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The influence of the loss of functional body hair on the water budgets of early hominids

Estimates are presented of the net daytime thermal loads, and associated drinking water requirements, experienced by fully haired and naked skinned hominids adopting quadrupedal and bipedal postures in open equatorial environments. Naked hominids could probably have tolerated higher environmental temperatures and levels of metabolic heat production, but this would have required the expenditure of large amounts of water. At normal levels of metabolic activity, a naked skin actually reduces the water requirements of bipedal hominids exposed to temperature regimes typical of the African savannah. A naked skin confers no such advantage on a quadruped. The findings support the contention that bipedalism was the pre-adaptation necessary to make the loss of functional body hair a net thermoregulatory asset in such environments.

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Introduction

Humans are unusual among mammals of comparable body mass, and unique among primates, in the possession of a functionally naked skin. Although various hypotheses have been proposed to account for this conspicuous feature (Darwin, 1871; Hardy, 1960; Kushlan, 1985; Morgan, 1982; Morris, 1967), it is widely interpreted as an adaptation to the novel thermal stresses encountered during a shift from forested to more open savannah habitats (Harris, 1980; Wheeler, 1984, 1985; Zihlman & Cohn, 1986), which some authors also associate with the adoption of strenuous muscular activities such as diurnal hunting (Ardey, 1976; Brace & Montagu, 1977; Campbell, 1966; Eckhardt, 1987). If this latter view is correct, a naked skin would be a relatively recent acquisition when compared with other hominid features such as bipedalism, since there is no indication in the fossil record that active hunting was a significant aspect of hominid ecology before 2 m.y.a.

A naked skin has several alleged benefits in high temperature environments. The loss of functional body hair, or more specifically the relatively static insulatory layer of air trapped by it, increases the thermal conductance of the animal, allowing more heat to be dissipated by non-evaporative means. However, it should be noted that this is only advantageous if environmental temperatures do not exceed that of the body, since when this gradient is reversed the loss of insulation will increase the rate at which heat is gained from the surroundings. The less restricted airflow resulting from the absence of a trapped boundary layer also increases the rate at which sweat can be evaporated from the surface of the skin (McClellan, 1963). This potential can only be fully utilised if sweat gland secretion is capable of matching the higher rate of evaporation and sufficient drinking water is available. In addition, the efficiency of this process is greater from a naked skin, since where a coat is present some of the secreted fluid evaporates from the hairs, taking most of its latent heat of vaporisation from the air rather than the body of the animal.

Theoretically, these factors could have conferred two distinct thermoregulatory advantages on early hominids; the greater maximum rates of sweat evaporation increase the combined levels of high environmental temperatures and muscular activity which can be tolerated without inducing hyperthermia, and higher potential rates of non-evaporative heat

loss, together with more efficient sweating, reduce the demand for drinking water. Although these arguments are superficially attractive, there are two major problems which must be addressed before they can be considered as satisfactory candidates for the primary selection pressures responsible for the initial evolution of a functionally naked skin by hominids.

First, it needs to be demonstrated that the reduction of body hair would actually have been a net thermoregulatory asset in savannah environments. This would only have been the case if the benefits, in terms of increased rates of endogenous heat dissipation, outweighed the cost of additional environmental heat gain. Considerations of the energetics of mammals at high ambient temperatures alone (Eckhardt, 1988; McArthur & Clarke, 1987) are of limited relevance since they do not take into account the high levels of solar radiation experienced in open equatorial environments. In such conditions, a dense coat of body hair can act as a shield, reflecting and re-radiating much of the incident energy before it reaches the skin surface. Consequently, the loss of this insulatory barrier can actually increase, rather than reduce, the thermal loads experienced by the animal (Parer, 1963; Macfarlane, 1976), even when ambient air temperatures do not exceed that of the body.

Second, if there are thermoregulatory advantages associated with a naked skin in open equatorial environment it must be explained why other similarly sized savannah mammals, ranging in ecology from herbivores to persistence hunters, have all retained coverings of body hair. Clearly, special factors need to be identified which would have only favoured the evolution of a naked skin by hominids. One important consideration could be the reliance of humans and higher primates on whole-body, rather than selective brain, cooling when exposed to heat stress (Hayward & Baker, 1969; Mitchell *et al.*, 1987; Taylor, 1974, 1977). This shifts the emphasis from panting, utilising the evaporation of fluid from the internal linings of the upper respiratory tract, to sweating from the external surfaces of the body to remove excess heat. Another crucial feature of hominids could have been their unique posture and mode of terrestrial locomotion. By dramatically reducing the area of the body exposed to the most intense fluxes of direct solar radiation, bipedalism minimises the costs otherwise associated with a naked skin (Wheeler, 1984). It also confines those areas of skin at greatest risk of thermal and UV-B damage to the head and upper shoulders, where they can be protected by the retention of only a relatively small area of hair cover (Wheeler, 1985).

By quantifying the thermal loads on naked and haired hominids, this present paper aims to determine whether the loss of body hair would have actually decreased or increased the thermoregulatory stress experienced during the day in open equatorial environments. To investigate whether posture has a significant influence on the relative costs and benefits of a naked skin, estimates of the thermal and water budgets of both bipedal and quadrupedal hominids have been calculated.

The thermal exchange of haired and naked hominids in open equatorial environments

The net amounts of energy gained by quadrupedal and biped hominids were estimated using a model previously described (Wheeler, 1991*b*) for calculating these environmental loads throughout a clear equatorial day. Full details of the methods used, and any assumptions made, are contained in this earlier paper.

The model relates to a hypothetical early hominid, proportioned intermediately between reconstructions of *Australopithecus afarensis* and the Chimpanzee *Pan troglodytes*; standing

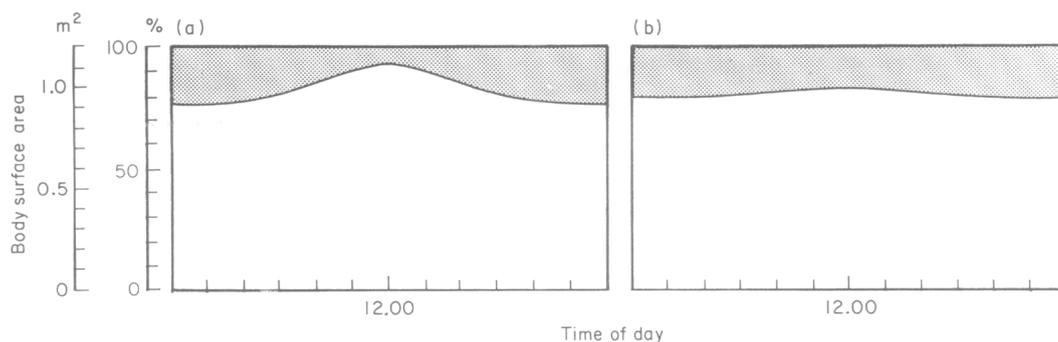


Figure 1. The relationship between the area of the body surfaces exposed to direct solar radiation (▨) and time of day for (a) bipedal and (b) quadrupedal fully haired hominids as determined in experiments with scale models.

1.25 m high, with a mass of 35 kg and total body surface area of 1.2 m². It is assumed that a constant core temperature of 37°C is maintained throughout the day.

Energy budgets have been calculated for four different temperature regimes with maximum air temperatures, at a standard reference height of 200 cm above the ground (T_{200}) of 30, 35, 40 and 45°C. Air temperatures peak at 14.00, 1 h later than the 5°C higher maximum attained by the surface of the 40 cm tall ground vegetation (T_g). The temperature profiles actually experienced by bipedal and quadrupedal hominids throughout the remainder of each day were calculated as previously described (Wheeler, 1991*a,b*). The present paper continues to adopt the notation in which the environmental temperature regime throughout any particular day is described by quoting the maximum of T_{200} and T_g only. For example, 30/35°C denotes a day on which the peak values of T_{200} and T_g are 30 and 35°C, respectively. Wind speed was taken as a relatively low 1 m.s⁻¹.

It has been assumed that the haired hominids were covered in a dark blackish coat, similar to that of the living African apes, absorbing 80% of the incident short wave solar radiation. Since it is more difficult to make assumptions about the thermal conductance of the coat of early hominids two different sets of thermal budgets have been calculated. One is for a thermal conductance of 5 W.m⁻².°C⁻¹, the other a less insulating coat of 10 W.m⁻².°C⁻¹. The latter is closer to the 8.3 W.m⁻².°C⁻¹ reported for *P. troglodytes* exposed to positive heat loads at high environmental temperatures, experimental determinations from other living primates ranging from 5.3–12.5 W.m⁻².°C⁻¹ (Johnson & Elizondo, 1979; Mahoney, 1980; Stitt & Hardy, 1971; Taylor, 1977). To estimate the total environmental heat load on hominids in the two postures the net gains through the shaded and unshaded surfaces of the body were calculated separately and combined, weighted according to their contribution to the total surface of the animal (Figure 1).

Estimating the thermal budget of a naked hominid is more complex as its body surface is divided into four, rather than just two, areas where different conditions of energy exchange prevail (Figure 2). It has been assumed that the hypothetical naked hominid retained hair on its head and upper shoulders covering 15% of its total surface area (Wheeler, 1985). The temperatures of the exposed and shaded portion of these surfaces, and the resulting energy exchange through them, were calculated in the same way as for the corresponding areas on fully haired hominids with a thermal conductance of 5 W.m⁻².°C⁻¹. Energy exchange through naked areas was calculated assuming the temperature of the skin was 37°C, since in

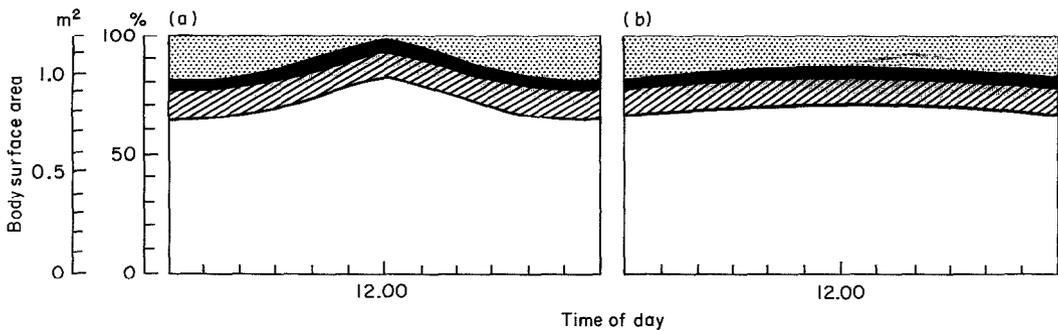


Figure 2. The relationship between the areas of the body exposed to direct solar radiation and time of day for (a) bipedal and (b) quadrupedal naked hominids. The surfaces have been divided into four regions; naked exposed (▨), naked shaded (□), haired exposed (■) and haired shaded (▩), the haired areas on the head and upper shoulders totalling 15% of the body surface. These areas were determined in experiments with appropriately marked scale models.

mammals dependent on sweating to dissipate excess heat the evaporation of fluid must prevent the temperature of this surface rising above that of the core. Although this assumption allows energy gains during periods of net positive heat load, with which the present study is concerned, to be accurately estimated, it should be noted that it could result in overestimates of the losses during the cooler early morning and late afternoon when peripheral vasoconstriction could lower skin temperature to conserve energy. The exposed skin would have required dense melanin pigment to protect it from the damaging effects of ultraviolet radiation and would therefore probably have been similar in colour to that of modern negroid and aboriginal races. The calculations assume this naked skin absorbs 80% (Jacques *et al.*, 1955) of incident short wave radiation and has an emissivity to longer wavelength thermal radiation of unity.

The resulting thermal budgets of haired and naked hominids in quadrupedal and bipedal postures are shown in Figures 3(a) & 4(a). The values plotted represent the net environmental heat loads on the animals, which are the total amounts of energy gained from all external sources not lost by subsequent re-radiation, convection and conduction. Positive values above the baseline show heat gains which must be dissipated by evaporative cooling if the animal is to maintain a body temperature of 37°C. Conversely, negative values represent losses which must be replaced by metabolic heat production to maintain homeothermy. It can be clearly seen that, as expected, reducing the surface insulation of the hominid increases the rates of both energy gain and loss during periods of positive and negative heat load, respectively.

To calculate the total thermal load requiring evaporative dissipation an estimate of endogenous metabolic heat production must be added to these external loads. The metabolic rates of standing, but stationary, mammals are consistently about 1.7 times basal metabolic rate (BMR) (Taylor, 1974), the equivalent of 82.9 W for a 35 g hominid with a predicted BMR of 48.8 W. Since approximately 10% of metabolic heat production is lost by evaporation from the linings of the respiratory tract, this leaves an additional 74.6 W to be dissipated by the evaporation of sweat from the skin surface. The total heat loads requiring dissipation by cutaneous evaporation are shown in Figures 3(b) & 4(b). Studies on the energetics of modern humans and other living mammals indicate that total mean diurnal metabolic heat

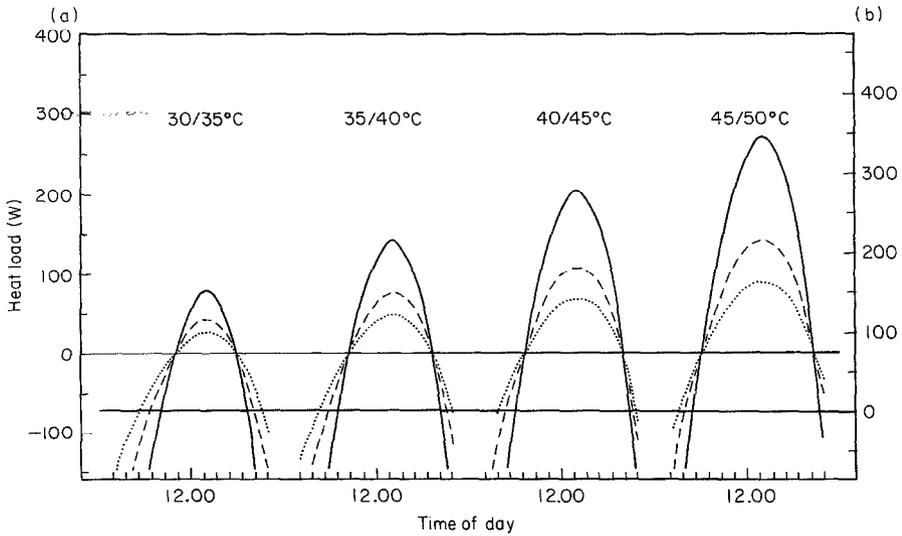


Figure 3. (a) Environmental and (b) total diurnal heat loads requiring dissipation by cutaneous evaporation experienced by naked (—) and fully haired [with thermal conductances of 10 (---) and 5 (···) $W.m^{-2}.^{\circ}C^{-1}$] quadrupedal hominids exposed to four different temperature regimes. The total loads assume the endogenous heat production of a stationary 35 kg hominid is 1.7 times its predicted BMR (shaded), of which approximately 10% is lost by internal evaporation from the linings of the respiratory tract.

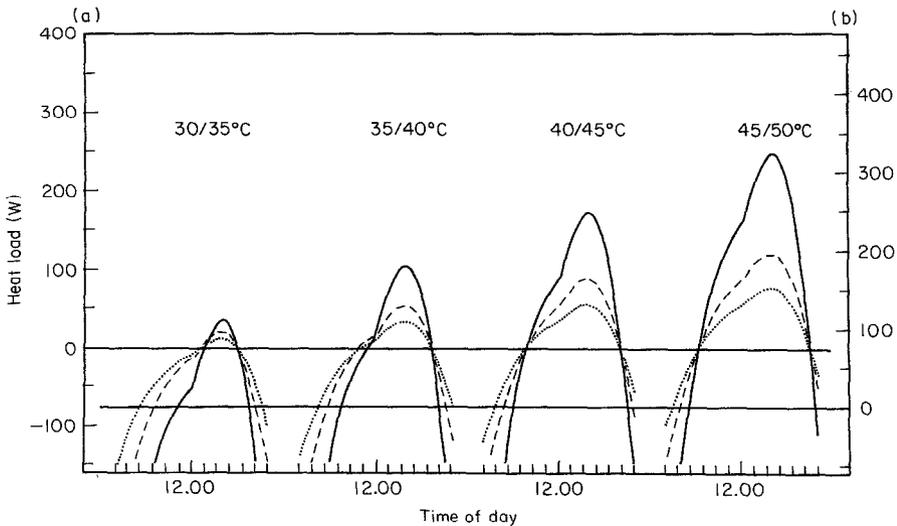


Figure 4. (a) Environmental and (b) total diurnal heat loads requiring dissipation by cutaneous evaporation experienced by bipedal hominids exposed to four different temperature regimes. For explanation see Figure 3.

production, which includes the heat generated by activities such as locomotion, would typically have been about twice BMR (Wheeler, 1991*b*).

The thermoregulatory drinking water requirements of haired and naked hominids

The total amount of energy requiring evaporative dissipation throughout the day at any given level of mean metabolic expenditure is represented by the area bounded by the corresponding baseline and the curve about it. The amounts of water required to remove these loads can therefore be calculated using its specific latent heat of vaporisation of 2410 J.g^{-1} at 37°C (Kerslake, 1972). Water budgets have been calculated assuming that fluid evaporating from the surface of a naked skin takes all this energy from the body of the hominid. As already discussed, the transfer of heat during sweating can be less efficient where body hair is present. Consequently, two estimates of the thermoregulatory water requirements of hominids retaining body hair have to be calculated; one assuming the process is 100% efficient and the other that only 80% of the energy is taken from the body, the residual 20% coming from the surrounding air as some water evaporates from the fibres of the coat.

The calculations are further complicated by the fact that the food consumed to fuel the given level of metabolic expenditure will also supply some of the water demand, both as preformed water and an end product of cellular respiration, thereby reducing the required drinking intake. A more comprehensive discussion of the contribution of these factors, as well as the additional problem of respiratory and insensible losses, is given in Wheeler (1991*b*). All the estimates produced in the present paper are based on a "dry" diet containing 12.5 kJ.g^{-1} and 15% by mass of water. This corresponds to a diet consisting primarily of relatively dry fruits and seeds, with a few more succulent items such as berries and invertebrates. It has previously been shown that even the inclusion of a large proportion of meat in the diet would have a relatively minor influence on the estimated water budgets (Wheeler, 1991*b*).

The resulting estimates of the thermoregulatory water budgets of quadrupedal and bipedal hominids at increasing levels of metabolic expenditure are shown in Figures 5 and 6, respectively. The values shown are the net amounts of drinking water required to replace all diurnal cutaneous and respiratory losses. If complete water budgets over a 24 h cycle were required, then the relatively low nocturnal respiratory and insensible losses, in addition to estimates of the amount excreted in urine and faeces, would also need to be included (Wheeler, 1991*b*).

The thermoregulatory advantages of a functionally naked skin in open equatorial environments

It is apparent from the results obtained that there is no simple answer to the question as to whether a naked skin constitutes a net thermoregulatory asset for hominids in savannah conditions, since this is influenced by environmental temperature, activity level and posture. However, they do show that the loss of functional body hair would have both increased the maximum heat load which could be tolerated and, perhaps more importantly, under certain circumstances reduced the drinking water requirements of these animals.

(i) Tolerance of high environmental and endogenous heat loads

Under all temperature regimes examined the peak thermal loads on hominids retaining body hair cover were substantially less than on those with a naked skin (Figures 3 & 4). However,

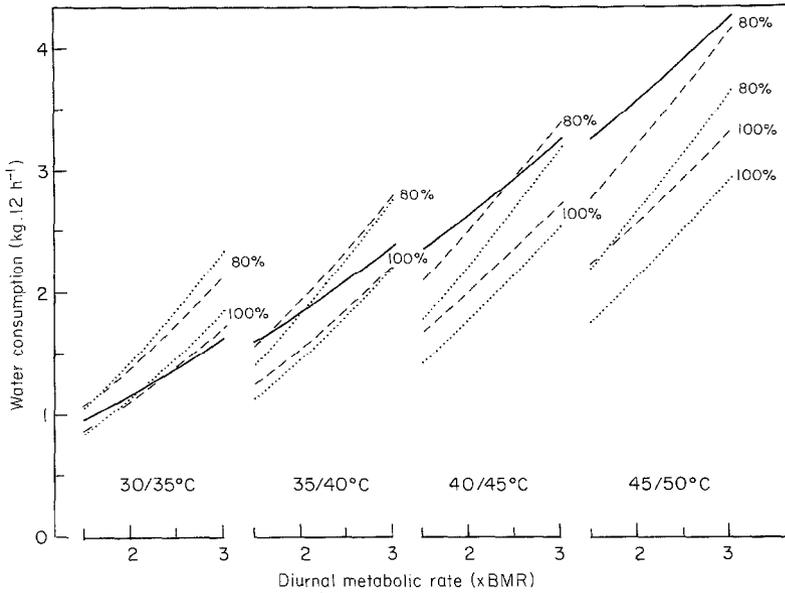


Figure 5. Relationships between the diurnal thermoregulatory drinking water requirements of naked (—) and fully haired, [with thermal conductances of 10 (---) and 5 (···) $\text{W}\cdot\text{m}^{-2}\cdot^{\circ}\text{C}^{-1}$] quadrupedal hominids and metabolic expenditure during exposure to four different temperature regimes. Two sets of estimates for fully haired hominids are shown, assuming efficiencies of heat transfer during sweating of 80 and 100%. To produce estimates of the total drinking water intakes of these animals estimates of nocturnal evaporative, faecal and urinary losses would need to be added to the values shown.

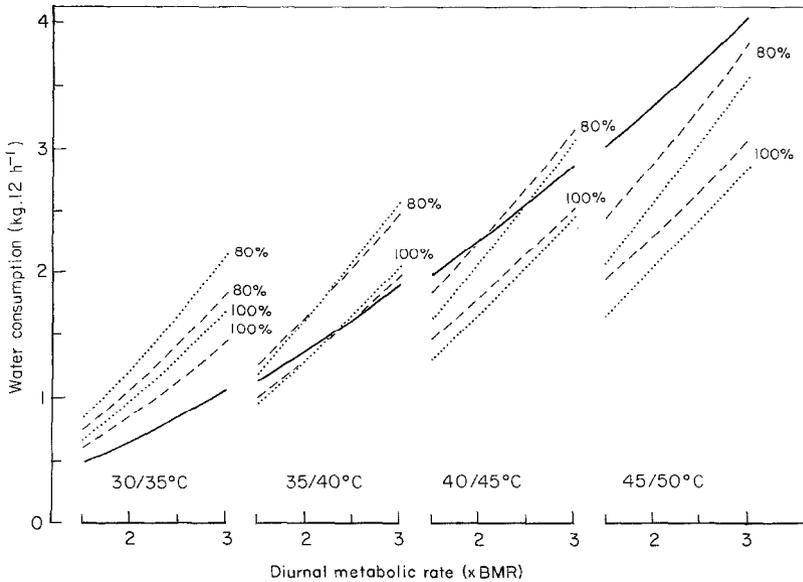


Figure 6. Relationships between the diurnal thermoregulatory drinking water requirements of bipedal hominids and metabolic expenditure during exposure to four different temperature regimes. For explanation see Figure 5.

even at low levels of metabolic expenditure, about 1.7 times BMR, these reduced thermal loads can still exceed the maximum rates of cutaneous evaporative cooling reported for modern haired hominid primates of approximately 100 W.m^{-2} (Wheeler, 1991*b*). In contrast, the maximum rate of heat dissipation of modern humans, in excess of 500 W.m^{-2} (Lee, 1964), can cope with the greater peak thermal loads on a naked skin even when exposed to the hottest temperature regime examined in the present study. Of course, earlier naked hominids would only have been able to match this if their maximum rates of fluid secretion were comparable to the elaborate eccrine sweat gland system of modern humans.

Therefore, the results confirm that in open equatorial conditions a naked hominid with well developed cutaneous sweat glands could tolerate more extreme environmental temperatures than one retaining dense body hair. However, the costs of maintaining a stable body temperature in such circumstances are extremely expensive. The large amounts of drinking water required to utilise this potential advantage means that it would probably have little ecological significance in such environments, beyond allowing unavoidable exposures to brief periods of extreme thermal stress to be survived. It is also evident that naked savannah hominids could sustain higher levels of muscular activity without inducing hyperthermia, but again only if the necessary amounts of drinking water were available.

(ii) Thermoregulatory drinking water requirements

Under certain, less extreme, circumstances the results suggest that the loss of body hair can actually save water. Whether a naked skin increases or decreases thermoregulatory water loss is determined by the relative importance of two phases of the day when different conditions of energy exchange prevail (Figures 3 & 4). The first is the hottest period of the day when the animal is gaining energy from its surroundings. It is during this period that body hair will be advantageous in reducing the heat load requiring evaporative dissipation. The second occurs before and after this period when, although there is no net environmental heat gain, water is still required to dissipate some or all of the endogenous metabolic heat production. This is when a higher conductance will be advantageous by facilitating the non-evaporative loss of body heat. Consequently, a naked skin will only reduce drinking water requirements when savings during these latter periods outweigh the costs of the additional energy gain during the former.

Under the highest temperature regimes examined the period of net environmental energy gain predominates for hominids in both quadrupedal (Figure 3) and bipedal (Figure 4) postures, resulting in those with a naked skin having higher drinking water intakes at all levels of metabolic expenditure (Figures 5 & 6). At lower environmental temperatures the periods when evaporative cooling is utilised solely to remove body heat and a naked skin saves water, become increasingly important. The temperature below which this advantage of a naked skin starts to outweigh its costs during the hottest part of the day is dependent on the mean metabolic expenditure of the hominid, with higher levels of endogenous heat production shifting the balance in favour of a loss of body hair.

Posture also has a major influence on the range of temperature regimes over which a naked skin conserves water. Taking the most likely situation of an efficiency of heat transfer during sweating of close to 100% and a mean metabolic expenditure during the day of approximately twice BMR (Wheeler, 1991*b*), a naked skin confers no overall advantage to a quadrupedal hominid on days when maximum air temperatures exceed about 29°C (Figure 7). In contrast, a loss of functional body hair reduces the net thermoregulatory drinking water consumption of a biped at maximum temperatures up to almost 35°C .

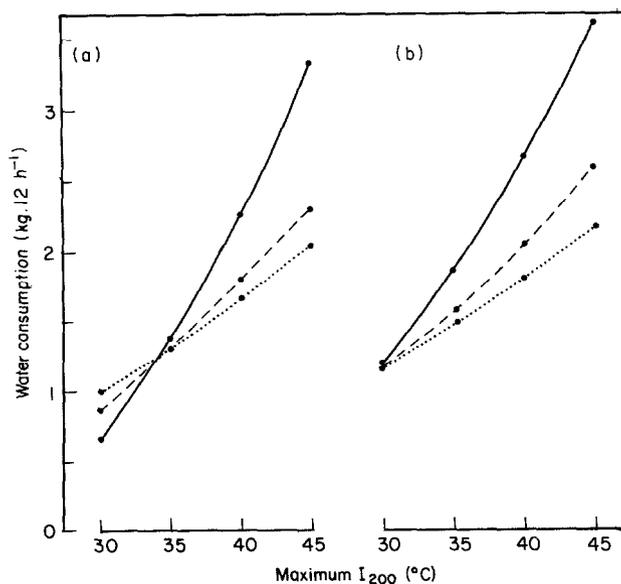


Figure 7. Relationships between the diurnal thermoregulatory water requirements of naked (—) and fully haired [with thermal conductances of 10 (---) and 5 (···) $\text{W} \cdot \text{m}^{-2} \cdot ^{\circ}\text{C}^{-1}$] hominids in (a) bipedal and (b) quadrupedal postures and maximum air temperature, T_{200} . It should be noted that the values depicted are not the losses resulting from continual exposure to the temperatures shown, but those occurring during exposure to the temperature regimes of which these are the maximum air temperature reached. Both figures are for a mean diurnal metabolic expenditure of twice BMR and assume the evaporation of sweat removes heat from both naked and haired skin with an efficiency of 100%.

How much lower than these temperatures a functionally naked skin would have constituted an overall thermoregulatory asset is uncertain, since factors other than just diurnal heat stress and water conservation are involved. At night, when ambient air temperatures can fall considerably in open savannah environments, the loss of body hair can be a liability, as the main thermoregulatory problem is the retention of body heat. During this colder period of each 24 h cycle, behavioural strategies such as roost site selection and huddling may have been important, and in later humans the acquisition of fire and clothing would have greatly alleviated the problem. In earlier hominids, the temperature regime below which such energetic considerations would have outweighed the benefits of any reduction in water consumption afforded by a naked skin cannot be determined with any certainty, since this will have depended on the relative importance of conserving these two resources. However, since this lower limit will be independent of locomotory posture, the range of environmental temperatures over which a naked skin could have been an overall thermoregulatory asset would have been wider for bipeds than quadrupeds. Interestingly, days with maximum air temperatures between 29 – 35°C , the range across which the loss of body hair could only have had a selective advantage for bipedal hominids, are some of those most typical of the equatorial African savannah.

In summary, the results obtained in the present study support the view that the primary selection pressures responsible for the loss of functional body hair in hominids were thermoregulatory. In addition to preventing hyperthermia during brief exposures to extreme thermal stress, the calculated thermal loads show that a naked skin could have reduced the drinking water requirements of early hominids foraging in open savannah environments.

Consequently, unless precluded by other factors such as heat loss at night, body hair reduction could have commenced immediately after the evolution of bipedalism, more than 2 My before there is any evidence that behaviours such as active diurnal hunting were important to their mode of life. However, the findings support the suggestion (Wheeler, 1984) that the acquisition of a naked skin could not have preceded this postural change, which itself may have evolved in response to similar thermoregulatory pressures (Wheeler, 1991*b*). Therefore, the unique combination of bipedalism and a dependence on whole body, as opposed to selective brain, cooling are probably the two factors which account for the evolution of a naked skin in humans and its absence among other savannah mammals of comparable body mass.

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