Harrison *et al.*, 1977).

In 2003, this same 'ectoparasite hypothesis' was presented as a new hypothesis in *Biology Letters* by Pagel & Bodmer, receiving considerable media interest.

Did Darwin get it right?

In *The Descent of Man, and Selection in Relation to Sex*, Darwin argued that man, or rather primarily woman,

became divested of hair for ornamental purposes and that women subsequently transmitted the sexual advantage of nakedness almost equally to their offspring of both sexes. Darwin (1871) had also collected evidence that many species had evolved features that were in themselves inconvenient or injurious, but that were retained because they were attractive to the opposite sex. However, Darwin's hypothesis has serious defects. For example, the characteristics that are sexually esteemed are often indicative or suggestive of good health, such as lustrous hair or plumage (see Andersson, 1994), whereas the first stages of hair loss would seem more indicative of ill-health (mange, debility or alopecia) rather than of fitness to survive (Morgan, 1990). Furthermore, expensive sexual signal for the purposes of sexual selection are usually seasonal, and generally develop after sexual maturation. Although *H. sapiens* males are generally considered to prefer less hairy females (Darwin, 1871), and sexual selection may have facilitated the evolution of nakedness (Rantala, 1999; Pagel & Bodmer, 2003), Darwin's hypothesis does not explain what initial selective advantage would have caused males to start to prefer more naked females (see Fisher, 1930; Kokko *et al.*, 2002). This may be due to the fact that in the late nineteenth century, there was no real understanding of the role of parasites and pathogens in natural selection (Pagel & Bodmer, 2003).

Recently, Harris (2006) has proposed that human nakedness is not the result of Darwinian selection. Instead, she suggests that hairlessness is the result of parental (usually maternal) selection (Harris, 2006). She proposes that as in premodern societies, mothers use infanticide as a method of birth control, the mothers's decision to kill the baby may have been prevented if the infant met the standard of beauty prescribed by the mother's culture. This hypothesis, however, is based on the view prevalent in the social sciences – long held but incorrect – that standards of beauty are arbitrary cultural conventions that are distinct from natural and sexual selection (see e.g. Etcoff, 1999; Berry, 2000). In fact, sexual and parental preferences with regard to infant attractiveness evolved because they enhance reproductive success (see e.g. Grammer *et al.*, 2003). Thus, they cannot be considered as separate from 'Darwinian selection'.

Conclusions

Most prevailing theories explaining human nakedness assume that nakedness was an adaptation to the savannah environment (e.g. Kushlan, 1985; Wheeler, 1985). After hominids abandoned Africa about two million years ago (Zihlman & Cohn, 1986) for northern latitudes with a cooler climate, a hairy coat would surely have been beneficial. However, man adapted to northern latitudes by changing the colour of the skin, not by regaining hair. Thus, according to most of the prevailing hypotheses, human nakedness is a ghost of our evolutionary past. Only the ectoparasite theory proposes that selection pressure toward nakedness may have continued down to modern times.

Acknowledgements

I thank J.J. Ahtiainen, R.V. Alatalo, J. Holmes, V. Kauko, S. Kuukasjärvi, S. Koistinen, E.T. Valtonen, O. Tammisalo, J. Taskinen and J. Viitala for their valuable comments on earlier drafts of the paper. Special thanks are due to A.M. Bailey, C. Soligo and an anonymous referee, who gave fruitful comments on the final version of the paper, and Ellen Valle who checked the language.

References

- Amaral, L.Q. (1996). Loss of body hair, bipedality and thermoregulation: comments on recent papers in the journal of human evolution. *J. Hum. Evol.* **30**, 357–366.
- Andersson, M. (1994). *Sexual selection*. Princeton: Princeton University Press.
- Ardrey, R. (1976). *The hunting hypothesis*. London: Collins.
- Bailey, A.M. & Prociv, P. (2000). Persistent head lice following multiple treatments: evidence for insecticide resistance in *Pediculus humanus capitis*. *Australas. J. Dermatol.* **41**, 250–254.
- Belt, T. (1874). *The naturalist in Nicaragua*. London: John Murray.
- Berry, D.S. (2000). Attractiveness, attraction, and sexual selection: evolutionary perspectives on the form and function of physical attractiveness. In *Advances in experimental social psychology*, 32: 273–342. Zanna, M.P. (Ed.). San Diego: Academic.
- Brace, C.L. (1966). What ever happened to hairy man? *Science* **153**, 362.
- Brace, C.L. & Montagu, A. (1977). *Human evolution*. 2nd edn. New York: Macmillan.
- Campbell, B.G. (1966). *Human evolution*. Chicago: Aldine.
- Cuanne, S.C. (1980). The aquatic ape theory reconsidered. *Med. Hypoth.* **6**, 49–58.
- Darwin, C. (1871). *The descent of man, and selection in relation to sex*. London: John Murray.
- Darwin, C. (1888). *The descent of man, and selection in relation to sex*. 2nd edn. London: John Murray.
- Dixon, A.F., Halliwell, G., East, R., Wignarajah, P. & Anderson, M.J. (2003). Masculine somatotype and hirsuteness as determinants of sexual attractiveness to women. *Arch. Sex. Behav.* **32**, 29–39.
- Dunbar, R. (1991). Functional significance of social grooming in primates. *Folia Primatol.* **57**, 121.
- Ebling, J. (1985). The mythological evolution of nudity. *J. Hum. Evol.* **14**, 33–41.
- Ellis, D. (1986). Proboscis monkey and the aquatic ape. *Sarawak Mus. J.* **36**, 251–262.
- Etcoff, N. (1999). *Survival of the prettiest: the science of beauty*. New York: Anchor/Doubleday.
- Evans, P.H.R. (1992). The paranasal sinuses and other enigmas: an aquatic evolutionary theory. *J. Laryngol. Otol.* **106**, 214–225.

- Fisher, R.A. (1930). *The genetical theory of natural selection*. Oxford: Oxford University Press.
- Foley, R. (1987). *Another unique species: patterns in human evolutionary biology*. London: Longman.
- Folstad, I. & Karter, A.J. (1992). Parasites, bright males, and the immunocompetence handicap. *Am. Nat.* **139**, 603–622.
- Glass, B. (1966). Evolution of hairlessness in man. *Science* **152**, 294.
- Gould, S.J. (1977). *Ontogeny and phylogeny*. Cambridge, MA: Harvard University Press.
- Grammer, K., Fink, B., Møller, A.P. & Thornhill, R. (2003). Darwinian aesthetics: sexual selection and the biology of beauty. *Biol. Rev.* **78**, 385–407.
- Hardy, A.C. (1960). Was man more aquatic in the past? *New Scientist* **7**, 642–645.
- Harris, J.R. (2006). Parental selection: a third selection process in the evolution of human hairlessness and skin color. *Med. Hypoth.* **66**, 1053–1059.
- Harrison, G.A., Weiner, J.S., Tanner, J.M. & Barnicot, N.A. (1977). *Human biology*. Oxford: Oxford University Press.
- Hassanloo, Z., Fenton, M.B., DeLaurier, J.D. & Eger, J.L. (1995). Fur increases the parasite drag for flying bats. *Can. J. Zool.* **73**, 837–842.
- Johanson, D. & Blake, E. (1996). *From Lucy to language*. Verona: Editoriale Bortolazzi-Stein.
- Johansson, D.C., Masao, F.T., Eck, G.G., White, T.D., Walter, R.C., Kimbel, W.H., Asfaw, B., Manega, P., Ndessokia, P. & Suwam, G. (1987). New partial skeleton of *Homo habilis* from Olduvai Gorge, Tanzania. *Nature* **327**, 205–209.
- Klein, R.G. (1999). *The human career: human biological and cultural origins*. 2nd edn. Chicago: University of Chicago Press.
- Kokko, H., Brooks, R., McNamara, J.M. & Houston, A.I. (2002). The sexual selection continuum. *Proc. Roy. Soc. Lond. B* **269**, 1331–1340.
- Kushlan, J.A. (1980). The evolution of hairlessness in man. *Am. Nat.* **116**, 727–729.
- Kushlan, J.A. (1985). The vestimentary hypothesis of human hair reduction. *J. Hum. Evol.* **14**, 29–32.
- La Lumiere, L.P. (1981). The evolution of human bipedalism. *Phil. Trans. Roy. Soc. Lond. B* **292**, 103–107.
- Leakey, M.D. (1971). *Olduvai gorge: excavation in beds I and II, 1960–1963*. Cambridge: Cambridge University Press.
- Leakey, R.E. & Lewin, R. (1977). *Origins*. New York: Dutton.
- Leshin, M. & Wilson, J.D. (1981). Mechanisms of androgen-mediated hair growth. In *Hair research*: 205–209. Orfanos, C.E.W., Montagna, W. & Stüttgen, W. (Eds). Berlin: Springer.
- Mahoney, S. (1980). Cost of locomotion and heat balance during rest and running from 0 to 55 °C in patas monkey. *J. Appl. Physiol.* **49**, 789–800.
- Morgan, E. (1972). *The descent of woman*. New York: Bantam.
- Morgan, E. (1982). *The aquatic ape*. London: Souvenir Press.
- Morgan, E. (1985). The aquatic hypothesis. *New Scientist* **1405**, 11–13.
- Morgan, E. (1990). *The scars of evolution*. London: Souvenir Press.
- Morris, D. (1967). *The naked ape*. London: Jonathan Cape.
- Morris, D. (1977). *Manwatching. A field guide to human behaviour*. Oxford: Elsevier International Projects.
- Morris, D. (1994). *The human animal*. London: BBC Books.
- Mount, L.E. (1979). *Adaptation to thermal environment*. London: Edward Arnold.
- Olson, W.S. (1966). What ever happened to hairy man? *Science* **153**, 362.
- Pagel, M. & Bodmer, W. (2003). A naked ape would have fewer parasites. *Biol. Lett.* **270** (Suppl. 1), S117–S119.
- Rantala, M.J. (1999). Human nakedness: adaptation against ectoparasites? *Int. J. Parasitol.* **29**, 1987–1989.
- Rogers, A.R., Iltis, D. & Wooding, S. (2004). Genetic variation at the MC1R locus and the time since loss of human body hair. *Curr. Anthropol.* **45**, 105–108.
- Scholander, P.F. & Schevill, W.E. (1955). Counter-current vascular heat exchange in the fins of whales. *J. Appl. Physiol.* **8**, 279–282.
- Schwartz, G.G. & Rosenblum, L.A. (1981). Allometry of hair density and the evolution of human hairlessness. *Am. J. Phys. Anthropol.* **55**, 9–12.
- Sokolov, W. (1962). Adaptations of mammalian skin to the aquatic mode of life. *Nature* **192**, 464–466.
- Stephensson, W. (1972). *The ecological development of man*. Sydney: Angus and Robertson.
- Tiggemann, M. & Lewis, C. (2004). Attitudes toward women's body hair: relationship with disgust sensitivity. *Psychol. Wom. Quart.* **28**, 381–387.
- Tobias, P.V. (2003). Encore Olduvai. *Science* **299**, 1193–1194.
- Toth, N. & Schick, K. (1993). *Making silent stones speak: human evolution and the dawn of technology*. New York: Simon and Schuster.
- Verhaegen, M.J.B. (1985). The aquatic ape theory: evidence and possible scenario. *Med. Hypothesis* **16**, 17–32.
- Verhaegen, M.J.B. (1987). Aquatic ape theory and speech origins: a hypothesis. *Speculations Sci. Technol.* **11**, 165–170.
- Westermarck, E. (1894). *The history of human marriage*. London: Macmillan and Co.
- Wheeler, P.E. (1984). The evolution of bipedality and loss of functional body hair in hominids. *J. Hum. Evol.* **30**, 357–366.
- Wheeler, P.E. (1985). The loss of functional body hair in man: the influence of thermal environment, body form and bipedality. *J. Hum. Evol.* **14**, 23–28.
- Wheeler, P.E. (1990). The significance of selective brain cooling in hominids. *J. Hum. Evol.* **19**, 321–322.
- Wheeler, P.E. (1991a). The thermoregulatory advantages of hominid bipedalism in open equatorial environments; the contribution of increased convective heat loss

- and cutaneous evaporative cooling. *J. Hum. Evol.* **21**, 107–115.
- Wheeler, P.E. (1991*b*). The influence of bipedalism on the energy and water budgets of early hominids. *J. Hum. Evol.* **21**, 117–136.
- Wheeler, P.E. (1992*a*). The thermoregulatory advantages of large body size for hominids foraging in savannah environments. *J. Hum. Evol.* **23**, 351–362.
- Wheeler, P.E. (1992*b*). The influence of the loss of functional body hair on the energy and water budgets of early hominids. *J. Hum. Evol.* **23**, 379–388.
- Wheeler, P.E. (1993). The influence of stature and body form on hominid energy and water budgets: a comparison of *Australopithecus* and early *Homo* physiques. *J. Hum. Evol.* **24**, 13–28.
- Wheeler, P.E. (1994). The foraging times of bipedal and quadrupedal hominids in open equatorial environments (reply to Chaplin, Jablonski & Cable, 1994). *J. Hum. Evol.* **27**, 511–517.
- Wheeler, P.E. (1996). The environmental context of functional body hair loss in hominids (reply to Amaral, 1996). *J. Hum. Evol.* **30**, 367–371.
- Zahavi, A. (1975). Mate selection: a selection for a handicap. *J. Theor. Biol.* **53**, 205–213.
- Zihlman, A.L. & Cohn, B.A. (1986). Responses of hominid skin to savanna. *South Afr. J. Sci.* **82**, 89–90.

Copyright of Journal of Zoology is the property of Blackwell Publishing Limited and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.