PHYSIOLOGICAL ANIMAL ECOLOGY

TEMPERATURE AND THERMOREGULATION

1.6 Control systems

When the first vertebrates emerged on land some 400 million years ago they immediately enjoyed the great advantage of extracting oxygen from a medium (air) with a high oxygen content and a low density. This advantage eventually led to the evolution of homeothermic, or endothermic, mammals and birds, with a constant body temperature and a metabolic rate some four to eight times greater than their ectothermic ancestors. The advantages of terrestrial life and physiological control over thermoregulation are many and varied but there is a price to pay, namely dehydration as a result of the ventilation of the respiratory surfaces. We will examine later the interesting adaptations that have evolved to compensate for the risk of dehydration. Let us first examine the control systems involved in both endothermic and ectothermic thermoregulation. Temperature control lends itself to systems analysis, and there have been very sophisticated analyses of the control, particularly for humans.

In Fig. 1.9 a simple model depicts the central nervous system as a black box receiving afferent information from cold and warm sensors situated in both the periphery and the core of the body. This information is integrated and produces the appropriate efferent response. Sweating, shivering and non-shivering thermogenesis, and to a large extent panting, are restricted to true endotherms (mammals and birds), while ectothermic animals (the rest of the animal kingdom) can at best use only changes in vasomotor tone and behaviour. The latter two responses are naturally used extensively by endotherms as well.
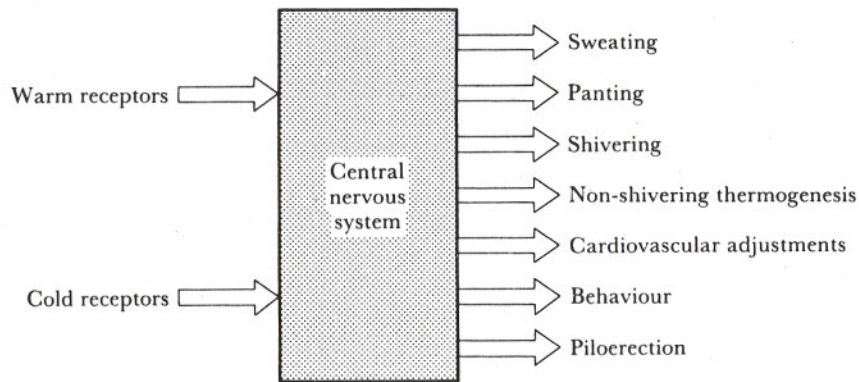
Figure 1.9 The thermoregulatory system as a black box which receives information from warm and cold receptors, and actuates appropriate effector mechanisms to dissipate, generate or conserve heat.

This simple model has been expanded frequently to provide mathematical and engineering models, expressed in the analogous terms of a proportional controller. In parallel with efforts to understand the systems characteristics of temperature control better, there has been a concerted effort to identify the anatomical elements and physiological function of the controller. Neurochemical and neurophysiological approaches were employed. In the neurochemical approach, putative neurotransmitters and their antagonists have been introduced into the nervous system. It has been possible to produce the entire repertoire of thermoregulatory responses in several animal species by micro-injecting minute amounts of various neurotransmitters at appropriate brain locations. The same neurotransmitter will elicit appropriate responses in species as diverse as the sheep and the giant monitor lizard, suggesting a very ancient origin for the neurochemical mechanisms. However, no unifying neurochemical model has emerged capable of explaining responses across species, nor in different thermal circumstances, and there are so many methodological problems associated with current techniques that one cannot be optimistic about achieving a coherent model.

The neurophysiological approach has been much more successful. Neurones capable of functioning as temperature sensors have been identified in peripheral tissue (especially the face and scrotum), and in the central nervous system, of several species (see Fig. 1.10). They have firing rates which either increase (warm sensors) or decrease (cold sensors) with temperature change in the physiological range, and their characteristics are very similar in all species studied, including ectotherms. The modern techniques of brain slice recording and neuronal culture have established that single neurones can act as biological thermometers without any connection to other neurones; on the other hand, there are neurones in the brain which function as interneurones capable not only of integrating afferent input from tempera-
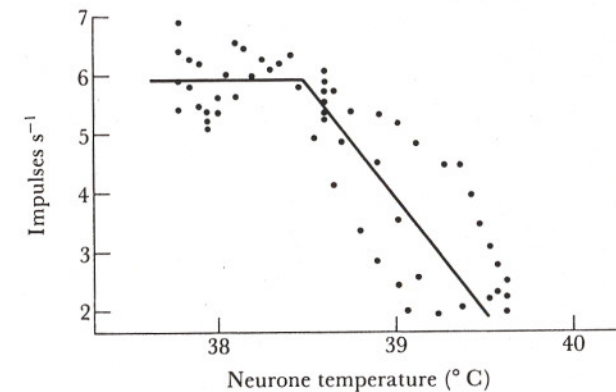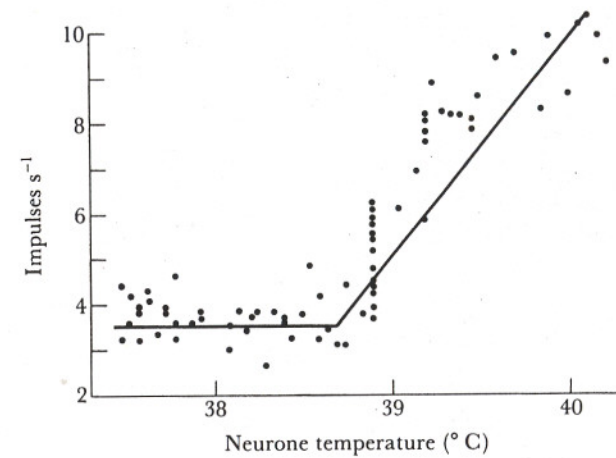
Figure 1.10 Temperature–activity patterns of hypothalamic neurones in a conscious rabbit. A miniature heat exchanger was implanted in the rabbit's hypothalamamus, and microelectrodes were used to measure firing rates of nearby neurones. Most hypothalamic neurones have a firing rate which is not affected by local temperature. Some have a firing rate which increases with temperature within the normal range of brain temperatures (top) or decreases with temperature over the same range (bottom). Redrawn from Hellon (1967).

ture sensors in different body regions, but also capable of integrating the thermoregulatory control system with other control systems, like that responsible for maintaining body fluid volume.

1.7 Metabolic rate and thermoneutral zones

Basal metabolic rate is a medical term invented for humans. It describes the minimum amount of energy required to support essential life processes such
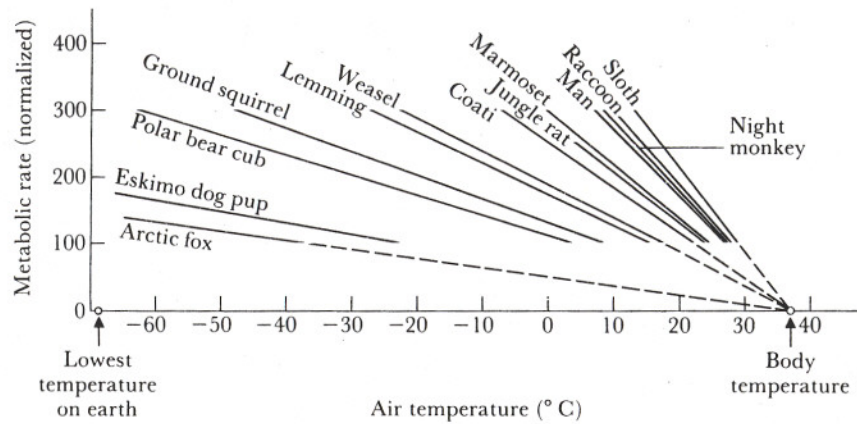
Figure 1.11   Regression lines fitted to measurements of the metabolic rate of various mammals in relation to air temperature. The resting metabolic rate of each species, in the absence of cold stress, is given the value 100%, making it possible to compare widely differing species. The slope of the regression line is a measure of conductance, and Arctic animals typically have much lower conductances than tropical animals. Redrawn from Scholander *et al.* (1950a).

as heart function, respiration, muscle tonus, etc. when the subject is at complete rest, in the post-absorptive state (i.e. food has not been eaten during the past 12 hours) and in a thermally neutral environment. It is seldom possible to comply with all these conditions when studying animals and instead we describe the conditions of the experiment and rather speak of standard or resting metabolic rate. If we expose an endothermic animal to a wide range of temperatures and simultaneously measure its metabolic rate we shall find a temperature range within which metabolic rate will not change. The width of this so-called thermoneutral zone will depend largely on the conductance and body size of the animal concerned. This important principle is well illustrated in Fig. 1.11 which shows that well-insulated Arctic animals, such as the Arctic fox, have very wide thermoneutral zones and only raise their metabolic rates when exposed to temperatures as low as −40 °C. In contrast, naked humans have a very narrow neutral zone and in the case of some small mammals the zone is merely a single point on the temperature axis.

If we recall the conductance equation (eqn [1.7]), we can see that polar animals, as expected, have much lower conductances than tropical animals; their slopes are much flatter. Also, the equation predicts that if the lines are extrapolated to the *x*-axis they intercept this axis at body core temperature, about 37 °C for most mammals. Interestingly, the extrapolated conductance curve for birds does not intercept the *x*-axis at body temperature, presumably

because birds can change their shape and therefore their conductance markedly by fluffing their feathers out and changing their posture.

Because an increased metabolic rate represents an energy cost to the animal, various physiological adaptations have evolved to reduce this potential energy wastage. These include summer aestivation in the case of desert animals, hibernation during winter and even a daily torpor in the case of very small endotherms such as humming-birds and shrews.

The increase in metabolic rate with declining ambient temperature, shown in Fig. 1.11, is largely the consequence of shivering of skeletal muscle. Shivering is an emergency procedure and animals will go to great behavioural lengths to avoid having to employ it. Shivering produces a large amount of heat but not all the heat is stored, because the muscle activity induces increased blood flow, and the extra flow results in heat loss from the body surface. Human shivering efficiency (i.e. percentage heat stored) is about 50%, which is nevertheless much higher than the efficiency of exercise as a means of generating heat to overcome cold, about 20%. During voluntary activity of a muscle, shivering is inhibited, which means that the effects of exercise and shivering are not additive. Also, the pathways responsible for activating shivering in voluntary muscle are separate to the pathways serving motor function in the same muscles and can be traced back through separate spinal tracks to the posterior hypothalamus.

In addition to shivering, certain mammals, particularly small ones, are capable of producing large amounts of heat by so-called non-shivering thermogenesis (NST). To test if an animal is capable of NST it is first given the opportunity to become cold-adapted by exposing it to low ambient temperatures and preferably a declining photoperiod. It is then given noradrenaline while its heat production is measured either directly in a calorimeter or indirectly by recording the oxygen consumption. Animals capable of NST will respond with a rapid, almost instantaneous, increase in heat production. The mechanism whereby NST operates at the cellular level involves sympathetic stimulation of β-adrenoreceptors in brown adipose tissue (BAT), and the dissipation of proton gradients across the mitochondrial membranes in this tissue. We shall discuss the phenomenon in some detail in Chapter 3. Non-shivering thermogenesis is an efficient means of heat production and is extensively used by small mammals when emerging from torpor and hibernation, as well as by the neonates of large mammals, including man.

1.8 Colour

The colours displayed by vertebrate animals have been the subject of much speculation among zoologists, geneticists and animal scientists. The subject is a complex one, particularly when considering the effect of opposing natural selection pressures. For example, it may be beneficial for an animal to be white in colour to match its background (so-called crypsis) and thereby
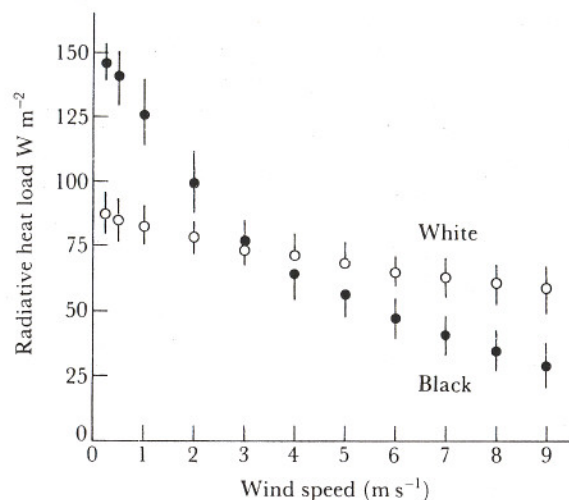
Figure 1.12   Radiant heat load transferred to the skin under black or white pigeon plumages, as a function of wind speed. Plumages were maximally erected, and exposed to 900 W m^{-2} of simulated solar radiation. Redrawn from Walsberg *et al.* (1978).

escape predation, while at the same time black may be beneficial for thermoregulation and a brilliant display of colours may make it easier to attract mates. Under conditions of natural selection these opposing selection pressures are resolved by the most important vector in the complex of selection pressures. Study of animal colour proceeds from a misleadingly anthropocentric base too. Many non-human animals are completely colour-blind and those with colour vision may have completely different spectral sensitivity.

In addition to these complexities, we must also realise that the plumage and pelage of birds and mammals are not merely plain physical surfaces to which we can assign an absorption or reflectance value. Of great importance to the thermal biologist is the degree to which heat will penetrate through the pelages or plumages of different colours and thereby affect the heat gain of the animal. The biologist must also study heat exchange under natural conditions, when factors other than radiation, such as wind speed, become important considerations when evaluating colour. For example, Walsberg *et al.* (1978) have shown that, although black pigeons absorb a greater radiative heat load than do white pigeons in still air, this difference is progressively reversed as the wind velocity exceeds 4 m s^{-1}. Similar results were obtained by Lombard (1989) working on the plumages of black cormorants and white gannets in a wind tunnel. Walsberg (1983a) believes that irradiation penetrates more deeply into white plumages and heat gain is therefore less affected by the surface disruption of the plumage at higher wind speeds (Fig. 1.12).

Plate 1.1   Polar bears are protected from the cold by a thick pelage and layer of subcutaneous fat. It is thought that the white hairs act as optic fibres to convey short-wave radiation from the surface of the pelage to the skin surface, thereby warming the skin. (Photo: courtesy of Tom Ulrich.)

Surface reflectance of a pelage can therefore provide misleading data and penetrance of the radiation should always be measured. Øritsland and Ronald (1978) found that the reflectance values for three dark brown *Mustela* species were very similar (0.30–0.35), whereas the transmission of energy through their pelages varied two-fold. Also, Grojean *et al.* (1980) maintain that hollow, transparent hairs in polar bears act like optic fibres to guide short-wave radiation towards the darkly pigmented skin, thereby increasing the depth of penetration of the radiation and consequent heat gain. These results, in conjunction with the excellent adaptation exhibited by pitch-black ravens in hot deserts, suggest the almost absurd idea that black may be the ideal colour for thermoregulation in the desert and white ideal for the polar regions.

Remember also that colour affects only the reflectance and absorption of short-wave radiation (mostly within the visible range) and that the absorption of long-wave radiation is not affected by colour (see Fig. 1.8). In the desert large amounts of short-wave radiation are absorbed by the desert surface, which then heats up and re-radiates this energy as long-wave radiation. It follows that small animals living very close to the substrate will gain heat largely through long-wave re-radiation and colour becomes less important. In polar regions the high reflectance of snow and ice causes high levels

of short-wave radiation (including ultraviolet radiation), hence the fairly rapid tanning of skiers even under very cold conditions. Evaluating colour is therefore a complex procedure and we must remember that many animals, by merely altering their orientation, posture or seeking out a favourable microclimate can readily compensate for the relatively small thermal disadvantage due to their colour. Nevertheless, it is an important ecophysiological concept as the following simple examples should show.

1.8.1 Chameleons

It is generally accepted today that the dramatic colour changes which chameleons exhibit serve largely to facilitate behavioural thermoregulation. Chameleons are ectothermic animals and rely on sunbasking and shade-seeking to regulate their body temperatures. When they are cold they disperse the melanin pigment in their integumentary cells so as to facilitate the absorption of short-wave, visible radiation. The colour changes are accompanied by changes in the shape of the body and the orientation of its long axis. For example, when warming up chameleons take on the shape of a broad leaf and orientate laterally towards the sun's rays. When they are exposed to excessively high temperatures the long axis of the body is orientated parallel to the solar beam, thereby reducing the profile area exposed to direct radiation, and they turn a pale colour (Burrage, 1973).

1.8.2 Amphibians

Generally speaking, amphibians are not efficient thermoregulators and remain in shaded moist habitats. Nevertheless, there are several interesting exceptions. For example, we have found that certain species of tree frog are able to blanch completely white when exposed to strong solar radiation. In cool conditions, when they need to raise their body temperature the frogs release the pituitary hormone melanophore-stimulating hormone (MSH), which disperses the melanin granules and they become almost black, so maximising the absorption of visible radiation. These little frogs are ecophysiologically interesting in other ways too; they are almost waterproof, which is most unusual for an amphibian (Withers *et al.*, 1982; Kobelt and Linsenmair, 1986).

1.8.3 Birds

The colours of birds range across the complete spectrum from drab grey through pure white, pitch-black to the brilliance of humming-birds. Colour in birds is employed for a variety of reasons: crypsis, thermoregulation and optical signalling are the most important. Optical signalling and crypsis have obvious advantages but the thermoregulatory importance of colour is more

subtle. For example, the Cape cormorant, a pitch-black bird, tends to overheat when nesting on rocky islands. To cool itself it employs a form of rapid thermal panting. Because these birds have no access to fresh water one would expect that thermal panting would cause excessive concentration of body fluids, but apparently the efficient salt glands that discharge in their nasal sinuses compensate adequately for this stress. Why then are these animals black, rather than white like the gannets which nest next to them? The answer is to be found when one observes them foraging. They dive deeply in chase of their favourite prey, the pilchard, and to reduce buoyancy their feathers are hydrophilic or 'wettable'. This property brings the cold sea water (12 °C) into direct contact with the surface of their skins (35 °C) and heat drains rapidly from their bodies. As soon as foraging is complete, however, they return rapidly to the shore, spread their wings and orientate the maximum surface area to the sun. It is then that the black colour becomes a major advantage; they soak up solar radiation and warm their bodies without wasting valuable nutrients by shivering. The white gannets, on the other hand, have hydrophobic feathers and do not become wet during their short power dives after their prey, which is closer to the sea surface. They therefore have no need to enhance their sun-basking and their white colour with its high reflectance is an advantage during nesting. Analysis of the advantage of the cormorant's black colouring shows that interpretation of why an animal is a particular colour requires a knowledge of the animal's total ecology and life style. This point is further illustrated by the bedouin goat example described below, and the desert raven mentioned previously.

1.8.4 Mammals

The effect of natural selection on the colour of mammals is equally complex. The colour patterns of wild ungulates in the savannahs of Africa are remarkably similar. With obvious exceptions, the pelage is usually a fawn to light fawn in colour. This colour is probably a compromise or optimisation to ensure reasonable reflectance of incident solar radiation as well as good crypsis against the blonde to light brown colour exhibited by the savannah vegetation for most of the year. The springbok (Fig. 1.13) has been studied in considerable detail (Hofmeyr and Louw, 1987). On cold mornings it orientates the long axis of the body laterally to the sun's rays and the dark brown stripe that runs bilaterally along the flanks facilitates the absorption of solar heat. As air temperatures begin to rise, the animals start to orientate parallel to the solar beam, thereby reducing the profile area exposed to direct solar radiation by as much as 50% (Fig. 1.14). The white colour of the rump and face also increases reflectance when this orientation is employed. Finally, the ventral surface in the springbok, as in many antelope, is pure white, which assists in reflecting short-wave radiation that is reflected off the substrate.

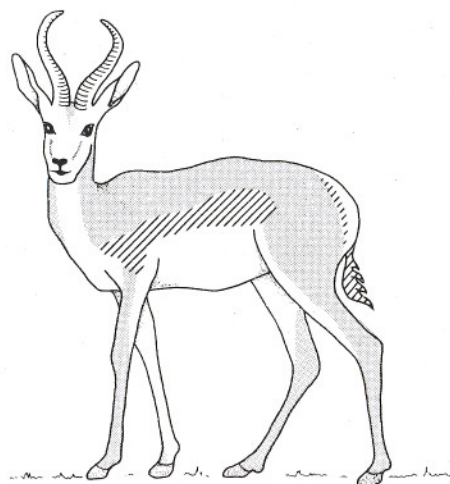In the context of the ecophysiology of African mammals the black and

Figure 1.13 Lateral view of a springbok, illustrating its colour pattern: fawn shading, dark brown (diagonal lines) and white (remainder).
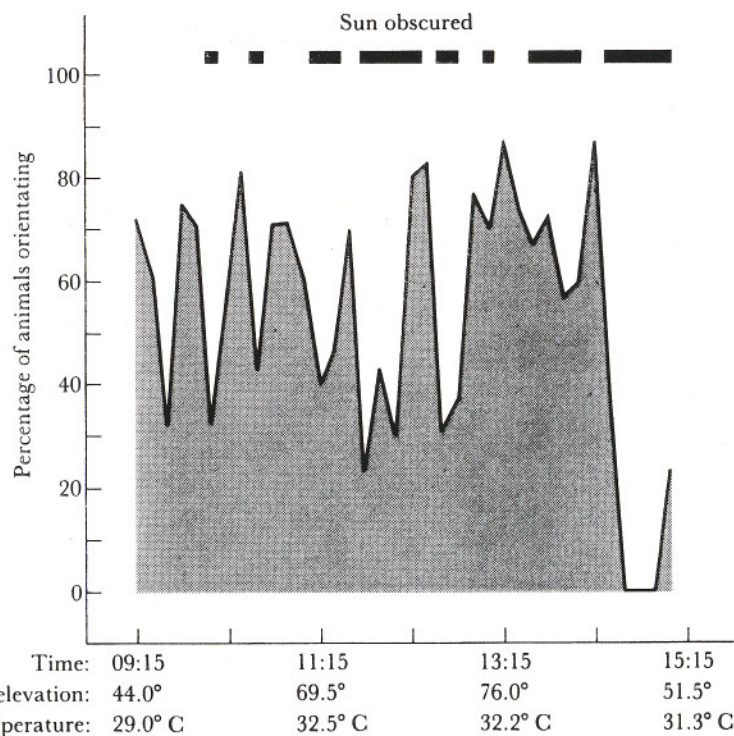
Figure 1.14 Percentage of springbok in a herd orientating the long axis of the body towards the sun. Bars at the top indicate when the sun was fully or partially obscured.

white stripes of zebras still remain a mystery. Some zoologists believe that the stripes enhance crypsis but the evidence is not convincing. We have measured the surface temperature of the stripes and, as expected, the skin surface covered by black stripes heats up more rapidly, and for short periods black stripes can attain a higher equilibrium temperature than the white stripes can. Zebras employ the same orientation behaviour as springbok, described above, and it is noteworthy that the ratio of black stripes to white is much higher on the flanks than on the rump. This pattern would facilitate warming when the animal is orientated at right angles to the solar beam and increase reflectance when the rump is presented to the sun. A really convincing explanation of the zebra's remarkable colour pattern is, however, still awaited.

Any consideration of the colour of ungulates would be incomplete without discussion of that fascinating small ruminant, the bedouin goat. Amiram Shkolnik of Tel-Aviv University has shown clearly that, in winter conditions, when the nutritional stress is at its peak in the Negev Desert, the metabolic rate of black goats standing in the sun is 25% lower than that of white goats. This difference apparently arises because the black goats absorb more solar radiation, and so have to expend less energy in shivering to maintain their body temperatures. Over a long dry winter the difference in metabolic rate can mean the difference between survival and death and the Bedouin have for centuries favoured the black colour in their selective breeding practices. The black colour of the goats is a disadvantage in the hot desert summer and black goats lose more water by sweating and panting than the white goats. Fortunately, however, bedouin goats have a remarkable ability to store very large amounts of water in their rumens and, even in summer conditions, only need to drink every second day.

1.9 Evolution of endothermy

Endothermy and the ability to maintain a constant body temperature would seem to have obvious advantages. Endothermic homeotherms, *inter alia*, maintain the temperature of their nervous systems at a constant level, locomote rapidly, have invaded cool and cold regions of the globe, and have become nocturnal predators. All these attributes have advantages, but care should be taken to avoid the anthropocentric view that endothermy is the apogee of evolutionary development. One need only mention the overwhelming success of the insects or the very extensive adaptive radiation of the teleosts to challenge that view. Moreover, endothermy has a high energy cost, requiring a metabolic rate 4–8 times greater, per gram of tissue, than that of most ectotherms. The energy demand, in turn, requires an increase in the respiratory ventilation rate and consequently increases the danger of both desiccation and disturbance to acid–base balance. Food requirements are also increased. It would be more circumspect to conclude
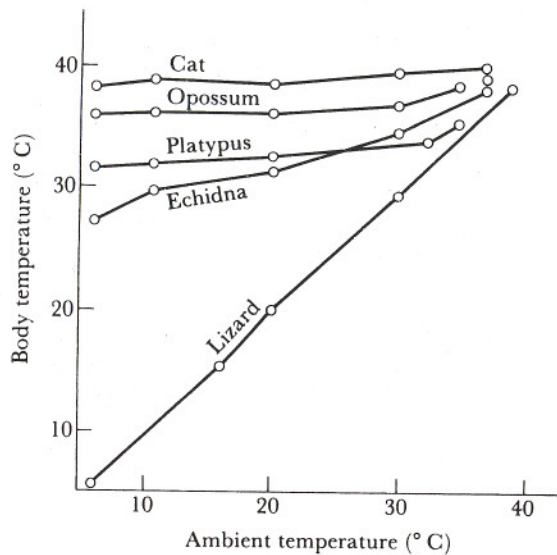
Figure 1.15 Variations of body temperature in a reptile (lizard), two monotremes (echidna and platypus), a marsupial (opossum) and a placental mammal (cat) caused by exposure for 2 hours to ambient temperatures between 5 and 40 °C. Redrawn from Martin (1980).
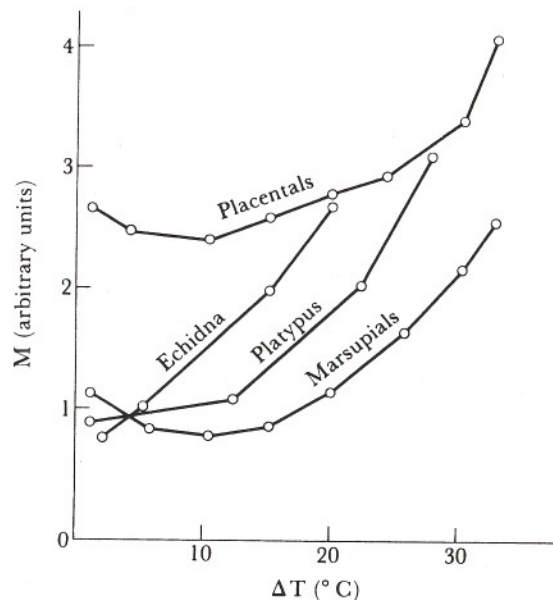

Figure 1.16 Metabolic rates of typical placental mammals, typical marsupials, and two monotremes (echidna and platypus) plotted against the difference between body temperature and ambient temperature, (ΔT). The curves of placentals and marsupials represent the results of experiments on several species of each kind. Redrawn from Martin (1980).

that endothermy, in spite of representing a quantum jump in evolutionary history, has conferred major advantages only to certain classes of animals within their specific niches. Humans have naturally exploited their advantages to the fullest through their concurrent intellectual development, which has allowed them to gain ascendancy over all other animals.

Much has also been made of the differences in body temperature among monotremes, marsupials and eutherian mammals as well as in their responses to cold (Figs 1.15 and 1.16). The initial inference that was drawn suggested that thermoregulation in the non-eutherian mammals was primitive and still evolving towards that of the eutherians. Today, however, these differences are considered to be the result of specialisation, analogous to that of the oryx antelope, which apparently can survive body temperatures of 45 °C in the desert. We also now know that some eutherian mammals, like naked mole rats, are poikilothermic, apparently more 'primitive' than the echidna.

The high metabolic rate of endotherms is achieved largely through a greater concentration of mitochondria and apparently also through the occurrence of two different functional forms of mitochondria in endotherms. For example, when comparing ectothermic mitochondria (frog) with endothermic mitochondria (rat) Akhmerov (1986) found that he could distinguish an endothermic mitochondrion in which oxidative phosphorylation was uncoupled, thereby producing heat and not ATP. The respiration of succinate in the absence of ADP was also five times greater in rat mitochondria than in frog mitochondria. The greater concentration of mitochondria in endotherms imparts additional advantages to these animals, not least of which is the ability of endotherms to undertake vigorous sustained exercise, because of their ability to maintain high rates of aerobic metabolism. This phenomenon has been examined in some detail by Bennett and Ruben (1979) and Bennett (1987), who conclude that high and stable body temperatures improve locomotor performance (Fig. 1.17). However, Bennett and Ruben (1979) caution that ectothermic vertebrates should not necessarily be considered easy prey for endotherms. The ectotherms' lower energy requirements for thermoregulation and efficiency of food utilisation allow them to occupy niches entirely unsuitable for endotherms. Their escape behaviour is often very successful and they can even pursue endotherms, provided that they need only short bursts of activity.

To summarise, then, endotherms and ectotherms have many thermoregulatory attributes in common, including similar control circuitry. Endotherms do, however, have special attributes, which must have evolved over a long period of geological time. There were probably intermediate forms maintaining lower body temperatures, such as the 25 °C of modern tenrecs. Once endothermy had been established, various 'spin-off' advantages could develop such as improved and continuous cortical function, improved care of young, and lactation. Improved cortical function may have led to increased
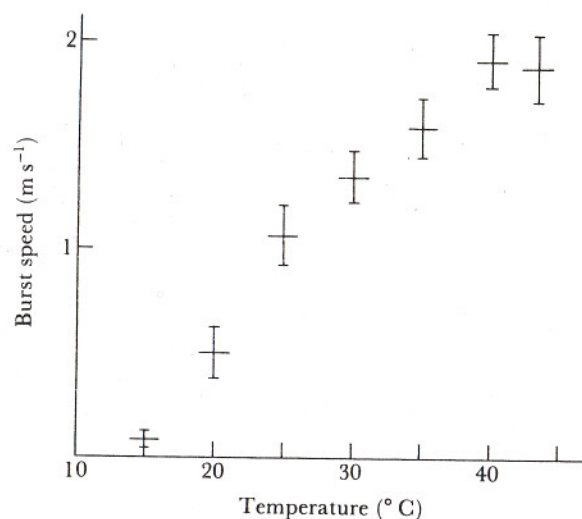
Figure 1.17 Burst speed as a function of body temperature in the desert iguana *Dipsosaurus dorsalis*, shown as mean ± 95% confidence interval. Data from Bennett (1980).

relative brain size or encephalisation. The possibilities for speculation are endless and fascinating but one should guard against simplistic explanations of such a complex process of evolution.

1.10 Fever (pyrexia)—aberration or adaptive response?

Almost everyone has experienced the discomfort which a fever causes—the cold shivers and eventual profuse sweating are well-known symptoms of this condition. In certain diseases such as malaria these responses are greatly exaggerated and very debilitating for the patient. What may be just a temporary unpleasant experience for a human may be lethal for other animals, where debility may mean inability to forage, or to escape a predator. The question therefore arises whether fever is merely a symptom of the disease or does it have survival or adaptive value? Before answering this question let us examine how thermoregulation changes during a bout of fever, as well as the physiological mechanisms involved in the production of fever.

During the first phase of fever a human patient feels cold and may experience cold shivers. This usually prompts him to clothe himself more warmly or use warmer bedclothing. The shivering will eventually disappear as the body temperature reaches a new elevated set point. Sweating then often occurs when the fever resolves. During the fever, the human mammal uses both behavioural and physiological responses to maintain body temperature at a new level. It is important to note that fever is not an uncontrolled hyperthermia but constitutes precise thermoregulation about a new elevated
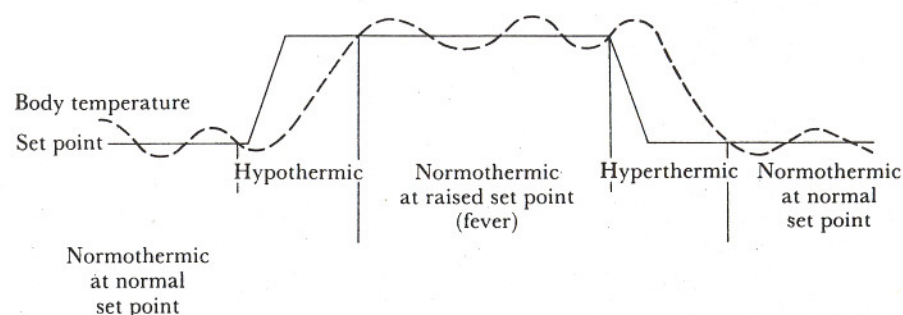
Figure 1.18 The thermal course of a fever. The system behaves as if the set point for body temperature were elevated at the beginning of the fever, and returned to normal at the end of the fever. Thermoregulatory effector mechanisms are initiated to bring the actual body temperature to the set point, as if the patient is hypothermic at the beginning of the fever and hyperthermic at the end. Redrawn from Bligh (1973).

set point (Fig. 1.18). A process similar to that in humans occurs in many other species of endotherm too.

The sequence of physiological events which accompany fever is complex and not yet completely understood. The flow diagram in Fig. 1.19 is a broad outline of these events. A variety of stimuli such as antigens, chemicals and particularly microbial agents can entrain the fever response. Exposure of an animal to these stimuli leads to the production of an endogenous pyrogen by the white blood cells (mostly monocytes and macrophages). Several endogenous pyrogens have been identified and are now even cloned. The endogenous pyrogen induces several secondary processes, one of which is a disturbance to the neurochemistry of the brain, which results in the elevated body temperature. Other processes include release of proteins by the liver, changes in serum metal ion concentrations, and a variety of hormonal events.

We return now to the question of whether or not fever has survival value. There is little doubt now that the release of endogenous pyrogens has a beneficial effect on the host. For example, they reduce the amount of circulating iron in the bloodstream, thereby inhibiting the reproduction of invasive pathogens.

The subsidiary question of whether the pyrexia, the elevated body temperature, contributes to the survival value remains unresolved. Hippocrates (Ancient Greek Father of Medicine) thought fever was advantageous, but modern doctors tend to treat fevers with antipyretic drugs, such as aspirin, which prevent the pyrexia without blocking other components of the fever. The first modern attempt to answer this question was made by the American physiologists Linda Vaughn, Harry Bernheim and Matt Kluger, who realised that lizards, because they are ectotherms and good behavioural thermoregulators, would be ideal material with which to test the hypothesis; no one had previously envisaged that ectotherms might develop fever. They first
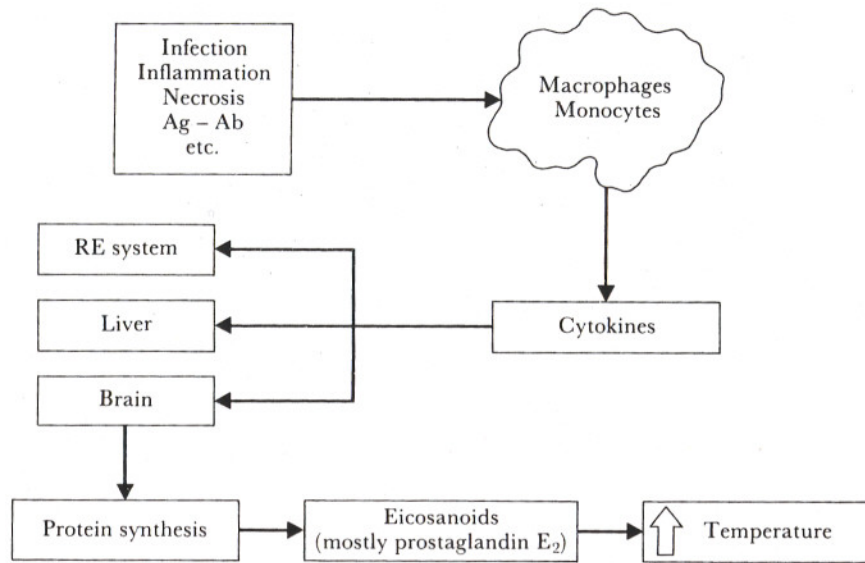
Figure 1.19 Outline of the biochemical events resulting in fever. In response to infection, inflammation, necrosis, antigen–antibody reactions and other stimuli, macrophages and monocytes release cytokines (interleukin 1, interleukin 6, tumour necrosis factor) which act on many organs, including the brain, where they initiate further protein synthesis and release of eicosanoids (primarily prostaglandin E_2). Modified from Mitchell and Laburn (1985).

placed desert lizards (*Dipsosaurus dorsalis*) in a thermal gradient which allowed them to select body temperature behaviourally, normally about 37 °C. When these lizards were injected with a bacterium pathogenic to reptiles (*Aeromonas hydrophila*), they selected a higher body temperature, about 42 °C, by remaining for longer periods at the warm end of the gradient (Vaughn *et al.*, 1974). Subsequently, Kluger *et al.* (1975) performed an even more significant experiment by again injecting *D. dorsalis* with live *A. hydrophila* and dividing them into five groups, which were held in incubators at 34, 36, 38, 40 and 42 °C, respectively. The lizards were unable to thermoregulate behaviourally in the incubators and merely acquired the temperature of the surrounding air. The results of the experiment showed a significantly higher rate of survival at higher temperatures, which suggests that fever may indeed have survival value.

More recently, Boorstein and Ewald (1987) carried out an even more sophisticated experiment using the grasshopper *Melanoplus sanguinipes*. They allowed the grasshoppers to eat food contaminated with a natural pathogen. The infected grasshoppers immediately sought out a warmer environment, and achieved an elevated body temperature. If prevented from attaining the high body temperature, the grasshoppers had severely compromised survival; again, pyrexia seemed to have survival value.

A survival value for fever would please the Darwinist who believes that all life processes must at one time or another have had a selective advantage to allow their development. If fever is as universally operative as the above studies would suggest, then it may have very ancient evolutionary origins; it has even recently been observed in a species of leech (Cabanac, 1989). However, as any biologist might expect, as further studies on the potential survival value of fever have accumulated, the picture has become increasingly complex and ambiguous (see Mitchell *et al.*, 1990). Almost 40 ectothermic species have now been tested, and about two-thirds develop fever. Among lizards, fever appears to be confined to one family, Iguanidae. In only a very few of the ectotherms tested has the pyrexia been demonstrated to have survival value. Whether it has survival value in endotherms is still unknown. There are advantages in using antipyretic drugs during fever, particularly because they reduce several unpleasant symptoms. Since short courses of aspirin, and other antipyretic drugs used by doctors, seldom have adverse effects, it seems advisable to continue to use antipyretics during fever, while we gather further information.