Temperature Regulation

The temperature of most animals follows passively that of the surroundings. It would seem advantageous if they could free themselves from the vagaries of this environmental variable, and in this chapter we shall deal with animals that keep their body temperature more or less independent of the environmental temperature.

Birds and mammals live through most of their lives with body temperatures that fluctuate no more than a few degrees. We shall consider these animals first, and then discuss what other animals have achieved in keeping their temperature independent of the environment.

First, we should clarify what we mean by *body temperature*, by no means a simple concept. Second, to maintain a constant temperature, the heat gained and the heat lost from the organism must be equal. To understand these two processes, we must be familiar with the simple physics of heat transfer.

In a *cold environment* a high temperature can be maintained by reducing the heat loss and/or increasing the heat gain (heat production). Most birds and mammals do this very well. However, some mammals and a few birds seem to give up the fight against cold and permit their temperature to drop precipitously; they go into torpor or hibernation. Nevertheless, temperature regulation is not abandoned; on the contrary, hibernation is a well-regulated physiological state.

In a *hot environment* the problems of maintaining the body temperature are reversed: The animal must keep the body temperature from rising and is often compelled to cool itself by evaporation of water.

Not only birds and mammals, but certain other animals are amazingly adept at keeping their temperature above that of the environment. This applies, for example, to lizards that bask in the sun, to many insects, and amazingly, even to some fish that maintain parts of their body at temperatures approaching those of "warm-blooded" animals.

TABLE 7.1 Heat production in the major organs of a man at rest (body mass, 65 kg; heat production, 1872 kcal per day = 78 kcal per hour = 90.65 W). The main internal organs weigh about 5 kg but account for 72% of the total heat production. [Aschoff et al. 1971]

Organ	Organ mass		% of body mass		Heat production at rest		% of total	
	kg		% of body mass		kcal h^{-1}		% of total	
Kidneys	0.29		0.45		6.0		7.7	
Heart	0.29		0.45		8.4		10.7	
Lungs	0.60	5.03	0.9	7.7	3.4		4.4	72.4
Brain	1.35		2.1		12.5		16.0	
Splanchnic organs[a]	2.50		3.8		26.2		33.6	
Skin	5.00		7.8		1.5		1.9	
Muscle	27.00	59.97	41.5	92.3	12.2		15.7	27.6
Other	27.97		43.0		7.8		10.0	
Total	65.00		100.0		78.0		100.0	

[a] Abdominal organs, not including kidneys.

BODY TEMPERATURE OF BIRDS AND MAMMALS

What is body temperature?

The heat produced by an animal must be transported to the surface before it can be transferred to the environment. Therefore, the surface of the organism must be at a lower temperature than the inner parts, for if the temperature were the same throughout, no heat could be transferred. The conclusion is that the temperature of an organism of necessity cannot be uniform throughout.

If we examine where in the mammalian body heat production takes place, we find that some parts produce more heat than others. In humans the organ of the chest and the abdomen, although they make up less than 6% of the body mass, produce 56% of the total heat (Table 7.1). If we include the brain, which in humans is large and has a high heat production, we have accounted for 72%, or more than two-thirds of the total heat production, in less than 8% of the body mass.

We can therefore consider that the body consists of a core where most of the heat is produced, and a much larger shell that includes skin and muscles and produces only a small fraction of the total body heat.
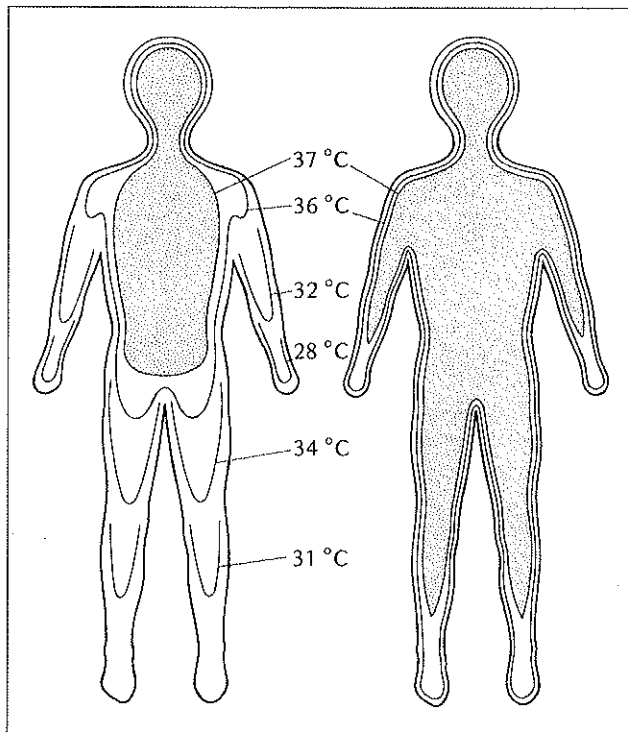
During exercise, the situation is different, for the total metabolic rate may increase 10-fold or more. Most of this increase occurs in the muscles (including the diaphragm and other respiratory muscles). During exercise, then, for the internal temperature to remain constant, more than 10 times as much heat as was produced at rest must be transported to the surface of the organism.

Temperature distribution in the body

The inner, or core, temperature remains reasonably constant, but this does not mean that the temperature throughout the core is uniform. Organs that have a high rate of heat production may be warmer than others, but they are cooled by the blood (i.e., the venous blood that leaves these organs is warmer than the arterial blood). The temperature differences in the core may be as much as 0.5 °C from one site to another. We therefore cannot speak about a single core temperature, but for practical purposes the deep rectal temperature is often used as a representative measure.

The surface temperature of a person who is in

FIGURE 7.1 Temperature distribution in the body of a person at room temperatures of 20 °C (left) and at 35 °C (right). The isotherms, which indicate sites of equal temperature, show that, at 35 °C room temperature, a core temperature of 37 °C (shaded area) extends into the legs and arms. At 20 °C room temperature, the temperature gradients in the shell extend throughout the legs and arms, and the core temperature is restricted to the trunk and head. [Aschoff and Wever 1958]

can calculate a mean body temperature from multiple measurements at various sites, provided we have a weighting procedure to apply to the various measurements. However, mean body temperature calculated from multiple measurements is physiologically relatively meaningless.

We have already seen that the core temperature does not represent the heat status of the whole body, that the temperature of the shell can vary widely, and that the depth in the body to which the shell temperature extends can change drastically. A change in the temperature of the shell means that the total amount of heat in the body changes, although the core temperature may remain constant. If a person moves from a room temperature of 35 °C to 20 °C, the drop in shell temperature may involve a heat loss of 200 kcal (>800 kJ) from the shell. The magnitude of this much heat becomes clear when we realize that it corresponds roughly to 3 hours' resting metabolism of the person.

"Normal" body temperature of birds and mammals

Daily fluctuations in core temperature

The core temperature of humans and of other mammals and birds undergoes regular daily fluctuations. Within 24 hours these fluctuations are usually between 1 and 2 °C. Diurnal animals show a temperature peak during the day and a minimum at night; nocturnal animals show the reverse pattern. However, these daily cycles are not caused directly by the alternating periods of activity and rest, for they continue even if the organism is at complete rest.

The daily body temperature pattern of many mammals and birds consistently follows the light cycle. When the towhee (*Pipilo aberti*) is kept in 12 hours of darkness and 12 hours of light, its body temperature follows a cycle synchronized with the light cycle. At a room temperature of 23 °C, the core temperature at night is about 39 °C and when the light comes on, it rapidly rises to nearly 42 °C

heat balance is always lower than the core temperature. This means that the arterial blood that flows to the shell loses heat and returns as colder venous blood. This is, of course, how most of the heat produced in the core is brought to the surface or, in other words, how the core organs are cooled. Depending on the circumstances (external temperatures and the need for heat loss), the surface temperature varies a great deal. Also, the underlying tissues, including a large part of the muscle mass, can take on temperatures considerably below the core temperature (Figure 7.1).

What is the mean temperature of the body? We

FIGURE 7.2 When the towhee (a finch, *Pipilo aberti*) is kept at a constant room temperature of 23 °C, its body temperature varies with the light cycle. When the lights come on at 0600 hours, the body temperature rises by nearly 3 °C, to drop again when the lights go off at 1800 hours. If the room temperature is reduced to 5 °C, the body temperature cycle is similar, but at a slightly higher level. [Dawson 1954]

Hour of day
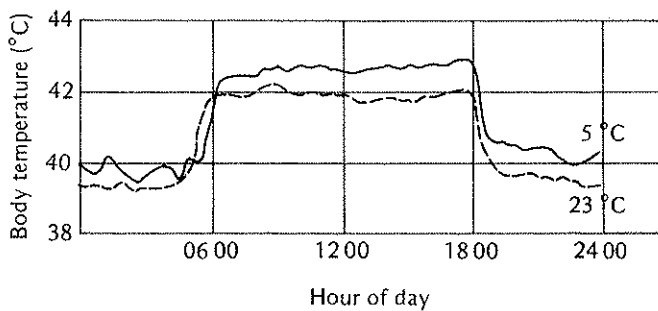
(Figure 7.2). At a different room temperature (5 °C, for example) the core temperature follows the same day-and-night cycle, although it is, on the average, about 0.5 °C higher than the corresponding core temperature measured at 23 °C.

Similar temperature cycles have been recorded in a variety of other birds from several different families. Diurnal forms always have the highest temperature during the day and nocturnal species at night. One example of a nocturnal bird is the flightless kiwi (*Apteryx*) from New Zealand. Its core temperature is lower than in most other birds, with a daytime mean of 36.9 °C. At night, which is the normal period of activity for the kiwi, the temperature increases to a mean of 38.4 °C (i.e., at night the temperature is about 1.5 °C higher than in the daytime) (Farner 1956).

Both the temperature cycle and the corresponding cycle in metabolic rate can be reversed by reversing the periods of light and dark. This shows that the cycle is governed by the illumination. However, even if all variations in the light are removed and the animals are kept in continuous uniform light, their temperature variations continue on nearly the same timing. This is called the *free-running period*, and because it persists without any

external cues, it must be inherent in the organism; it must be a truly endogenous cycle.

The cycle is self-sustained in the sense that, in the absence of external timing cues, it continues for days, weeks, and even months. It remains extremely regular, but its duration usually is not exactly 24 hours. As a result, the timing of a free-running cycle in the absence of an external cue gradually drifts away from the environmental 24-hour day-and-night cycle.

We have now seen that the temperature of the body core and shell may differ greatly and that there are regular variations of several degrees that make measurements of the core temperature meaningful only if we also have information about activity, the time of day, and the usual temperature cycle of the animal.

Temperature differences among animal groups

If we disregard variations that amount to a couple of degrees, we see that the usual or "normal" core temperature is almost uniform within each of the major groups of warm-blooded vertebrates, but that there are characteristic differences among the groups (Table 7.2).

Allowing for the fact that it is difficult to establish what is normal body temperature for a given animal, and disregarding variations caused by external conditions and activity, we can as a rule of thumb say that most birds maintain their body temperature at 40 ± 2 °C, eutherian mammals at 38 ± 2 °C, marsupials at 36 ± 2 °C, and monotremes at 31 ± 2 °C. Small birds may have somewhat higher body temperatures than large birds (McNab 1966), but in mammals there is no clear relationship between body size and body temperature (Morrison and Ryser 1952). For marsupials the available information is insufficient to show whether there is any relationship between body size and body temperature.

The fact that the so-called primitive groups – insectivores, marsupials, and especially monotremes – consistently have low body temperatures

TABLE 7.2 Approximate normal and lethal core temperatures of some major groups of mammals and birds. The lethal temperatures are based on observations made under a wide variety of conditions. There is rather consistently an approximately 6 °C interval between the normal and the lethal temperatures for the same animal.

Animal	Approximate normal core temperature (°C)	Approximate lethal core temperature (°C)
Monotreme (echidna)	30–31[a]	37[a]
Marsupials	35–36[b]	40–41[e]
Insectivore (hedgehog)	34–36	41[f]
Man	37	43
Eutherian mammals	36–38[c]	42–44[g]
Bird (kiwi)	38[d]	
Birds, nonpasserine	39–40[b]	46[h]
Birds, passerine	40–41[b]	47[i,j]

[a] Schmidt-Nielsen et al. (1966).
[b] Dawson and Hulbert (1970).
[c] Morrison and Ryser (1952).
[d] Farner (1956).
[e] Robinson and Morrison (1957).
[f] Shkolnik and Schmidt-Nielsen (1976).
[g] Adolph (1947).
[h] Robinson and Lee (1946).
[i] Calder (1964).
[j] Dawson (1954).

raises some interesting evolutionary problems. These groups are considered to be very ancient and presumably have had more time than more recent groups to evolve toward a high body temperature, if this is "desirable" or advantageous. Have they remained in their more "primitive" stage because they have lacked the capacity to evolve in this direction? They have certainly been successful as witnessed by their ability to survive for so long.

The fact is that we do not fully understand the advantages of any given body temperature. In any event, it would be a mistake to interpret a low body temperature as a sign of "primitive" and thus inadequate temperature regulation. It has been said that the egg-laying echidna is halfway to being a cold-blooded animal and is unable to regulate its body temperature adequately. In fact, the echidna is an excellent temperature regulator and can maintain its core temperature over a wide range of ambient temperatures down to freezing or below, although it has a poor tolerance to high temperature (Schmidt-Nielsen et al. 1966).

The approximate lethal body temperatures for the various groups of warm-blooded vertebrates are given in the last column of Table 7.2. It seems that the lethal temperature is regularly at roughly 6 °C above the normal core temperature. Thus, the echidna dies when its body temperature reaches 37 °C, which is a normal temperature for placental mammals and well below the normal temperature for birds. The margin of safety remains uniformly at about 6 °C from group to group, but we do not know why the lethal temperature is at such a constant level relative to the normal core temperature.

Temperature of cold-climate animals

Do Arctic birds and mammals maintain body temperatures within the same range as species from warmer climates?

To answer this question the body temperatures of a number of Alaskan birds and mammals were measured while the animals were exposed to a wide range of low air temperatures. The birds studied belonged to 30 different species and ranged in weight from 0.01 to 2 kg. In air temperatures from +20 °C down to −30 °C, their mean body temperature was 41.1 °C, which is within the normal range for birds from moderate or tropical climates.

Arctic mammals of 22 species, weighing from 0.1 to 1000 kg, were exposed to temperatures down to −50 °C, and one species (the white fox) even to −80 °C. The individuals of all species maintained their body temperatures within normal mammalian limits. The mean for all the observed species was 38.6 °C, which is about 0.5 °C higher than the previously reported mean temperature for a large number of mammals from temperate regions, but this difference is considered insignificant (Irving and Krog 1954).

We can therefore conclude that Arctic birds and

mammals maintain body temperatures characteristic of their groups, although they live in some of the coldest areas on earth.

Animals in natural conditions

In contrast to the large amount of information on body temperature in captive and laboratory animals, there are few long-term studies on animals under natural conditions. The development of methods to measure temperature with transducers that transmit information by radio (telemetry) has made it possible to obtain recordings from unrestrained and completely undisturbed animals.

Surgical implantation of such a telemetric unit has enabled the monitoring of the temperature of a single animal for as long as 1 year. When this technique was used on sheep grazing under field conditions, the daily range of the deep body temperature was less than 1 °C regardless of sun, rain, or storm. The total temperature range observed during a whole year from summer to the most severe winter was 1.9 °C, from 37.9 to 39.8 °C (Bligh et al. 1965).

Fever

Fever is an increase in body temperature that usually is associated with microbial or virus infections. Similar increases in body temperature can be produced by the injection of killed bacteria. These contain substances, *pyrogens,* that are the cause of the fever reaction. The organism behaves as if the set point of a thermostat has been increased by a few degrees and now regulates as if it wants to maintain the increased temperature.

Fever is definitely not a failure of temperature regulation. If a person with fever is challenged with cooling, increased heat production serves to maintain the higher temperature, and vice versa if an extra heat load is applied. The processes of temperature regulation respond as expected, except that the reactions revolve around the higher body temperature.

The concept that fever represents a well-regulated resetting of a "thermostat" is further supported by the following experiment. If a pyrogen is injected into a dog, the animal develops a fever. However, if heat is applied locally only to the hypothalamus, where the temperature regulation center is located, the fever in the body is suppressed. The body behaves as if the higher "set-point" has already been reached. This indicates that the bacterial pyrogen does not somehow damage the regulatory mechanism in the hypothalamus, but that a certain hypothalamic temperature is "desirable," and when this has been attained, no further heating is called for (Andersen et al. 1961).

Both mammals and birds develop fever after becoming infected with bacteria, but it is unclear whether the fever is beneficial or harmful. An interesting attempt at settling this much-argued question has been made by studying, not warm-blooded mammals or birds, but a cold-blooded animal, the lizard *Dipsosaurus dorsalis.* When *Dipsosaurus* is placed in an environment where there is a range of temperatures, it selects a preferred temperature where it tends to remain so that it maintains body temperature of about 38.5 °C. If the lizard is injected with an appropriate bacterial suspension, it seeks a somewhat warmer environment and maintains a higher body temperature, a "fever" of approximately 2 °C.

Amphibians and fish show similar reactions in response to bacterial pyrogens (Reynolds et al. 1976; Kluger 1977). They select a warmer environment and thus maintain higher preferred body temperatures, demonstrating that the "fever" response is present in a broad range of vertebrates and not only in the warm-blooded mammals and birds. Even cockroaches, when injected with bacteria and placed in a thermal gradient, prefer temperatures significantly elevated over what they normally do (Bronstein and Conner 1984).

Let us return to the question of whether fever is beneficial or harmful. An answer has been sought by performing the following experiment on *Dipsosaurus.* Five groups of lizards were infected with bacteria (*Aeromonas hydrophila*) and kept at uniform constant temperatures. One group was kept

at a neutral 38 °C, two groups at lower temperatures (36 and 34 °C), and two at higher temperatures (40 and 42 °C). There was a striking correlation between survival and temperature; all the animals at the lowest temperature died in less than 4 days; survival increased with temperature and was highest in the animals at 42 °C. This is approximately the same temperature that injected animals voluntarily chose if they were allowed to select their temperature (Kluger et al. 1975). In these animals, then, a clear beneficial effect was associated with the higher body temperature.

The ability to maintain a constant body temperature, as birds and mammals do, and the ability to reset the temperature with full maintenance of regulation as occurs in fever, require extraordinary capacities of the physiological mechanisms for heat exchange. Before we discuss these mechanisms we will need an elementary knowledge of the physics of heat transfer.

TEMPERATURE, HEAT, AND HEAT TRANSFER

In the preceding section we were concerned with temperature, and the concept of heat was mentioned only incidentally. It is important to understand the difference between these two physical quantities and to realize that the measurement of temperature does not necessarily give any information about heat.

Temperature is usually measured in degrees Celsius (°C), although in physical chemistry and thermodynamics we use absolute temperature expressed in kelvins (K).*

In biology heat is usually measured in calories, and 1 calorie (cal) is defined as the amount of heat needed to raise the temperature of 1 g water by 1 °C. The calorie is not a part of the International System of Units (the SI System), but the term is so common that it will remain in use for some time to come. For conversion to SI units, 1 cal = 4.184 joules (J).

To heat 1 g water from room temperature (25 °C) to the boiling point (100 °C) requires 75 cal of heat. To raise the temperature of 100 g water by 75 °C requires 7500 cal (7.5 kcal). In both cases the initial and final temperatures are the same, and temperature alone therefore gives no information about the amount of heat added. If we know the amount of water, however, we can calculate the amount of heat from the temperature change, for by definition, the heat needed to raise the temperature of 1 g water by 1 °C is 1 cal. The amount of heat needed to warm 1 g of substance by 1° is known as the *specific heat capacity* of that substance.† The specific heat capacity of water is 1.0 cal g^{-1} $°C^{-1}$, which compared with that of other substances is very high. The specific capacity of rubber is 0.5, of wood 0.4, and of most metals 0.1 or less. The specific heat capacity of air is 0.24 cal g^{-1} $°C^{-1}$, and because the density of air is 1.2 g per liter (at 20 °C), the heat capacity of 1 liter of air is 0.3 cal $°C^{-1}$.

The amount of heat needed to increase the temperature of the animal body is slightly less than the amount needed to heat the same mass of water. The mean specific heat capacity of the mammalian body is about 0.8. Thus, to increase the temperature of a 1000-g mammal by 1 °C requires about 800 cal. The exact value for the specific heat capacity of the animal body varies somewhat. For example, the specific heat capacity of mouse bodies was found to vary between 0.78 and 0.85 with a mean of 0.824 (Hart 1951).

The bulk of the body is water, which has a specific heat capacity of 1.0, and the other components – proteins, bone, and fat – tend to reduce

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* Absolute zero is at −273.15 °C. Celsius temperature (T_C) relates to absolute temperature (T_K) as follows: $T_K = T_C + 273.15$.

† It is recommended that the word *specific* before the name of a physical quantity be restricted to the meaning "divided by mass" (Council of the Royal Society 1975).

this value. Fat is particularly important, for its amount can vary within wide limits, and its specific heat capacity is only about 0.5.

For many purposes it is sufficient to use a mean value of 0.8 for the specific heat capacity of the animal body, for in order to determine a change in heat content, we must know the mean body temperature, and as we have seen, this variable is very difficult to determine with accuracy.

Physics of heat transfer

For a body to maintain a constant temperature, there is one absolute requirement: Heat loss must exactly equal heat gain. For an animal to maintain a constant temperature, heat must be lost from the body at the same rate it is produced by metabolic activity.

As we have seen, metabolic heat production can easily increase more than 10-fold with activity, and unless heat loss is increased in the same proportion, body temperature will rise rapidly. Furthermore, the conditions for heat loss vary tremendously with external factors such as air temperature and wind. An understanding of the physiological mechanisms involved in the regulation of heat production and heat loss requires an elementary knowledge of the physics of heat transfer.

Whenever physical materials are at different temperatures, heat flows from a region of higher temperature to one of lower temperature. This transfer of heat takes place by *conduction* and by *radiation*. A body cannot lose heat by conduction or radiation unless its environment, or some part of it, is at a lower temperature than the surface of the body. There is, however, a third way to remove heat: the *evaporation* of water. These three ways of heat transfer – conduction,* radiation, and

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*Transfer of heat between a surface and a fluid (gas or liquid) in contact with it takes place by conduction. Mass movement in the fluid, termed *convection*, contributes to renewal of fluid in the boundary layer and thus complicates the conductive heat transfer (see later in this chapter).

FIGURE 7.3 Heat flow in a uniform conductor depends on its cross section, the temperature gradient, and the material from which it is made.
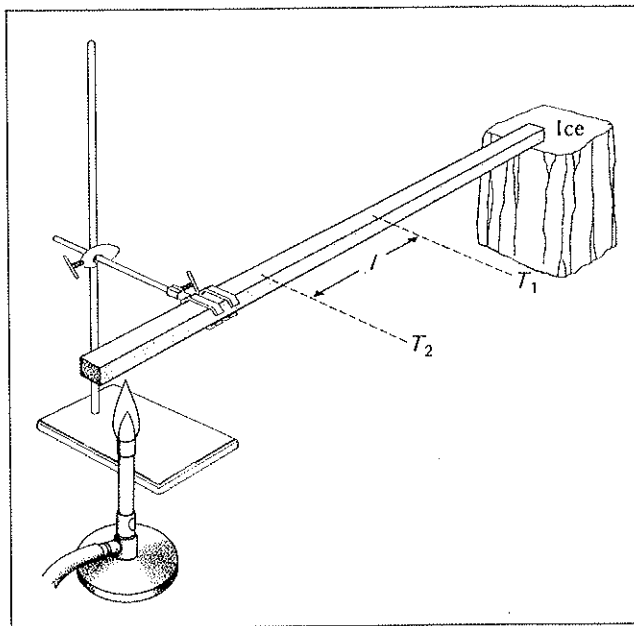
evaporation – are the only means available for the removal of the heat produced in the metabolic activity of living organisms.

Conduction

Conduction of heat takes place between physical bodies that are in contact with each other, whether they are solids, liquids, or gases. Conduction of heat consists of a direct transfer of the kinetic energy of molecular motion, and it always occurs from a region of higher temperature to one of lower temperature.

Assume that we have a uniform conductor in which we keep one end warm and the other cold (Figure 7.3). The rate of heat transfer by conduction $\dot{Q}$ can now be expressed as:

$$\dot{Q} = k\,A\,\frac{T_2 - T_1}{l}$$

where k is the thermal conductivity of the conductor, A is the area through which the heat flows

TABLE 7.3 Thermal conductivities (k) for a variety of common materials. [Hammel 1955; Hensel and Bock 1955; Weast 1969]

Material	k (cal s^{-1} cm^{-1} °C^{-1})
Silver	0.97
Copper	0.92
Aluminum	0.50
Steel	0.11
Glass	0.002 5
Soil, dry	0.000 8
Rubber	0.000 4
Wood	0.000 3
Water	0.001 4
Human muscle	0.001 1
Adipose tissue	0.000 51
Air	0.000 057
Animal fur	0.000 091

(normal to the direction of heat flow), and T_2 and T_1 are the temperatures at two points separated by the distance l. The fraction $(T_2 - T_1)/l$ is known as the *temperature gradient* and stands for the temperature difference per unit distance along the conductor.

This expression for heat flow in a conductor can be stated in simple intuitively obvious terms. Heat flow increases with the thermal conductivity (k) of the conducting material, with increasing cross-sectional area (A) of the conductor, and with an increased temperature difference between two points T_2 and T_1. Increasing the distance (l) between two given temperatures, T_2 and T_1 (if these remain unchanged), decreases the amount of heat flow.

The thermal conductivity coefficient (k), is an expression for how easily heat flows in a given material. Values for the thermal conductivity of some common materials are given in Table 7.3. As we know, metals are excellent conductors and have high conductivity coefficients. Glass and wood are poorer conductors; water and human tissues have slightly lower conductivities again, but of a similar order of magnitude. The similarity between the thermal conductivities of human tissue and water is, of

course, attributable to the fact that most tissues consist of roughly two-thirds to three-quarters water. Air and animal fur have very low thermal conductivities, which means that their insulation value (resistance to heat flow) is high. The main reason the thermal conductivity of fur is low is the large amount of air trapped between the hairs. Other materials that enclose a high proportion of air (e.g., felt, woolen fabrics, down) are also poor conductors or excellent insulators.

The simple equation for heat conduction given above unfortunately applies only when heat flows through a plane object such as a wall. Most animal surfaces are curved, and this makes the conduction equation considerably more complex. For practical purposes, we can consider the heat flow as dependent on temperature gradients and area, but if we wish to make a quantitatively satisfactory analysis of heat transfer in an animal, it is necessary to apply a more rigorous treatment of the physics of heat transfer.

Convection

The transfer of heat in fluids is almost invariably accelerated by the process of *convection*, which refers to mass movement of the fluid. Assume a cold fluid in contact with a warm solid surface. Heat flows into the fluid by conduction, and the fluid adjacent to the surface becomes warmer. If the fluid is in motion, the warm fluid adjacent to the solid surface is replaced by cold fluid, and the heat loss from the solid surface is therefore speeded up. Mass flow, or convection, in the fluid thus facilitates heat loss from the solid, although the transfer process between solid and fluid remains one of conduction.

Convection in a fluid may be caused by temperature differences or by external mechanical force. Heating or cooling of a fluid usually changes its density, and this in turn causes mass flow. For example, if a warm solid surface is in contact with a cold fluid, the heated fluid expands and therefore rises, being replaced by cool fluid. In this case the mass flow, or convection, is caused by the temperature difference and is called *free* or *natural con-*

vection. This term applies also if the wall is colder than the fluid and the fluid adjacent to the wall becomes denser and sinks.* Free convection, of course, can take place both in air and in water and contributes substantially to the rate of heat loss from living organisms.

Motion in the fluid can also be caused by external forces, such as wind, water currents, or an electric fan. Convection caused by external forces, as opposed to density changes, is referred to as *forced convection*.

Because convection depends on mass transfer in fluids, the process is governed by the rather complex laws of fluid dynamics, which include such variables as the viscosity and density of the fluids, in addition to their thermal conductivity. Convective heat loss does not depend only on the area of the exposed surface. Variables such as the curvature and the orientation of the surface give rise to rather complex mathematical expressions, which cause great difficulties in the analysis of the heat transfer from an animal. As we shall see below, however, we can find practical means for analyzing the heat transfer between an animal and the environment that circumvent the need for an exact analysis of the physical processes involved.

Radiation

Heat transfer by radiation takes place in the absence of direct contact between objects. All physical objects at a temperature above absolute zero emit electromagnetic radiation. The intensity and the wavelength of this radiation depend on the temperature of the radiating surface (and its emissivity, which we shall discuss below). All objects also receive radiation from their surroundings. Electromagnetic radiation passes freely through a vac-

* Water has a higher density at +4 °C than at the freezing point. This is of great importance in bodies of fresh water, but in most physiological situations the anomalous density of water is of no significance. Sea water does not exhibit the anomalous density properties at near-freezing temperature (see also page 226).

uum, and for our purposes atmospheric air can be regarded as fully transparent to radiation.

The *intensity* of radiation from an object is proportional to the fourth power of the absolute temperature of the surface. This is expressed by the *Stefan-Boltzmann law* for heat radiation flux:

$$\dot{Q}_R \propto \sigma T^4$$

where T is the absolute temperature of the radiating surface (in kelvin, K), and σ is Stefan-Boltzmann's constant $(1.376 \times 10^{-12}$ cal s^{-1} cm^{-2} K^{-4} or 5.67×10^{-8} W m^{-2} K$^{-4})$. Because the amount of heat or energy radiated increases with the fourth power of the absolute temperature, the emission increases very rapidly indeed with the surface temperature.

The *wavelength* of the emitted radiation depends on the surface temperature, and the hotter the surface, the shorter is the emitted radiation. As the surface temperature of a heated object increases, the radiation therefore includes shorter and shorter wavelengths.

The radiation from a heated piece of iron just barely begins to include visible red light when its temperature is about 1000 K. If heated further, it emits shorter wavelengths (i.e., more visible radiation is included). Therefore, as the temperature increases, the visible color shifts from red to yellow to white. The sun's radiation, which has its peak in the visible part of the spectrum, corresponds to a surface temperature of about 6000 K and includes an appreciable amount of radiation in the near ultraviolet as well.

Objects that are close to physiological temperatures emit most of the radiation in the middle infrared. For example, the infrared radiation from the living human skin $(T \simeq 300$ K) has its peak at about 10 000 nm. As visible light is between 450 and 700 nm, the radiation from human skin includes no visible light. (The visible light from the skin that we perceive is, of course, only reflected light, and in darkness we see no light from the skin.)

Figure 7.4 shows how the wavelengths and intensity of emitted radiation change with the tem-

FIGURE 7.4 The thermal radiation from a body depends on its surface temperature, in regard to both the spectral distribution of the radiation and its intensity. The higher the surface temperature, the shorter is the wavelength and the higher is its intensity. This figure shows the spectral distribution of the thermal radiation from the sun (6000 K), a red-hot stove (1000 K), and the human body (300 K). [Hardy 1949]
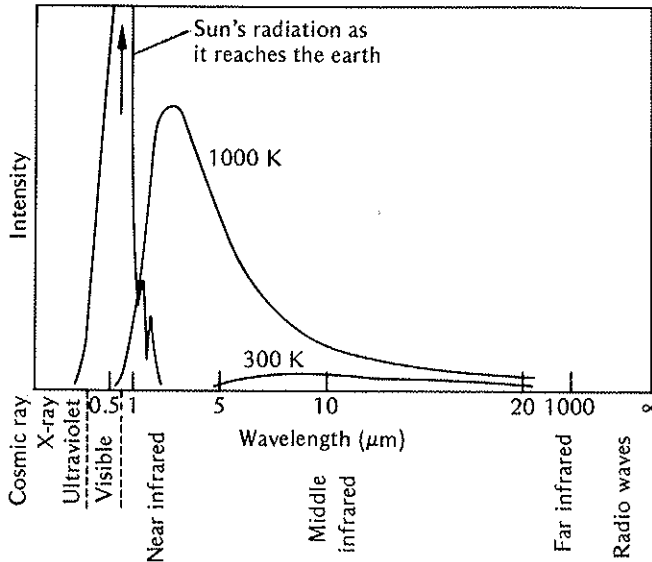
perature of the radiating surface, as described in the preceding two paragraphs.

The next concept to consider is *emissivity*. The simplest way to approach this concept is to consider first the *absorptivity* of a surface for the radiation that falls on it. A black body, by definition, absorbs radiation completely in all wavelengths and reflects nothing. The absorptivity of a completely black body is therefore 100%. (Although we often think of "black" in relation to visible light, the physical concept applies to all wavelengths).

In contrast to a black body, the surface that reflects all radiation is a perfect reflector, and its absorptivity is zero. This condition is approached by a highly polished metallic surface (e.g., a silver mirror). Because incident radiation is either absorbed or reflected, absorptivity and reflectivity *must* add to 1 (or 100%). If 30% of incident radiation is reflected, 70% is absorbed, and so on.

Usually, the absorptivity (and thus reflectivity) is different in different wavelengths of incident radiation. In visible light we recognize this as the color of objects; an object we perceive as yellow reflects mostly yellow light and absorbs other components of the visible light. In the middle infrared, which is of the greatest interest in connection with heat radiation at physiological temperatures, most surfaces are black bodies. The human skin, for example, absorbs virtually 100% of incoming infrared radiation, and thus is a black body in these wavelengths, irrespective of whether it is light or dark in the visible light.

The concept of surface *absorptivity* should now be clear, and we can return to the *emissivity*. The two are numerically equal, a fact that can be intuitively understood from the following. Consider an object suspended in a vacuum within a hollow sphere of uniform wall temperature. The object within the sphere receives radiation from the wall of the sphere, part of which is absorbed and part of which is reflected. Likewise, the object radiates to the spherical surface, and part of this radiation is absorbed while part is reflected. (The reflected portion, in turn, is either intercepted by the suspended object or reaches another point of the sphere.)

When the system is in equilibrium, the object has attained the temperature of the surrounding spherical surface, and the absorbed and emitted radiations from the object are now precisely equal. If this were not so, the object would not be at the temperature of the sphere. This would be a physical impossibility, for otherwise we could tap energy from the system and have the makings of a *perpetuum mobile*. As a practical example, take a highly reflective metal coffee pot that has a reflectivity of 95% (i.e., an absorptivity of only 5%). Its emissivity, therefore, is also 5% (i.e., the polished coffee pot loses heat by radiation very slowly).

Let us next consider that the object within the sphere is nearly black and has an absorptivity of 99%. This object obviously will attain the same temperature as a highly reflective silver object similarly suspended, although the latter may have an

absorptivity of only 1%. For each object at equilibrium the absorbed and the emitted radiations are precisely equal. The final temperature will be the same for both, but the highly reflective object will need longer to reach it.

To repeat, an object of high absorptivity also has high emissivity. A body that is a perfect emitter in a given wavelength is also a perfect black body in the same wavelength, and vice versa.

Human skin, animal fur, and all sorts of other nonmetallic surfaces have high absorptivities in the middle infrared range of the spectrum, between 5000 and 10 000 nm. For all practical purposes human skin is black in this range, and there is no difference between heavily pigmented and unpigmented skin. The difference we perceive is in the visible region of the spectrum, but because no radiation is emitted in this range, the difference in pigmentation does not influence radiation from human skin.

As a consequence of the high absorptivity in the middle infrared, emissivity is also close to 100% in this region. Consequently, heat losses by radiation from pigmented and unpigmented skins are about equal; both radiate as virtually black bodies. The same is true of radiation from animal fur, which likewise is independent of the color in the visible part of the spectrum.

Failure to appreciate this simple physical fact has led to some ill-conceived speculation in regard to animal coloration. For example, it has been suggested that black-colored animals lose heat by radiation faster than white-colored ones. Because the emission of radiation in the infrared has no relation to visible coloration, a difference in emissivity in the infrared can be established only by direct measurement in this range of the spectrum. No such differences have been found.

Skin and fur color may, however, be important to the heat absorbed from solar radiation, which has its peak intensity in the visible range. About half of the energy carried in solar radiation falls within what we call the visible light (Figure 7.4), and it is important to the heat balance whether this light is absorbed or reflected. When exposed to di-rect solar radiation, dark-colored skin or fur absorbs more of the incident energy than light-colored skin or fur.

Net heat transfer by radiation. If two surfaces are in radiation exchange, each emits radiation according to *Stefan-Boltzmann's law*, and the net radiation transfer ($\dot{Q}_R$) between them is:

$$\dot{Q}_R = \sigma \epsilon_1 \epsilon_2 (T_2{}^4 - T_1{}^4) A$$

in which σ is Stefan-Boltzmann's constant, ϵ_1 and ϵ_2 are emissivities of the two surfaces, T_1 and T_2 are their absolute temperatures, and A is an expression for the effective radiating area.* If the environment is a uniform sphere, A is a simple expression of the integrated "visible" surface in the direction of radiation.

If the environment is nonuniform, however, and in particular if it includes a point source of heat (such as the sun), the integration of the surfaces of exchange becomes more complex. In this regard, situations in nature are extremely complex, and to describe in exact terms the total heat transfer is very difficult. Nevertheless, once the elementary physics of radiation exchange is understood in principle, we can readily avoid some erroneous conclusions such as those relating to the role of surface pigmentation.

A practical simplification. Although radiation heat transfer changes with the fourth power of the absolute temperature, we can use a simplified expression, provided the temperature difference between the surfaces is not too great. Within a temperature range of about 20 °C, the error of not using the rigorous Stefan-Boltzmann equation can often be disregarded, and, as an approximation, we can regard the radiation heat exchange as being proportional to the difference in temperature between the two surfaces. For small temperature differences, the error is relatively insignificant, but it becomes increasingly important the greater the temperature difference.

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*This equation for net radiation transfer assumes that one or both surfaces has an emissivity close or equal to unity.

We will not use this simplification and regard the radiation heat exchange as proportional to the temperature difference. The rate of heat loss from a warm-blooded animal in cool surroundings consists of conduction and radiation heat loss (for the moment disregarding evaporation). Because both can be considered proportional to the temperature difference $(T_2 - T_1)$, their sum will also be proportional to $(T_2 - T_1)$, or:

$$\dot{Q} = C \ (T_1 - T_1)$$

in which all the constants that enter into the heat-exchange equation have been combined to a simple proportionality factor, C.

We shall later return to the application of this simplified equation in the discussion of heat loss from warm-blooded animals in the cold.

Evaporation

The evaporation of water requires a great deal of heat. To transfer 1 g water at room temperature to water vapor at the same temperature requires 584 cal (2443 J). This is an amazingly large amount of heat, for when we consider that it takes 100 cal (418 J) to heat 1 g of water from the freezing point to the boiling point, we see that it takes more than five times again as much heat to change the liquid water into water vapor at the same temperature.

The amount of heat required to achieve the phase change from liquid water to vapor is known as the *heat of vaporization* (H_v). The heat of vaporization changes slightly with the temperature at which the evaporation takes place: At 0 °C the H_v is 595 cal per gram water; at 22 °C it is 584 cal per gram; and at the boiling point, 100 °C, it is 539 cal per gram.

In physiology it is customary to use the figure 580 cal per gram water, which is an approximation of the value for vaporization of water at the skin temperature of a sweating person, about 35 °C.

The measurement of heat loss by vaporization of water has one great convenience: It suffices to know the amount of water that has been vaporized. When a person is exposed to hot surroundings, he cools himself by evaporation of sweat from the general body surface, but a dog evaporates most of the water from the respiratory tract by panting. The amount of heat transferred per gram water is, of course, the same in both cases (i.e., we do not have to know the exact location or the area of the evaporating surface).

The respiratory air of mammals and other air-breathing vertebrates is exhaled saturated with water vapor, and therefore there is normally a considerable evaporation of water from the respiratory tract, even in the absence of heat stress. This evaporation must, of course, be included in any consideration of the total heat balance of an animal, which is the subject we shall now discuss.

HEAT BALANCE

We have repeatedly emphasized that for the body temperature to remain constant, heat loss must equal heat gain. The body temperature does not always remain constant, however. Assume that heat loss does not quite equal the metabolic heat production, but is slightly lower. The body temperature inevitably rises. This means that part of the metabolic heat remains in the body instead of being lost, and the increase in body temperature thus represents a storage of heat.

If the mean body temperature decreases, which happens when heat loss exceeds heat production, we can regard the excess heat loss as heat removed from storage. The amount of heat stored depends on the change in mean body temperature, the mass of the body, and the specific heat capacity of the tissues (which for mammals and birds usually is assumed to be 0.83).

The heat exchange between the body and the environment takes place by the three means described above: conduction (including convection), radiation, and evaporation. Usually each of these represents a heat loss from the body, but this is not always so. When the air temperature exceeds the body surface temperature, heat flow by conduction is to, not from, the body. When there is a strong radiation from external sources, the net radiation

flux may also be toward the body. Evaporation is nearly always a negative entity, but under unusual circumstances it could be reversed; this happens, for example, when a cold body comes in contact with moist warm air.*

We can enter these variables into a simple equation:†

$$H_{tot} = \pm H_c \pm H_r \pm H_e \pm H_s$$

in which

H_{tot} = metabolic heat production
 (always positive)
H_c = conductive and convective heat exchange
 (+ for net loss)
H_r = net radiation heat exchange
 (+ for net loss)
H_e = evaporative heat loss (+ for net loss)
H_s = storage of heat in the body
 (+ for net heat gain by the body)

The three components of heat exchange – conduction, radiation, and evaporation – depend on external factors, among which the most important

*When a human with a skin temperature of, say, 35 °C, enters a Turkish steam bath in which the air is nearly saturated and above 40 °C, there is an immediate condensation of water on his skin. In this case the direction of evaporation heat exchange is the reverse of the usual. In the sauna bath, however, the air is usually dry, and the visible moisture seen on the skin shortly after entering the sauna is sweat.

† It is important to note that no work term appears in this equation. For heat balance, the equation is correct as it stands. However, if oxygen consumption is used to estimate metabolic rate and to calculate heat production, external work must be considered, for that fraction of the oxygen consumption that goes to perform external work does not appear as heat in the body. For example, a flying bird uses probably 20% of its metabolic rate to impart acceleration to the air through which it flies (ultimately this external work degenerates into heat in a trail of decaying air vortexes). For a flying bird, therefore, only 80% of the oxygen consumption represents heat released within the body, and only this part enters into the heat balance equation as metabolic heat (H_{tot}) to be dissipated through the means to the right of the equality sign. This also means that the caloric equivalent of oxygen (4.8 kcal formed per liter oxygen consumed) cannot be used to calculate the heat production of an animal performing external work.

single factor is temperature. It is obvious that heat losses increase when the external temperature falls. If, however, external temperature rises, the heat losses decrease, and if external temperature exceeds body surface temperature, both conduction and radiation heat exchange may be from the environment to the organism. The total heat gain is then the sum of heat gain from metabolism plus heat gain from the environment. This situation still permits the maintenance of a constant body temperature (storage = 0), provided evaporation is increased sufficiently to dissipate the entire heat load.

The physiological responses in cold and in heat differ in many respects, and it is convenient to treat the two conditions separately. We shall first deal with temperature regulation in cold surroundings, and afterward discuss temperature regulation in the heat.

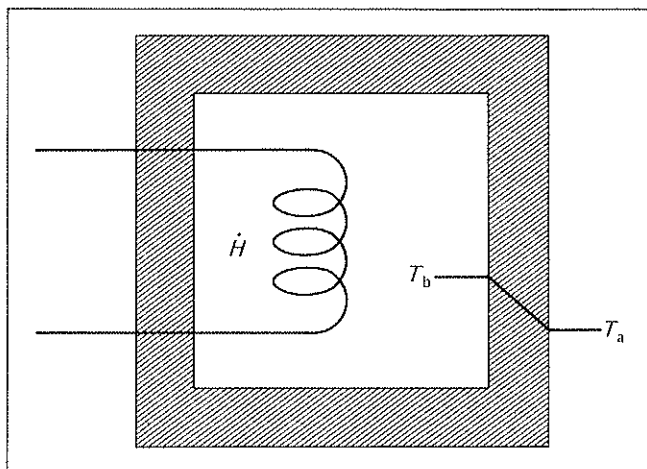## Temperature regulation in the cold: keeping warm

To maintain a constant body temperature, an animal must satisfy the steady-state condition in which the rate of metabolic heat production ($\dot{H}$) equals the rate of heat loss ($\dot{Q}$). For the moment we will consider that the heat loss (in the cold) takes place only through conduction (including convection) and radiation, and that heat loss through evaporation can be disregarded.* To describe the heat loss we will use the simplified equation that relates heat loss ($\dot{Q}$) to ambient temperature as developed in the preceding section:

$$\dot{H} = \dot{Q} = C\,(T_b - T_a)$$

This equation simply says that the rate of metabolic heat production equals the rate of heat loss, which in turn is proportional to the temperature difference between the body and the environment ($T_b - T_a$). The term C is a conductance term that will be discussed later.

*At moderate to low temperature, evaporation takes place primarily from the respiratory tract, at a rate corresponding to a few percent of the metabolic heat production.

FIGURE 7.5 An insulated box is maintained at a given temperature (T_b) by a heater supplying heat at the rate $\dot{H}$. If the outside temperature (T_a) is lowered, T_b can be maintained constant by increasing the rate of heat input in proportion to the temperature difference $(T_b - T_a)$. This is a model of thermoregulation in a mammal.
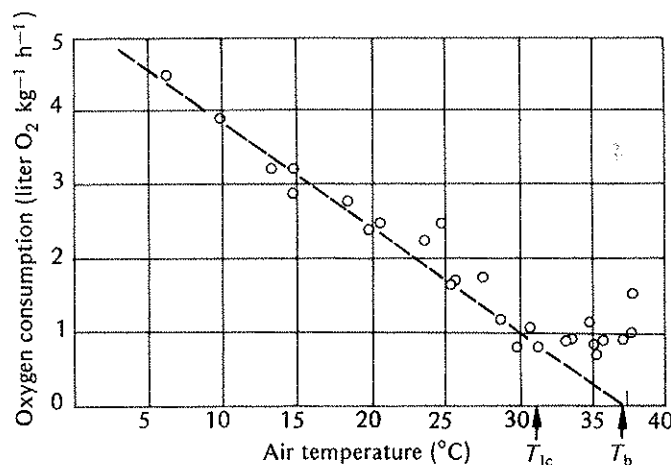

FIGURE 7.6 The oxygen consumption of the pygmy possum (*Cercaertus nanus*) at various ambient temperatures. Below a certain point, the lower critical temperature (T_{lc}), the oxygen consumption increases linearly with decreasing ambient temperature. [Bartholomew and Hudson 1962]

What can an animal do to maintain the steady state? Among the terms in the above equation, ambient temperature (T_a) is one an animal can do little about, short of moving to a different environment. To adjust to an unfavorable T_a, an animal can adjust only three remaining terms: heat production $(\dot{H})$, the conductance term (C), or body temperature (T_b). As we are concerned with the maintenance of the body temperature (T_b), we are left with adjustments to be made either in heat production $(\dot{H})$ or in the conductance term (C). (The third alternative, a change in body temperature, does occur in hibernation, a subject to be discussed later.)

Increase in heat production

Although heat production (metabolic rate) cannot be turned down below a certain minimum level, increased metabolic rate permits a wide range of adjustments. The major ways in which heat production is increased are through (1) muscular activity and exercise, (2) involuntary muscle contractions (shivering), and (3) so-called nonshivering

thermogenesis. The last term refers to an increased metabolic rate that takes place without noticeable muscle contractions.

To clarify the role of increased heat production, let us consider a simple physical model of an animal (Figure 7.5). An insulated box is equipped with an electric coil that delivers heat at the rate $\dot{H}$. The temperature inside the box (T_b) is therefore higher than the ambient temperature (T_a). If we lower the ambient temperature (T_a), the temperature within the box can be maintained only by increasing the rate of heat input $(\dot{H})$. The increase in $\dot{H}$ must be proportional to the increase in temperature difference as long as the insulation (or conductance) in the wall remains unchanged.

This is precisely the situation for an animal exposed to cold. The lower the ambient temperature, the greater the increase in metabolic rate needed to stay warm. In Figure 7.6 we see that below a certain ambient temperature, called the *lower critical temperature* (T_{lc}), the metabolic rate increases linearly with decreasing temperature. Above the critical temperature, heat production, which cannot be

FIGURE 7.7 The metabolic rates of various mammals in relation to air temperature. The normal resting metabolic rate for each animal, in the absence of cold stress, is given the value 100%. Any increase at lower temperature is expressed in relation to this normalized value, making it possible to compare widely differing animals. [Scholander et al. 1950a]
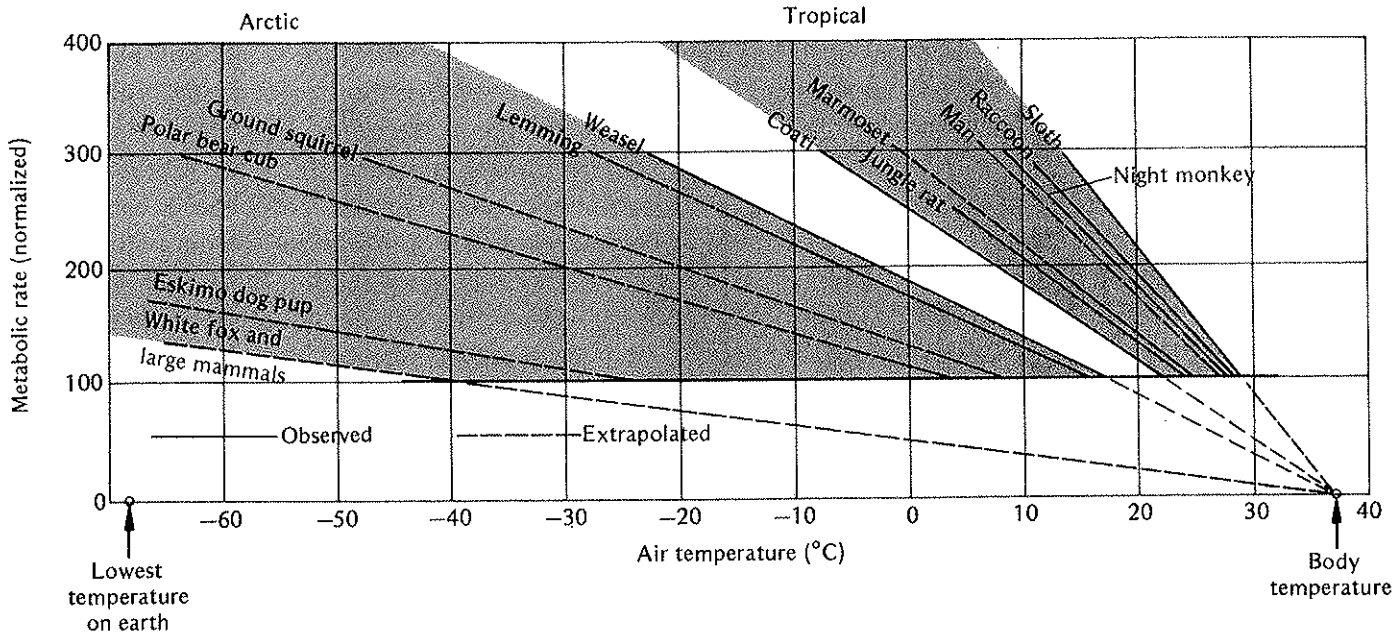
reduced lower than the resting metabolic rate, remains constant as temperature is increased.

If we imagine an animal that can reduce its metabolic rate further, less and less heat is needed to keep warm as the outside temperature (T_a) is increased. When T_a reaches T_b, no heat is lost from the animal, and no heat input is needed to maintain T_b. This is quite feasible for our model in Figure 7.5; the straight line that describes its heat loss relative to changing air temperature intersects with the abscissa when T_b equals T_a. The straight line that describes the heat production of the mammal in Figure 7.6 likewise extrapolates to the abscissa to intersect at the temperature of the body.

If we want to compare a variety of different animals, we can conveniently do so if we assign to the normal resting metabolic rate of each the value 100%. This has been done in Figure 7.7, where we can see that most tropical mammals have critical temperatures between +20 and +30 °C; below these temperatures their metabolic rates increase rapidly.
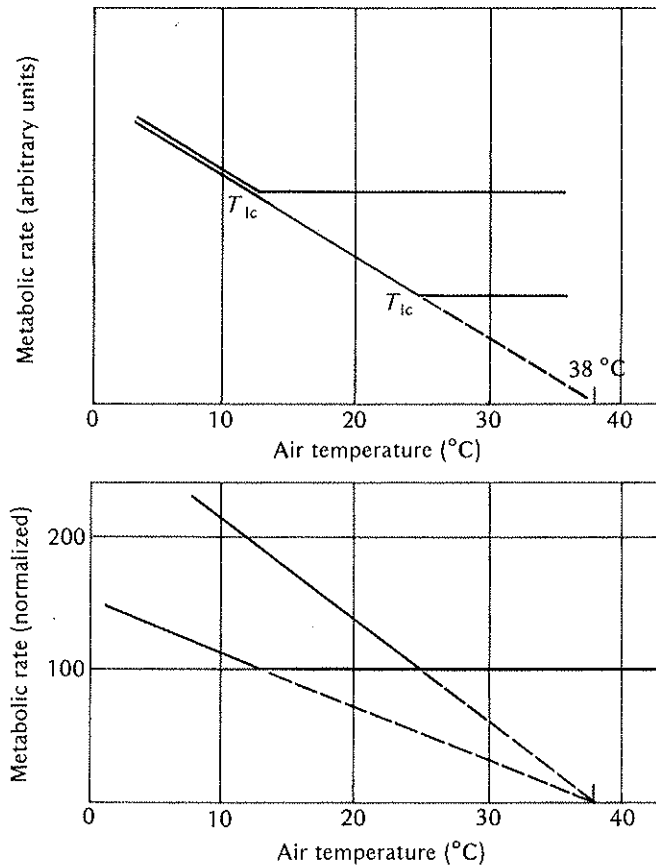
Arctic mammals, however, have much lower critical temperatures, and a well-insulated animal such as an Arctic fox does not increase its metabolic rate significantly until the air temperature is below −40 °C.

The slopes of the lines in Figure 7.7 can be regarded as an expression of the conductance term (C) in the equation we have been using.* As a rule, tropical mammals have high conductances, and Arctic mammals low conductances (high insulation values). As a consequence, a tropical mammal, because of its high conductance (low insulation), must increase its metabolism drastically for even a moderate temperature drop.

For example, a monkey with a body temperature of 38 °C and a lower critical temperature of 28 °C must double its metabolic rate for a further 10° drop

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*When the data have been normalized by assigning to the resting heat production the value of 100%, the slope does not indicate conductance in absolute units.

FIGURE 7.8 If two animals have the same body temperature and the same conductance, but have different resting metabolic rates, they will also have different lower critical temperatures (top). If their metabolic rates are normalized to 100%, this procedure will suggest, incorrectly, that they have different conductance values (bottom).

*thermoneutral zone** is much greater in the Arctic animal and the metabolic response to cold is less pronounced than in tropical mammals. The way the graph is drawn, however, is in some ways misleading. Assume that we examine two mammals of equal size and equal conductance value, but that one has a metabolic rate in the thermoneutral zone that is twice as high as the other. If, instead of normalizing the metabolic rate at 100%, we plot their actual metabolic rates (Figure 7.8), the lower critical temperature will be different for the two animals, but below this temperature, the two animals must expend the same number of calories to keep warm.

It is therefore obvious that the location of the lower critical temperature (the width of the thermoneutral zone) by itself is not sufficient information about how well adapted an animal is to cold conditions. Information about the level of the resting metabolic rate, or better, the conductance value, is also necessary to evaluate the relationship between energy metabolism and heat regulation.

Conduction, insulation, and fur thickness

Conductance, in the sense it has been used above, is a measure of the heat flow from the animal to the surroundings. The term includes the flow of heat from deeper parts of the body to the skin surface and from the skin surface through the fur to the environment. When conductance is low, the insulation value is high. In fact, insulation is the reciprocal value of conduction.†

Our discussion is concerned with animals in the cold, where the fur is a major barrier to heat flow. The insulation values of the fur from various animals differ a great deal. Some data, plotted relative to the thickness of the fur, are shown in Figure 7.9.

in the temperature, to 18 °C. An Arctic ground squirrel, on the other hand, which has a lower critical temperature at about 0 °C, will not need to double its metabolic rate until the temperature has dropped to nearly −40 °C. The Arctic fox, with its lower critical temperature at −40 °C, should be able to sustain the lowest temperatures measured in Arctic climates (−70 °C) with less than a 50% increase in its metabolic rate.

The difference between Arctic and tropical animals is very clear in Figure 7.7. The width of the

*The *thermoneutral zone* is the temperature range within which the metabolic heat production is unaffected by a temperature change.

†*Thermal conductance* (heat flow per unit time per unit area per degree temperature difference) has the units $W\ m^{-2}\ °C^{-1}$ (or $cal\ s^{-1}\ cm^{-2}\ °C^{-1}$). *Insulation* is the reciprocal of conductance, and its units are therefore $W^{-1}\ m^2\ °C$ (or $cal^{-1}\ s\ cm^2\ °C$).
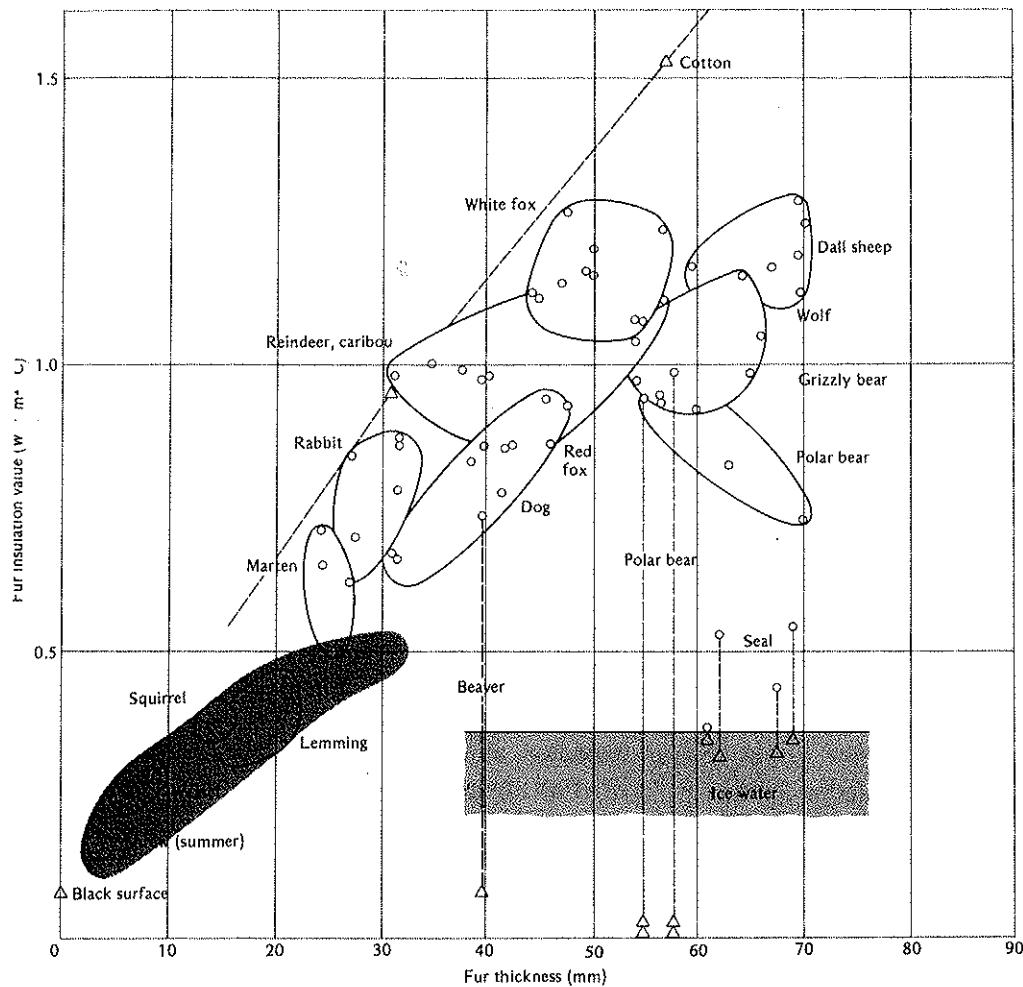
FIGURE 7.9 The insulation value of animal fur is related to fur thickness. Because small mammals of necessity carry relatively short fur, they have poor insulation compared with larger animals. Insulation values for fur in air are indicated by open circles; values for fur submerged in water, by triangles. Insulation values for fur (ordinate) are measured in air or water at 0 °C with the inside of the fur maintained at 37 °C. The sloping broken line represents the insulation values of cotton of various thicknesses. In this figure the insulation value of 4 cm of fur is about 1 W^{-1} m^2 °C, which equals 41 840 cal^{-1} s cm^2 °C. For 1 cm thickness of fur the insulation value will be one-fourth, or 10 460 cal^{-1} s cm^2 °C. The conductance value (the reciprocal of insulation) is therefore 0.000 096 cal s^{-1} cm^{-2} $°C^{-1}$, which is in good agreement with the value for fur listed in Table 7.3. [Scholander et al. 1950b]

As expected, the insulation value increases with the thickness of the fur and reaches a maximum for some of the larger animals that have thick fur, such as the white fox.

Among the smaller animals there is a clear correlation between fur thickness (and insulation) and the size of the animal. A small animal must have relatively short light fur or it could not move about. This is particularly true for the smallest mammals, small rodents and shrews. Because of their relatively poor insulation, these animals must either take advantage of microclimates (e.g., by living in burrows) or hibernate to escape the problem of keeping warm.

The polar bear is interesting, for its open and coarse fur provides poor insulation relative to its thickness. More important, when polar bear skin is submerged in ice water, most of the insulation value

of the fur is lost, and heat transfer is 20 to 25 times faster than in air. If the water is agitated (as it would be when the bear is swimming), the heat loss is increased even more, some 50 times. This is because water penetrates to the skin surface, dislodging all air from the fur. When in water, the polar bear is helped by subcutaneous blubber, which affords insulation (see later in this chapter).

The skin of the seal has a relatively thin fur, but a heavy layer of blubber affords considerable insulation. Therefore, the difference in insulation value for seal skin in air and in water is not very great. In air, seal skin with the blubber attached has only a slightly better insulation value than the skin of a lemming (i.e., 60 to 70 mm of mostly blubber insulates about as well as 20 mm of fur). When the seal skin is submerged in water, the insulation value is reduced, but not as drastically as for polar bear skin.

It is well known that the thickness of animal fur changes with the seasons and that winter fur is heavier and presumably affords better insulation than the thinner summer fur. The seasonal changes that have been measured are greatest in large animals and relatively insignificant in small rodents. The black bear, for example, in summer loses 52% of the insulation value of its winter fur (i.e., the summer pelt affords less than half the insulation of the winter pelt). The smallest seasonal change observed in a sub-Arctic mammal was a 12% reduction of the winter value in the muskrat (Hart 1956).

Conductance in birds

As we have seen, the conductance values for mammals in the cold require that the metabolic rates increase in proportion to the imposed cold stress. The straight lines describing the metabolic rates at low temperature extrapolate to body temperature, showing that mammals fit our assumed model (Figure 7.5).

For birds the situation is not so simple. Some birds conform to the mammalian pattern with metabolic curves that extrapolate to body temperature. Other birds, however, deviate from this pattern.

FIGURE 7.10 The oxygen consumption of the pigeon and of the roadrunner increases at low temperature, but the regression lines do not extrapolate to the body temperature of the animal as they commonly do in mammals. [Calder and Schmidt-Nielsen 1967]
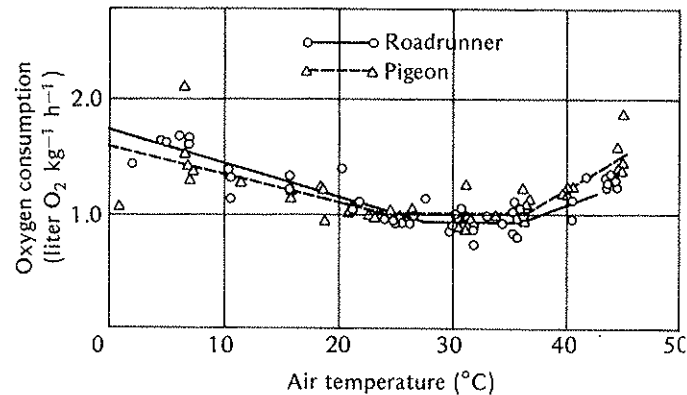

For example, the metabolic heat production of pigeons and roadrunners does not increase as much as expected at low ambient temperature (Figure 7.10). For these birds the metabolic line extrapolates, not to the body temperature of about 40 °C, but to a much higher temperature, well above 50 °C.

There is only one possible explanation for such a slope: The bird does not adhere to the simple equation $H = C\ (T_b - T_a)$, where C remains constant at low temperature.

One way to explain the observed regression line is to assume that the conductance value (C) gradually decreases with falling ambient temperature (T_a). The other way to achieve a change in slope is to permit the body temperature (T_b) to decrease. The birds represented in Figure 7.10 maintained normal body temperatures, and the question is then: how can conductance change gradually as the ambient temperature decreases?

One way to decrease conductance is to raise the feathers and withdraw feet and head as far as possible into the feathers, and birds do this in the cold. Another way is to allow the peripheral tissues to undergo an appreciable temperature drop while the core temperature is maintained. The drop in shell temperature has several effects: Circulation in the

FIGURE 7.11 Body temperature of a willow tit (*Parus montanus*) during the night hours at three different ambient temperatures. The records are from midafternoon one day to the following morning. (Reinertsen and Haftorn 1986).
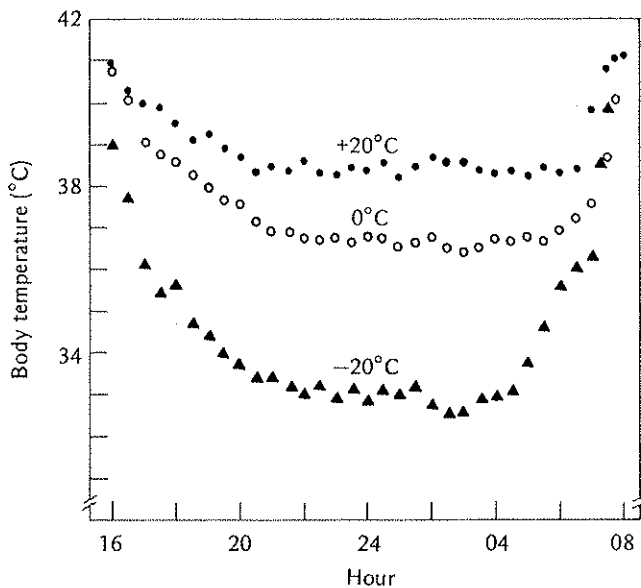
shell is decreased, shell thickness is increased, and the volume of the core is reduced. Each of these variables contributes to a change in conductance and permit the maintenance of core temperature.

A change in conductance can also be combined with a drop in core temperature, and this could achieve even greater savings. Small birds in northern climates have serious problems in winter. The ambient temperature is low, snow covers the ground, and the days are short with only a couple of hours of weak daylight. How do small birds manage through the winter?

Studies in Norway show that the willow tit (*Parus montanus*) uses both a decreased conductance and a drop in core temperature to survive from day to day in winter. The drop in core temperature is greater at low ambient temperature (Figure 7.11) and may be as great as 10 °C. Even at an ambient temperature as high as 20 °C the drop may be nearly 4 °C, which represents an energy saving of 35% compared to what it would cost to maintain day-

time temperature during the night (Reinertsen and Haftorn 1986).

The relative savings of dropping the core temperature are not as great at lower ambient temperatures, but in combination with other adjustments it enables the bird to remain in subarctic regions during the winter. The birds use food storage, they find sheltered roosting places, and they assume a sleeping posture that utilizes heat conservation to the fullest.

Huddling

Among the penguins of the Antarctic the most striking is the large emperor penguin (*Aptenodytes forsteri*), which lives under colder conditions than any other bird and has the unique characteristic of breeding during midwinter.

As winter approaches, emperor penguins leave the open water and walk on the sea ice for 50 or 100 km toward the permanent ice shelf to the rookeries. There the female lays a single egg, which is placed on the feet of the male, who remains at the rookery to incubate the egg while the female returns to the sea to feed.

While incubating, the male stands on the ice for over 2 months in air temperatures that may be as low as −30 to −40 °C with high wind velocities. The female usually returns to the rookery with a full stomach about the time the egg hatches; she feeds the chick while the male returns to the sea to feed.

Emperor penguins can feed only at sea, and to sustain himself during the long fast the male begins the period with large deposits of subcutaneous fat. The fast may exceed 100 days, and by the end the male may have lost up to 40% of his initial body weight.

How much energy is needed for the long walk to and from the rookery, and how much is needed to keep warm in the Antarctic cold? And do penguins keep warm? These questions have been the subject of detailed studies (LeMaho et al. 1976; Pinshow et al. 1976).

The penguins do keep warm; their body temper-

HUDDLING PENGUINS Chicks of the emperor penguin photographed on the ice-covered Antarctic breeding grounds. The chicks huddle together and thus reduce the surface area exposed to cold air. This behavior leads to a substantial reduction in the metabolic cost of keeping warm in the frigid climate. The group in this photo contains about 50 birds; a few have momentarily raised their heads to watch the photographer. [Courtesy of Yvon LeMaho, University of Lyon, France]

ature remains at the normal 38 °C during the entire breeding period. How much fuel do the birds need for this and how much for walking?

A large male penguin may weigh 35 kg when he leaves the sea and may have lost 15 kg at the end of the fast. The amount of energy needed for walking can be determined by training penguins to walk on a treadmill in the laboratory and determining their oxygen consumption. This shows that walking 200 km to the breeding grounds and back to the sea may require the use of about 1.5 kg of fat.

Is the remainder sufficient to keep the bird warm for several months of starvation while he incubates the egg?

One might expect penguins to have physiological characteristics that distinguish them from other birds, such as a thermoneutral zone extending to extremely low temperatures (i.e., a very low thermal conductance). This is not the case. Penguins have a thermal conductance to be expected for any bird of the same body size, and their lower critical temperature is at −10 °C, far above the usual Ant-

arctic winter temperatures. The metabolic rates of penguins under laboratory conditions at temperatures similar to those in nature suggest that perhaps 25 kg of fat would be needed to keep warm during the winter, and this by far exceeds the reserves that even a large male carries.

The apparent contradiction is explained by the behavior of the penguins in the rookery, where they huddle together in large groups that may number several thousands. The metabolic rates of huddling penguins have not been determined, but weight loss, which presumably results from metabolism of fat, is a good indication. Single emperor penguins in the cold lose about 0.2 kg per day; huddling penguins lose only about half as much, about 0.1 kg. Huddling together helps, and it is easy to understand why. Instead of being exposed to the cold on all sides, a major part of each bird's surface is in contact with neighboring penguins. When two bodies have the same temperature, there is no heat flow between them. Huddling together obviously is a prerequisite for survival and for the success of breeding. Why the emperor penguins choose to breed in winter is another question that remains unanswered.

Other animals also huddle together to keep warm, although they may be less spectacular than the penguins. Huddling reduces the exposed surface, thus reducing the cold stress and the metabolic requirements for heat production. This is of particular importance for newborn mammals and bird nestlings that live together as a litter: They can remain warm in the absence of the parent for longer periods, and the young animal's decreased dependence on the use of energy for heat production permits faster growth.

Insulation in aquatic mammals

Many seals and whales live and swim in the near-freezing water of the Arctic and Antarctic seas. Not only are the temperatures low, but water has a high thermal conductance and a high heat capacity, and the thermal loss to water is therefore much higher than to air of the same temperature. The heat conductivity coefficient for water is about 25 times as high as for air, but because convection, both free and forced, plays a major role, the cooling power of water may under some circumstances be even greater, perhaps 50 or even as high as 100 times as great as for air.
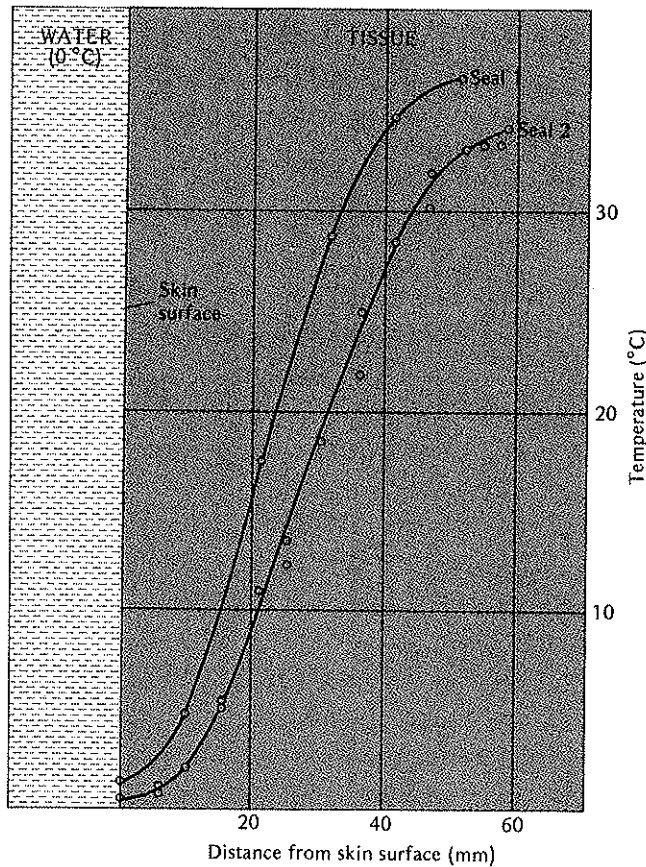
What can seals and whales do about their heat balance in water with such cooling power? Evidently they manage quite well, for both seals and whales are far more numerous in cold water than in the tropics. As there is nothing they can do about the water temperature (short of moving to warmer seas), they have a limited choice. They could either (1) live with a lowered body temperature, (2) increase the metabolic rate to compensate for the heat loss, or (3) increase the body insulation to reduce the heat loss.

With regard to body temperature, seals and whales are similar to other warm-blooded animals; their usual temperature is around 36 to 38 °C (Irving 1969). We must therefore look at the other possibilities for an explanation of their ability to live in ice water.

The metabolic rate has been measured in several species of seals and in some dolphins (porpoises), but not in any of the large whales, which are rather unmanageable as experimental animals. Most of these animals have resting metabolic rates about twice as high as would be expected from their body size alone (Irving 1969). In the harp seal (*Phoca groenlandica*), an Arctic species, the metabolic rate remained the same in water all the way down to the freezing point; in other words, even the coldest water did not cause the heat loss to increase enough to require increased heat production. The lower critical temperature for the harp seal in water is thus below freezing and has not been determined (Irving and Hart 1957).

The third possibility, an effective insulation, is obviously the main solution to the problem. Both seals and whales have thick layers of subcutaneous blubber that afford the major insulation. Measurements of the skin temperature support this concept, for the temperature at the skin surface is nearly
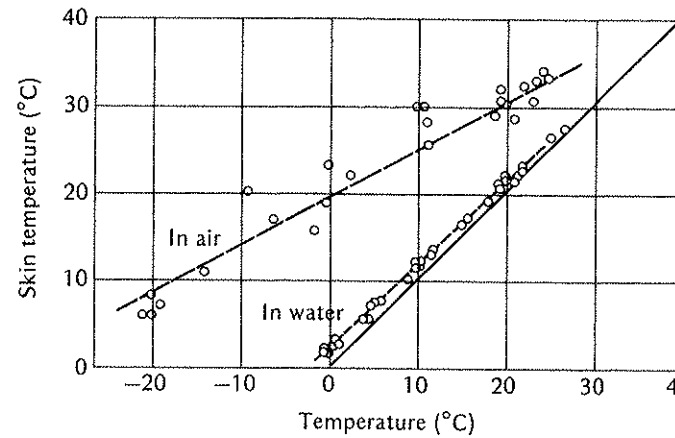
FIGURE 7.12 The temperature of the skin surface of a living seal immersed in ice water is nearly identical to that of the water. Most of the insulation is provided by the thick layer of blubber. [Irving and Hart 1957]

FIGURE 7.13 The skin surface temperature of seals in air and water. Solid line indicates equality of skin and environmental temperature. [Hart and Irving 1959]


substantial layer of blubber that seems to be of major importance when the polar bear swims in ice water. Without the layer of blubber, the semi-aquatic way of life would seem impossible (Øritsland 1970).

If seals and whales are so well insulated, how do they manage to avoid overheating when the water is warmer or when the metabolic rate is increased during fast swimming? If a seal is removed from water and placed in air, its skin temperature increases considerably (Figure 7.13). The higher skin temperature is necessary for dissipation of heat to the air, due to the reduced cooling power of air relative to water. The increase in skin temperature results from an increased blood flow through the blubber to the superficial layer of the skin, which is well supplied with blood vessels. This system of cutaneous blood vessels permits a precise regulation of the amount of heat that reaches the skin surface and thus is lost to the environment.

We can now see that the main difference in insulation between aquatic and terrestrial mammals is that the insulator of the aquatic mammals (the blubber) is located internally to the surface of heat dissipation. Therefore, the blood can bypass the insulator, and heat dissipation during heavy exer-

identical to that of the water (Figure 7.12). If the surface temperature is nearly the same as that of the water, very little heat can be transferred to the water. The temperature gradient is sustained by the blubber, and at a depth of some 50 mm (roughly the thickness of the blubber), the temperature is nearly at body core temperature.

In Arctic land mammals the temperature gradients are different. The surface temperature of the body skin under the fur is regularly within a few degrees of core temperature (Irving and Krog 1955), and most of the insulation therefore resides outside the skin surface. The polar bear, whose fur loses most of its insulation value in water, also has a

SEAL BLUBBER This cross section of a frozen seal shows the thick layer of blubber. Of the total area in the photo, 58% is blubber and the remaining 42% is muscle, bone, and visceral organs. The measuring stick is graduated in inches. [Courtesy of P. F. Scholander, University of California, San Diego]
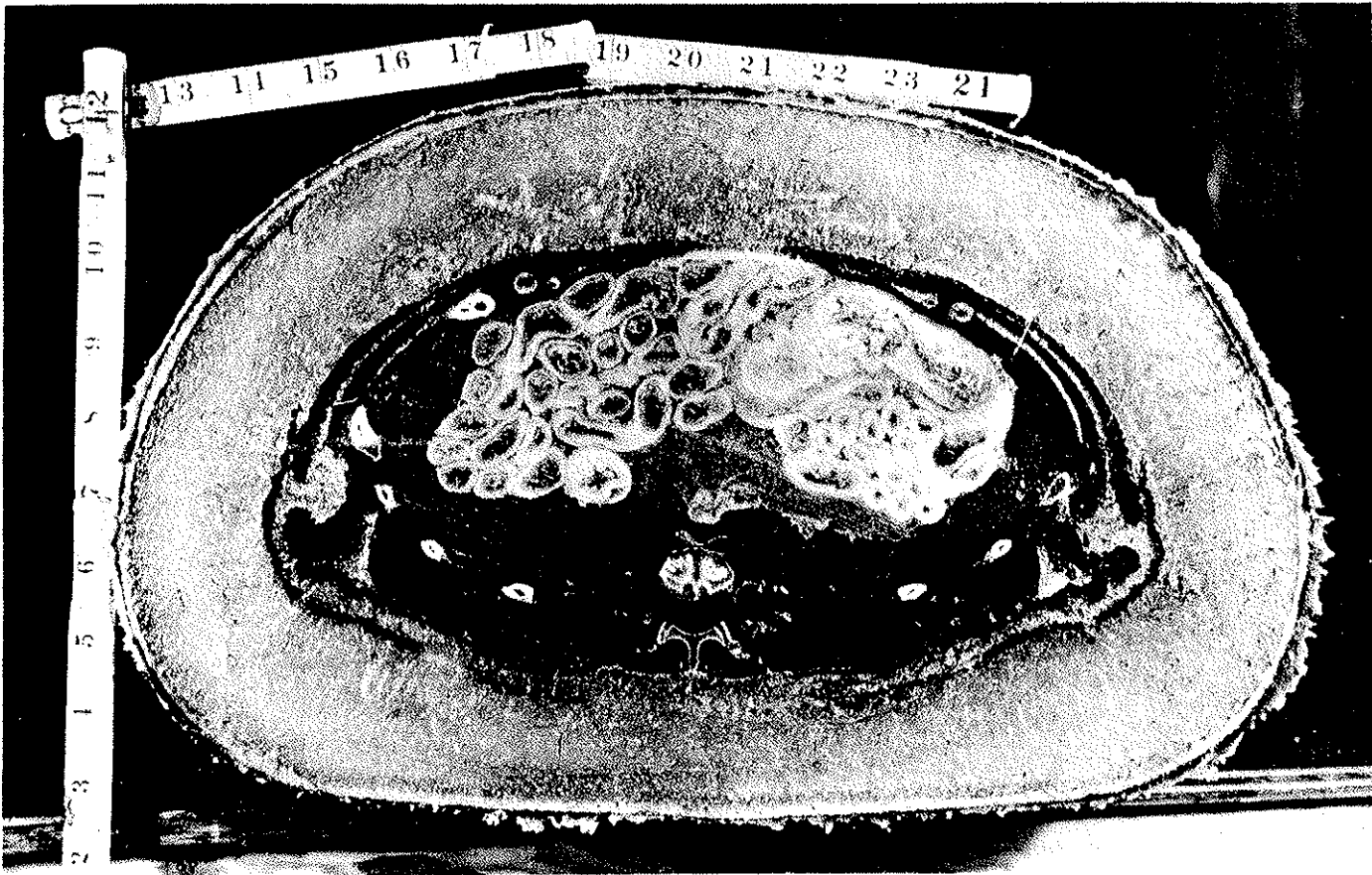
tion or in warm water can be independent of the insulator. Terrestrial animals, in contrast, have the insulator located external to the skin surface. Therefore, they cannot modulate the heat loss from the general skin surface to any great extent and must seek other avenues of heat loss when they need to dissipate excess heat to the environment (Figure 7.14).

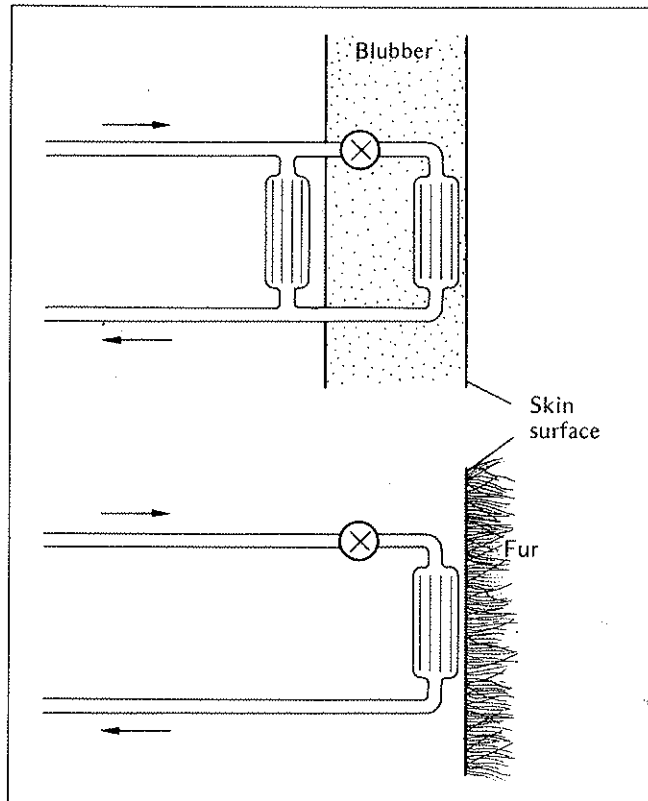### Distribution of insulating material

We must remember that furred Arctic animals cannot afford to insulate all parts of the body equally well; they also need surfaces from which heat can be dissipated, especially during exertion. Because the main part of the body is well insulated for max-

imum heat retention, they need thinly covered skin areas on the feet, face, and other peripheral locations, from which heat loss can take place when the demand for heat dissipation increases.

Estimates of the fraction of the body surface area that is covered with fur of different thicknesses suggests that some animals have considerable flexibility in regulating their conductance by changes in posture. Estimates on a male guanaco (a relative of the llama) are shown in Table 7.4 and in diagrammatic form in Figure 7.15 (Morrison 1966).

Because the thermal conductance through fur is inversely related to the thickness of the fur, the nearly bare areas can potentially transfer much more heat than the heavily furred areas. With the limbs

FIGURE 7.14 The insulation afforded by blubber can be bypassed when the need for heat dissipation increases. Fur, in contrast, is located outside the skin surface and its insulation value cannot be drastically changed by a bypass.
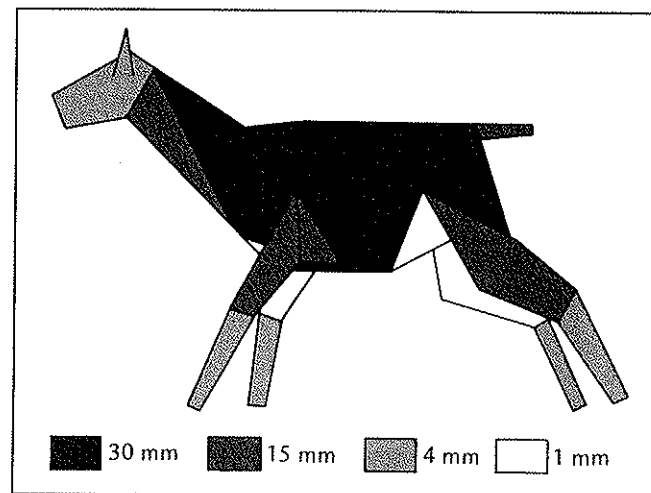

TABLE 7.4 Partitioning of surface areas with fur of different thickness in the South American guanaco (*Lama guanicoe*). About 40% of the area is covered by heavy fur, but almost 20% is nearly bare and permits extensive modulation of heat dissipation. [Morrison 1966]

	Depth of fur (mm)	Percent of total skin area
Nearly bare	1	19
Short hair	4	20
Medium-length hair	15	20
Long hair	30	41

FIGURE 7.15 Distribution of fur of different thicknesses on the body of the guanaco. Areas on the chart are proportional to measured areas on the animal. [Morrison 1966]

30 mm   15 mm   4 mm   1 mm

extended and their surfaces fully exposed, the bare areas can serve as "heat windows" that can account for more than half the total heat transfer.

A guanaco lying or standing in a normal position would have the bare areas on the inside of the legs opposed, and this would reduce surface heat transfer by one-half. If the animal were to curl up to cover as much as possible of the remaining short-haired areas, surface conductance would be at a minimum: only one-fifth of that for the stretched out animal. Other animals have similar short-haired areas whose role in heat transfer can be modulated by changing their exposure and by changing the blood flow to these areas, thus giving a great deal of flexibility in the regulation of heat loss.

Heat exchangers

Seals and whales have flippers and flukes that lack blubber and are poorly insulated. These appendages are well supplied with blood vessels and receive a rich blood supply. This means that these relatively thin structures with their large surfaces can lose substantial amounts of heat and aid in heat dissipation, but how is it possible to avoid excessive heat loss from the flippers when heat needs to be conserved? If the blood that returns to the body