CHAPTER 1

TEMPERATURE AND THERMOREGULATION

1.1 Introduction

It would be naïve to try to select the 'most important' environmental factor affecting life when, for example, the absence of a few milligrams of any one of several trace elements from the diet of a large mammal will lead to severe illness and eventual death. Nevertheless, no one would deny that temperature has a profound effect on all life processes and so warrants careful study and analysis. Such study requires familiarity with the basic effects of temperature on chemical reaction rate and with the well-known Q_{10} effect.

Life is sustained by a complex of biochemical reactions and the molecules involved in these reactions possess kinetic energy, that is, they are in constant motion. If we raise the temperature of reacting molecules from 30 to 40 °C we increase their kinetic energy by about 3%, yet the reaction velocity may increase 200–300%. The reason for the disproportionate increase can best be explained by referring to Fig. 1.1. The feasibility of a reaction taking place is determined by the energy barrier to the reaction, known as the activation energy. According to the Arrhenius principle, a relatively small percentage change in the average kinetic energy of a population of molecules may result in a relatively large change in the fraction of molecules having energy greater than the activation energy. This phenomenon is the basis of the profound effect of temperature upon life processes.

It is customary to describe the effect of temperature on a life process in terms of the Q_{10}:

$$Q_{10} = \text{Velocity } (T + 10\,^{\circ}\text{C})/\text{Velocity } (T\,^{\circ}\text{C}) \qquad [1.1]$$

Because the biochemical reaction velocity does not increase linearly with the temperature, Q_{10} is not a constant for a particular reaction, but itself varies with temperature. It is important, therefore, to specify the range of temperature over which a Q_{10} was measured.

The more chemical reactions upon which a living organism depends, the greater the effect of temperature on its functioning, and the human brain, with its multiple synaptic connections, is potentially the most temperature sensitive of all living tissues. Yet, if we look around any room in which 20–30

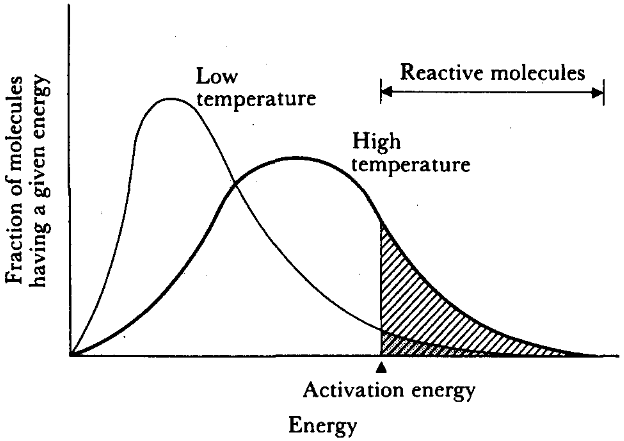


Figure 1.1 **Distribution of energy in a population of molecules at a low and high temperature. Only those molecules having energy equal to or greater than the activation energy are reactive.**

persons are gathered, we will very likely find one who can tune and play a string instrument, one who can solve a differential equation, perhaps one who can write some poetry; probably all will be able to use complex speech patterns for communication and exercise fine motor control over their voluntary muscles. It is not therefore surprising to find that human body temperatures are remarkably constant. It seems likely that the development of the impressive intellectual ability of humans was and still is dependent on very fine thermal control over the central nervous system. One only has to observe the deranged behaviour of humans in whom brain temperatures have even been slightly disturbed to realise the importance of a regulated brain temperature.

The development of the ability to regulate body temperature may have been a prerequisite for the development of complex nervous systems. Many other authors consider the advantage of a constant body temperature to be that enzymes work best at constant temperature. We should remember, however, that enzymes have a remarkable ability to adapt to different prevailing temperatures, for example through development of iso-enzymes, which are enzymes with the same function but with different temperature-dependent kinetics. The enzymic processes which sustain bacteria living in below-freezing sea water are basically the same as those which sustain bacteria in hot-water springs. Also, even in an animal which does have a constant body temperature, enzymes are required to act at different temperatures. The enzyme thrombin, for example, must play its role in preventing leakage from blood vessels whether the potential leak occurs in the human heart, at 37 °C, or a few seconds later in the finger tip, at less than 20 °C.

In those animals which do regulate their body core temperatures, many vertebrates and some invertebrates, the regulated temperature usually lies in the range of 32–42 °C. Having a body temperature above air temperature allows some metabolic heat to be dissipated without evaporating valuable body water (see McArthur and Clark, 1987). However, no one has advanced a valid physical, chemical or biological reason why the regulated temperatures lie in a specific range. A hypothesis, as good as any other, is that the range represents the ocean temperatures at the time at which terrestrial life emerged. Alternative explanations will be presented later.

Perhaps because it is relatively easy to measure temperature accurately when compared with many other ecophysiological variables, an enormous literature on thermal biology has accumulated over the past decades. We cannot hope to cover it extensively here and will therefore concentrate on key principles.

1.2 Terminology

1.2.1 Body temperature

Animal temperatures vary with the time of day and among and between species. In those animals which have a temperature different from environmental temperature, different parts of the body exhibit different temperatures. There is therefore no such thing as a single 'body temperature'. Representative temperatures usually are those of deep body tissue measured through a convenient orifice; standard practice is to use the rectum or cloaca.

Examples of animals which regulate temperature well are:

Monotremes	30–31 °C
Marsupials	35–36 °C
Eutherian mammals	36–40 °C
Birds, non-passerine	39–40 °C
Birds, passerine	40–41 °C

The amplitude of the circadian rhythm in body temperature is related to body size, with smaller animals tending to exhibit the greater amplitude, a consequence of their lower thermal inertia. There are exceptions; the camel has an unexpectedly large circadian variation. Another important rhythm of body temperature is that associated with reproductive cycles; in most women, for example, body temperature rises about 0.5 °C at ovulation.

Relatively few species (all mammals or birds) regulate body temperature accurately all the time. A great many more species regulate well for part of each day, by using thermoregulatory behaviour. The temperature which they then select to maintain is known as the 'preferred' or 'eccritic' body temperature for that species, though a better term is 'selected' body temperature.

1.2.2 Homeothermy vs. poikilothermy

Because the historical terms 'cold-blooded' and 'warm-blooded' are illogical, the terms 'homeothermic' and 'poikilothermic' were introduced to describe animals with a well-regulated and a variable body temperature respectively. Another classification of thermoregulation describes animals as 'endothermic' (producing heat within their own tissues to thermoregulate) or 'ectothermic' (relying on gained heat from the environment when thermoregulating).

The categorisations endothermic–ectothermic and homeothermic–poikilothermic are independent (Figs 1.2 and 1.3). In theory, any ectotherm can be homeothermic, given a suitable habitat. However, if an animal is habitat independent and homeothermic, it must be an endotherm. Not all animals display the same thermoregulatory pattern at all times. Some alter the pattern according to environmental circumstances. For example, some moths, beetles and carpenter bees, usually ectotherms, employ endothermic mechanisms before and during flight. Nor do all species in an order have the same pattern; most mammals are homeothermic endotherms, but the naked mole rats, fossorial mammals, appear to be typical poikilotherms.

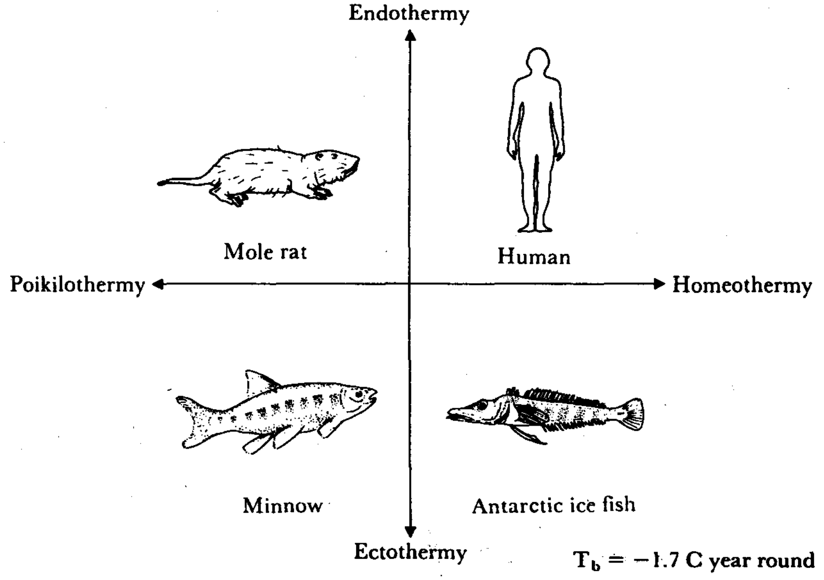


Figure 1.2 **Categorisation of thermoregulatory abilities, with typical examples. There are very few true homeothermic ectotherms, though many ectotherms do maintain an almost constant body temperature, given an appropriate thermal environment.**

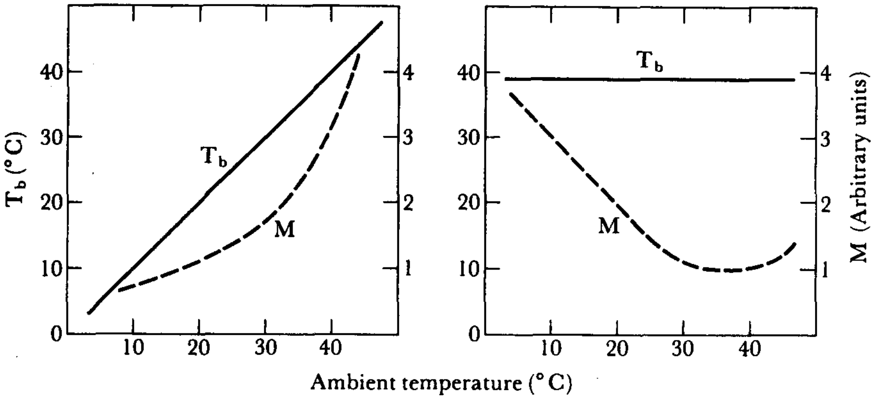


Figure 1.3 **Body temperature (T_b) and metabolic rate (M) of a typical poikilothermic ectotherm (left) and homeothermic endotherm (right) in relation to ambient temperature.**

1.2.3 Behavioural vs. physiological thermoregulation

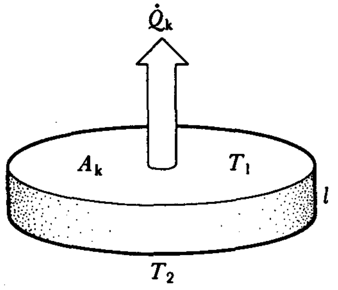
Caution is always advocated in discriminating between 'behavioural' and 'physiological' phenomena because they are indistinguishable at the level of the physics and chemistry (physiology) of cells. Nevertheless, a strong convention exists which describes the use of site selection, position and posture for temperature regulation as behavioural thermoregulation, and the use of endogenous metabolic heat production, cardiovascular adjustment, and evaporation as physiological thermoregulation.

1.3 Physics of heat exchange

Heat is a synonym for the total kinetic energy of all the molecules in a system, and all systems with temperatures above absolute zero (−273 °C) contain heat. Temperature, on the other hand, is a measurement of the mean kinetic energy of the molecules in a system. When two systems with different temperatures are placed in contact, heat flows from the one with the higher temperature to the one with the lower temperature. The rate at which heat will flow between them cannot be determined from the difference in their temperature alone (Bartholomew, 1982). Let us examine the most important avenues of heat gain and heat loss which animals experience, and the most important factors affecting the rate of heat exchange.

1.3.1 Conduction

Conduction is the movement of heat by interaction of adjacent molecules without the mass motion of the medium through which the energy transfer takes place.



$$\dot{Q}_k = C_k\, A_k\, \frac{T_2 - T_1}{l}$$

Figure 1.4 **Rate of heat flow ($\dot{Q}_k$) through a segment of conductor of thickness l and area A_k, and face temperatures T_1 and T_2.**

The rate of heat transfer by conduction ($\dot{Q}_k$) through a segment of material can be expressed by the equation shown in Fig. 1.4. The thermal conductivity coefficient (k) is a number which describes the ease with which heat flows by conduction through given material. For example, the k value for silver is 0.41, for wood 0.0001 and for air 0.000 024 W mm^{-1} $°C^{-1}$. The last figure explains the important insulative function of air trapped in animal fur and protective clothing.

From the conduction equation we can deduce that the most important factors affecting heat gain or loss from an animal by conduction, other than the k value, are the surface areas involved and the temperature gradients between the animal and the environment.

Heat transfer by conduction therefore is of great importance to those animals in which there is a large contact area with a solid surface, such as snakes and many invertebrates. High rates of heat transfer with the solid substrate may have contributed to the development of poikilothermy in fossorial mammals like golden moles and mole rats. In humans walking or standing, even on snow or ice, very little heat is gained or lost by true conduction as only small areas of the body (soles of the feet) are in direct contact with a solid medium.

1.3.2 Convection

Consider a naked human with a skin temperature of 35 °C standing in a room with completely still air (air temperature 25 °C). Comparatively little heat will be lost through the soles of the feet because of the small surface area. However, because of the temperature gradient of 10 °C between the entire surface of the rest of the body and the surrounding air, kinetic energy will be transferred from the surface of the skin to the boundary layer of air adjacent to the skin. As the air molecules gain kinetic energy, they will move upward

and away from the skin creating fluid currents. The heat loss is no longer by conduction, but by means of 'free convection'. If we were now to turn on a fan, heat loss will be increased even further by so-called 'forced convection', because the boundary layer is removed more rapidly by the external wind. Convection is thus the movement of heat through a fluid (either liquid or gas) by mass transport in currents.

For an animal in a moving fluid, the rate of heat loss is governed by the equation:

$$\dot{Q}_c = C_c A_c V^n (\bar{T}_s - T_f) \qquad [1.2]$$

where $\dot{Q}_c$ (W) is the rate of convective heat loss, A_c (m^2) the area of the animal participating in the convective heat exchange, V (m s^{-1}) the fluid speed, $\bar{T}_s$ (°C) the mean surface temperature of the animal, and T_f (°C) the fluid temperature. The exponent n depends on the size of the animal and the range of fluid speeds over which the equation is applied: for a typical mammal or bird in air, $n \simeq 0.5$, so that convective heat transfer is approximately proportional to the square root of wind speed. The coefficient C_c varies not only with animal size but also with physical properties of the fluid, including density: convective heat loss rate reduces with altitude. More important, convective heat transfer is so rapid in water that it is very costly for any aquatic animal to maintain a body temperature different to water temperature, and most do not do so. Naked humans are unable to regulate body temperature in water colder than about 15 °C, a temperature above that of most of the world's ocean water. For a more detailed analysis of the physics of forced and free convection, see Mitchell (1974).

Remember that when air or water temperatures are above body temperature then heat gain is accelerated by convection. For this reason the Bedouin shelter from hot desert winds while naïve Europeans seek out wind on the mistaken understanding that wind always has a cooling effect. Wind speed is of crucial importance at low air temperatures, and the wind chill factor is a measure of the combined effect of air temperature and wind on cooling and evaporation. A person exposed to an air temperature of −40 °C and a 50 km h^{-1} wind would lose heat as if exposed to −80 °C in still air. The record low for our planet is −87 °C (1958) at USSR Antarctic base. The incremental effect of wind speed is, however, particularly noticeable at low wind speeds for two reasons. One derives from the convective heat transfer equation: $\sqrt{V}$ increases three-fold between 0.1 and 1 m s^{-1}, but only 15% between 30 and 40 m s^{-1}. The other is biological: at fairly low speeds the natural lie of the animal's coat (pelage) is disturbed, thereby allowing cold air currents to reach the skin.

The fluid speed (V) in the convective heat transfer equation (eqn [1.2]) is the relative speed of body and fluid, so the equation refers as well to an animal moving through a fluid or to a fluid moving past an animal. Flying and swimming animals particularly are subjected to high convective heat loss; some birds will deliberately dangle their legs to enhance heat loss when flying in hot environments.

1.3.3 Radiation

Radiation is energy exchange by means of electromagnetic energy which travels at the speed of light and needs no medium of propagation. The rate of radiant heat transfer between an animal and its environment is given by

$$\dot{Q}_r = C_r A_r((\bar{T}_s + 273)^4 - (\bar{T}_r + 273)^4) \qquad [1.3]$$

where $\dot{Q}_r$ (W) is the rate of radiant heat loss, A_r (m^2) the area participating in the radiant heat transfer, and $\bar{T}_r$ (°C) the mean radiant temperature of the surroundings, that is, the surface temperature of objects exchanging radiation with the animal. The coefficient C_r incorporates the Stefan–Boltzmann constant as well as the emissivities of both the animal's surface and of the solid surfaces making up the radiant environment.

Heat from animal bodies is emitted in the middle infra-red (5–20 μm). Heat is gained by animals from direct solar radiation, mostly within the visible range (0.4–0.7 μm), but also from reflected visible energy as well as re-radiated long-wave radiation. In the case of direct solar radiation and reflected sunlight the colour of the animal has an important influence on the coefficient C_r as more energy within these wavelengths is reflected by light colours than by dark colours. Dark colours, in turn, absorb more energy than light colours under these conditions. It is important to note, however, that direct sunlight heats up the surface of the earth and this energy is re-radiated in the form of long-wave radiation, the absorption of which is not affected by colour. Based on these principles one would expect animals in polar regions to be black where the incident radiation is mostly visible energy (sunlight and reflected sunlight from snow and ice) and in hot deserts we would expect animals to be light-coloured. However, there is no simple relationship between thermal environment and animal colour. Indeed, some colours seem paradoxical. Polar bears are white and therefore one expects them not to be able to use solar warming well. In the white-hair coat (pelage), however, the individual hairs may act like optical fibres and reflect short-wave energy through the pelage to the surface of the skin. Also many desert animals are pitch-black in colour. The desert raven's black plumage absorbs a large amount of solar radiation and the tips of the feathers can reach temperatures as high as 80 °C. Very little of this heat actually reaches the skin surface, however, as the air trapped beneath the plumage acts as an insulative barrier between the feathers and the skin. Also, the tips of the feathers reach a temperature well in excess of the air temperature even on a hot day and the high thermal gradient encourages heat loss by both convection and radiation. Similar circumstances may prevail in the case of other black desert animals.

1.3.4 Change of state

Change of state in biological systems involves either the change of state of liquid water into water vapour or vice versa and either the uptake or release of the latent heat of vaporisation or condensation respectively. Rate of heat loss via this avenue is influenced mainly by vapour pressure gradients, surface areas and wind speed.

Consider a naked human standing in direct sunlight on a hot day. If the environmental temperature exceeds the body surface temperature, the only way in which the subject can lose heat is by evaporating water by sweating, as humans do not exhibit thermal panting. The lower the water vapour pressure of the air the faster the sweat will evaporate. If the wind speed increases, the boundary layer next to the skin, which is saturated with water vapour, will be disrupted, thereby increasing the vapour pressure gradient from the skin to the surrounding air and accelerating evaporative cooling. Naturally the larger the surface area involved, the greater the potential cooling effect. Per kilogram of body mass, humans lose more water through sweating than any other member of the animal kingdom, and access to such powerful cooling helps to maintain the temperature of their central nervous systems at a very constant temperature.

Because rates of evaporation and convection both depend fundamentally on the properties of the boundary layer near the body surface, the equation describing evaporative heat loss from the body surface looks very like the convection equation:

$$\dot{Q}_e = C_e A_e V^n (P_{\mathrm{H_2Os}} - P_{\mathrm{H_2Oa}}) \qquad [1.4]$$

where $\dot{Q}_e$ (W) is the rate of evaporative heat loss, A_e (m^2) the area participating in evaporation, $P_{\mathrm{H_2Os}}$ (kPa) the saturated water vapour pressure at body surface temperature, and $P_{\mathrm{H_2Oa}}$ the water vapour pressure of ambient air. The exponent n has exactly the same value as in the convection equation, that is, about 0.5 for typical mammals. The coefficient C_e depends on the same physical properties as C_c, but also includes a factor accounting for how wet the body surface is. Because this factor is very difficult to measure, the equation is seldom used. Rather, use is made of the rate of mass loss of the animal as an indirect measure of evaporation rate. Then:

$$\dot{Q}_e = \lambda \dot{m} \qquad [1.5]$$

where λ (J g^{-1}) is the latent heat of evaporation of water, and $\dot{m}$ (g s^{-1}) the rate of mass loss.

If an animal evaporates water predominantly via the respiratory tract, the surface evaporation equation no longer applies, but the mass loss equation does. Evaporation from the respiratory tract can also be determined by measuring ventilation rate and the water content of inspired and expired air.

The driving force for evaporation is the water vapour pressure gradient.

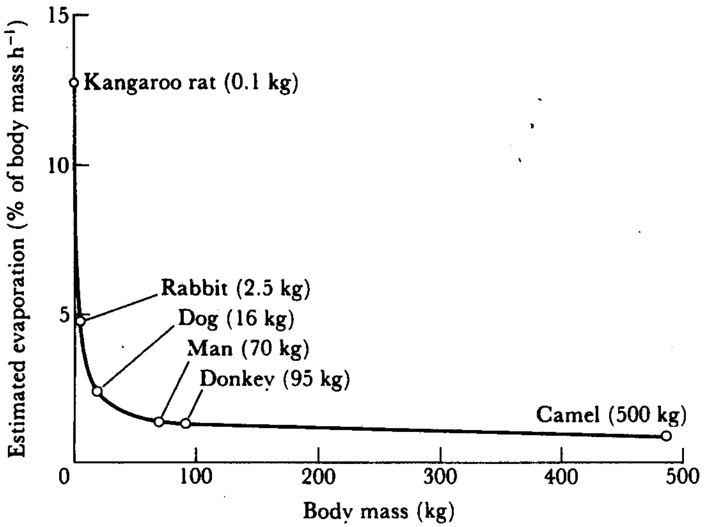


Figure 1.5 **Estimated rates of evaporation of water necessary to maintain a constant body temperature for various mammals standing at rest in a typical desert environment. Heat load is proportional to body surface area, and available water is proportional to body mass, so small animals, with a high surface area relative to mass, are disadvantaged. Redrawn from Schmidt-Nielsen (1964).**

Meteorologists like to express the water vapour concentration in air in terms of the relative humidity. Simplistic deductions based on relative humidity can, however, be misleading. For example, evaporation from a human takes place faster in air at 90% relative humidity, 15 °C temperature, than in air at 40%, 30 °C, because vapour pressure rises rapidly with temperature (see Chapter 2). It is perfectly possible to evaporate sweat into air with 100% relative humidity, provided the temperature is low enough.

The combination of high air temperature and high humidity, on the other hand, results in very high vapour pressure, and poor or absent evaporative cooling. Based on these physical principles, Richards (1973) speculates that when the unfortunate victims of the infamous 'Black Hole of Calcutta' incident were crammed into a small prison cell, air temperature must have risen rapidly to skin temperature. The prison cell was poorly ventilated and consequently the atmospheric air soon became saturated from the sweat and expired air of the prisoners. Body temperatures must have risen swiftly under these conditions with rapid onset of heat death. Similar conditions prevail inside space suits, and a good deal of the paraphernalia carried by astronauts on space walks is concerned with removing heat.

Birds and mammals are the only animals that regularly employ active evaporative cooling. Some lizard species will pant but usually as an emergency measure only. Birds do not sweat but most do employ thermal panting. Small mammals never sweat because of the danger of dehydration (see Fig. 1.5). For example, if a small mouse were to sweat it would become fatally dehydrated within a few hours. Instead, they use behavioural mechanisms to escape from heat to a more favourable microclimate. Again, in an emergency, small mammals like rats and bats will cover their body surfaces with saliva. Some large animals both sweat and pant (e.g. most large antelope, sheep and cattle), some only pant (e.g. dogs, pigs and wildebeest). Rhinos sweat but elephants do not; they dilate the blood vessels to their large ears, which then act as thermal windows for radiant and convective cooling. Flapping of the ears increases convective cooling through these thermal windows.

1.3.5 Newton's Law of Cooling

Newton's Law of Cooling, expressed in its simplest form, states that the rate of cooling of an inert body is proportional to the difference in temperature between the centre of that body and the surrounding medium:

$$\dot{T}_b = C_N(T_b - T_a) \qquad [1.6]$$

where C_N represents the Newtonian cooling constant of the particular body, T_b is the temperature of the body (and $\dot{T}_b$ its rate of change) and T_a is the ambient temperature. In other words, if the body is incapable of producing heat, the rate of heat loss will decrease exponentially as the body's temperature approaches that of the environment (see Fig. 1.6).

The concept provided by Newton's Law has been useful in analysing and testing various hypotheses in thermal biology. For example, if the heating

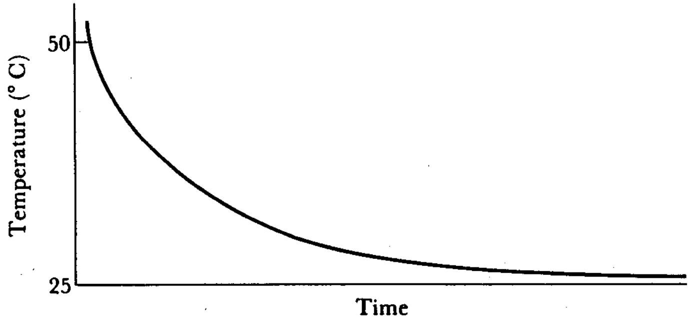


Figure 1.6 **Temperature of a body heated to above 50 °C and then placed in an environment of 25 °C, cooling according to Newton's Law. The temperature (T_t) at a time t is given by the equation**

$$T_t - T_f = (T_i - T_f)e^{-t/\tau}$$

where T_i and T_f are the initial and final temperatures, and τ the time constant.

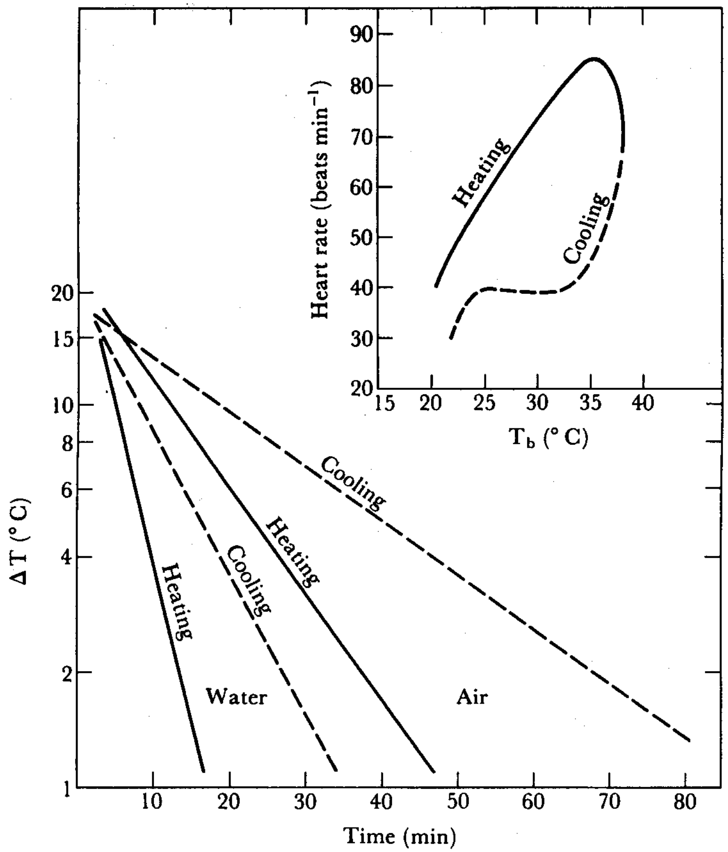


Figure 1.7 **Difference in temperature (Δ*T*) between body core and environment, as a function of time, during heating and cooling of the Galapagos marine iguana (*Amblyrhynchus cristatus*) between 20 and 40 °C, in water and air. The rates of heating and cooling are much faster in water than in air, because of the much higher heat transfer coefficient at the animal surface. In both water and air, the rate of cooling is lower than the rate of heating, a deviation from Newton's Law, implying that the rate of heat transfer within the iguana differs during heating and cooling. Such differences usually result from a change in the cardiovascular status, which is reflected in the hysteresis in the relationship between heart rate and body temperature (T_b) during heating and subsequent cooling. Modified and redrawn from Bartholomew and Lasiewski (1965).**

and cooling rates of the Galápagos marine iguana in air and water are drawn on a semi-logarithmic plot, a great deal of information can be gleaned from the results (Fig. 1.7). First, the rate of cooling and heating in water is swifter than in air because of the better heat transfer in water. Also, in both cases rates of heating are more rapid than cooling rates. For an inanimate body, rates of cooling and heating must be equal, according to Newton's Law, so unequal rates imply active thermoregulation by the animal. In the case of the marine iguana, it is adjustments in cardiovascular function, particularly vasomotor tone, which affect the transport of heat between the core and the periphery and vice versa.

Tracy (1972) has cautioned against the indiscriminate use of Newton's Law when studying the thermal adaptations of homeotherms. He argues that the effects of wind speed and animal size must be evaluated separately. Similarly, Bakken (1976) maintains that the analysis of cooling curves obtained by plotting log (body temperature − air temperature) vs. time is generally inaccurate.

1.3.6 Conductance

Notwithstanding its potential inaccuracies, Newton's Law has allowed the introduction of the concept of conductance into thermal ecophysiology, and measurements of conductance have allowed important insights into thermal adaptations. If the body undergoing Newtonian heating or cooling has mass *m* (g) and specific heat *p* (J g^{-1} °C^{-1}), then its rate of heat transfer with the environment $\dot{Q}$ (W) is

$$\dot{Q} = mp\dot{T}_b = mpC_N(T_b - T_a) \qquad [1.7]$$

The term mpC_N is called the conductance (K); it differs from the heat transfer coefficients described earlier in that it defines heat transfer from the core of the body, rather than its surface, to the environment, and is influenced by vasomotor tone, subcutaneous fat, etc.

If a non-evaporating animal reaches thermal equilibrium at a particular ambient temperature, then its heat loss to the environment must equal its metabolic heat production:

$$\dot{Q}_m = K(T_b - T_a) \qquad [1.8]$$

Hence, the slope of equilibrium metabolic heat production plotted against air temperature is the negative of the conductance.

1.3.7 Size, shape, time constants and thermoregulation

An animal's size has a profound effect on its thermoregulation. The most important size parameter affecting thermoregulation is the ratio of surface area to body mass. Bearing in mind the allometric relationship between the relative surface area and the body mass of an animal, which scales to the power of 0.66, the smaller an animal the greater the relative surface area and, all other factors being equal, the faster it will gain or lose heat. A desert ant crawling across a hot desert dune has an extremely high relative surface area and gains heat very rapidly from the environment. Nevertheless, if it can retreat to a cool micro-environment (shade of a pebble) it can unload its heat very rapidly and continue on its journey for a limited time. In contrast, an elephant has a huge volume and a small relative surface area. It gains and loses heat very slowly; it has high thermal inertia.

For similar reasons, juveniles of a sand-dune lizard can use the dying rays of the sun to remain active in the late afternoon, but have to bury in the sand in the middle of the day, when the adults are active (Seely *et al.*, 1990).

Small animals also tend to have high conductance, which exacerbates their rate of heat loss in cold environments. Small endotherms, depending upon environmental circumstances, will generally be obliged to produce more heat per gram of tissue than large animals, whereas large animals may experience difficulty in getting rid of excess heat even though they generate far less heat than small animals per unit body mass.

Animal shape also influences heat exchange. Having body elements with a filament-like geometry minimises radiant heat gain and maximises convective heat loss for animals exposed to the sun, so the ant's shape also contributes to its ability to be active in the desert sun. Similarly, the typically rotund shape of polar animals, like the polar bear or Arctic ptarmigan, maximises radiant heat gain and minimises convective heat loss.

An animal's size, shape and conductance all influence the rate at which it will reach a new equilibrium of body temperature after a change of thermal environment. The approach to a new equilibrium temperature is exponential, so the rate of approach can be expressed in terms of the 'time constant', the time taken for $(1 - 1/e) \approx 63\%$ of the full change in temperature to occur. The time constant may be measured as the negative reciprocal of a log-linear plot of body temperature against time, following a change in thermal status; changes in slope of this plot indicate active physiological thermoregulation.

The time constant is a useful parameter for interspecific comparisons of rates of heat transfer. It also quantifies well the responses of a single species to different thermal challenges. For example, the time constant for naked humans transferred from a neutral to a hot environment is about 40 min, while it is over 3 hours following transfer from a neutral to a cold environment, reflecting activation of heat conservation mechanisms.

1.4 Measuring temperature and heat transfer

In the past several decades the measurement of temperature of both animals and their environments has become progressively more accurate and easier to accomplish. The introduction of thermistors, electronically compensated thermocouples, thermopiles, infra-red thermometers and radiotelemetry have all contributed towards this improvement. For further details, and particularly to avoid common errors, the reader is referred to an excellent practical guide by D. M. Unwin (1980) called *Microclimate Measurements for Ecologists.*

Although standard micrometeorological measurements are of great value to the thermal biologist, it would be very useful to have a single index which expresses heat transfer. Several recent studies in the field have used the 'standard operative temperature'. Standard operative temperature is a concept originally developed by Gagge (1940) for analysing human heat transfer and is the temperature of an ideal isothermal black body enclosure with standard convection conditions, which would produce the same net sensible heat flow for the same animal surface temperature. It is therefore an index of sensible heat flow to and from the environment. It can be calculated from standard micrometeorological variables, but in practice it is measured by constructing a model of exactly the same dimensions as a representative animal of the species being studied. The model is fitted with thermometers and is covered with the pelt of the animal being studied. These taxidermic models can then be placed in strategic positions, for example in full sunlight, in burrows, in the shade or various positions above ground or in a tree while their temperatures are being monitored. Using this method Chappell and Bartholomew (1981) studied the thermal energetics of the antelope ground squirrel in its southern Californian desert habitat. They found that standard operative temperature in unshaded areas was 30 °C above the upper critical temperature of the ground squirrels and 20 °C above air temperature for much of the day. In these conditions the maximum time that the animals could tolerate surface exposure was 7–9 min. Their findings supported the hypothesis that thermoregulation in this ground squirrel involves cycles of transient hyperthermia followed by periods of rest in underground burrows when heat is dissipated passively. For further details of the method consult Bakken (1980) and for interesting application to measuring the energetic cost of free existence see Weathers and Nagy (1980).

Because the construction of taxidermic models for measuring operative temperature is quite involved and time-consuming and because the measurements they give are species specific, many thermal biologists choose to use the simpler, but similar, measure of 'black bulb temperature'. The standard black bulb or globe thermometer in meteorology is a hollow copper sphere 150 mm in diameter, painted matt black and fitted with a thermometer which measures the temperature at the centre of the sphere. The black bulb or globe temperature will integrate several environmental variables namely radiation, wind speed and air temperature. As long as an animal does not change emissivity, globe temperature is a reasonable index of the animal's heat transfer in the prevailing environmental conditions, though it clearly cannot account for evaporative or metabolic processes. Seely *et al.* (1990) have shown the advantage of globe temperature over air temperature and substrate temperature in explaining the way lizards employ the thermal mosaic on an apparently homogeneous desert sand dune.

An approach which combines aspects of the black bulb thermometer and the taxidermic model is to construct a metal cylinder the same size as the study animal, paint it black and fit it with a thermometer in order to monitor its interior temperature. Very small cylinders the size of ants or bees can be made. In this way Louw and Nicolson (1983) were able to measure a critical minimum temperature required for flying in carpenter bees with better predictive value than normal air temperature.

1.5 The heat balance and the complexity of heat exchange in an outdoor environment

Thermal flux through an organism is usually described by the deceivingly simple equation:

$$\dot{Q}_m + \dot{Q}_w + \dot{Q}_k + \dot{Q}_r + \dot{Q}_c + \dot{Q}_e = \dot{Q}_s \qquad [1.9]$$

where $\dot{Q}_m$ is the metabolic rate, $\dot{Q}_w$ is the rate of energy expenditure on physical work, $\dot{Q}_k$, $\dot{Q}_r$, $\dot{Q}_c$ and $\dot{Q}_e$ are the rates of heat transfer by conduction, radiation, convection and evaporation with the environment, and $\dot{Q}_s$ is the rate of heat storage, which equals zero when the organism is in thermal equilibrium. Although the concept is simple, the measurement of all the variables in an outdoor environment is exceedingly complex (see Porter and Gates, 1969, see Fig. 1.8).

Because of their complexity, complete heat balances have seldom been attempted. A famous study is the analysis of the heat balance of a lizard by Bartlett and Gates (1967). Studies on African mammals have shown that one of the most important avenues of heat gain in a hot arid environment is via re-radiation of long-wave radiation from the surface of the soil. These and other studies have also highlighted the importance of surface areas, particularly the profile area exposed to direct solar radiation, as well as the importance of thermal gradients between the organism and the environment. Also of importance is wind speed, the nature of the integument (pelage) and, in the case of man, clothing. These structures can act as thermal shields resulting in the exchange of heat at the surface of the animal without eliciting any physiological responses.

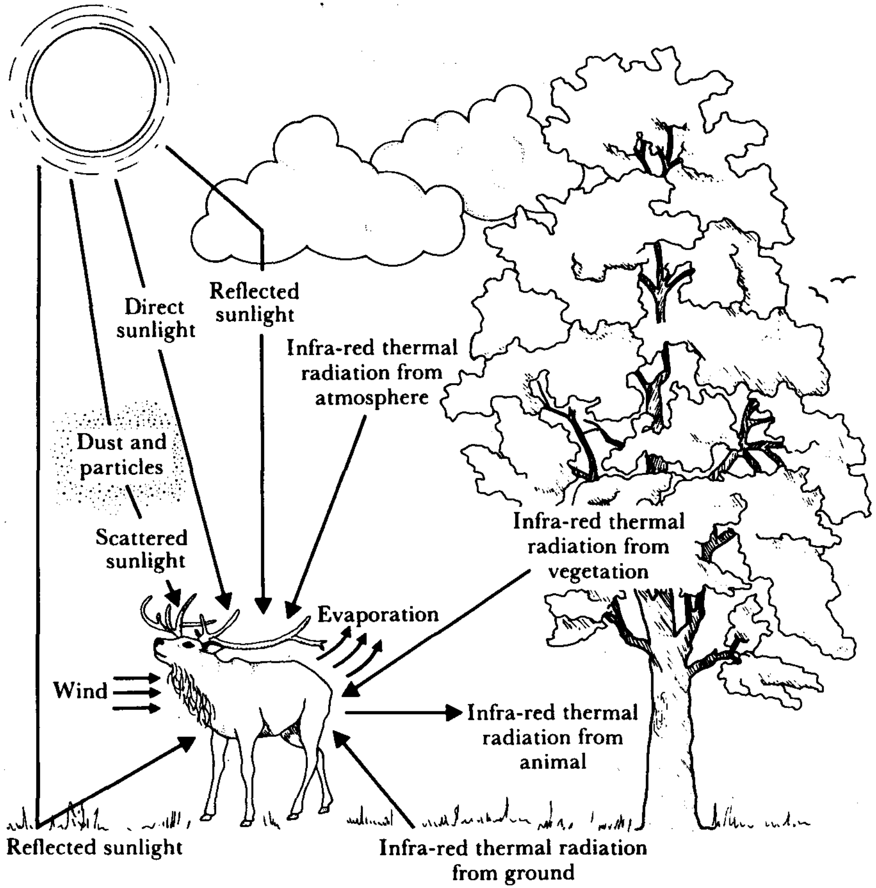


Figure 1.8 Avenues of heat transfer between an animal and an outdoor environment. Redrawn from Porter and Gates (1969).