Ann. Rev. Anthropol. 1983. 12:259–84

HUMAN HEAT TOLERANCE: An Anthropological Perspective

Joel M. Hanna

Departments of Physiology and Anthropology, University of Hawaii at Manoa, Honolulu, Hawaii 96822

Daniel E. Brown

Department of Anthropology, University of Hawaii, Hilo, Hawaii 96720

INTRODUCTION

Within the complex of characteristics which we recognize as distinctly human are usually listed bipedalism, hairlessness, a large brain, and a symbolic linguistic ability. Each of these characteristics is genetically coded and probably represents a response to selective pressures at some time in the past. In each case we see a continuation and elaboration of adaptive patterns which characterize the order Primates.

Among our human adaptations we must also include the ability to tolerate heat. Human heat tolerance is the result of a series of adaptations which have been genetically encoded. All normal members of the species are born with a highly specialized complex of thermoregulatory sweat glands and a sensitive control system. It is a plastic system whose response and efficiency becomes more pronounced with prolonged and intense stimulation. The ability to respond to heat is seen in all extant human populations, regardless of the environment in which they now live or how many generations they have been removed from the heat (22). For those groups living in hot environments, the employment of cultural mechanisms has served as a buffer mediating between the hot macroenvironment and the organism. Still it is clear that physiological adaptations remain of paramount importance in daily survival (80). As is the case with other human characteristics, we seem to have taken advantage of our primate heritage, and with the aid of selection, extended our capacity beyond that of the other members of the order.

0066–4294/83/1015–0259$02.00

In this paper we will consider several aspects of heat tolerance and adaptation. First we take an evolutionary perspective, relating human heat tolerance to that of other animals and considering how it could have occurred. Then there is a discussion of hot environments and heat exchange with them. Finally, we examine the response to heat of contemporary humans and discuss various factors which influence individual response.

EVOLUTIONARY CONSIDERATIONS

Mammals have evolved a number of adaptations to enhance survival in hot environments. These include thick coats of hair, spreading of saliva over the surface of the body, perspiration, temporary storage of heat through increasing body temperature, panting, and heat avoidance by seeking refuge in the shade or underground (90, 105). Many species combine several of these adaptations to enhance heat tolerance. Camels, for example, have thick hair, store significant amounts of heat (to be released at nighttime), perspire, and drink large quantities of water. These techniques can be employed individually or in combination as the situation requires (90). The order Primates has generally been conservative and has employed fewer mechanisms. Prosimians and New World monkeys rely upon the primitive mammalian pattern of saliva spreading accompanied by panting. This combination is not particularly effective for primates because they cannot survive above ambient temperatures of 38°C (59, 94). Some prosimians and New World forms have also adopted a nocturnal schedule to avoid heat.

Old World monkeys, apes, and humans have evolved in a different direction through elaboration of thermoregulatory sweat glands dispersed over the surface of the body. These specialized glands, called eccrine glands, are also found in the lower primates, but at a much lower density, and they produce measurable perspiration only on the palms, soles, and the volar surfaces of the tail (94). Their function seems to be tactile rather than thermoregulatory and their contribution to the maintenance of body temperature is negligible (56). At some point after the separation of the New World from the Old World monkeys, selection favored the development of a greater heat tolerance. This was accomplished by wetting of the general body surface with eccrine glands becoming more dispersed, more numerous, and more active. This was an effective development allowing macaques and baboons to survive at environmental temperatures exceeding 40°C (48, 69). Humans show a continuation of this trend, with the highest capacity for heat loss through evaporation of perspiration exceeding that of monkeys by a significant amount (23). Unfortunately, physiological studies have not been extended to other types of monkeys (tropic forest dwellers, for example) or to the great apes, but on the basis of the anatomical distribution of eccrine glands, these primates also seem inferior to humans in sweat capacity (73, 95).

The evolutionary events leading to our high level of heat tolerance remain obscure; however, it seems safe to assume that the adaptation occurred in a hot environment with daily accessibility to drinking water and probably involved periodic bouts of intense physical activity. That a hot environment was involved seems obvious. Eccrine glands are thermoregulatory so that an increase in capacity, number, and distribution would suggest selection for heat. It is difficult to determine, based on current human physiological adaptations alone, whether human heat tolerance developed under hot-dry or hot-wet conditions. Evaporation of perspiration, and thus cooling power, is most effective in dry conditions, making an adaptive strategy emphasizing enhanced eccrine gland activity appropriate for hot-dry conditions (27). On the other hand, the need for a constant and plentiful water supply to provide a substrate for perspiration can be a great limitation for humans in dry heat. Evaporation is not so effective in a hot-humid environment, but since water is usually easily available, prodigious sweating over the entire body surface will maximize evaporative cooling without leading to fatal dehydration.

One must turn to the fossil record for information concerning the conditions under which humans may have developed their heat adaptations. The oldest unambiguous evidence for hominid remains stem from areas of eastern and southern Africa which at present are savanna or open woodland environments (14). It seems likely that similar environmental conditions were present in these areas during Plio-Pleistocene times. In the lower Omo basin, for instance, palynological studies suggest that xerophytic plants predominated about 2.0 million years ago (7), with grassland environments mixed with shrubs and some trees (12). Also, existing presently, as well as in the Plio-Pleistocene, are a variety of microenvironments, including those associated with rivers, streams, and lakes, where water favored limited woodlands. Plio-Pleistocene hominid sites from East Africa are generally found near water sources (e.g. Olduvai Gorge, Hadar, Lake Turkana), whereas later habitations were often located in drier areas (50).

Looking beyond the Plio-Pleistocene into the Early Miocene, much of East Africa was probably heavily forested, with later Miocene uplifting of the Rift Valley highlands creating a rain shadow which led to the drier climates of later times. The drying trend, which is marked by an increase in faunal turnover, began about 16 million years ago (98). It may have been during this period that hominid ancestors were first confronted with hot-dry environmental conditions. Thus, it may well be that early hominid evolution took place under hot-dry conditions. This, however, is far from certain.

More clearly implicated by the development of rapid response and high capacity of eccrine glands in acclimatized human subjects is selection for high levels of physical activity. The rapid response and high capacity in acclimatized man implicates selection for the high heat loss required during intensive physical activity. Well acclimatized humans can sustain a perspiration rate of 2*l* per hour (51). This is adequate to lose 1200 kcal of heat per hour or the equivalent of the heat generated by running 12 miles per hour or running 5-minute miles. This exceeds most levels of activity. For short time periods, a sweating rate of 4*l* per hour has been reported (23). This represents a heat loss potential above our ability to produce heat through working. This excess capacity for heat loss is probably related to high levels of heat production associated with intense work of short duration.

There is a curious problem in that heat loss is related to water availability. In order to dissipate the large quantities of heat associated with intense work, equal quantities of water must be consumed. Yet men cannot store water nor can they dehydrate to a significant degree. Humans have a limited capacity to dehydrate. Less than 3 percent of body water can be lost with no decrease in function (63), and for longer duration of heat loss, water must be replenished continuously, a significant limiting factor. Additionally, there is a problem of replacement. Most other animals can drink prodigious quantities of water after exposure to heat and so replace that lost through evaporation (1). Humans do not have this capacity. We are limited to about 1*l* at a time, which is scarcely the amount of water lost during an hour's moderate work (90). It is not clear why we do not have a larger capacity for rehydration considering the high capacity of the sweat glands. Furthermore, even if water is readily available, men working in the heat will drink less than that lost through perspiration. Adolph (1) has called this voluntary dehydration. Voluntary dehydration has been seen during work in the heat under a variety of conditions ranging from heavy industrial tasks (41) to primitive village agriculture in New Guinea (9). There is a gradual dehydration so by the end of the working period those involved have sustained significant water loss. This deficit is gradually replaced during meals and at other times so that rehydration is complete by the next day (40). Thus, there is a partial uncoupling of thirst from actual water requirements. This means that activity level will not be directly tied to and limited by water availability. These then are major elements of human heat tolerance: high capacity for heat loss, availability of water, and a loss of sensitivity for immediate water need.

In an evolutionary perspective there are several situations in which this complex of adaptations could have occurred. First, an adequate technology may have existed such that water could be carried, perhaps in large bird eggs or in gourds. The !Kung San employ such technology today (68); however, it is difficult to envision primitive men carrying several kilograms of water, while periodically engaging in vigorous activity. A second possible situation involves a thorough knowledge of the environment, its flora and fauna. Precise knowledge of surface water and plant resources would allow movement from place to place. Contemporary San and Australian aborigines have been able to acquire adequate amounts of water in this manner (68).

A third solution is to remain within a day's range of a water supply. Hunters or foragers could thus leave in the morning and return in the evening or, if necessary, the next evening. This would set conditions for voluntary dehydration and favor the uncoupling of thirst from water deficit. In the perspective of human evolution, some anthropologists (18, 61) have suggested that the establishment of a home base with daily foraging and return was a major step in human social evolution. A certain supply of water would contribute to the establishment of a home base. If a home base near water were established, several other benefits would accrue. The proximity of water and associated vegetation would provide a cool microclimate. This would be especially helpful to the very young, who have a limited heat tolerance because of an inadequate sweating capacity, and to pregnant women, who have the additional heat load of several kilograms of tissue which is metabolically very active. Remaining at a home base would have benefited these important segments of the population by reducing their thermal burden.

Several anthropologists, including Coon (17), LeBarre (54), and Montagu (67), have attempted to tie heat tolerance to hair loss. The basic argument is that body hair impedes heat loss, and its removal permits free circulation of the air to the skin allowing greater evaporation. Newman (70) objects, arguing that (*a*) there is no evidence to support a hair coat as a barrier to heat loss, and (*b*) removal of hair exposes the body surface to solar heat gain and may actually increase heat load. The first point has not been supported by experimental evidence. Weiner (101) has cited experimental evidence showing a direct relationship between thickness of hair coat and heat loss. The hair coat is especially undesirable at low levels of air movement where it restricts evaporation. Similarly, a recent study of macaques by Johnson & Elizondo (48) shows that the hair coat of the rhesus monkey may be a significant barrier to heat dissipation when compared to hairless man. With respect to Newman's second point, there is little doubt that exposure of the skin to solar radiation increases body heat load. In hot, dry conditions, clothed men are more tolerant than unclothed men. If heat tolerance and hair loss are related, we suggest the selection must have occurred during bouts of strenuous activity when solar heat gain is less critical than immediate heat dissipation. This may represent a trade between acceptance of an increased heat load due to radiation and an ability for rapid heat loss. Such conditions could have been bursts of running in pursuit of game or strenuous digging of roots and tubers, activities not typically observed in nonhuman primates.

An alternative relationship between hair loss and heat tolerance has been suggested by Robertshaw (79). He suggests "It has been speculated that eccrine sweating in man became necessary because of the loss of hair and that glands previously confined to the glabrous surfaces of the palms and soles spread to the other parts of the skin surface (p. 119)." While this hypothesis cannot simply be rejected, the high density of eccrine glands over the skin surface (relative to other mammals) is a characteristic of Old World monkeys and the great apes (73, 95). It would thus seem that loss of hair has simply enhanced their effectiveness rather than causing them to spread. Regardless of how the development of heat tolerance and hair loss are related, they are complementary.

HOT MACROENVIRONMENTS

An understanding of biological and cultural heat adaptations requires a knowledge of heat exchange and some salient characteristics of the environment in which it occurs. Adaptive responses involve the creation and maintenance of a favorable microclimate within a larger and more stressful macroclimate. The microclimate acts as a buffer, restricting heat gain while promoting heat loss. The center of the system is the human body, the core of which includes the brain, lungs, viscera, and other organs which function only within a narrow temperature range. Elevation of core temperature by only a few degrees is fatal. The core is surrounded by a shell of other tissues—the muscles and skin—whose temperature is variable (11, 51, 58). The shell interacts directly with the microclimate to facilitate heat loss.

Humans generate heat by normal metabolic processes and must ultimately lose this heat to the macroenvironment in order to maintain a constant internal body temperature. The effectiveness of the heat removal process depends, in large part, on the gradient of heat between the body core and the external environment. In simple terms, human ability to adjust to heat depends on only three factors: the magnitude of the heat gradient between the macroenvironment and the body core, the rate of heat exchange between the interior and skin surface, and the rate at which metabolic heat is produced. Various aspects of the macroenvironment clearly have a direct effect on the first two factors, and they may also have an indirect effect on the rate of metabolic heat production by limiting the types or amount of physical work that humans can perform.

An initial understanding of how environmental features can affect human heat tolerance may be gained through examination of the processes of heat transference between the body and the macroenvironment. These processes are radiation, conduction, convection, and evaporation.

Heat Exchange with the Environment

RADIATION Radiative heat exchange occurs between objects in line of sight of each other. Heat is exchanged through the gain or loss of electromagnetic energy at a wide span of wavelengths. Energy is emitted from one object to another, and thus heat is lost from the first object. Net radiative heat change, or the difference between energy lost through emission and gained through absorption, depends upon an object's temperature and reflectance, the temperatures and reflectances of all objects visible to it, the surface area of the object, and the surface area of features visible to the object (46, 51).

For human heat adaptation, the most significant type of radiative heat transfer is between the sun and the body surface. The amount of solar radiation at the earth's surface, or insolation, varies depending upon season, latitude, time of day, amount of moisture and dust in the atmosphere, and altitude (71, 85). Interestingly, direct solar radiative heat gain in standing individuals, particularly in the tropics or during summer, is less around noon than at about 9 AM or 3PM, since less area is exposed to the sun at noon (97). Another consideration in solar radiative heat gain is the reflectance of the skin, which significantly differs among individuals and between populations. "White" skin reflects about 30–40 percent of total solar radiation, while "black" skin reflects 18 percent or less (37).

CONDUCTION Conduction is a process similar to diffusion, involving molecule-to-molecule transferal of heat between surfaces that are in physical contact with each other. The amount of thermal conductance depends upon temperature differences between touching surfaces, the area of contact between them, and the thermal conductivity of the materials (20, 32).

In consideration of human heat gain or loss through conduction, the chief route is through body surface contact with the ground (or floor). Conductive heat exchange is maximized in the supine position and minimized when standing. Conductive heat gain from surfaces with temperatures above that of the body core may be minimized by wearing sandals or shoes made of material with low thermal conductivity (high insulation) and maintaining a standing posture. Of the four processes of heat exchange between the skin surface and the macroenvironment, conduction usually has the least significance for human adaptation (36).

Within the organism the process of conduction is the major means for heat transfer from the body core to the surface. Heat is conducted through layers of tissue or via the blood. The thickness and composition of the shell therefore can greatly influence the rate of heat exchange between the core and the environment.

CONVECTION Convective heat transfer refers to the exchange of heat between an object and a moving fluid (liquid or gas). This is frequently divided into two types of heat exchange: natural (or free) convection and forced convection. Natural convection occurs when an object is in contact with a calm, non-moving gas or liquid. The temperature difference between the object and the fluid causes vertical movements of the fluid due to density-buoyancy effects (62). Forced convection occurs when some outside force causes the fluid to move (e.g. in air, barometric pressure differences or electric fans may cause this movement). With forced convection, natural convection becomes of negligible importance (37). If air temperature is lower than body core temperature, convective heat loss can be elevated by artificially increasing air velocity or by exposing the maximum amount of body surface area to natural air movements. On the other hand, with air temperature above 38°C, any breeze will increase heat load and at above 45°C air convection will add more heat than can be lost by evaporation (8).

EVAPORATION When a substance is converted from a liquid to a gas under isothermal conditions, energy in the form of heat is required to drive the process. This energy requirement, the latent heat of vaporization, has a characteristic value for a unit mass of a given substance at a given temperature. The latent heat of vaporization of water is approximately 0.58 kcal/g at 30°C (32), hence a liter of water will remove 580 kcal of heat.

Evaporation of water from the skin surface is dependent on skin temperature, water vapor pressure of ambient air, the surface area of exposed skin, and the amount of water available for evaporation on the skin surface. The principle means by which humans provide moisture for evaporative cooling is by active perspiration from eccrine glands. Additionally, water used to humidify air in the respiratory tract, insensible perspiration (diffusion of water to the skin surface), and the behavioral application of water to the skin surface all add to evaporative heat loss.

Heat Balance

Body heat content as related to heat exchange with the environment may be represented by the following equation (11, 51):

$$M_b + M_a \pm S = E \pm R \pm K \pm C$$

The left side of the equation is a summary of body heat production and content. M_b is basal heat production and is thus the amount of heat generated by living tissue at rest. M_a is additional heat produced through physical activity. S is the amount of heat contained by the body. In the heat S may be increased to reduce strain on the heat loss effectors. On the right side of the equation are the avenues of heat exchange discussed above: E, R, K, and C are evaporation, radiation, conduction, and convection respectively. Excluding S, over any short period of time the equation may be unbalanced, but to maintain equilibrium the two sides must balance in the long term.

Several variables in the macroenvironment have important, direct effects on heat exchange. These include: ambient temperature, insolation (and thus cloudiness and particulate matter in the atmosphere), temperatures and reflectances of objects in line-of-sight, the surface areas of these objects, temperature and thermal conductivity of the ground, wind velocity, and water vapor pressure (or humidity) of the air. A number of biometeorological indices have been developed, such as comfort indices, to sum the factors in the macroenvironment contributing to heat stress; these indices are useful only for specific purposes and under specific conditions (28, 34, 51). For adaptive considerations, air temperature and humidity are perhaps the most important factors and are the variables used for dividing the macroenvironment into two major types of significance for human heat tolerance: hot-dry and hot-humid environments.

Hot-Dry Macroenvironments

Hot-dry climates are represented in the extreme by hot deserts, although many nondesert areas such as savannas, or the Intermediate Tropical Zone, are seasonably hot-dry. It is in hot-dry climates that environmental temperatures above that of the body core are most frequently encountered. Under these conditions it is possible to gain body heat by convection and conduction.

A primary feature of hot deserts is their dryness. Deserts can be defined as land areas where the annual rainfall in centimeters is a smaller number than the mean annual temperature in degrees Celsius plus 16.5 (39). The aridity permits high insolation values because of the usually dry, cloudless skies, and thus desert environments have a high solar radiative heat load (26). Deserts are also exceedingly hot in mid-day. Records from North Africa indicate temperatures of 80°C are not uncommon (15). The high daytime temperature in deserts tends to increase air movement, leading to increased convective heat gain. Conversely, cloudless night skies favor the rapid reradation of heat into space, resulting in cool nights (2, 15). Hot deserts are also characterized by sparse vegetation and therefore shade and humid microenvironments are rare. Human adaptation to hot deserts then must also extend beyond heat adaptation: low availability of food (both caloric and protein) and water (8, 90) resources also become significant limiting factors. Even when water is available, it may be unusable because of high salinity (8, 100), and the cool nights may necessitate adaptations to cold stress as well as to heat.

Some regions not usually considered as deserts are seasonally hot-dry. These include: many tropical grassland regions with alternating wet and dry seasons; hot steppes, which are characterized by extreme variability in precipitation, often with low predictability; temperate or cool deserts, with summer temperatures as high as those found in hot deserts; and temperate steppes with short, hot summers (64, 100). These seasonally hot-dry areas tend to have more vegetation than hot deserts because rainfall, when it occurs, is more frequent during cool seasons when there is less evaporation (100). This lowered evaporation rate during part of the year makes water more available to human inhabitants.

During hot-dry seasons these regions, like hot deserts, are characterized by hot days and cold nights, although the ranges are not so extreme.

Hot-Humid Macroenvironments

Hot-humid areas differ in several ways from the hot-dry environments discussed above. Because of cloudiness and moisture in the atmosphere, insolation values are lower, and thus ambient temperatures are lower. Concomitantly, the more opaque atmosphere limits reradiation of heat from the ground, favoring warmer nighttime temperatures. Temperature variations tend to be less extreme and seldom rise above human body core temperature. While tropical rainforest is the extreme representation of hot-humid zones, hot-wet environments also include a wide distribution of local climates, some of which may be seasonally cold and dry as well (38).

For human heat adaptation, the primary problem in humid environments is the reduced effectiveness of evaporation as a cooling mechanism. However, because objects in line-of-sight are usually cooler than body core temperature, especially when there is extensive vegetation cover (55), radiative heat loss occurs. Convective cooling is also very important, as air temperature is also lower than core temperature. Because of this, microclimate ventilation is an important consideration in hot-wet environments.

Because of the high humidity, vegetation is extensive and diverse (16, 54). Shade and water are usually plentiful for humans, permitting reduction of solar heat gain and the replenishing of body water lost in perspiration (70). Another potential problem is the relatively constant diurnal temperature. Intensive activity cannot be scheduled to cool parts of the day as is common in hot-dry areas. Human parasites and disease factors find hot-humid conditions congenial, and thus such water-associated infections as malaria, trypanosomiasis, schistosomiasis, enteric diseases, as well as many fungal and nematode infections, are prevalent (10). These infections can add to the heat burden by virtue of their febrile effects.

MICROENVIRONMENTS

Moran (68) has defined microclimate as "The climatic condition, especially the temperature, nearest the individual. Refers to the creation of environmental conditions different from those in the general area." For humans in heat, the ideal microclimate is below skin temperature, has a vapor pressure favoring evaporative heat loss, and is protected from conductive, convective, and radiation heat gain. It is within this extrasomatic zone that behavioral and social adaptations play a major role by maintaining a favorable microclimate within the microenvironment.

The goal of these adaptations is to maintain a cool and relatively dry shell of air about major portions of the body surface to facilitate heat loss. The physiological adaptations to be discussed later facilitate heat transfer from the core and working muscles into this microenvironment so that thermal equilibrium of the core can be maintained.

Microenvironment Adaptations to Dry Heat

Human adaptive techniques include material cultural adjustments and behavioral adaptations. Material culture provides habitations and clothing which establish a favorable microclimate and counter the high potential of radiation, convection, and conductive heat gain. Behavioral techniques center largely upon avoidance.

Material cultural adaptation to hot-dry environments are similar to those observed in cold environments. Lee (56), Rapoport (77), Wulsin (106), and Moran (68) have discussed housing and may be consulted for details. There are a number of techniques which seem common to hot-dry areas. 1. Houses are constructed to delay the entry of heat. High heat capacity materials such as adobe and stone are desirable because they can absorb large amounts of heat before passing it into the interior. The stored heat is lost at night by radiation and convection. The net effect is to dampen temperature fluctuations so that interior temperatures remain moderate. An added bonus is warm indoor temperatures during the cool evening. Houses of the Pueblo Indians of the Southwest provide a good example of the application of this principle. 2. A simple alternative to massive construction is excavation into the earth. The mean temperature of the subsoil is more comfortable than the surface with its extreme variations and is much cooler during the day. Rapoport (77) has described Middle Eastern communities with the entire village constructed several meters beneath the surface. Pit houses in the American Southwest and elsewhere are examples. 3. If habitation is to be above ground, a compact geometry minimizing surface area to internal volume is desirable. This proportionally reduces solar heat gain as well as convective heat gain from desert winds. 4. Houses can also be built close together, thereby increasing the internal volume with a disproportional increase in surface area. Such compact building also provides for mutual shading of some exterior walls and provides wind protection. This can be extended to villages and towns with multiple-story houses and canyon-like streets. 5. Limiting the size and number of windows, as well as provisioning them with shutters, reduces convective and radiative heat entry. 6. Painting in a light color or whitewashing reflects much radiation and reduces radiative heat gain. 7. If adequate water is available, plants can be used as primitive air conditioners by taking advantage of their transpiration, planting them close to walls for shade and cooling. Rapoport describes an ingenious tropical Spanish design employing plants. The house design includes two courtyards with a gallery extending between them. One courtyard is of flagstone and the other well planted. As the sun warms the stoneyard, air rises pulling the cooler air through the structure by convection. 8. Kitchens and cooking areas can be built away from residential structures to prevent heat entry.

Clothing is a second aspect of material culture which provides protection against the extremes of the macroclimate. Although clothing reduces abrasions and prevents sunburn, an equally important effect is to reduce solar heat gain (2). This, in turn, reduces the level of perspiration required to maintain equilibrium. Henschel & Hanson (42) have shown that well-acclimatized men wearing an army desert uniform perspire 30 percent less than unclothed men at rest. This represents a reduction in heat load of about 165 kcal/hr. There are also benefits in terms of reduced core temperature and heart rate. Adolph (2) calculates wearing clothing in the desert gives about half the protection of an awning or a building.

Desert clothing has adaptive value in that it stops radiation at some distance from the skin surface and converts it to heat which can then be lost into the air. Additionally, the insulative effects of trapped air reduce heat transmission to the skin surface (2). The addition of a light reflective surface may reduce heat gain even more.

Clothing is less advantageous at work than at rest because of the need to lose internally generated heat. Henschel & Hanson (42) calculate the sweat reduction as about 15 percent at work. Design principles for hot desert garments are also similar to those for cold climates (51). The material should be permeable to water permitting evaporation, but should act as a barrier to radiation and convective heat gain. Loose fitting, baggy clothing is desirable in that it favors ventilation and evaporation from the skin surface. A light-colored external garment may reflect radiation, reducing heat gain. Wulsin (106) has discussed the application of some of these principles by residents of hot desert areas.

Microenvironment Adaptations to Humid Heat

In the humid tropics, the problems associated with heat are quite different. Solar radiation is less of a problem as temperatures are lower than in the desert. The major thermoregulatory problem is the high humidity which reduces the effectiveness of evaporative heat loss (70).

Houses are constructed for shade and protection from rain, yet they must provide adequate ventilation. The dominant feature is the roof. Ideally, it is a huge parasol with steeply sloping sides to shed rainfall and large overhangs to provide the maximum protection. Materials of a low heat capacity are favored because diurnal temperature variation is not great and heat storage provides no benefit (77). Grass or thatch are ideal because solar radiation striking a damp roof evaporates water and aids in cooling. Humid tropic houses normally have a long, narrow geometry to achieve maximum ventilation. In some cases, elevated platforms may be employed to escape rain puddling and to allow more adequate convective cooling. A variation is seen in Polynesia where elevated stone platforms move the living floor several meters above ground level. Conductive heat transfer into the subsoil may aid in maintaining a cool micro-environment.

The obvious problem in constructing houses in the humid tropics is how to provide for privacy while retaining unrestricted ventilation. The privacy can be solved with curtains, blinds, or other movable temporary partitions. In some cases, permanent walls made of loosely joined bamboo or similar material are a compromise, allowing some degree of privacy but also permitting an appreciable degree of air flow.

There is a single simple rule for humid tropical clothing—the least amount possible. Given the high humidity and modest solar heat input, it is desirable to leave most of the skin uncovered (80).

There are a variety of other behavioral adaptations to the heat, including culturally sanctioned behavior, special foods and drinks, behavior scheduling, etc. These will not be considered here because of space limitations, but they have been reviewed elsewhere (36, 68, 76, 77, 106).

BIOLOGICAL ADAPTATIONS TO HEAT

If the temperature of the microenvironment cannot be maintained at comfortable levels, a series of physiological responses is initiated. These increase heat loss via evaporation and enhance heat transfer from the core to the shell. At ambient temperatures between 24–29°C, most resting unclothed humans are in thermal equilibrium such that metabolic heat is dissipated by a combination of factors discussed above (51). As ambient temperature increases, there is a gradual increase in body heat content, and the thermoregulatory centers in the brain begin a series of responses to increase conductive heat transfer from the core to the shell and to evaporate water from the surface.

Dermal Blood Flow

The initial response to increased body heat content is an elevated dermal blood flow. Venous blood flow is shifted from internal veins to superficial veins where it can be cooled before entering the core. There is a compensatory vasoconstriction in other areas to maintain blood pressure (107). This presents an efficient and metabolically economical mechanism for rapid transfer of heat to the shell. Peripheral skin blood vessels dilate under the influence of the sympathetic nervous system and an as yet unidentified transmitter (21, 84). The active vasodilation caused by transmitter accounts for most of the increased surface blood flow, and according to Rowell (88), is regulated by central core temperature. As blood flow increases through direct arteriovenous shunts, large quantities of blood are shifted into the extremities, especially the hands and feet. These are superb heat exchangers by virtue of their large surface areas and low metabolic heat production (5). The general increase in skin temperature also is beneficial in promoting loss of heat from the surface by radiation and convection.

Cardiovascular Response

The increased surface blood flow may induce an increase in cardiovascular activity, specifically increases in heart rate and blood pressure. The tachycardia seems to be a response to pooling of blood in cutaneous circulation (81, 107). If physical activity is required, the strain on the heart is increased. It must maintain flow to working muscles as well as to the skin. In acute exposure to heat, it is this increased cardiovascular strain which leads to fatality and accounts for the excess deaths of the elderly and young during heat waves (24).

Perspiration

As skin temperature increases, the sweat glands begin to function. This occurs at about 35°C skin temperature, but the starting point is subject to considerable individual variation (35). The appearance of perspiration is not uniform but the pattern is regional, starting on the trunk and progressing distally to include the extremities (44). The sweating mechanism will be carefully matched to thermal needs. When sweating has been adequate to reduce the temperature of blood perfusing the thermoregulatory center, the rate of production will be reduced until an equilibrium is established. If core temperature continues to climb, however, sweat producton may not continue to increase. Before the surface is completely saturated, hidromeiosis (sweat gland fatigue) can occur and reduce output. Hidromeiosis probably results from blockage of duct openings because of hydration of the surrounding skin (51) since it appears in humid exposures more frequently than dry exposures.

Thus, the physiological response of humans to a hot ambient temperature is rather simple: blood is shifted to the surface, cardiovascular activity maintains blood flow and rapid heat transfer within the organism, while sweating physically removes heat from the skin surface.

Eccrine Glands

The effectiveness of human evaporative heat loss is the work of the eccrine sweat glands. These are so specialized and developed in humans that Montagna (66) considers them one of our characteristic organs. They can be contrasted with apocrine sweat glands which are found in the skin of most mammals. Apocrine glands are associated with hair follicles, secrete a lipid rich, viscous fluid, and are poorly innervated (53, 79, 89). In mammals such as the horse and the sheep, they produce thermal sweat (90, 105). In primates a phylogenetic trend is seen as the ratio of eccrine to apocrine glands increase from prosimians to man (73, 95). In humans, eccrine glands are spread over the surface and apocrine glands are confined to the axilla and groin (13, 53).

Eccrine glands consist of a coiled region within the dermis and a duct through the epidermis to the surface of the skin. The innermost coiled portion secretes a fluid similar to plasma, and the coiled and tubular portions contain a series of active transport systems to reabsorb some solutes (13). The glands are sensitive to acetylcholine and to circulating hormones such as aldosterone, so that the composition of the final fluid reflects general body water and electrolyte balance as well as immediate thermal needs.

Eccrine glands are found on the hairless portions of the body surface at densities ranging from 52 glands/cm^2 on the thigh to 240/cm^2 on the dorsum of the hand. These densities exceed those reported for other animals (102). In terms of heat loss, their effectiveness can be appreciated from the following: a horse can perspire at a rate of 100 gm/m^2/hr, a camel at 250 gm/m^2/hr, and a human in excess of 500 gm/m^2/hr (27).

The activity of eccrine glands is regulated by the sympathetic nervous system with acetylcholine serving as the postsynaptic transmitter. The function of the glands is under complex control with local skin temperature and central core temperature playing roles (51). The central receptors in the hypothalamus monitor body heat content carefully, such that a small increase in the temperature of the blood perfusing the hypothalamus leads to a rapid onset of thermal perspiration over large areas of the body. The central hypothalamic center is presumably involved in control of patterned, nonthermal eccrine function such as emotional and gustatory sweating (13). Local heating of the skin also causes local thermal sweating (29), and under many circumstances it can be more important than central input (57). Drugs and hormones can also mediate sweating.

Factors Influencing Individual Response

ACCLIMATIZATION Of the myriad of factors known to influence individual response to heat, the state of acclimatization is without doubt the most important. Acclimatization seems to be a universal human capacity, and degree of acclimatization is a major contributor to individual variation in response. The process of acclimatization is illustrated in a study reported by Strydom & Wyndham (96). Twelve white South African men from temperate regions with no recent heat exposure served as subjects. They were required to perform moderate work (1560 ft.lb/min, 212 m.kg/min) in a hot, humid environment (33/34°C; 90/93°F wet/dry) for a period of 4 hours. The work consisted of stepping onto a box at a rate of 12 times per minute. Their responses are shown in Figure 1 and are characteristic of acute heat response in unacclimatized humans. Sweating rate is low, heart rate is high—approaching maximum levels—and core temperature reaches pathological levels. Several of the men could not complete the test.

The acclimatization procedure involved repeating the test each day for 10 consecutive days. The changes are also recorded in Figure 1. Sweat rate has

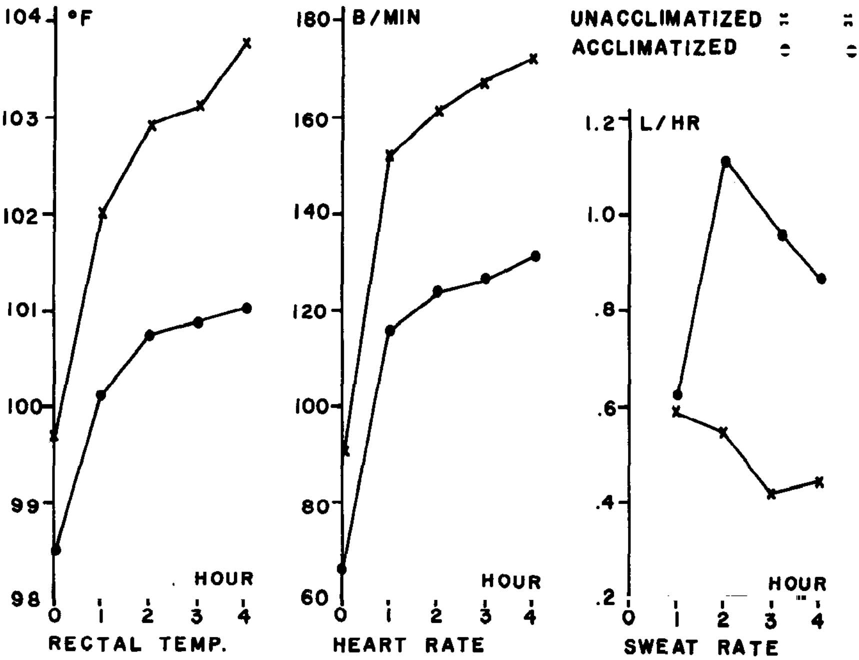

Figure 1 Physiological changes during acclimatization to heat. Responses are recorded during a 4-hour work period in a hot, humid environment. Acclimatization leads to increased sweat loss, which reduces core temperature and cardiovascular stress. After Strydom & Wyndham (96).

doubled and the resulting increase in heat loss has reduced cardiovascular activity and reduced core temperature. These observations have been repeated in a number of studies (23, 29, 60, 107). The actual exposure time required is less than 100 minutes per day (60) irrespective of the thermal environment for the rest of the day.

The remarkable aspect of the acclimatization response is the ease by which it is accomplished. It is rapid, effective, and will occur even though the trials are performed in a temperate climate in winter. Furthermore, all normal people who have been tested can acclimate. As Edholm & Weiner (22, p. 151) note, "even with long continued life in temperate or cold climates over many generations without exposure to hot or tropical conditions, the ability to acclimatize is retained." Studies on macaques (47) have confirmed that a similar, but less dramatic acclimatization may occur in other primates.

The major factor promoting acclimatization is an increase in sweat gland output and an increase in sensitivity to the thermal environment. Sweating begins at a lower skin temperature (5, 51), the capacity for production is increased by severalfold, and "inactive" glands may be activated (52). This permits core temperature to remain at a lower value and concomitantly reduces circulatory strain (87). In addition to a higher output of perspiration, there is a reduction in sodium and chloride loss (83). This may reflect general body water balance rather than sweat gland adjustment (103). However, the end result is the same. Acclimatization yields a greater electrolyte economy through a reduction in sodium and chloride loss in sweat. The kidneys also reduce sodium loss and respond rapidly with a reduction in water loss if dehydration occurs (90).

The stimulus for acclimatization is closely related to physical activity, because natural acclimatization is always accompanied by work. However, in a series of laboratory studies, Fox (29) demonstrated that acclimatization will develop in proportion to the degree of rise in body temperature. Fox and associates developed a plastic suit which enabled the temperature of a resting individual to be raised to any level and maintained in a steady state. Acclimatization changes paralleled those seen in other studies, confirming that elevated temperature and not work was the acclimatizing stimulus (29).

Acclimatization also seems to involve a change in pattern of sweat gland recruitment. Hofler (44) found that unacclimatized men sweated most profusely about the trunk and gradually recruited sweat glands from the limbs and other parts of the body surface. After acclimatization, the pattern was reversed such that sweating was most perfuse about the limbs with the trunk being recruited later. The higher surface area to mass ratio of the limbs and their lower level of metabolic activity makes them potentially better sources for loss of metabolic heat. Such a reversal in pattern of recruitment would provide a much more efficient vector for heat loss at no increase in energy expenditure and could actually reduce the perspiration required to maintain thermal equilibrium (36).

In summary, humans acclimate to heat in a rapid and effective manner. Acclimatization involves increased sweating which reduces body temperature and circulatory strain. The stimulus is elevated body temperature for short periods over several consecutive days. In addition to a higher rate of perspiration, acclimatization also involves a greater sensitivity to environmental heat, as evidenced by the lower temperature at which sweating begins, as well as a redistribution of recruitment patterns and a greater sodium and chloride economy.

Anecdotal observations may cause us to question the idea that acclimatization leads to increased sweating because newcomers to the topics seem to perspire more than indigenes. Newcomers are most likely storing more heat and beginning to perspire at higher skin and core temperatures than natives, hence they have greater heat stores to lose. This requires more perspiration once sweating begins.

AGE There is a close relationship between an individual's age and heat tolerance. Development of sweat gland function in youth and reduction in cardiovascular functions in the aged are the major factors involved. Neonates are extremely vulnerable to extreme heat because their sweating capacity is limited. All sweat glands are formed at birth, but many are inactive. Hey & Katz (43) estimate that a newborn's sweat glands produce only one third the adult levels of perspiration, even though they are more densely packed. This reduced capacity puts them at risk for heat-related problems. Ellis (24) has shown that during a 15-year period in the U.S., the heat-aggrevated death rates in infants under a year of age was the highest of any age group save those over 50.

As the child grows, the integument stretches, density of sweat glands fall, and capacity increases. Essential to the process is activation of formed glands. Kuno (53) has summarized evidence suggesting a critical period in the first 2 ½ years during which time activation occurs. It is during this period that the sweating capacity of children increases. Because there seems to be no additional activation, this developmental phenomenon has been used to account for the observation that natives in hot climates have more active glands than those from temperate climates (53). Exposure to heat during infancy is presumably the activating stimulus. Knip (52) has recently summarized evidence that deactivation and reactivation may occur in adulthood.

Older adults are at highest risk for heat-induced death (24). The major problem seems to be lack of acclimatization and reduced physical activity in the elderly. The elderly who maintain physical condition fare as well as middle-aged men in moderate heat (19, 82). It is only at high levels of physical activity in the heat that the fit and healthy older individual may be less tolerant (82).

SEX DIFFERENCES A large number of studies have compared men and women in humid and dry heat with the general conclusion that both sexes respond to heat and acclimatize in the same manner, but women tend to begin sweating at a higher skin temperature, sweat less, and store more heat (30, 91, 108). Weinman et al (104) reported that at equal exercise intensity active women had better performance in humid heat than inactive men. When the sexes are matched in terms of physical fitness and level of work, there are only trivial differences in the heat (45, 49, 72). Horstman & Christensen (45) have presented evidence that active women may acclimatize at a faster rate, but again the difference seems trivial. Thus, with respect to heat tolerance, there seems to be no important difference between the sexes if physical condition is equal.

PHYSICAL ACTIVITY Physical activity leads to physical fitness which is closely related to heat tolerance. Well-trained men more easily tolerate heat, and training actually enhances the level of heat tolerance (33, 74). Training is beneficial even if it takes place in a temperate environment with no ambient heat load (75). The opposite is also true—acclimatization to heat has a positive effect on work performance and improves maximum work capacity (92). As we have noted previously, "Physical fitness and heat tolerance both involve greater sweating and improvement in cardiovascular function so they probably cannot be separated" (36).

BODY SHAPE AND PROPORTION Among the earliest established correlates of human variation were the "ecological rules" of Allen and Bergmann. These rules hold that peoples living in warm climates have longer extremities and a lesser body mass than those living in cold climates. Roberts (78) has summarized the data and arguments. The underlying assumption is that a higher surface area to mass ratio in homeotherms is beneficial in terms of heat loss. There are a number of qualifications which limit the usefulness of this attractive hypothesis. Malnutrition and infectious disease are epidemic in the tropics, and these could reduce body size and proportions. These notwithstanding, stature, weight, and limb length are phenotypically plastic and have a significant environmental input. In this context, studies of growth are helpful. Eveleth (25) studied American middle-class children reared in Brazil and found them to be more linear than expected. Stinson & Frisancho (93) compared the children of Andean migrants to the Amazon jungle with children living in the Andes. Those reared in the jungle were more linear, the length of the extremities clearly greater. Dietary factors, parasitic infection, or selective migrations could play some critical role; however, the lengthening of extremity in tropical areas is part of a developmental process. This corresponds to evidence from animal studies. Whittow (105) describes pigs reared outdoors in a cold environment as having shorter legs than littermates reared within a heated enclosure. The mechanism is probably blood flow to the developing extremities. In the cold, body thermal balance takes precedence, so blood flow is reduced and full genetic potential is not reached. In a warm environment the full potential is realized.

A linear body build is of advantage in hot climates if it promotes heat loss; however, this advantage is limited to some conditions. Experimental studies in climatic chambers show body temperature responds most obviously to level of physical activity (51) and that level of physical fitness is more important than surface area to mass proportions (4). During mild heat exposure surface area does provide an advantage for heat loss (92), but as amibient temperature increases, linear individuals may actually be at a disadvantage. At high environmental temperatures, the heat gain via convection and radiation can be greater than the heat loss advantage conferred by the greater surface area, thus a more compact body build may be favored (4).

Despite the simplicity and attractiveness of Bergmann's and Allen's rules for exploration of variation in human body form, a thermal explanation cannot be accepted uncritically. Other factors such as physical activity are more important than body shape during work. Also, body shape can be modified by disease, malnutrition, and other factors; and there also remains the possibility that extremity exposure to cold during the development process is more important than thermal demands during work in shaping final body configuration.

BODY FAT Excess body fat is probably detrimental in hot climates. Heavier individuals are more subject to heat-related death (58) and have greater stress during heat acclimatization (58, 65, 86). Reduced physical activity may be involved, but obesity per se may also play a role. Bar-Or et al (4) studied obese and lean women working in six environmental conditions ranging from cool to hot. In all conditions, the obese women sweated more profusely, stored more heat, and maintained higher heart rate. Fat did not appear to hinder heat transfer from core to shell because skin temperatures were also higher in the obese. The investigators suggested several factors linking obesity to heat tolerance. First and least important was surface area to mass ratio. As noted previously, at higher temperatures the obese obtain some advatage through lower environmental heat gain. Second, adipose tissue has less water than other tissues and hence can absorb less heat. This promotes a greater heat load on nonfat tissue and reduces heat tolerance. Third, obese individuals have lesser cardiovascular fitness than nonobese. Even if there are no pathological problems, obesity leads to an increased blood volume which is distributed to adipose tissue (99). This places greater strain on the cardiovascular system.

SKIN COLOR While skin color seems to vary in response to the ultraviolet level in solar radiation (31), thermobiologists have also considered its potential influence on heat regulation (55). White and dark skin are similar in terms of thermal exchange except, all else being equal, dark skin absorbs 30 to 40% more sunlight than white skin (6, 37). This must be dissipated as heat. Baker (3) reported that when blacks and whites are tested unclothed in the desert, blacks seem to show higher level heat storage than whites, presumably because of greater heat gain via radiation. There has been no confirmation of this observation. The thermal advantage of white skin was slight, and we agree with Blum (6, p. 54), "it seems necessary to assume that the possession of dark skin should be a disadvantage to the Negro, as regards to heat load and life in hot desert areas, but that the disadvantage is not a great one and probably of little importance under his usual condition of life."

ETHNICITY The influence of ethnicity on the ability to tolerate heat has been the subject of much speculation in the anthropological as well as in the popular literature. Implicit has been the assumption that people indigenous to hot environments are better able to tolerate heat than non-natives. The phenomenon of acclimatization has been largely unappreciated and the existing differences magnified. In some cases adaptation to a hot climate has been viewed as an adaptation to solar radiation rather than to heat. European literature, for example, focused upon the "actinic" or "chemical" rays of the sun (76). Protecting fair-skinned residents from these rays required heavy clothing and special spinal pads which simply impaired heat loss. Darker-skinned, less clothed natives tolerated the heat with greater ease.

Only recently have controlled experimental investigations begun to unravel ethnic differences in heat tolerance. People living in all major hot zones have been studied, and we have outlined details of this work in an earlier paper (36). In general, all people studied are capable of acclimatizing and achieving a high level of heat tolerance. This does not mean that all people respond in a similar manner. Some sweat more profusely, some tend toward greater heat storage, but the observed differences are generally small and not important for survival. The conclusions of Strydom & Wyndham (96) are probably still valid: differences in the state of acclimatization are probably more important than any other factor in producing differences in heat tolerance.

With this point in mind, we should consider the one ethnic factor which has emerged in several studies. Well-acclimatized Europeans show a tendency toward higher levels of sweat production than do natives of hot climates in similar states of acclimatization. The reported differences are usually small, but Strydom & Wyndham (96) observed rates of well-acclimatized Europeans to exceed those of similarly acclimatized Bantu by up to 250 cc per hour (Figure 2). The accumulated difference was over 600 cc in 4 hours. If Europeans do indeed perspire more heavily, there are a number of possible causes. One is that the Europeans are drinking more, hence maintaining a higher level of hydration. Alternatively, there may be a more "economical" sweating pattern in indigenes as has been previously suggested. It does not seem to be related to sweat gland density for density of functioning sweat glands does not seem to have an ethnic component (52). Regardless of the locus or even the reality of the phenomenon, Euporeans tolerate heat as well as any other people studied, and the work on ethnic variation has reinforced the view that intense selection for heat tolerance antedates contemporary human ethnic variation.

CONCLUSIONS

Humans are remarkably well adapted to tolerate heat whether derived from environmental or from metabolic sources. This adaptation apparently developed early in hominid evolution and permitted successful colonization of

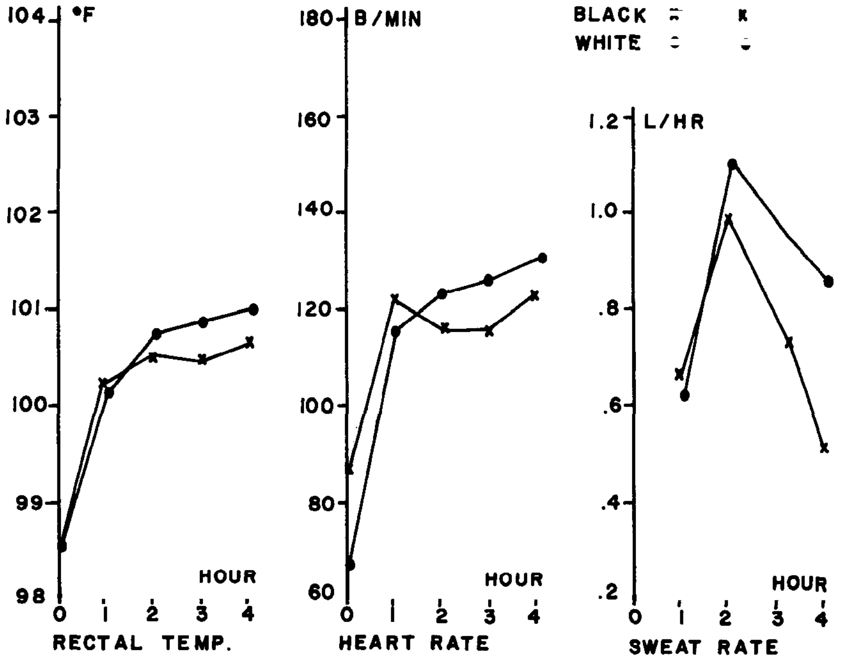

Figure 2 Ethnic differences in response to heat are seen when well-acclimatized black and white men are compared in a hot environment. The white men sweat more profusely, but maintain similar core temperatures and heart rates. These data are presented by Strydom & Wyndham (96). Other studies have yielded similar—but less extreme—differences.

savanna and other hot environments. Apparently, the selective pressures were very stong and included a behavioral component with high levels of physical activity. The major adaptation was a high-capacity sweating response, an improvement upon specialized sweat glands existing in the order Primates. The adaptation came with a price, however: the necessity for a reliable daily water supply. We have speculated that the necessity for water may have contributed to the establishment of a home base for hominid social groups. This base, in turn, may have been a critical factor in human sociocultural evolution.

In contemporary humans, cultural activities are an important means for adjustment to many environmental problems, yet biological adaptations seem of primary importance in adaptation to heat. These include cardiovascular adjustments and diversion of blood flow to surface areas which facilitate heat loss accompanied by active sweating and evaporative heat loss. Repeated exposure results in improvement in the system with a quicker onset, higher rate and increased sweating capacity. It is this ability to acclimatize found in all humans which accounts for most of the individual variation in response to heat.

Literature Cited

1. Adolph, E. F. 1947. The human body and the desert. In *Physiology of Man in the Desert*, ed. E. F. Adolph et al, pp. 16–32. New York: Wiley
2. Adolph, E. F. 1949. Desert. In *The Physiology of Heat Regulation and the Science of Clothing*, ed. L. W. Newburg, pp. 330–38. Philadelphia: Saunders
3. Baker, P. T. 1958. Racial differences in heat tolerance. *Am. J. Phys. Anthropol.* 16:282–305
4. Bar-Or, O., Lundergren, H. M., Buskirk, E. R. 1969. Heat tolerance in exercising and obese women. *J. Appl. Physiol.* 26:403–9
5. Belding, H. S., Hatch, T. F. 1963. Relation of skin temperature to acclimatization and tolerance to heat. *Fed. Proc.* 22:881–83
6. Blum, H. F. 1961. Does the melanin pigment of human skin have adaptive value? *Q. Rev. Biol.* 36:50–63
7. Bonnefille, R. 1976. Palynological evidence for an important change in the vegetation of the Omo basin between 2.5 and 2 million years ago. In *Earliest Man and Environments in the Lake Rudolf Basin*, ed. Y. Coppens et al, pp. 421–31. Chicago: Univ. Chicago Press
8. Briggs, L. C. 1975. Environment and human adaptation in the Sahara. In *Physiological Anthropology*, ed. A. Damon, pp. 93–129. New York: Oxford Univ. Press
9. Budd, G. M., Fox, R. H., Hendrie, A. L., Hicks, K. E. 1972. A field survey of thermal stress in New Guinea villages. *Philos. Trans. R. Soc. London Ser. B* 268:393–400
10. Burnet, M., White, D. O. 1972. *Natural History of Infectious Disease*. Cambridge: Cambridge Univ. Press. 4th ed.
11. Burton, A. C., Edholm, O. G. 1955. *Man in a Cold Environment*. London: Arnold
12. Carr, C. J. 1976. Plant ecological variation and pattern in the lower Omo basin. See Ref. 7, pp. 432–67
13. Champion, R. H. 1970. Sweat glands. In *An Introduction to the Biology of the Skin*, ed. R. H. Champion, T. Gillman, A. J. Rook, R. T. Simms, pp. 175–83. Philadelphia: Davis
14. Clark, J. D. 1980. Early human occupation of African savanna environments. See Ref. 38, pp. 41–71
15. Cloudsley-Thompson, J. L. 1964. Terrestrial animals in dry heat: Introduction. In *The Handbook of Physiology, Vol. 4: Adaptation to the Environment*, ed. D. B. Dill, pp. 447–50. Baltimore: Williams & Wilkins
16. Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–10
17. Coon, C. S. 1955. Some problems of human variability and natural selection in climate and culture. *Am. Nat.* 89:257–80
18. DeVore, I. 1964. The evolution of social life. In *Horizons in Anthropology*, ed. S. Tax, pp. 25–36. Chicago: Aldine
19. Dill, D. B., Consolazio, F. C. 1962. Responses to exercise as related to age and environmental temperature. *J. Appl. Physiol.* 17:645–48
20. Eckert, E. R. G., Drake, R. M. Jr. 1972. *Analysis of Heat and Mass Transfer*. New York: McGraw-Hill
21. Edholm, O. G., Fox, R. H., McPherson, R. 1957. Vasomotor control of cutaneous blood vessels in the forearm. *J. Physiol.* 139:455–65
22. Edholm, O. G., Weiner, J. S. 1981. Thermal physiology. In *The Principles and Practice of Human Physiology*, ed. O. G. Edholm, J. S. Weiner. London: Academic
23. Eichna, L. W., Park, C. R., Nelson, N., Horvath, S. M., Palmes, E. D. 1950. Thermal regulation during acclimatization to a hot dry environment. *Am. J. Physiol.* 163:585–87
24. Ellis, F. P. 1972. Mortality from heat illness and heat-aggrevated illness in the United States. *Environ. Res.* 5:1–58
25. Eveleth, P. B. 1966. The effects of climate on growth. *Ann. NY Acad. Sci.* 134:750–59
26. Fitzpatrick, E. A. 1979. Radiation. In *Arid-Land Ecosystems: Structure, Functioning and Management*, ed. D. W. Goodall, R. A. Perry, 1:347–72. Cambridge: Cambridge Univ. Press
27. Folk, G. E. 1976. *Textbook of Environmental Physiology*. Phildelphia: Lea & Febiger
28. Fox, R. H. 1965. Heat. In *The Physiology of Human Survival*, ed. O. G. Edholm, A. L. Bacharach, pp. 53–80. London: Academic
29. Fox, R. H., Goldsmith, R., Hampton, I., Hunt, T. 1967. Heat acclimatization by controlled hyperthemia in hot dry and hot wet climates. *J. Appl. Physiol.* 22: 39–46
30. Fox, R. H., Loftedst, B., Woodward, P., Eriksson, E., Werkstrem, B. 1969. Comparison of thermoregulatory function in men and women. *J. Appl. Physiol.* 26: 444–53

31. Frisancho, A. R. 1979. *Human Adaptation*. St. Louis: Mosby
32. Gates, D. M. 1980. *Biophysical Ecology*. New York: Springer
33. Gisolfi, C., Robinson, S. 1969. Relation between physical training, acclimatization and heat tolerance. *J. Appl. Physiol.* 26:530–34
34. Givoni, G. 1974. Biometeorological indices. In *Progress in Biometeorology. Vol. 1, Part 1A. Micro- and Macro-Environments in the Atmosphere: Their Effects on Basic Physiological Mechanisms of Man*, ed. S. W. Tromp, pp. 138–45. Amsterdam: Swets & Zeitlinger BV
35. Goldman, R. 1978. Prediction of human heat tolerance. In *Environmental Stress: Individual Human Adaptations*, ed. L. J. Folinsbee, J. A. Wagner, J. F. Borgia, B. L. Drinkwater, J. A. Gliner, J. F. Bedi, pp. 53–70. New York: Academic
36. Hanna, J. M., Brown, D. E. 1979. Human heat tolerance: Biological and cultural adaptations. *Yearb. Phys. Anthropol.* 22:163–86
37. Hardy, J. D. 1949. Heat transfer. See Ref. 2, pp. 78–108
38. Harris, D. R. 1980. Tropical savanna environments: definition, distribution, diversity, and development. In *Human Ecology in Savanna Environments*, ed. D. R. Harris, pp. 3–27. London: Academic
39. Healy, J. R. 1968. *Inventory of Research on Desert Regional Types*. Tucson: Office Arid Lands Stud., Univ. Ariz.
40. Henschel, A. 1964. Minimal water requirements under conditions of heat and work. In *Thirst*, ed. M. J. Wayner, pp. 19–28. New York: Macmillan
41. Henschel, A., Coppola, S. A. 1972. *Occupational Exposure to Hot Environments*. Washington DC: US Dep. HEW
42. Henschel, A., Hanson, H. E. 1959. Heat stress in a desert environment. *Proc. Am. Soc. Mech. Eng.* 210:1–4
43. Hey, E., Katz, G. 1969. Evaporative water loss in the newborn baby. *J. Physiol.* 210:1–4
44. Hofler, W. 1968. Changes in regional distribution of sweating during acclimatization to heat. *J. Appl. Physiol.* 25: 503–6
45. Horstman, D. H., Christensen, E. 1982. Acclimatization to dry heat: Active men vs active women. *J. Appl. Physiol.* 52: 825–31
46. Incropera, F. P., DeWitt, D. P. 1981. *Fundamentals of Heat Transfer*. New York: Wiley
47. Johnson, G. S., Elizondo, R. S. 1975. A thermal balance study in *Macaca mulatta* before and after heat acclimatization. *Fed. Proc.* 34:455 (Abstr.)
48. Johnson, G. S., Elizondo, R. S. 1979. Thermoregulation in *Macaca mulatta:* a thermal balance study. *J. Appl. Physiol.* 46:268–77
49. Kamon, E., Avellini, B. 1979. Responses to heat of men and women equal in surface area and aerobic capacity. *Fed. Proc.* 38:1296. (Abstr.)
50. Kennedy, G. E. 1980. *Paleo-Anthropology*. New York: McGraw-Hill
51. Kerslake, D. M. 1972. *The Stress of Hot Environments*. Cambridge: Cambridge Univ. Press
52. Knip, A. S. 1977. Ethnic studies on sweat gland counts. In *Physiological Variation and its Genetic Basis*, ed. J. S. Weiner, pp. 113–23. New York: Halsted
53. Kuno, Y. 1956. *Human Perspiration*. Springfield: Thomas
54. LaBarre, W. 1964. Comments on the human revolution. *Curr. Anthropol.* 5: 147–50
55. Ladell, W. S. S. 1964. Terrestrial animals in humid heat: Man. See Ref. 15, pp. 625–59
56. Lee, D. H. K. 1964. Terrestrial animals in dry heat: Man. See Ref. 15, pp. 551–82
57. Leibert, J., Candas, V., Vogt, J. 1979. Effect of rate of change in skin temperature on local sweating rate. *J. Appl. Physiol.* 46:306–11
58. Leithead, C. S., Lind, A. R. 1964. *Heat Stress and Heat Disorders*. Phildelphia: Davis
59. LeMaho, V., Goffart, M., Rochas, A., Felbabel, H. 1981. Thermal regulation in the only nocturnal Simian: the night monkey *Aotus trivirgatus*. *Am. J. Physiol.* 240:R156–65
60. Lind, A. R., Bass, D. E. 1963. Optimal exposure for development of heat acclimatization. *Fed. Proc.* 22:705–8
61. Lovejoy, C. O. 1981. The origin of man. *Science* 211:341–50
62. Lowry, W. P. 1969. *Weather and Life*. New York: Academic
63. Marriott, H. L. 1950. *Water and Salt Depletion*. Springfield: Thomas
64. McGinnies, W. G. 1979. Arid-land ecosystems—common features throughout the world. See Ref. 26, pp. 299–316
65. Minard, D., Copman, L. 1963. Elevation in Body Temperature. In *Health in Temperature: Its Measurement and Control in Science and Industry*, ed. J. D. Hardy, pp. 527–43. New York: Reinhold
66. Montagna, W. 1962. *The Structure and Function of Skin*. New York: Academic

67. Montagu, M. F. A. 1964. Natural selection and man's relative hairlessness. *J. Am. Med. Assoc.* 187:356–57
68. Moran, E. F. 1982. *Human Adaptability*. Boulder, Colo: Westview Press
69. Newman, L. M., Commings, E. G., Miller, J. H., Wright, M. 1970. Thermoregulatory responses of baboons exposed to heat stress and scopolamine. *Physiologist* 13:217–18
70. Newman, R. W. 1970. Why is man such a sweaty, thirsty, naked animal: a speculative review. *Hum. Biol.* 42:12–27
71. Nieuwolt, S. 1977. *Tropical Climatology*. London: Wiley
72. Paolone, A. M., Wells, C. L., Kelly, G. T. 1978. Sexual variations in thermoregulation during heat stress. *Aviat. Space Environ. Med.* 49:715–19
73. Perkins, E. M. 1975. Phylogenetic significance of the skin of New World monkeys. *Am. J. Phys. Anthropol.* 42: 395–424
74. Piwonka, R., Robinson, S. 1967. Acclimatization of highly trained men to work in severe heat. *J. Appl. Physiol.* 22:2–12
75. Piwonka, R., Robinson, S., Gay, V., Manalis, L. 1965. Preacclimatization of men to heat by training. *J. Appl. Physiol.* 20:379–84
76. Planalp, J. M. 1971. *Heat Stress and Culture in North India*. Spec. Tech. Rep. US Army Inst. Environ. Med., Natick, Mass.
77. Rapoport, A. 1969. *House Form and Culture*. Englewood Cliffs, NJ: Prentice Hall
78. Roberts, D. F. 1972. *Climate and Human Variability*. Reading, Mass: Addison-Wesley
79. Robertshaw, D. R. 1979. Apocrine glands. In *Dermatology in General Medicine*, ed. T. B. Fitzpatrick, A. Z. Eisen, K. Wolff, I. M. Friedberg, K. F. Austey, pp. 118–21. New York: McGraw Hill
80. Robinson, S. 1949. Tropics. See Ref. 2, pp. 338–50
81. Robinson, S. 1972. Cardiovascular and respiratory reactions to heat. In *Physiological Adaptations*, ed. M. K. Yousef, S. M. Horvath, R. W. Bullard, pp. 77–98. New York: Academic
82. Robinson, S., Belding, H. S., Consolazio, F. C., Horvath, S. M., Turrell, E. S. 1965. Acclimatization of older men to work in heat. *J. Appl. Physiol.* 20:583–86
83. Robinson, S., Robinson, A. H. 1954. Chemical composition of sweat. *J. Physiol.* 34:202–20
84. Roddie, I., Shepard, J., Whelan, R. 1957. The contribution of constrictor and dilator nerves to skin vasodilation during body heating. *J. Physiol.* 136:489–97
85. Rosenberg, N. J. 1974. *Microclimate: The Biological Environment*. New York: Wiley
86. Ross, F. 1966. Medical problems related to the hostile environment, III: problems related to heat. *Southwest. Med.* 47:137–48
87. Rowell, L. B. 1974. Human cardiovascular adjustments to exercise and thermal stress. *Physiol. Rev.* 54:75–159
88. Rowell, L. B. 1978. Human adjustments and adaptations to heat stress—where and how? See Ref. 35, pp. 1–27
89. Sato, K. 1977. The physiology, pharmacology and biochemistry of the eccrine sweat gland. *Rev. Biochem. Physiol. Pharmacol.* 79:51–132
90. Schmidt-Nielsen, K. 1964. *Desert Animals*. Oxford: Oxford Univ. Press
91. Shapiro, Y., Pandolf, K. B., Avellini, B. A., Pimentel, N. A., Goldman, R. F. 1980. Physiological responses of men and women to humid and dry heat. *J. Appl. Physiol.* 49:1–8
92. Shvartz, E., Shapiro, Y., Magazanik, A., Meroz, A., Birnfeld, H., et al. 1977. Heat acclimatization, physical fitness and responses to exercise in temperate and hot environments. *J. Appl. Physiol.* 43:678–83
93. Stinson, S., Frinsancho, A. R. 1978. Body proportions of highland and lowland Peruvian Quechua children. *Hum. Biol.* 50:57–68
94. Stitt, J. T., Hardy, J. D. 1971. Thermoregulation in the squirrel monkey. *J. Appl. Physiol.* 31:48–54
95. Straus, W. L. 1950. Microscopic anatomy of the skin of the gorilla. In *Anatomy of the Gorilla*, ed. W. K. Gregory, pp. 214–21. New York: Columbia Univ. Press
96. Strydom, N. B., Wyndham, C. H. 1963. Natural state of heat acclimatization of different ethnic groups. *Fed. Proc.* 22: 801–9
97. Terjung, W. H., Louie, S. S.-F. 1971. Potential solar radiation climates of man. *Ann. Assoc. Am. Geogr.* 61:481–500
98. Van Couvering, J. A. H., Van Couvering, J. A. 1976. Early Miocene fossils from East Africa: Aspects of geology, faunistics and paleoecology. In *Human Origins: Louis Leakey and the East African Evidence*, ed. G. L. Isaac, E. R. McCown, pp. 155–207. Menlo Park, Calif: Benjamin
99. Vaughan, R. W., Conahan, T. J. 1980. Cardiopulmonary consequences of morbid obesity. *Life Sci.* 26:1–9

100. Walton, K. 1969. *The Arid Zones*. Chicago: Aldine
101. Weiner, J. S. 1971. *The Natural History of Man*. Garden City, NY: Doubleday Anchor
102. Weiner, J. S. 1977. Human ecology. In *Human Biology*, ed. G. A. Harrison, J. S. Weiner, J. M. Tanner, N. S. Barnicot, pp. 389–484. New York: Oxford
103. Weiner, J. S. 1977. Variation in sweating. See Ref. 52, pp. 125–37
104. Weinman, K., Slabochora, Z., Bernaur, E., Morimoto, T., Sargent, F. 1967. Reactions of men and women to repeated exposures to humid heat. *J. Appl. Physiol*. 22:533–38
105. Whittow, G. C. 1973. Evolution of thermoregulation. In *Comparative Physiology of Thermoregulation*, ed. G. C. Whittow, 3:202–58. New York: Academic
106. Wulsin, F. R. 1949. Adaptations to climate among non-European peoples. See Ref. 2, pp. 3–69
107. Wyndham, C. H., Benade, A. J. S., Williams, C. G., Strydom, N. B., Goldin, A., Heynes, A. J. 1968. Changes in central circulation and body fluid spaces during acclimatization to heat. *J. Appl. Physiol*. 25:586–93
108. Wyndham, C. H., Morrison, J. F., Williams, C. G. 1965. Heat reaction of male and female Caucasians. *J. Appl. Physiol*. 20:357–64

Annual Review of Anthropology
Volume 12, 1983

CONTENTS

(*Continued*)

CULTURAL-SOCIAL ANTHROPOLOGY

INDEXES