Hominine morphology, climatic determinism and an alternative hypothesis

Climatic determinism is an established hypothesis to explain phenotypic selection of hominine physique. Adaptations to heat and cold stress are, however, probably physiological rather than morphological. This paper advances an alternative hypothesis which relegates the influence of the climate to an indirect role only. Athletes select themselves into events for which their physiques are appropriate. ‘Field eventers’ are, in Sheldon’s terminology, mesomorphic and ectopenic (muscular and lacking in linearity). ‘Track eventers’, other than sprinters, have balanced physiques and are ectomorphic (linear). Distance runners are usually small and walkers tall. All are endopenic (lacking in the fat component). The physique of the northern (Inuit and Gurkhas) and southern (Bantu and San) study populations had morphological affinities with the physiques of the field and track eventers respectively. Northern populations, hunting megafauna over hilly terrain and sometimes through snow, need physiques of strength in body and leg. Southern populations, running down medium-size game, need the physique of distance runners. The physique of these contemporary populations may therefore be explained in terms of adaptations to the recent demands of hunting a particular range of fauna in a given physico-geographical environment. The pleomorphism and relative endomorphy of the White subjects can be explained by the relative sedentism associated with the adoption of agriculture. The hypothesis also explains the extreme physiques of Pygmies and Nilotics. The thermoregulatory and the alternative ‘task demand’ hypotheses, however, are not incompatible. The small size of the San hunter, for example, whilst having an undoubted biomechanical advantage, will assist rather than hinder thermoregulation.

Introduction

It has been widely argued that the diversity of human and hominine physique is a response to thermoregulatory considerations and that climate plays a major role in exerting selection pressure on the phenotype (Roberts 1973). This thermoregulatory hypothesis, sometimes known as the ‘eco-geographical’ (Mayr 1956), relates body area to volume, and thus mass and metabolism, and derives from the rules of Bergmann (1847) and Allen (1877). Bergmann’s rule states that: ‘Within a single wide-ranging species of warm-blooded animals, the subspecies or races in colder climates attain greater body size than those in warmer climates’. The rule is related to Newtonian cooling, in which an object with a high surface-area-to-volume ratio is subject to more rapid heat loss than one with a lower ratio (Hanna et al. 1989). The rule has also been reformulated to include humidity as well as temperature so that a smaller size is said to be associated with hot humid conditions and a larger size with cooler or drier conditions (Mosimann & James 1979).
Bergmann's rule is biologically plausible, has exerted a major influence and has almost achieved the status of dogma (Scholander 1955). There now exists an extensive supporting bibliography advanced by climatic determinists (Wilber 1957). In general mammals are said to confirm the theory and exceptions to be few (Allee & Schmidt 1951; Mayr 1956), but for primates, who show marked ecogeographical variation, there are contradictions and controversy (Albrecht et al., 1990). Some have been sceptical and argued that the size of the surface area of a mammal is of minor importance in heat conservation (Scholander 1955; Irving 1957; Wilber 1957; McNab 1971; Geist 1987). Reinig (1939) found mammalian size clines radiating more or less in any geographical direction.

Bergmann's rule has been advanced as an explanation for the observed diversity of physique in modern and recent human populations (Coon et al. 1950; Schreider 1950; Schreider 1951; Newman 1953; Roberts 1953; Brues 1959; Hiernaux et al., 1975; Crognier 1981; Jacobs 1985; Katzmarzyk and Leonard 1998). Trinkaus (1981), whilst in general favouring climate as the explanation for differences in body form, had reservations and Abbie noted that the Australian aborigines of the hot humid north were certainly no smaller than those of the cool temperate south (commentary on Newman 1963). Austin and Lansing (1986) devised a mathematical model for simulation of human thermoregulation and applied it to four sets of data representing varying body sizes and shapes. They concluded that the body surface area/weight ratio is inversely related to core temperature and heat storage under moderate conditions, but the relationship is not very strong.

This paper examines the role of climatic determinism and offers an alternative hypothesis to explain hominine pleomorphism. The term 'hominine' will be used throughout to encompass: 1) the Homo clade back to the origin of hunting involving the persistent pursuit of game 2) contemporary and early modern humans and 3) Neanderthals.

**Climatic determinism**

Bergmann's rule, applied to the problem of thermoregulation in heat-stressed humans, assumes that all unit areas of the surface of the body have an equal potential for heat dissipation. If true this assumption would suggest the importance of the ratio of area to volume in an unclothed heat-stressed human (Wheeler 1993). The assumption, however, is in part wrong (Porter 1993). Evaporative heat loss is much more efficient than heat loss by radiation and convection (Kuno 1956; Mount 1979; Clark & Edholm 1985). Running, in other than cold conditions, makes extreme thermoregulatory demands which can be met only by evaporative heat loss. Sweat glands are not evenly distributed over the body surface but are concentrated in the upper half of the body and, in particular, in the palms of the hands and the scalp. The hands and the scalp are two specialised heat dissipating organs (Porter 1993). The morphology of trunk and limbs and the area to volume relationship are, therefore, partly irrelevant in circumstances of heat stress, but they may not be wholly irrelevant. Small bodied and linear (ectomorphic) runners on the savannah, such as the San, have a large skin area to body mass ratio. As all parts of the skin sweat to some extent, or receive sweat descending from other areas, small size will ensure a greater relative area from which to lose heat under conditions of heat stress. This may, in part, explain the small size and ectomorphic physique of the San (Porter 1996), but there is also a biomechanical advantage (see below). This reasoning receives support from the work of Austin and Lansing (1986) recorded above. They found some thermoregulatory advantage for small body size. Their model took account of evaporative heat loss from the skin. The finding that two African populations had longer limbs standardised for