RESISTANCE TO HEAT IN MAN AND OTHER ANIMALS

Duncan Mitchell

Human Sciences Laboratory, Chamber of Mines of South Africa, Johannesburg

Of the many adverse effects of heat stress in animals, those particularly important in animal production are the effects on metabolism and reproduction (Hafez, 1968). When the body temperature of domestic animals, especially those subjected to intensive feeding, rises, appetite declines and metabolic rate drops. As a result of the lower metabolic rate, growth rate is depressed. Under controlled conditions in a group of four calves of the same breed and age, Bianca (1963) found that the calf which exhibited the lowest rectal temperature during experimental heat stress also gained weight at a rate 30 per cent higher than the rate of the calf which exhibited the highest rectal temperature. Milk and egg production are also influenced by low metabolic rate. Milk production in dairy cows adapted to European climates falls off if the ambient temperature exceeds 20°C (Hafez, 1968; Bianca, 1971).

Intolerance of high environmental heat stress adversely affects reproduction in a number of ways (Brown, 1971; Bianca 1970). Male animals lose fertility as a result of damage to spermatozoa and reduction in libido. The fertilization rate of females declines. Fewer embryos reach maturity, and those that do survive tend to result in miniature offspring.

This paper deals with the basic physiological mechanisms underlying resistance to heat. Hopefully, it will also demonstrate how animal species can differ in their heat tolerance, and how, within one species, individual animals may exhibit different degrees of reaction to heat. The paper is biassed towards man and the other large mammals, and towards research carried out in the Human Sciences Laboratory of the Chamber of Mines of South Africa.

The problem of resistance to heat will be approached from the point of view of control systems. The control approach may seem unnecessarily complex, but negative feedback control of body temperature is common to all animals which regulate their temperature. For a completely different approach to the problem of resistance to heat and a review which includes many aspects omitted here, the reader is referred to a paper by Belding (1969).

Negative feedback control

A negative feedback control system, when subjected to a disturbing influence, reacts in such a way as to oppose the effect of the disturbance. All negative feedback control mechanisms have certain common characteristics. These characteristics are shown in Figure 1.

A disturbance acting on the body being controlled will cause some parameter to depart from its prevailing value. Sensors detect that the parameter has changed. Information about the change is generated. The "feedback" information is compared with reference information. The

difference between the feedback information and the reference information is known as the error signal. It is the error signal which determines the magnitude of the corrective action of the control system. The error signal stimulates some control elements to generate control actions. The control actions, acting on the controlled system, oppose the effect of the disturbance.
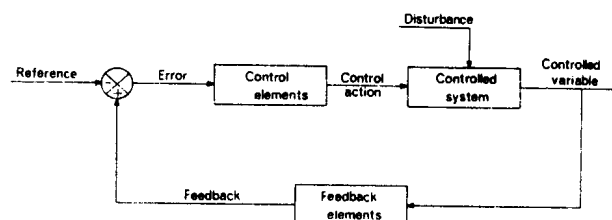

Fig. 1. – *Negative feedback control system* (from Mitchell, D., Snellen, J.W. & Atkins, A.R., 1970, by courtesy of Springer-Verlag).

The negative feedback control system of Fig. 1 serves as an adequate basic model for many biological control systems, including the control of body temperature. A variety of animals, when threatened by a thermal disturbance which tends to change their body temperature, will undertake some corrective action to oppose the effects of the disturbance. The action may be predominantly behavioural (Heath, 1970). Some desert reptiles, for example, will continually adjust their positions to achieve exposure to such a combination of sun and shade that their body temperature stays remarkably constant over many hours of the day (Cloudsley-Thompson, 1971).

The characteristics of behavioural temperature regulation are also found in highly developed animals. Man attempts to avoid exposing his naked body to extremes of heat and cold by the use of clothing. However, in the higher animals, and particularly in birds and mammals, conscious behavioural control is heavily supplemented by unconscious control within the body. This unconscious control is known as autonomic temperature regulation.

It is due to differences in the sophistication of the control system that some animals are able to control their body temperature better than others. Also, adaptation to the thermal environment is brought about by appropriate modifications to the control system. Let us therefore discuss the anatomical and physiological counterparts of the actions and elements in Fig. 1, and use them to investigate resistance to heat. First, we need to identify those animals which regulate their body temperatures.

Temperature regulators and conformers

The classification of animals into "warm-blooded"

and "cold-blooded" is one of several categorizations of classical physiology which are no longer tenable. Desert lizards, classically cold-blooded, may indeed have higher blood temperatures than hibernating mammals, which are classically warm-blooded. The alternative terms "homeothermic" and "poikilothermic" are preferable semantically. The homeotherms are those animals in which variations in body core temperature are confined to narrow limits (arbitrarily defined) despite much larger variations in ambient temperature. Poikilotherms, on the other hand, exhibit a large variability of core temperature as a proportional function of ambient temperature.

However, even the terms homeothermic and poikilothermic are not adequate to describe those animals which control their body temperatures and those which do not. Some animals with efficient thermoregulatory systems allow their body temperatures to vary over many degrees. Recently, therefore, it has been proposed that the terms "temperature regulators" and "temperature conformers" be used. Temperature regulators have a core temperature which is regulated to some extent by autonomic and/or behavioural processes. Temperature conformers have core temperatures which follow ambient temperature proportionally.

Vertebrates of all classes can regulate their core temperatures (Stromme, Myhre & Hammel 1971), but even among the mammals, the sophistication of the temperature regulatory system varies a great deal. Modern comparative physiologists describe a full spectrum of systems in mammals ranging from the monotremes to man (Dawson, 1972). It is, however, not possible to predict the nature of the temperature regulatory system simply from the phylogenetic position of the mammal (Robertshaw & Taylor, 1969). It is surprising to find, for example that some primates, for example the Japanese monkey, show little or no autonomic regulatory reactions to heat (Nakayama, Hori, Nagasaka, Tokura & Tadaki, 1971).

One also finds undeniable evidence of deliberate temperature regulation among the invertebrates. Some moths and locusts regulate their patterns of flight and rest to maintain body temperature within about a 5°C range during activity (Heath, 1970; Heath, Hanegan, Wilkin & Heath, 1971). Other insects, for example the cicada, move between sunlight and shade in such a way that body temperature varies only a few degrees (Heath et al., 1971). These insects must be considered temperature regulators, at least during their active periods. One suspects that future research will reveal evidence of temperature regulation among many invertebrates.

While many animals show an ability to regulate their body temperatures at times, surprisingly few can regulate their temperatures all the time. Behavioural regulators can control their body temperatures only within certain environmental limits. Outside these limits they are reduced to a state of torpor in which their thermal reactions are those of temperature conformers. Possession of an autonomic temperature regulatory system does not necessarily confer on an animal the ability to regulate his temperature

continuously under all conditions. Many mammals hibernate. During hibernation the characteristics of autonomic regulation disappear except for an alarm which causes hibernators to wake if their temperatures fall too low (Heller & Hammel, 1971).

Man and the agriculturally important animals are, of course, amongst those whose temperature regulatory systems are active at all times.

Behavioural and autonomic regulation

It is a basic thesis of this paper that all temperature regulation can be described in terms of the negative feedback control system of Fig. 1. Where, then do behavioural and autonomic regulation differ? Clearly, they differ at least in control actions. Sweating, panting and shivering are typical autonomic control actions, whereas changes of posture and changes of position are typical behavioural control actions, Behavioural control actions involve the conscious participation of the animal, autonomic actions do not (Cabanac, 1972). Current evidence suggests that, apart from differences in control actions, behavioural temperature regulation and autonomic temperature regulation are remarkably similar mechanisms (Stitt, Adair, Nadel & Stolwijk, 1971; Hammel, 1971. Cabanac, 1972).

The idle basking of lizard in the sun may seem to the casual observer to be a haphazard means of regulating temperature. However, it has now been amply demonstrated that behavioural regulation is well controlled and leads to body temperature levels being maintained within quite narrow limites. A number of ingenious studies have revealed close relationships between body temperature and such behavioural control actions as grooming in rats (Hainsworth & Stricker, 1970; Stricker & Hainsworth, 1971), positional changes in lizards (Cabanac & Hammel, 1971), postural changes in lizards (De Witt, 1971), voluntary work in rats (Corbit, 1969), and self-actuated changes in thermal conditions in a climatic chamber in monkeys(Carlisle, 1971) and lizards (Regal, 1971).

The controlled system

In temperature regulation, the controlled system is the body of the regulating animal. There are several aspects of body morphology which affect resistance to heat.

The first of these is simply the body mass. A heavy animal has a large thermal inertia (Schmidt-Nielsen, 1962). A given heat load, if uncompensated by the animal, will lead to a bigger temperature rise in a small animal than in a larger one. Small animals are at a distinct disadvantage in hot environments (McNab, 1970). In fact, small animals native to desert environments conscientiously avoid exposing themselves to the heat (Schmidt-Nielsen, 1962).

The second factor relating to body morphology is the ratio of mass to surface area. This ratio is the source of heated arguments among students of evolution, who see, or do not see, a relationship between the shape of certain animals and the climatic conditions under which they have evolved. The influence of the mass-to-surface ratio on resistance to heat cannot be clear-cut. In terms of environ-

mental heat load, an animal with a high mass-to-surface ratio is at an advantage because the ratio between its thermal inertia and its exposed area is high. However, if the heat load has a metabolic origin, rather than an environmental origin, it is an advantage to have a high surface area. At the Human Sciences Laboratory it has been found that small men working in hot humid environments are distinctly more likely to develop high body temperatures than are large men doing the same work, simply because the small men do not have sufficient area to dissipate their metabolic heat (Strydom, Wyndham & Benade, 1971).

A third factor related to body morphology is the extent of insulation offered by the animal's integument. Such insulation may be above or below the skin surface. Insulation below the skin surface impedes the transport of heat from the sites of generation within the body to the body surface. As a result, in many animals exposed to heat, fat deposits are limited to specific areas of the body and is not uniformly distributed subcutaneously (Cloudsley-Thompson. 1971).

Insulation above the skin surface may be an advantage or a disadvantage. It is an advantage provided the animal does not rely for cooling on the evaporation of water from its skin, because the benefit of evaporative cooling is much reduced if the evaporation does not take place on the skin surface (Cloudsley-Thompson, 1971). In unshorn fleeced sheep, for example, surface evaporation is ineffective in cooling the animal (Hofmeyr, Guidry & Waltz, 1969). However, in animals which do not rely on surface evaporative cooling, hair, fur, or feathers may be advantageous in that they offer a barrier to environmental heat load. The barrier is particularly useful when the animal is exposed to radiant heat. Sheep exposed to simulated solar radiation in hot environments show maximum heat tolerance when their fleece is about 40 mm long (Thwaites, 1967). Sheep standing in the sun may develop a temperature gradient in the wool of more than 1 ^{o}C per millimetre. Wool-tip temperatures may exceed 85 ^{o}C but the rate of heat flow through the fleece remains very low (Priestley, 1957).

A further anatomical factor influencing resistance to heat is the nature of the body surface. The surface properties affecting the absorption of radiation are especially important. Shorn white sheep skin absorbs about 60 per cent of the radiation in the wavelengths of the solar spectrum, and fleeced skin 75 per cent (Clapperton, Joyce & Blaxter, 1965). The absorptance of cattle hides varies from about 40 per cent for white hides, to more than 90 per cent for black hides, with red and brown hides absorbing 70 to 80 per cent (Riemerschmid & Elder, 1945; Stewart, 1954; Rhoad, 1940).

Animals with skin of high absorptance do not necessarily suffer the greatest solar heat load. The heat load reaching the skin surface depends not only on absorptance but also on the penetrance of radiation into the hide and the subsequent distribution of heat flow. Kovarik (1964) showed analytically, and Hutchinson & Brown (1969) confirmed experimentally that black hide colour does not necessarily render an animal maximally susceptible to solar

radiation.

The disturbance

Thermal disturbances may be of metabolic or environmental origin. In man, metabolic heat is the predominant source of thermal stress. The calorific value of oxygen in human combustion is about 20 kJ/litre (STPD). In the gold-mining industry, men work continuously for a full shift at a rate which demands an oxygen uptake of 1 litre/min or more (Morrison, Wyndham, Mienie & Strydom, 1968). They therefore develop power at a rate exceeding 300 W, and little, if any, of this power leaves the body in a form other than heat. The heat load on them is equivalent to that which they would experience if they were at rest but were exposed continuously to a still air environment with a temperature of 55 ^{o}C.

It is rare for any animal to maintain for many hours an exercise level such that the metabolic rate is several times the basal metabolic rate. Migrating birds presumably do so, although the energy costs of flying as a form of transport is low (Schmidt-Nielsen, 1971). Hunting dogs and foraging shrews might also do so. Man tolerates sustained high energy consumption as a way of life. His ability to do so is probably related to his extremely high sweating capacity (see below).

Environmental thermal disturbances may be conductive, convective, radiant or related to atmospheric water (Gates, 1968; Porter and Gates, 1969). Conductive heat stress can only be suffered by an animal having a large percentage of its surface area in contact with the ground, such as a snake. Such animals tend to use shade and burrows to avoid contact with hot ground. Convective heat stress requires air temperature higher than body surface temperature, and high air speed. Such air conditions are rare, even during the notorious "hot winds of ill repute" — the Sharav of Israel, the Chamsin of Arab countries, the Foehn of Switzerland or the Santa Ana of Southern California (Sulman, Danon, Pfeifer, Tal & Weller, 1970). Winds having a temperature of 40 ^{o}C and a speed of 35 m/s have been recorded in the Namib desert (G.N. Louw, personal communication), and these winds have a devastating effect on any animal that cannot escape them. Evaporative heat only constitutes a stress in the unusual event of condensation of atmospheric water occurring on an animal. Heat stress due to atmospheric water *per se* can arise in sheep, because the absorption of water by the fleece is an exothermic process (Thwaites 1967).

The most powerful environmental heat load is that associated with solar radiation. Most animals simply avoid exposing themselves to the solar radiation. However, exposure to the sun may be unavoidable in large animals resident in deserts or tropical savannahs.

One might easily believe that the overwhelming component of heat stress during solar radiation is direct short-wave radiation. However, direct solar radiation never strikes more than half the animal, and it is in the solar wavelength range that animals tend to have low absorptance (Kelly, Bond & Heitman, 1954). The importance
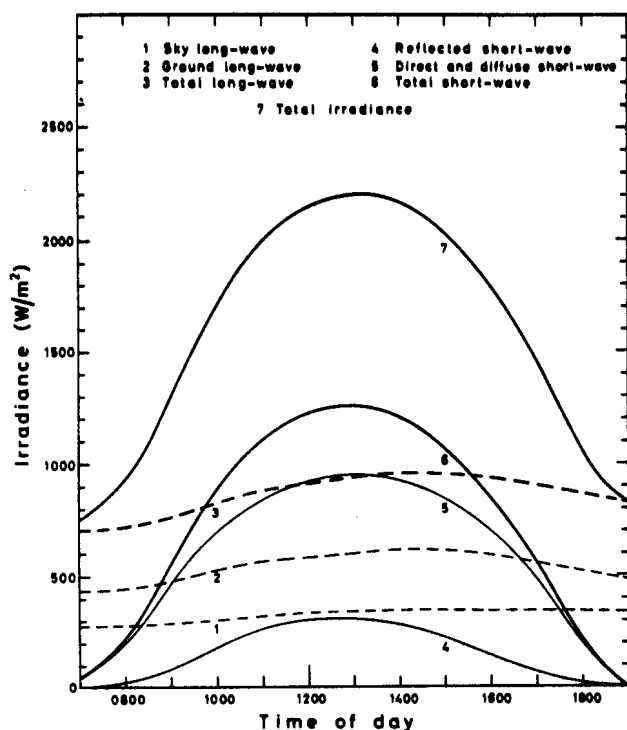
Fig. 2. — *Irradiance on a flat horizontal surface near Nairobi on a typical summer day* (redrawn from Finch, V.A., In press a, by courtesy of Miss Finch and the London Zoological Society).

of long-wave radiation from the ground and sky has been demonstrated recently in two excellent papers by Finch (In press 1972 a, b). She analysed the constitution of the summer radiant heat load near Nairobi at an altitude of 1650 m. Her results are shown in Fig. 2. The contributions of short-wave radiation (direct, diffuse and reflected) and long-wave radiation (air and ground) are about equal. Moreover, long-wave radiation is absorbed completely by all animals whereas many animals reflect a great deal of the short-wave radiation. Miss Finch found that an eland standing in the sun absorbed 40 per cent of the potential impinging radiation and a hartebeest 34 per cent. In the eland short-wave radiation contributed about half to the radiant heat load, but in the hartebeest only one third.

The controlled variable

The aim of temperature regulatory behaviour in animals is presumably the maintenance of the constancy of a body temperature, or combination of temperatures. The particular temperature which is controlled has not yet been identified. Core temperatures are always more stable than peripheral temperatures but this phenomenon is an inevitable consequence of the thermal structure of the body (Mitchell, Atkins & Wyndham, 1972). Body sites which might require rigid temperature control are those in which

a large number of enzymatic reactions occur (e.g. the liver) and those containing high densities of neurones (e.g. the brain).

One way of identifying the controlled variable is to investigate in which of the body sites local heating or cooling induces general control actions. Such experiments have indicated that control actions can be evoked by heating and cooling virtually any site in the body independently (Mitchell et al., 1972; Mitchell, 1972; Ingram & Legge, 1972).

One expects the controlled variable to be stable during thermal balance in all animals. It is therefore surprising to find that the stability of body temperature varies a great deal between animals. It is common experience that the body core temperature in a healthy resting man remains constant within about $1^{\circ}C$. Sheep also have remarkably constant body temperatures (Bligh, Ingram, Keynes & Robinson, 1965). The core temperature of camels, on the other hand, may rise by $6^{\circ}C$ between morning and evening (Schmidt-Nielsen, 1962). In the eland, the daily rise in core temperature may be between $3^{\circ}C$ (Bligh & Harthoorn, 1965) and $6^{\circ}C$ (Taylor, 1969 a).

The lability of body temperature in animals resident in arid areas probably reflects a mechanism by which water is conserved by using body mass as a thermal buffer (Schmidt-Nielsen, 1962). A camel may weigh 500 kg and an eland 1000 kg. A body temperature rise of $5^{\circ}C$ results from the storage of about 8000 and 16000 kJ respectively. If the heat had to be dissipated by evaporative cooling, rather than stored and dissipated at night by non-evaporative means, 3 and 6,5 kg of water would be required respectively.

In man and most other animals, elevation of tissue temperature above about $40^{\circ}C$ for several hours results in irreversible tissue damage and often in death. However, some animals have a remarkable ability to withstand high tissue temperatures. A rectal temperature above $45^{\circ}C$ for eight hours has been recorded in the oryx (gemsbok), without any apparent damage to the animal (Taylor, 1969b).

Feedback and integration

Investigation of the structure and function of neural pathways probably constitutes the most active field of research in temperature regulation today. Only a few aspects can be mentioned in this review. The reader is referred to other recent reviews for further details (Bligh, 1966; Hammel, 1968; Mitchell et al., 1972; Mitchell, 1972).

It is striking how similar the neural mechanisms are, in anatomy and physiology, in all types of temperature regulators. Neurones specifically sensitive to temperature have been found in temperature regulators ranging from lizards and fish (Hammel. 1971; Greer & Gardner, 1970; Hensel & Nier, 1971) to man (Hensel & Boman, 1960). The temperature sensors fall into two populations: those which respond with increased firing rate to increasing temperature, and those which respond to decreasing temperature. Although it has never been proved that these

154

sensors are involved in temperature regulation, they have the desirable properties. They provide neural information which is a sensitive and unambiguous measure of local temperature.

The afferent neural signals are collected and integrated in the central nervous system. In autonomic regulation, the integration is performed predominantly in the hypothalamus (Bligh, 1966), which contains a high density of temperature-sensitive neurones. Small local lesions in the hypothalamus destroy an animal's ability to regulate its temperature. Slight local heating or cooling of the hypothalamus evokes the full range of regulatory control actions, autonomic and behavioural. The cerebral pathways involved in behavioural regulation are not yet known.

Certain amines are involved in the processing of neural information in the hypothalamic area (Hellon, 1972). Of these, the most important are acetylcholine, noradrenaline, and 5-hydroxytryptamine. It is not yet known whether these amines are involved directly as neurotransmitters.

Whatever the mechanism of integration, efferent neural impulses are produced which are sufficient to stimulate the various control actions. In the case of autonomic regulation, efferent impulses are transported predominantly by sympathetic pathways (Hemingway & Price, 1968).

A control system such as that displayed in Fig. 1 is misleading in that it suggests that only one feedback pathway is involved in temperature regulation. There are in fact multiple pathways (Mitchell, et al., 1972). Some pathways serve to provide local modulation of central effects (Mitchell, et al., 1972; Mitchell, 1972). Others are independent local pathways. For example, sweating can be induced in some animals by an entirely peripheral mechanism (Jenkinson, 1969; Murray, 1966) and thus short-circuit the main feedback control system.

Control actions

The control actions exhibited by temperature regulators subject to heat stress are peripheral vasodilatation, sweating, panting, heat avoidance and a variety of other behavioural phenomena. Because of their relevance to man and the animals of agricultural importance, panting and sweating will be emphasized here.

Sweating and panting are means of cooling which employ the high latent heat of evaporation of water. Evaporating sweat in man has a latent heat of about 43 W min/g, slightly higher than that of pure water (Snellen, Mitchell & Wyndham, 1970). Sweating takes place from the skin surface and requires an adequate transfer of heat from body core to periphery. It is essentially an isothermal process (Mitchell, 1972) and thus precludes the attainment of high skin temperatures. During intense environmental heat stress, high skin temperature is an advantage because it reduces the heat load and increase re-radiation and convection to the environment (Finch, in press b). Panting involves evaporation from the respiratory tract. Some animals which pant rather than sweat may exhibit skin temperatures higher than core temperatures during hot periods of the day (Finch, in press b).

Man is a prodigious sweater. He can produce 35 g/m^2 min for short periods and 6 g/m^2 min for 24 hours (Belding, 1967). Sweating is considered to be a major avenue of cooling in cattle, but their glands can produce a maximum of about 3 g/m^2 min (McLean, 1963).

The ability of an animal to sweat is not related to phylogenetic position. Many non-primates sweat. Amongst primates, the baboon appears to sweat in much the same way as man does (Newman, Cumming, Miller & Wright, 1970), but the Japanese monkey not at all (Nakayama et al., 1971). The employment of sweating may be related
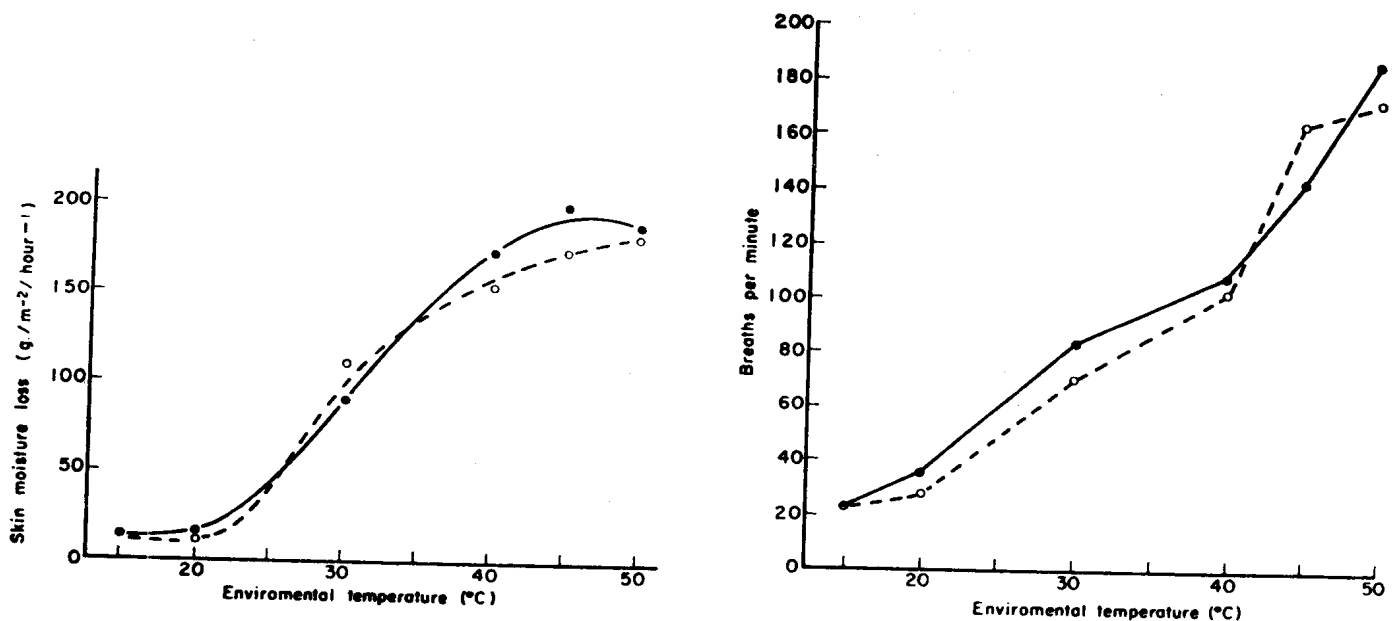

Fig. 3. — *Skin moisture loss (left hand diagram) and respiratory rate (right hand diagram) of new-born (solid circles) and year-old (open circles) calves at various environmental temperatures* (from Bianca, W. & Hales, J.R.S., 1970, by courtesy of Dr. Bianca & Baillière, Tindal & Cox).

to body size (Robertshaw & Taylor, 1969) although anomalies exist; the impala sweats (Maloiy & Hopcraft, 1971) but the wildebeest does not (Taylor, Robertshaw & Hofmann, 1969).

The existance of sweat glands does not imply that sweating is employed as a control action in temperature regulation (Jenkinson, 1969). Pigs have sweat glands but apparently do not sweat. Sheep sweat (Robertshaw, 1968) but it is doubtful whether their sweating has significance in temperature regulation (Hofmeyr et al, 1969). Only in man and a few other species (equines, camels, and rhinoceroses) are the sweat glands themselves innervated, and only in these species is sweating well controlled (Robertshaw, 1971).

Many animals both sweat and pant. These include cattle and several antelope (Taylor, Robertshaw & Hofmann, 1969; Taylor, Spinage & Lyman, 1969; Taylor 1969; Maloiy and Hopcraft, 1971). In animals which sweat and pant, both mechanisms are well regulated control actions, as Bianca & Hales (1970) have demonstrated in calves (Fig. 3).

Some animals do not sweat at all, but only pant. Typical among these are all the birds and the dog. Panting, as a means of evaporative cooling, is only inferior to sweating in those animals, such as man, which undergo sustained activity (Cloudsley-Thompson, 1971). Under resting conditions in hot environment wildebeest, which do not sweat at all, are no less heat tolerant than indigenous zebu cattle, which both pant and sweat (Taylor, Robertshaw & Hofmann, 1969).

Man does not pant. If he hyperventilates, he loses too much carbon dioxide in his lungs and soon develops respiratory alkalosis. Panting animals employ various techniques for minimising alkalosis. Dogs can contain the additional air flow required during panting to the upper respiratory tract (Schmidt-Nielsen, Bretz & Taylor, 1970). Wildebeest increase their effective dead space during panting (Taylor, Robertshaw & Hofmann, 1969). Cattle rapidly compensate for respiratory alkalosis by increased excretion of alkali in urine (Bianca, 1955).

It is therefore in the nature of the control actions that temperature regulators differ most. It seems that all temperature regulators have a neural network adequate to control their actions to heat. The success of their resistance to heat depends on the power of their control actions.

Modifications to control during growth and acclimatization

The control system in temperature regulators is subject to many types of modification, some normal and some pathological. Everyone is familiar with the pathological state known as fever, which is characterized by a sustained elevation in body temperature. There are two normal modifications which should be mentioned in this review. They are those associated with growth from the young animal to the adult, and with acclimatization.

Growth

The temperature regulatory system of a young animal often differs markedly from that of the adult. Bianca (1970) has pointed out a number of general differences between the young of various temperature regulators and their respective adults. Compared to the adult, young animals tend to have:

i) a smaller mass-to-surface ratio,
ii) poor thermal insulation
iii) a high metabolic rate,
iv) a large extracellular fluid volume,
v) a high vulnerability of dehydration,
vi) a higher sweat gland density,
vii) a greater plasticity of response.

The "greater plasticity of response" refers to his observation that strong thermal reactions, and large deviations in body temperature are much better tolerated by young animals than by adults. It is common experience that human children can, without apparent distress, run temperatures that would be extremely debilitating in adults.

The higher sweat gland density arise from the fact that the number of sweat glands apparently does not change after birth. Increase in surface area therefore results in a lower gland density.
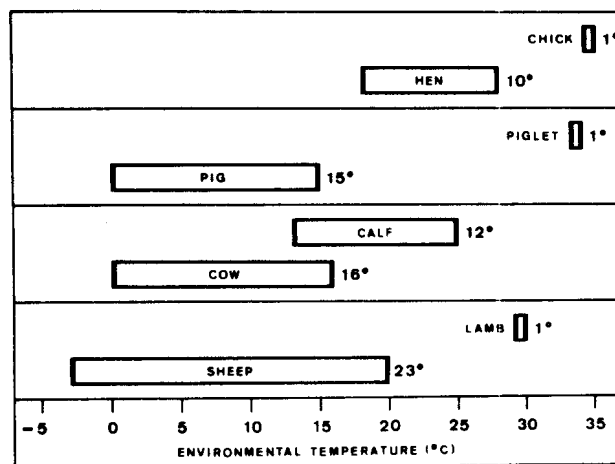

Fig. 4. — *Zones of thermal indifference for newborn and adults of four species* (from Bianca, W., 1970, by courtesy of Dr. Bianca and the International Journal of Biometeorology).

It is very important for those responsible for the husbandry of young animals to realise that the so-called "zone of thermal indifference" differs between young and adult. The zone of thermal indifference is the range of ambient temperatures associated with neither an increase in metabolism nor an increase in evaporation. Fig. 4, taken from Bianca (1970), shows the zones of thermal indifference for various animals. Notice, for instance, that adult sheep are thermally neutral over a wide range of temperatures extending to below freezing, whereas newborn lambs are neutral only over a 1°C range at 29°C.

Acclimatization

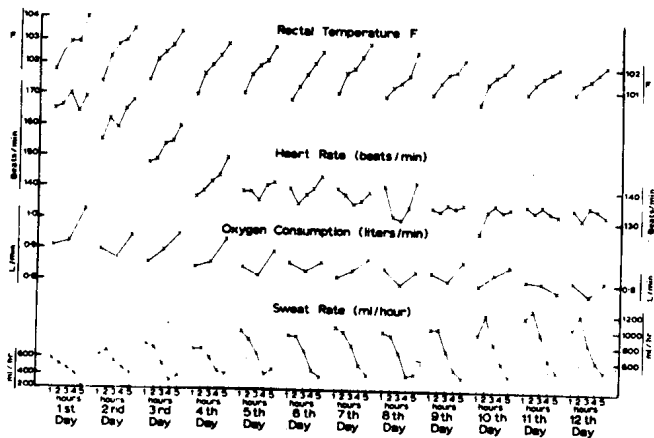Repeated exposure of an animal to high heat stress

Fig. 5. — *Typical acclimatization responses of working men exposed for five hours daily to hot humid environments* (from Strydom, N.B., *et al.*, 1966, by courtesy of Dr. Strydom and the American Physiological Society).
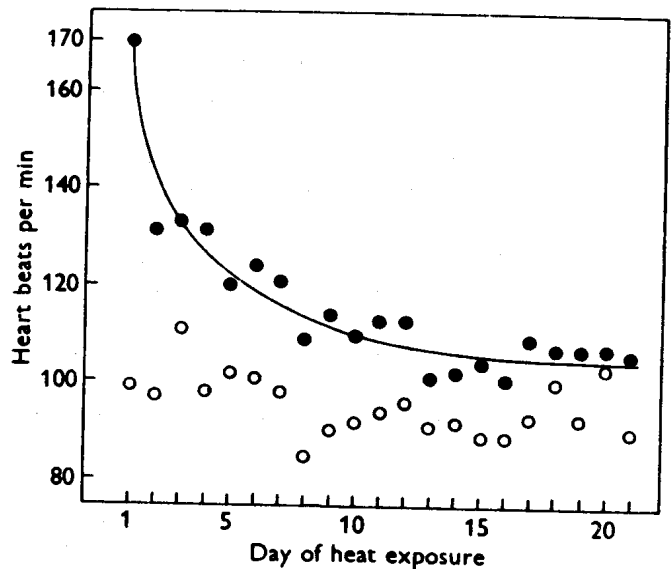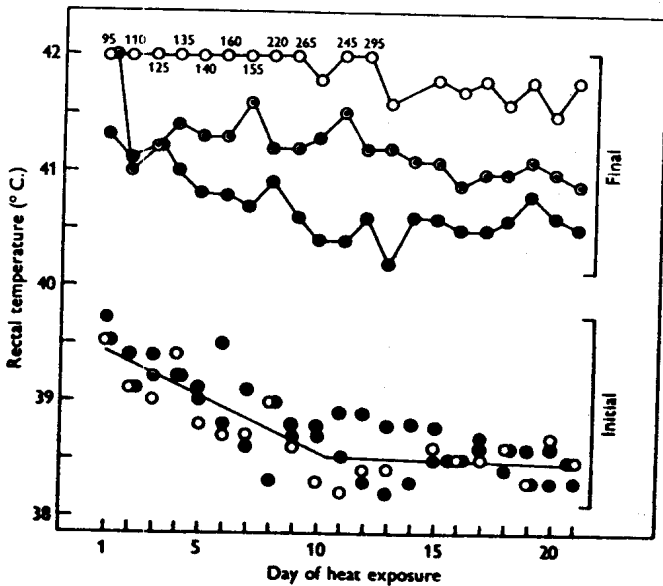
A great deal of research has been conducted into the physiological mechanisms of acclimatization in man and many other animals (Chaffee & Roberts, 1971). Fig. 5 shows the typical acclimatization response observed in working men exposed to humid heat at the Human Sciences Laboratory (Strydom, Wyndham, Williams, Morrison, Bredell, Benade & von Rahden, 1966). The important features are the increased sweat rate and the reduced heart rate, oxygen consumption and body temperature both before and during exposure to heat. Figure 6, from Bianca (1969), shows similar responses in calves exposed to heat.

Probably the most important single physiological adjustment in acclimatization, at least in man, is the stabilization of blood volume during heat stress. An unacclimatized man exposed to heat stress suffers the disastrous combination of peripheral vasodilation, and a loss of plasma volume (by sweating). Circulatory instability results. During acclimatization blood volume is increased. The mechanisms are not yet clear but are probably more related to protein shifts (Senay, 1970) than to the activity of hormones such as aldosterone and ADH.

Fig. 6. — *Rectal temperatures (left hand diagram and heart rates (right hand diagram, initial open, final solid) of three calves at the beginning and end of a 5 hr heat exposure, on 21 consecutive days* (from Bianca, W., 1959, by courtesy of Dr. Bianca and the Cambridge University Press).

generally leads to a progressive increase in the sensitivity of the temperature regulatory system and a reduction in the body temperature and circulatory strain (Wyndham, 1969). This process is known as acclimatization or acclimation. Continuous exposure of many generations of an animal species to heat stress leads, by genetic selection, to a population which, on average, is more heat tolerant. The latter process is adaptation. Ironically, natural adaptation to heat often results in an animal which is agriculturally less useful, while improvement of the agricultural properties of an animal by "genetic engineering" often results in an animal which is less heat tolerant (Bianca, 1971). The two goals are mutually exclusive from a metabolic viewpoint.

Natural exposure to life in hot regions confers some degree of acclimatization on men, but not nearly as much as that conferred by artificial exposure to work in the heat (Wyndham, 1969).

Conclusion

In conclusion, I should like to make a plea for support for research into the resistance to heat of animals in South Africa. There can be no doubt that resistance to heat is a requirement for any animal which is to be farmed or ranched successfully in South Africa. Two research directions suggest themselves: the improvement of heat

157

tolerance in domestic animals, and the utilization of natural-
ly heat-resistant game. It has been clearly demonstrated
with regard to heat resistance in animals that it is not
possible to extrapolate from the laboratory to the field,
nor from one environment to another (Finch, in press;
Murray, 1966; Brown, 1971). If we want to investigate
the resistance to heat of our animals, we must experiment
in the veld in South Africa.

References

BELDING, H.S., 1967. In: Thermobiology ed. A.H. Rose.
London: Academic Press.

BIANCA, W., 1955. J. agric. Sci., Camb. 45, 428.

BIANCA, W., 1959. J. agric. Sci., Camb. 52, 296.

BIANCA, W., 1963. J. agric. Sci., Camb. 60, 113.

BIANCA, W., 1970. Int. J. Biomet. 14 (suppl.), 119

BIANCA, W., 1971. Proc. Int. Union Physiol. Sci. 8,
157.

BIANCA, W. & HALES, J.R.S., 1970. Br. vet. J. 126, 45.

BLIGH, J., 1966. Biol. Rev. 41, 317.

BLIGH, J. & HARTHOORN, A.M., 1965. J. Physiol.,
Lond. 176, 145.

BLIGH, J., INGRAM, D.L., KEYNES, R.D. & ROBIN-
SON, S.G., 1965. J. Physiol., Lond. 176, 136.

BROWN, G.D., 1971. Aust. J. agric. Res. 22, 797.

CABANAC, H.P. & HAMMEL, H.T., 1971. J. Physiol.,
Paris, 63, 222.

CABANAC, M., 1972. In: Essays on Temperature Regu-
lation, ed. J. Bligh & R. Moore). Amsterdam: North-
Holland.

CARLISLE, H.J., 1971. J. Physiol., Paris, 63, 226.

CHAFFEE, R.R.J. & ROBERTS, J.C., 1971. Ann. Rev.
Physiol. 33, 155.

CLAPPERTON, J.L., JOYCE, J.P. & BLAXTER, K.L.,
1965. J. agric. Sci., Camb. 64, 37.

CLOUDSLEY-THOMPSON, J., 1971. New Scientist, 51,
132.

CORBIT, J.D., 1969. Science, 166, 256.

DAWSON, T.J., 1972. In: Essays on Temperature Regu-
lation, ed. J. Bligh & Moore. Amsterdam: North-
Holland.

DEWITT, C.B., 1971. J. Physiol., Paris, 63, 242.

FINCH, V.A., 1972a. In: Environmental Physiology of
Desert Animals. Symposia London Zool. Soc. No.
31. (In the press).

FINCH, V.A., 1972b. Am. J. Physiol. (In the press.)

GATES, D.M., 1968. Aust. J. Sci. 31, 67.

GREER, G.L. & GARDNER, D.R., 1970. Science, 169,
1220.

HAFEZ, E.S.E., 1968. In: Adaptation of domestic animals
ed. E.S.E. Hafez. Philadelphia: Lea and Febiger.

HAINSWORTH, F.R. & STRICKER, E.M., 1970. In:
Physiological and Behavioural Temperature Regu-
lation, ed. J.D. Hardy, A.P. Gagge & J.A.J. Stol-
wijk, Springfield: C.C. Thomas.

HAMMEL, H.T., 1968. Ann. Rev. Physiol. 30, 641.

HAMMEL, H.T., 1971. Proc. Int. Union Physiol. Sci. 8, 48.

HEATH, J.E., 1970. Physiologist, 13, 399.

HEATH, J.E., HANEGAN, J.L., WILKIN, P.J. & HEATH,
M.S., 1971. J. Physiol., Paris, 63, 267.

HELLER, H.C. & HAMMEL, H.T., 1971. Int. J. Biomet.
15, 231.

HELLON, R.F., 1972. In: Essays on Temperature Re-
lation, ed. J. Bligh & Moore. Amsterdam: North-
Holland.

HEMINGWAY, A. & PRICE, W.M., 1968. Anaesthesiology
29, 693.

HENSEL, H. & BOMAN, K.K.A., 1960. J. Neurophysiol.
23, 564.

HENSEL, H. & NIER, K., 1971. Pflügers Arch. Europ. J.
Physiol. 323, 279.

HOFMEYR, H.S., GUIDRY, A.J. & WALTZ, F.A., 1969.
J. appl. Physiol. 26, 517.

HUTCHINSON, J.C.D. & BROWN, G.D., 1969. J. appl.
Physiol. 26, 454.

INGRAM, D.L. & LEGGE, K.F., 1972. J. Physiol., Lond.
220, 283.

JENKINSON, D.M., 1969. In: The Exocrine Glands, ed.
S.Y. Botelho, F.P. Brooks & W.B. Shelley. Phila-
delphia: University of Pennsylvania Press.

KELLY, C.F., BOND, T.E. & HEITMAN, H., 1954.
Ecology 35, 562.

KOVARIK, M., 1964. Nature, Lond. 201, 1085.

McLEAN, J.A., 1963. J. agric. Sci. Camb. 61, 275.

McNAB, B.K., 1970. J. exp. Biol. 53, 329.

MALOIY, G.M.O. & HOPCRAFT, D., 1971. Comp. Bio-
chem. Physiol. 38A, 525.

MITCHELL, D., 1972. Human surface temperature: its
measurement and its significance in thermoregula-
tion. Doctoral thesis, University of the Witwaters-
rand, Johannesburg.

MITCHELL, D., ATKINS, A.R. & WYNDHAM, C.H., 1972.
In: Essays of Temperature Regulation, ed. J. Bligh
& R. Moore, Amsterdam: North-Holland.

MITCHELL, D., SNELLEN, J.W. & ATKINS, A.R., 1970.
Pflügers Arch. Ges. Physiol. 321, 293.

MORRISON, J.F., WYNDHAM, C.H., MIENIE, B. &
STRYDOM, N.B., J. S. Afr. Inst. Mining Metall.
69, 185.

MURRAY, D.M., 1966. J. agric. Sci., Camb. 66, 175.

NAKAYAMA, T., HORI, T., NAGASAKA, T., TOKURA,
H. & TADAKI, E., 1971. J. appl. Physiol. 31,
332.

NEWMAN, L.M., CUMMINGS, E.G., MILLER, J.L. &
WRIGHT, H., 1970: Physiologist 13, 271.

PORTER, W.P. & GATES, D.M., 1969. Ecol. Monogr.
39, 227.

PRIESTLEY, C.H.B., 1957. Aust. J. agric. Res. 8, 271.

REGAL, P.J., 1971. J. Physiol., Paris, 63, 403.

RHOAD, A.O., 1940. Proc. Am. Soc. Anim. Prod. 33,
291.

RIEMERSCHMID, G. & ELDER, J.S., 1945. Onderste-
poort J. vet. Sci. 20, 223.

ROBERTSHAW, D., 1968. J. Physiol., Lond. 198, 531.

ROBERTSHAW, D., 1971. Int. J. Biomet. 15, 263.

ROBERTSHAW, D. & TAYLOR, C.R., 1969. J. Physiol.,
Lond. 203, 135.

SCHMIDT-NIELSEN, K., 1962. Brody Memorial Lecture 11, Agricultural experiment Station, University of Missourie.

SCHMIDT-NIELSEN, K., 1971. Proc. Int. Union Physiol. Sci. 8, 100.

SCHMIDT-NIELSEN, K., BRETZ, W.L. & TAYLOR, C.R., 1970. Science, 169, 1102.

SENAY, L.C., 1970. J. Physiol., Lond. 210, 617.

SNELLEN, J.W., MITCHELL, D. & WYNDHAM, C.H., 1970. J. appl. Physiol. 29, 40.

STEWART, R.E., 1953. Agric. Eng. 34, 235.

STITT, J.T., ADAIR, E.R. & STOLWIJK, J.A.J., 1971. J. Physiol., Paris, 63, 424.

STRICKER, E.M.& HAINSWORTH, F.R., 1971. J. Physiol., Paris, 63, 430.

STROMME, S.B., MYRHE, K. & HAMMEL, H.T., 1971. J. Physiol., Paris, 63, 433.

STRYDOM, N.B., WYNDHAM, C.H. & BENADE, A.J.S., 1971. J.S. Afr. Inst. Mining Met. 72, 101.

STRYDOM, N.B., WYNDHAM, C.H., WILLIAMS, C.G., MORRISON, J.F., BREDELL, G.A.G., BENADE, A.J.S. & VON RAHDEN, M.J.E., 1966. J. appl. Physiol. 21, 636.

SULMAN, F.G., DANON, A., PFEIFER, Y., TAL, E. & WELLER, C.P. 1970. Int. J. Biomet. 14, 45.

TAYLOR, C.R., 1969a. Am. J. Physiol. 217, 317.

TAYLOR, C.R., 1969b. Scient. Am. 220, 89.

TAYLOR, C.R., ROBERTSHAW, D. & HOFMANN, R., 1969. Am. J. Physiol. 217, 907.

TAYLOR, C.R., SPINAGE, C.A. & LYMAN, C.P., 1969. Am. J. Physiol. 217, 630.

THWAITES, C.J., 1967. Res. Vet. Sci. 8, 463.

WYNDHAM, C.H., 1969. Environ. Res. 2, 442.