# 11 Human Regulation of Body Temperature and Water Balance

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SUMMARY

There is no evidence that the physiological characteristics distinguishing man from other primates evolved as adaptations to life on the savannah. On the contrary, many of these features, especially those concerned with the regulation of temperature and water balance, would have been positively maladaptive in such an environment.

## INTRODUCTION

In 1924 Raymond Dart discovered the first australopithecine skull in Taung, in a semi-arid region of South Africa. It was Dart who conceived the hypothesis that the ancestors of humans began to diverge from the apes because they migrated to a savannah-type environment. The theory appeared to represent the most straightforward method of connecting two pieces of 'evidence' – that is, Dart's supposedly savannah-dwelling hominid child and the belief that very much later human ancestors hunted big game on the African plains (Susman, 1987).

We now know that Dart's ideas were based, at least partly, on a misconception. He was convinced that the climate at Taung was as dry when the Taung baby lived there as it is today. It is now realised that the palaeo-environment of the Taung child was probably humid (Partridge, 1985; Brain, 1985). Moreover, the subsequent discoveries which have done so much to narrow the fossil gap have all been of hominids which lived and died near water (see Verhaegen, this volume, chapter 5). The savannah theory thus remains an artificial construction, a 'Just So Story' comparable with the hypothetical 'land bridges' in geology before the theory of plate tectonics.

Accounts of how our Plio-Pleistocene ancestors may have lived on the savannah include bouts of strenuous activity outside the gallery forest for hunting or digging (Hanna and Brown, 1983; but see Newman, 1970); dogged pursuit of swifter animals over one or two days (Carrier, 1984); and bipedal trekking after migrating herds of savannah ungulates (Sinclair, Leakey and Norton, 1986; but see Leutenegger, 1987; Verhaegen, 1987). Some of the more imaginative versions appear mutually contradictory. For example, the hypothesis of a foraging or hunting male accords ill

with Wheeler's meridian theory that our ancestors became bipedal to minimise direct solar radiation at midday, and retained a hairy heat shield only on top of the head (Wheeler, 1984, 1988; in imitation of D. H. K. Lee, in Newman, 1970; and in Schmidt-Nielsen, 1979, p. 89). If we accept this reasoning, it must have been the women who ranged over the plains at noon, while the balding and bearded males rested in the shade.

## ERECT POSTURE, NAKEDNESS AND SUBCUTANEOUS FAT

The suggestion has been made that erect posture and nakedness may have evolved to function in humans as a combined strategy of thermoregulation in an arid environment. In this connection it is noteworthy that (1) in no other species are hairlessness and erect posture found in combination, and (2) in no other species can either feature be shown to assist efficient temperature control on land.

Meerkats, prairie dogs and gerenuks frequently stand erect on extended hind limbs; kangaroos and several convergent rodents (for instance, *Pedetes, Dipodomys, Jaculus*) resort to bipedal locomotion when moving at speed, though their body posture with flexed hip and knee joints is very different from the human erect stance. But all these have retained a coat of fur which protects them from the sun (Montagna, 1965).

As for nakedness, it is found among real savannah or desert dwellers only in the underground tunnels of the naked mole-rat, a completely fossorial animal. In the African elephant and black and white rhino, which are functionally naked and live partly on the savannah, the hairlessness seems more of an affliction than an asset; these animals exploit every opportunity of wallowing to acquire a covering of mud as a protection against solar radiation. It is true that a few medium-sized savannah mammals, such as aardvarks, wart-hogs and hunting dogs, are comparatively sparsely haired. But this feature is unlikely to have evolved as a defence against the sun's heat, since these species spend the day in holes and are active at dusk or at night.

Humans lack the short reflective fur of diurnal savannah dwellers such as zebras and bovids, lions and camels (Wilson, 1979, pp. 752–3; Newman, 1970; Wheeler, 1984). Instead, they display a subcutaneous layer of white fat tissue, fairly evenly distributed over the surface of the central body parts and comprising on average around 20 per cent of body weight. This fat layer is (1) conspicuously absent in savannah mammals and conspicuously common in the larger aquatic ones, and (2) demonstrably maladaptive in a hot terrestrial environment.

There are no fat animals on the savannah, with the exception of small burrowing rodents or marsupials. In the case of these species, the fat is brown rather than white, internal or localised (for instance, in a fat tail) rather than subcutaneous and, unlike human fat, it is subject to seasonal

fluctuation. Among larger animals, the dromedary has occasional need of a fat store against food shortage, but here again the fat is highly concentrated (in the hump), varies with the animal's feeding condition, and fluctuates between 0.5 and 8 per cent of its body weight. The only fat animal which exploits the grasslands around the rivers is the hippopotamus, but it does this at night and stays in the water during the day.

In the case of marine mammals, however, the fat tissue is universal among the larger species. It varies from 20 to 25 per cent of the body weight in fast swimmers to more than 40 per cent in the slower species (Slijper, 1958, 1979).

The adaptiveness of this feature in water has been further illustrated by studies of human athletes. For example, blacks – in whom subcutaneous fat comprises a somewhat lower percentage of overall body weight than in other races – tend to be the swiftest runners over both short and long distances, but they are relatively poor swimmers (Ghesquiere and Bunkens, this volume, chapter 16). Successful swimmers are on average fatter than the winners of track events, and many long-distance swimmers are even grossly fat (Pugh and Edholm, 1955). The fat layer has been shown to be an effective barrier against heat loss in water. A study of a fat Channel swimmer revealed that when lying still in bath water at 18°C for more than one hour, he complained of no discomfort other than boredom, whereas another subject with much less subcutaneous fat complained of intense discomfort and showed a drastic drop in rectal temperature after fifteen minutes (Pugh and Edholm).

Clearly, the possession of the fat layer facilitates spending more time in the water. The result of one recent experiment even suggested that the converse may also be true. It was found in a study of slightly obese women that, without dietary restriction, an hour's daily walking or cycling reduced body weight by 10 and 12 per cent respectively after six months, while a daily swim caused a weight gain of 3 per cent over the same period (Gwinup, 1987). On land, on the other hand, subcutaneous fat has the dual disadvantage of reducing speed and, in hot climates, of acting as a heat trap. An extra weight of fat tissue equivalent to only 10 per cent of body weight seriously reduces speed. Even in temperate climates, no terrestrial animal that has to run for its life – be it as predator or prey – has much fat. Hares, for instance, which escape predators by running, have much less body fat than rabbits, which take refuge in their burrows.

Excess fat can constitute a real risk to humans taking exercise, especially in hot and sunny environments (Austin and Lanking, 1986). In fact, it has been calculated that most land-based sports other than walking and table tennis are up to ten times more likely to lead to fatalities than swimming, despite the additional danger of drowning incurred by swimmers

(Dolmans, 1987). And the same fat layer that is advantageous in water, with its high thermal conductivity, is a handicap to effective temperature control on land. Stranded dolphins, even in cool environments, soon die of hyperthermia. And Pribilof fur seals are seriously distressed by any activity on land at air temperatures of only 10°C (McFarland *et al.*, 1979, p. 773). The alleged danger of overheating on the savannah — sometimes advanced as the reason for hairlessness — would have been compounded by the evolution of the fat layer.

## BODY TEMPERATURE

In an endothermic species the normal temperature represents a compromise between the advantages and disadvantages of high body temperature in relation to its particular habitat and behaviour.

One of the advantages of high body temperature — especially the higher nervous tissue and muscle temperature — is the facilitation of faster reactions (McFarland *et al.*, p. 651). For every rise of 1°C, the velocity of the biochemical processes is more than doubled (compare the warming-up of athletes). Fast reactions are important in predators and their prey, in intra-species conflicts, and for birds in flight. For these purposes, generally speaking, the higher the nerve and muscle temperature, the better. The disadvantage lies in the high energy expenditure needed to sustain the temperature: the cost of keeping body tissues at about 38–42°C, as in most mammals and birds during the day, is enormous (Else and Hulbert, 1987). High temperatures may also incur other disadvantages — for example, problems of lipid and protein solubility and protein denaturation.

If the processes of thermoregulation in humans had evolved in response to a move from the trees to savannah, we would expect them to be characterised by a high normal temperature because of the need for speed, whether in flight or in pursuit, and a capacity to tolerate periods of higher temperature because of exposure to the tropical heat. Most hunted or hunting animals have a body temperature of at least 38°C. While the average rectal temperature in man is 37°C, in horses it is 38°C, in cattle and guinea pigs 38.5°C, in rabbits, sheep, dogs and cats 39°C, in goats 39.5°C (Slijper, 1958; Calloway, 1976). By contrast, animals which do not defend themselves by running away — such as hedgehogs, mole-rats, armadillos, monotremes, pottos and sloths — may have body temperatures lower than 35°C, and consequently incur much lower energy costs than other animals of the same size (Wilson, 1979, p. 747; McFarland *et al.*, 1979, p. 652; Calloway, 1976; Goffart, 1978).

If we exclude the group of slow-moving mammals listed above, a normal temperature as low as man's is found chiefly among the larger aquatic mammals. Hunting and hunted pinnipeds have a body

temperature like ours or slightly higher – for instance, 37.5°C in fur seals and 36.5°C in sea-elephants. But aquatic mammals that can afford to move slowly often have lower temperatures, which saves energy and allows longer submersion. Hippopotamuses and many cetaceans have body temperatures of about 35.5°C, sea-cows probably even lower (Slijper, 1958, p. 359). In other words, humans have a normal temperature resembling that of sea mammals, lower than most terrestrial ones, and markedly lower than that of any active savannah species. As well as possessing such a high basic temperature, animals living in exposed habitats evolve the capacity to survive periods when the diurnal air temperature is very high. The oryx, for example, can sustain a rectal temperature of 45°C and Grant's gazelle of 46.5°C for many hours, whereas humans feel ill if their rectal temperature rises to 38°C. Different mechanisms have been developed in warm-blooded animals for selectively keeping their brain temperature lower than the body temperature (Taylor and Lyman, 1972). These mechanisms, well developed in savannah dwellers, are poorly developed in humans (Cabanac, 1986), so that in man a rectal temperature of 41°C may result in permanent brain damage (Cabanac, 1986; Krupp and Chatton, 1981, pp. 1, 939).

In a savannah-type environment there is an unusually wide difference between day and night temperatures. Consequently, one final characteristic of thermoregulation in animals living in this environment is that they have evolved a wide range of body temperatures. Many show a fluctuation of more than 6°C between day and night temperatures: the oryx, for example, ranges between 38°C and 45°C, and the gazelle's rectal temperature may increase by 5 or 6°C during a single run, which – through muscular warming-up – has the advantage of enhancing its speed (Taylor, 1970; Taylor and Rowntree, 1973). At the other extreme are the medium-sized and large aquatic mammals which display almost no body temperature fluctuations. For instance, the core temperature of the East Siberian dolphin shows fluctuations of less than 0.5°C (Slijper, 1958, p. 205). Human metabolism seems to be adapted to fluctuations of less than 1°C (Schmidt-Nielsen, 1979, figure 4), although naked Australian aborigines after a single night's sleep under the desert sky may have body temperatures as low as 35°C (Kanwisher, 1977, p. 500). Running a marathon may raise the body temperature by two degrees, but rises greater than that can be fatal.

This factor is stressed in textbooks of physiology: 'The range of body temperature in a group of healthy persons is quite small. Indeed, the co-efficient of variation of body temperature in man is one of the smallest for which quantitative data are available' (Bell, Davidson and Scarborough, 1968). If we had been, as has been suggested, savannah-adapted over millions of years, it seems likely that we would have been able to accommodate with ease a temperature rise to more than 40°C in

the afternoon. The peak figures of death by heat-stroke in Greece in the hot summers of 1987 and 1988 suggest that man is anything but a savannah animal.

## WATER ECONOMICS

### Drinking water

Among the commonest of mammalian adaptations to a hot, dry habitat is a minimal dependence on drinking water. Many small savannah and desert mammals (burrowing and nocturnal) do not drink at all. The same is true of some of the African ungulates such as the eland and the oryx (Taylor, 1970). Carnivores usually need to drink more because their diet consists of relatively large amounts of protein, which requires a lot of water for its excretion in the urine (Schmidt-Nielsen, 1979, p. 125). Yet in desert habitats even carnivores such as fennecs have the capacity to survive without drinking. Many arboreal primates such as langurs almost never drink because the moisture in their vegetarian diet is sufficient for their needs (Napier and Napier, 1985, p. 151). If the ancestors of human beings had left the forests and gone into more open environments, they would have evolved the capacity to become more conservative with water as a means of adapting to their habitat.

Precisely the opposite it true. Humans, even without exercise and in temperate climates, have to drink much more than any other terrestrial mammal. Otherwise they would become susceptible to cystitis and other infections, kidney stones, and especially dehydration. Without intervention, a dehydration of about 10 per cent may be fatal for humans, whereas most animals can rapidly recover from a dehydration of 20 per cent. For instance, dogs can survive a dehydration of 17 per cent, cats 20 per cent, camels and donkeys 25 per cent (Wilson, 1979, p. 753; Schmidt-Nielsen, 1979, pp. 15, 62, 89, 123–5).

### Sweat production

Of all mammals, man has the highest sweat production (Newman, 1970). Montagna (1965) says: 'Sweating is an enigma that amounts to a major biological blunder; it depletes the body not only of water, but also of sodium and essential electrolytes'. But sweating is only one of the strategies mammals have evolved to prevent overheating. Many small mammals – such as rodents, marsupials and cats – use saliva instead of sweat for thermoregulation, spreading it over the more sparsely haired areas of the skin so that in evaporating it cools the body. Some larger mammals – such as dogs – reduce their body temperature by panting; others, like horses and cattle, sweat; sheep do both. But the maximum water loss per unit of skin surface in these species is always much smaller than in humans (Newman, 1970; Schmidt-Nielsen, pp. 54, 73, 83).

Although camels sweat, they have adapted to their arid environment by reducing water loss to a minimum; they do this by allowing their body temperature to rise during the day; the heat thus stored is given up at night without any expenditure of water. African hunting dogs (which, like dogs, do not sweat and do not salivate, and, unlike dogs, do not even pant) use the same strategy: they conserve water both by hiding in holes during the day and by allowing their body temperature to reach a level which in humans would be fatal, around 42°C (Kanwisher, 1977).

Of all the available strategies, human eccrine sweating combined with low body temperature is the least well adapted to savannah conditions and the least likely to have evolved in that type of habitat. As far as is known, fur seals are the only non-human mammals which sweat thermoactively through abundant eccrine glands (on their naked hind flippers) when they are overheated on land (G. A. Bartholomew, in McFarland *et al.*, 1979, p. 773).

**Other water losses**

Maximum urine concentration tends to vary according to the amount of water available in the environment and the diet (Table 11.1). Pigs and macaques, herbivores with a succulent diet, produce urine slightly more dilute than humans; that of freshwater beavers is much more dilute. On the other hand, the urine of dolphins is slightly more concentrated, and that of most land mammals like cats, dogs, sheep and rats is much more concentrated than in humans. In the savannah and desert dwellers, renal osmotic power is at the maximum. This seems to imply that human ancestors had ready access to a plentiful supply of fresh water or possibly brackish water, or at least to large quantities of fruits and fresh vegetables. Neither of these conditions is likely to have been fulfilled on the savannah. Even an evolution of only a few hundred thousand years in a mosaic gallery environment would have selected a higher urine concentration capacity.

The water content of human faeces tells a similar story. When camels drink daily, their faeces consist of 50–65 per cent water; when they have no access to drinking water, it is only 45 per cent (Schmidt-Nielsen, 1979, p. 61). Small desert rodents have a faecal water content in a similar range, between 45 and 50 per cent (Macmillen, 1972) as compared with about 70 per cent in the white rat. Human faeces normally consist of 75 per cent water (Diem and Lentler, 1978, p. 658).

The final channel of water loss is through exhaled air. Many animals in arid and semi-arid environments – such as kangaroos, giraffes and camels, as well as reindeer in the arctic desert – conserve most of the water breathed out from the lungs by utilising counter-current exchange of water during expiration. In humans, however, more saturated air is exhaled (Langman, 1985; Walker, Wells and Merrill, 1961).

Table 11.1 Maximum urine concentration in different mammals (Schmidt-Nielsen, 1979, pp. 181, 184; McFarland *et al.*, 1979, p. 674; Malvin and Rayner, 1968; Macmillen, 1972)

| Species | Maximum observed urine concentration in mOsm/l |
|---|---|
| Beaver | 520 |
| Pig | 1100 |
| Man | 1430 |
| Rough-toothed dolphin | 1700 |
| Bottle-nose porpoise | 1810 |
| Quokka (wallaby) | 2190 |
| Hill kangaroo | 2730 |
| Camel | 2800 |
| White rat | 2900 |
| Sheep | 3200 |
| Cat | 3250 |
| Small savannah mammals | 3900 or more |
| Australian hopping mouse | 9370 |

## Human water needs in hot, open environments

The total water expended by humans in sweat may easily reach 10 or 15 litres per day in hot and open environments (Newman, 1970; Schmidt-Nielsen, p. 12). Man needs to ingest water in large quantities to replace this loss. It might therefore be expected that he would have acquired the capacity to drink deep when water was available, and possibly to retain the water in his body.

As in the other instances quoted, the reverse is true. In the above-mentioned volume Schmidt-Nielsen makes this clear. Man's body is not adapted to store water: any excess taken in, for whatever reason, is rapidly excreted by the kidneys (p. 18). He has little, if any, ability to be trained to use less water (p. 22). When water is available, he is an unusually slow drinker. A very thirsty man can drink 3 per cent of his body weight in ten minutes, but a dehydrated camel, 30 per cent (p. 67). Moreover, when in danger of dehydration, man does not drink enough

to replenish the water loss even if a plentiful supply of water is available (p. 9).

Table 11.2 Human characteristics compared with those of
                aquatic and savannah mammals

| Humans | Aquatic mammals | Savannah mammals |
|---|---|---|
| Hind limbs in extension of trunk | All; resemblance with sea-lions | In gerenuk, suricata and prairie dog, for standing |
| Functionally naked skin | In all completely aquatic and many tropical semi-aquatic species, in Stellar sea-lion and elephant-seal | None; naked mole-rat is fossorial; elephant and rhinos need mud cover |
| Subcutaneous layer of white fat | In all medium-sized and larger species; usually thicker than in man | None |
| High drinking needs | In the freshwater semi-aquatic species (beaver) | None; except elephant (rhinos?) |
| Average rectal temperature less than 38°C | Probably all | None |
| Normal diurnal temperature fluctuation less than 1°C | Probably all | None; often 5°C and more |
| Eccrine sweat production for thermoregulation on land | Sea-lions (Pribilof fur seal); no sweat glands in completely aquatic species | None |
| Urine concerntration less than 1430 mOsm/l | Less than 1820 mOsm/l | More than 2400 mOsm/l |

## CONCLUSION

All the available evidence points to an extreme dependence on water in humans (Table 11.2). Even if our ancestors once lived in mosaic savannah environments, they would be expected to have evolved a more efficient system of water conservation than is in fact the case. 'Man suffers from a unique trio of conditions: hypotrichosis corpus, hyperhydrosis, and polydipsia' (nakedness, sweatiness and thirst) (Newman, 1970). Humans cannot withstand hyperthermia and cannot

store heat. They have abundant sweat and tears, rather saturated expiration and dilute urine, watery faeces, a low drinking capacity, a naked skin, a rather thick subcutaneous fat layer over the central body parts, a rather low body temperature and a small circadian temperature fluctuation.

Each of these features suggests that man evolved in an environment where water was permanently and abundantly available. In combination, they point irresistibly to the conclusion that wherever man evolved these characteristics, it could not have been on the savannah.

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