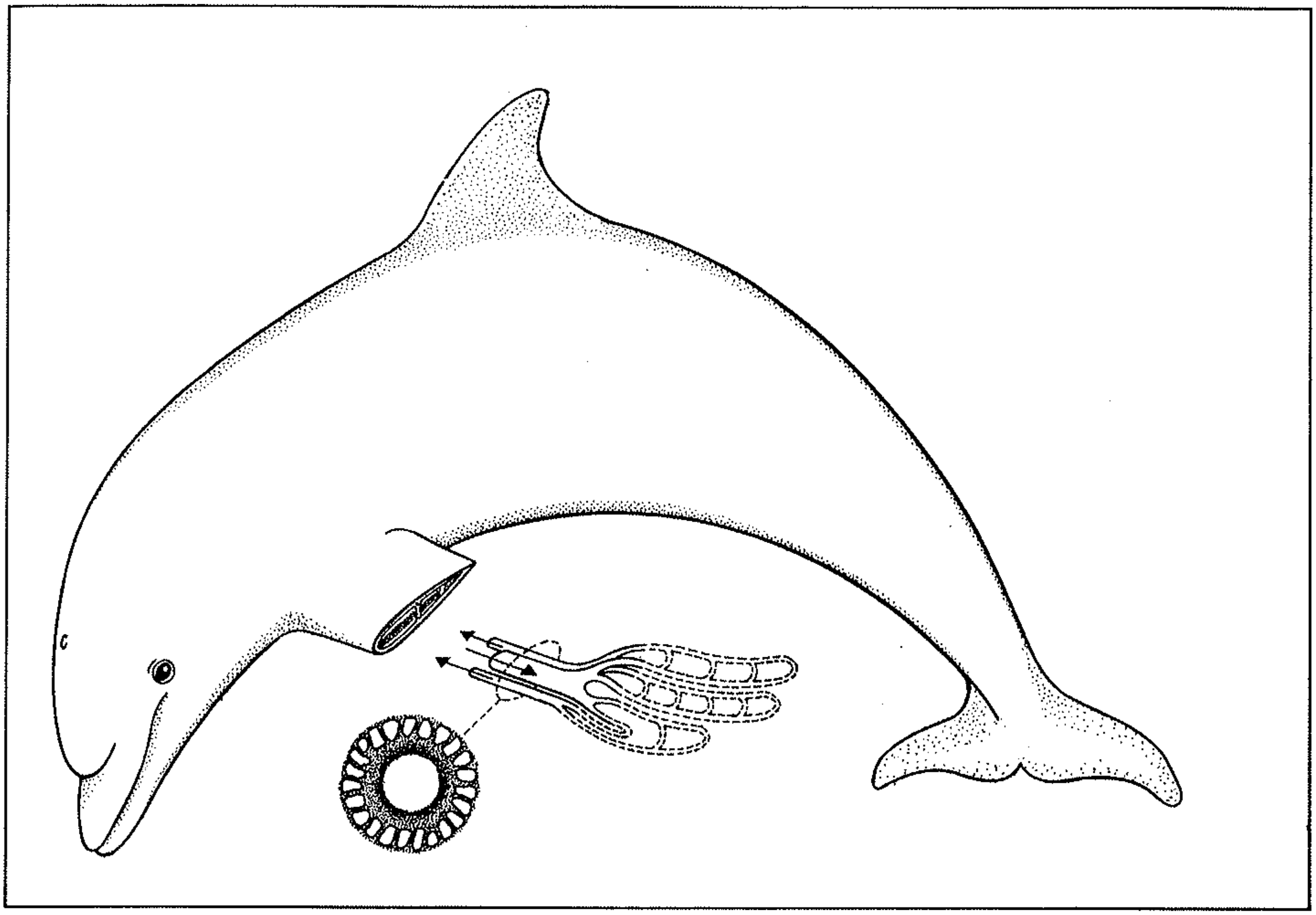
FIGURE 7.16 In the flippers and fluke of a dolphin (porpoise) each artery is surrounded by several veins. This arrangement permits the venous blood to be warmed by heat transfer from the arterial blood before it reenters the body. [Schmidt-Nielsen 1970]

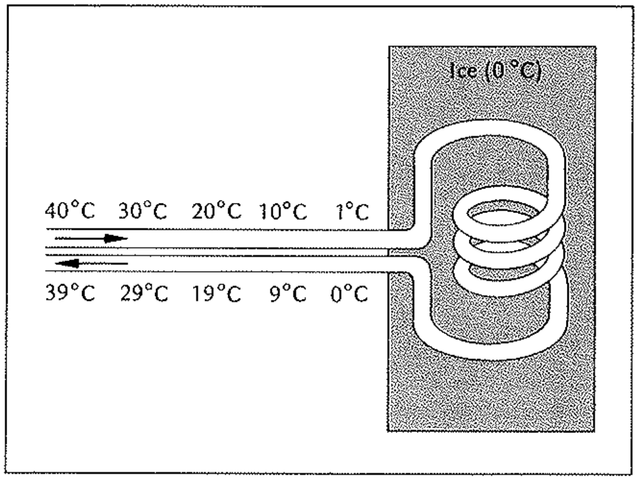


core from these appendages were at near-freezing temperature, the deeper parts of the body would rapidly be cooled.

Excessive heat loss from the blood in the flippers is prevented by the special structure of the blood vessels, which are arranged in such a way that they function as heat exchangers. In the whale flipper each artery is completely surrounded by veins (Figure 7.16), and as warm arterial blood flows into the flipper, it is cooled by the cold venous blood that surrounds it on all sides. The arterial blood therefore reaches the periphery precooled and loses little heat to the water. The heat has been transferred to the venous blood, which thus is prewarmed before it reenters the body. If the heat exchange is efficient, the venous blood can reach nearly arterial temperatures and thus contribute virtually no cooling to the core. This type of heat exchanger is known as a *countercurrent heat exchanger* because the blood flows in opposite directions in the two streams (Scholander and Schevill 1955).

A diagram of a countercurrent heat exchanger may help explain how it works (Figure 7.17). Assume that a copper pipe carries water at 40 °C into a coil suspended in an ice bath, and that the water returns in a second pipe located in contact with the first so that heat is easily conducted between them.

FIGURE 7.17 Model of a countercurrent heat exchanger. In this case heat is conducted from the incoming water to the outflowing water so that in the steady-state condition the outflowing water is prewarmed to within 1 °C of the incoming water. For explanation, see text.



As the water leaves the coil, it is very nearly at the temperature of the ice bath, 0 °C. As this water flows adjacent to the warmer pipe leading into the coil, it picks up heat and thus cools the incoming water. After some time a steady state of temperatures is reached, which may be as indicated in the diagram, depending on the conditions for heat exchange between the two pipes and their length.

For animals swimming in warm water, heat dissipation presents a greater problem than heat conservation. The anatomical arrangement of the heat exchanger is such that an increased blood supply and an increase in arterial blood pressure cause the diameter of the central artery to increase, and this in turn causes the surrounding veins to be compressed and collapse. The venous blood must now return in alternate veins, which are located closer to the surface of the flipper. Because the heat exchanger is now bypassed, the arterial blood loses heat to the water, and the venous blood returns to the core without being rewarmed, thus cooling the core. In this way the circulatory system of the flipper can function both in heat conservation and in heat dissipation.

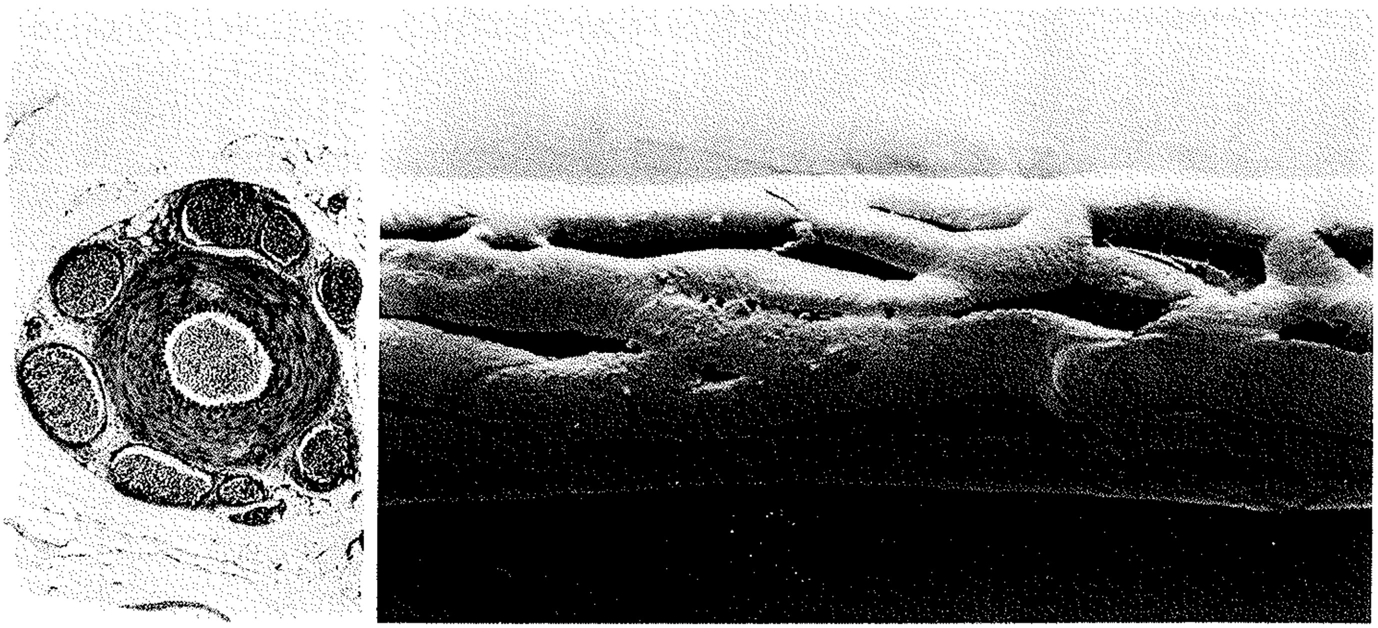
It is interesting that such countercurrent heat exchangers are found in a number of other animals. For example, sea cows, which live in tropical and subtropical waters, have heat exchangers in their appendages. This might seem unnecessary, for they live in warm water, but sea cows move slowly and have relatively low metabolic rates for their size, and thus would have difficulties unless they could reduce the heat loss from the appendages.

Heat exchangers in the limbs are not restricted to aquatic animals. Even in the limbs of humans some heat exchange takes place between the main arteries and the adjacent larger veins, located deep within the tissues. In cold surroundings most of the venous blood from the limbs returns in these deep veins, but in warm surroundings much of the venous blood returns in superficial veins under the skin and is thus diverted from heat exchange with the artery (Aschoff and Wever 1959).

In birds, heat exchange in the legs is very important, especially for birds that stand or swim in cold water. Unless the blood flowing to these thin-skinned peripheral surfaces went through a heat exchanger, the heat loss would be very great indeed. However, because of the heat exchanger the heat loss is minimal. A gull placed with its feet in ice water for 2 hours lost only 1.5% of its metabolic heat production from the feet, a quite insignificant heat loss (Scholander 1955).

Even some tropical animals have vascular heat exchangers in their limbs. In the sloth the artery to the foreleg splits into several dozen thin parallel arteries, which are intermingled with a similar number of veins. It may seem superfluous for a tropical animal to have such heat exchangers, but on a rainy and windy night the heat loss from an animal sleeping in the crown of a tree can be very great indeed.

The value of the heat exchanger in the sloth has been clearly demonstrated by immersing a limb in ice water. The blood temperature below the heat exchanger decreased drastically, but in the part of the foreleg above the heat exchanger the temperature of the venous blood was nearly at core temperature (Scholander and Krog 1957).



BLOOD VESSELS IN A BIRD LEG Cross section (left) and surface view of the blood vessels in the leg of a European rook (*Corvus frugilegus*), a crow-like bird. The thick-walled artery runs in the center and is surrounded by several thin-walled veins that branch and anastomose so that they virtually cover the artery (right). The diameter of the structure is 2 mm. [Courtesy of Uffe Midtgård, University of Copenhagen]

It has been suggested that the vascular bundles in the forelegs of the sloth and the loris have an entirely different function: that they are related to the ability of these climbing animals to maintain a strong grip (Buettner-Janusch 1966; Suckling et al. 1969). However, the vascular structure is located in the upper part of the foreleg, and the muscles responsible for the grasp are in the lower part. The fact that the blood runs through a bundle of arteries that join again into a single vessel cannot have any imaginable influence on the muscles in the lower part of the foreleg. The blood still contains the same oxygen and nutrients, and the only difference these muscles could detect would be a slightly decreased blood pressure, which certainly could not improve the strength of the grip.

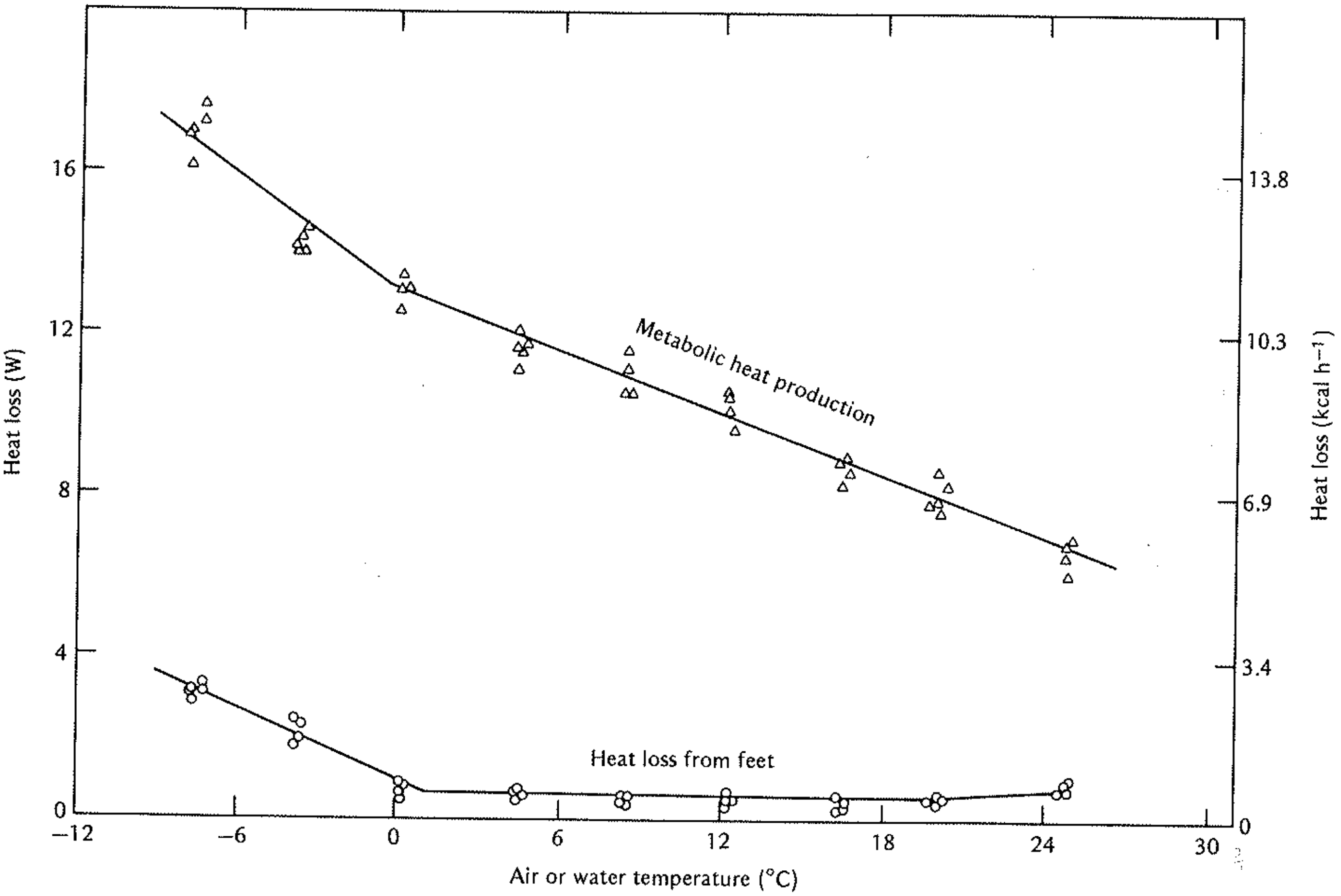
An animal in the cold has two opposed problems: to conserve heat and to keep peripheral tissues such as the feet from freezing. At ambient temperatures down to freezing, there is no conflict between the two; reduction in blood flow and cooling of the arterial blood in a heat exchanger help to minimize the heat loss.

However, when the temperature falls much below freezing, it is necessary to add enough heat to the peripheral tissues to keep them from freezing. The bare feet of the duck and other birds are suitable examples. As long as there is no danger of freezing, the heat loss from the feet is minimal, but as the temperature is lowered below 0 °C, the heat loss increases in proportion to the decrease in temperature (Kilgore and Schmidt-Nielsen 1975). The increase in heat drain is reflected in an increased metabolic heat production, appearing as a distinct inflection point in the metabolic curve (Figure 7.18).

Temperature regulation in the heat: keeping cool

We have seen that mammals and birds must increase their heat production in order to stay warm at ambient temperatures below a certain point, the

FIGURE 7.18 At low temperature, below 24 °C, the heat loss from the feet of a duck is a small fraction of the metabolic heat production. Below the freezing point the heat transferred to the feet (and lost tc the water) increases in proportion to the drop ir temperature. [Kilgore and Schmidt-Nielsen 1975]



lower critical temperature. We will now be concerned with what happens above this critical temperature.

Above the critical temperature the metabolic heat production (resting metabolic rate) remains constant through a range usually known as the *thermoneutral range* (see Figure 7.6). As before, for the body temperature to remain constant, metabolic heat must be lost at the same rate it is produced. If we return to the now familiar equation for heat balance, $\dot{H}=C\ (T_b-T_a)$, we see that if $\dot{H}$ and T_b remain constant and T_a changes, the conductance term (C) must also change.

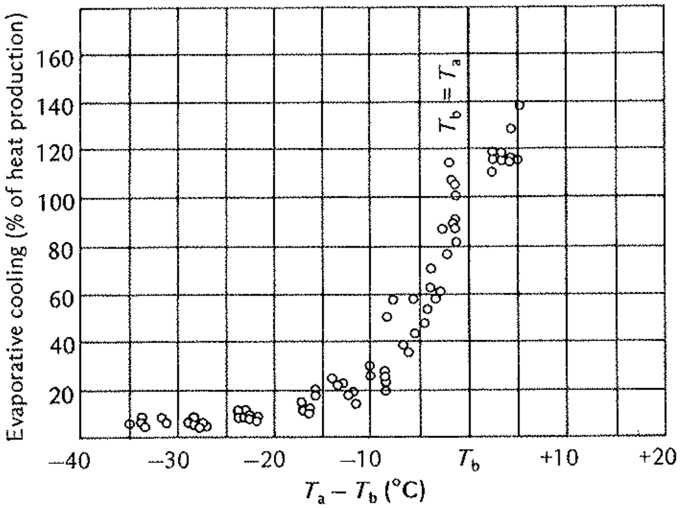
The conductance term refers to the total heat flow from the organism, and it can be increased in several ways. One way is by increasing circulation to the skin so that heat from the core is moved more rapidly to the surface. Another way is by stretching out and exposing increased surface areas, especially naked or thinly furred areas.

Let us return to the basic equation for heat balance (page 253):

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

As the ambient temperature increases, the conditions for heat loss by conduction and convection (H_c) and radiation (H_r) become increasingly unfavorable. Because the metabolic heat production

FIGURE 7.19 The cooling by evaporation in jackrabbits, expressed in percent of the simultaneous metabolic heat production. Evaporation increases as the difference between body temperature (T_b) and air temperature (T_a) decreases. As this difference approaches zero (body and air temperatures equal), the entire heat production (100%) is dissipated by evaporation. [Dawson and Schmidt-Nielsen 1966]



(H_{tot}) remains unchanged (or even increases slightly), the heat balance equation must increasingly emphasize the evaporation and storage terms (H_e and H_s).

In the discussions of heat regulation in the cold we disregarded heat removed by evaporation because it made up a fairly small fraction of the total heat exchange. At high temperature evaporation is the key item in the heat balance. Assume that we have increased the temperature of the environment to equal the body temperature of an animal. If the temperature of the environment equals the body temperature, there can be no loss of heat by conduction, and the net radiation flux approaches zero. If we now wish to maintain a constant body temperature (i.e., keep the storage term H_s at zero), the consequence is that the entire metabolic heat production (H_{tot}) must be removed by evaporation of water.

This prediction has been tested on a number of mammals and birds. When they are kept in air that equals their body temperature, those that are able to keep their body temperature from rising (not all species can) evaporate an amount of water that is equivalent to their metabolic heat production. An example is given in Figure 7.19, which shows that the desert jackrabbit (actually a hare) behaves according to the prediction.

The ambient temperature can, of course, increase further and exceed the body temperature, as frequently happens in deserts. In this event the body receives heat from the environment by conduction from the hot air, by radiation from the heated ground surface, and in particular by radiation from the sun.

Under these circumstances evaporation must be used to dissipate the sum of metabolic heat production and the heat gain from the environment. The possibility of storing heat is not a good solution, for as we saw before, animals have only limited tolerance to increased body temperature. Nevertheless, as we shall see later, even a moderate increase in body temperature can indeed be important for a desert animal.

To evaluate the importance of the heat load from the environment, consider how much water is used for evaporation (sweating) by a person in a hot desert. His total resting metabolic rate is about 70 kcal per hour, and this amount of heat, if dissipated entirely by evaporation, requires 120 ml, or 0.12 liter, water. We also know that a person exposed to the sun on a hot desert day may sweat at a rate of between 1 and 1.5 liters per hour. To make our calculations simple, let us say 1.32 liters per hour. If there is no change in his body temperature, and 0.12 liter is used to dissipate the metabolic heat, the excess of 1.2 liters used must be attributable to the heat gain from the environment. Thus the sum of conduction from the hot air, radiation from the hot ground, and radiation from the sun must require the evaporation of 1.2 liters of water. Therefore, in this example, the heat load from the environment is exactly 10 times as high as the metabolic heat production of the person at rest. If the body temperature were to increase by 1 °C, the storage of heat would be about 60 kcal, or the equivalent of 0.1 liter water evaporated – a fairly insignificant amount.

We now have a good idea of how important the environmental heat load can be when the temperature gradients are reversed, and it is worth considering how this affects animals. If a person were to continue evaporating at the indicated rate and had no water to drink, he would be near death from dehydration at the end of a single hot day in the desert. Yet the deserts of the world have a rich and varied animal life, although in most deserts there is no drinking water available. This requires further discussion.

The importance of body size

If we put a large block of ice outside in the hot sun, and a small piece next to it, the small piece will melt away long before the large block. If a big rock and a small pebble are placed on the ground in the sun, the pebble will be hot long before the big rock. The reason is that a small object has a much larger surface relative to its volume. If the big rock or block of ice is broken into many small pieces, numerous new surfaces, previously unexposed, are in contact with the warm air and receive solar radiation. Because of the many new exposed surfaces the total mass of rock heats up more rapidly and the crushed ice melts faster.

The relation between surface and volume of similar-shaped objects is simple. If a given cube is cut into smaller cubes with each side one-tenth that of the larger cube, the total surface of all the small cubes is 10 times that of the original cube. If the linear dimension of the small cube is one-hundredth of the larger one, the aggregate surface is 100 times the original, and so on. This rule holds for any other similar-shaped objects. Thus, any small body has a surface area that, relative to its volume, increases as the linear dimension decreases. Small and large mammals have sufficiently similar shapes that their body surface area is a regular function of the body volume, and the same rule applies.

Let us return to the animal in hot surroundings. Its total heat gain consists of two components: heat gain from the environment and metabolic heat gain. The heat gain from the environment by conduction and convection, as well as radiation from ground and sun, are surface processes, and the total environmental heat load therefore is directly related to the surface area. In Chapter 5 we saw that the metabolic heat production of a mammal is not quite proportional to body surface, but sufficiently close that, as an approximation, we can assume this to be so. Therefore, the total heat load – the sum of metabolic and environmental heat gain – is roughly proportional to the body surface area. This puts the small animal, with its larger relative surface, in a far more unfavorable position with regard to heat load than a large animal.

If a person in the desert must sweat at a rate of 1 liter per hour (which equals about 0.60 liter per square meter body surface area per hour), we can use the surface relationship to estimate or predict how much water other animals should evaporate under similar desert conditions in order to dissipate the heat load. We thus obtain a theoretical curve that predicts the amount of water needed to keep cool (Figure 7.20). The amount is an exponential function of body mass, and on logarithmic coordinates the curve will be a straight line.

However, Figure 7.20 is plotted on a linear ordinate in order to emphasize the exponential increase in water required if a small animal were to depend on evaporation to keep cool in the desert. Many small rodents weigh between 10 and 100 g and would have to evaporate water at a rate of 15 to 30% of their body weight per hour. As a water loss of between 10 and 20% is fatal for mammals, such rates of water loss are impossible. Obviously, because of their small size alone, desert rodents must evade the heat, which they do by retreating to their underground burrows during the day.

Large body size: the camel. Figure 7.20 shows that large animals, such as camels, derive a substantial advantage simply from being big. The benefit, however, does not increase much as the body size increases further. Theoretically, if a camel in

FIGURE 7.20 For a mammal to maintain a constant body temperature under hot desert conditions, water must be evaporated in proportion to the heat load. Because of the larger relative surface area of a small animal, the heat load, and therefore the estimated evaporation in relation to the body size, increases rapidly in the small animal. The curve is calculated on the assumption that heat load is proportional to body surface. [Schmidt-Nielsen 1964]

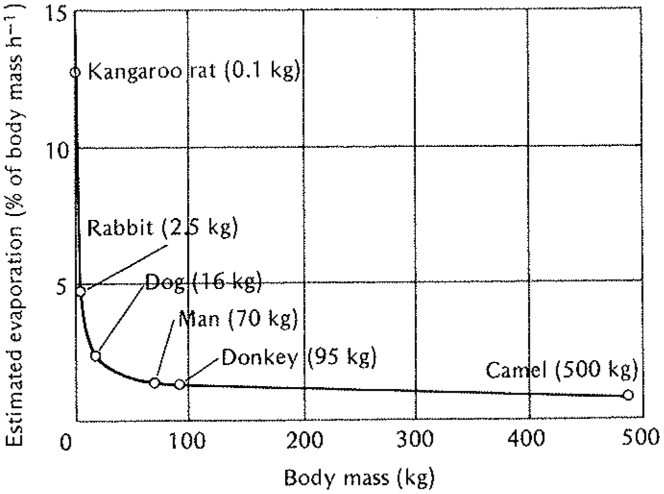
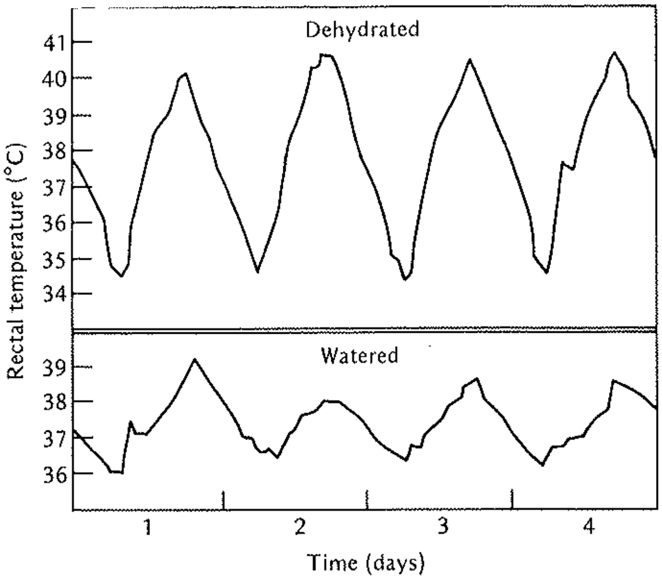


FIGURE 7.21 The daily temperature fluctuation in a well-watered camel is about 2 °C. When the camel is deprived of drinking water, the daily fluctuation may increase to as much as 7 °C. This has a great influence on the use of water for temperature regulation (see text). [Schmidt-Nielsen 1963]

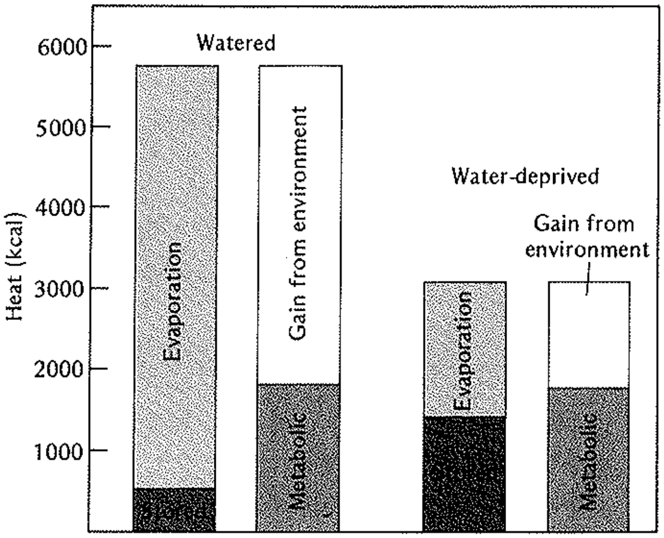


other respects were like a man, its body size would make it evaporate water at about half the rate of a man. The camel, however, is not a man and does not use this much water for heat regulation. As we shall see, the camel uses a combination of several approaches that help reduce the heat gain from the environment and thus the use of water.

First consider what a camel can do about two of the variables in the heat balance equation, evaporation (H_e) and storage of heat (H_s). Storage of heat is reflected in an increase in body temperature. In a normal camel that is watered every day and is fully hydrated, the temperature varies by about 2 °C, between about 36 and 38 °C (Figure 7.21). When the camel is deprived of drinking water, however, the daily temperature fluctuations become much greater (Schmidt-Nielsen et al. 1957). The morning temperature may be as low as 34 °C, and the highest temperature in the late afternoon may be nearly 41 °C. This large increase in body temperature during the day constitutes a storage of heat. For a camel that weighs 500 kg, the amount of heat stored by a 7 °C temperature rise corresponds to 2900 kcal of heat, which equals a saving of 5 liters of water. In the cool night, the stored heat can be unloaded by conduction and radiation without use of water.

The high body temperature during the day has a further advantage, beyond that of storing heat. When the body temperature is increased, the temperature gradient from the hot environment to the body (which determines the amount of heat gain from the environment) is reduced. This reduction in environmental heat gain is at least as important as heat storage with regard to water savings and is reflected in the reduced amount of water used. This is illustrated in Figure 7.22, which shows the heat balance of a small adult camel studied in the Sahara Desert. In the fully hydrated animal the evaporation during the 10 hottest hours of the day was

FIGURE 7.22 The change in body temperature of a camel deprived of drinking water greatly affects the heat gain from the environment and in turn the amount of water used for heat regulation (by evaporation). [Schmidt-Nielsen et al. 1957]



9.1 liters, corresponding to the dissipation of 5300 kcal heat. In the same camel when deprived of drinking water, the evaporation was reduced to 2.8 liters in 10 hours, corresponding to the dissipation of 1600 kcal heat. Thus, the use of water in the dehydrated camel was reduced to less than one-third that in the fully hydrated animal.

The main reason the camel uses substantially less water than a man (about 0.28 liter per hour in the camel compared with more than 1 liter per hour for a man who weighs about one-quarter as much) is the higher body temperature in the camel, which means both storage of heat and a reduced environmental heat gain. In contrast, man maintains his body temperature nearly constant at about 37°C, and thus does not store appreciable amounts of heat. A human also maintains much steeper gradients between the environment and his body surface, for the mean skin surface temperature of a sweating human is about 35°C.

One further important reason is that the camel has thick fur with a high insulation value. This imposes a heavy insulating layer between the body and the source of the heat and thus reduces the heat gain from the environment. The simplest way of testing the importance of this fur is to shear a camel. In one such experiment, the water expenditure of a camel, under otherwise similar conditions, was increased by about 50% when the animal was shorn.

We have now seen some of the major reasons for a lower-than-predicted (from body size alone) water loss in the camel: (1) heat is stored because of an increase in body temperature; (2) the increase in body temperature decreases the heat flow from the environment; and (3) the fur is a substantial barrier to heat gain from the environment.

The camel has one further advantage over humans: It can tolerate a greater degree of water depletion of the body. A human is close to the fatal limit when he has lost water amounting to between 10 and 12% of the body weight, but the camel can tolerate about twice as great a water depletion without apparent harm. As a result, the camel can go without drinking for perhaps 6 to 8 days under desert conditions that would be fatal in a single day to a human without water.

In the end, however, a camel must drink to replenish its body water, and when water is available, it may drink more than a third of its body weight. The immense capacity for drinking has given rise to the legend that a camel, before a long desert journey, fills its water reservoirs. In reality, the camel, like other mammals, drinks to replenish lost water and to restore the normal water content of the body, and there is no evidence that it overdrinks in anticipation of future needs.

Small body size: the ground squirrel. We saw earlier that because of their small size and large relative surface, small rodents should be unable to remain above ground and active during the day. Seemingly, the small ground squirrels of the North American deserts defy this conclusion. These small rodents, which weigh from less than one hundred to a few hundred grams, are often seen outside their burrows in the daytime. They move around quickly, dashing from one place to another; they frequently disappear in a hole, but soon appear again, often within minutes. During the hottest midsummer days they are less active in the middle of the day, but are often seen during the morning and late afternoon hours.

Usually, there is no free water available in their environment. How is it possible for ground squirrels to remain active during the day? Apparently, heat storage plays a great role, but not on a diurnal cycle, as for the camel.

When they are outside their burrows on a hot day, the ground squirrels heat up very rapidly. They cannot tolerate any higher body temperature than other mammals and die if heated to 43°C. However, a temperature of 42.4°C can be tolerated without apparent ill effects. As an active ground squirrel has become heated outside, it returns to the relatively cool burrow, were it rapidly cools off, helped by its large relative surface (Chappell and Bartholomew 1981). By moving in and out of the cool burrow the ground squirrel can rapidly pick up heat and rapidly unload it again and in this way avoid using water for evaporation. This permits it to move about and be active during the day.

Evaporation: sweating or panting

We know from our own experience that humans sweat to increase cooling by evaporation. Dogs, in contrast, have few sweat glands, and they cool primarily by panting – a very rapid, shallow breathing that increases evaporation from the upper respiratory tract. Some animals use a third method for increasing evaporation: They spread saliva over their fur and lick their limbs, thus achieving cooling by evaporation.

The amount of heat needed to evaporate 1 kg of water (580 kcal or 2426 kJ) is, of course, the same irrespective of the source of the water and where it is evaporated. Let us see if there are other differences that might make one method of evaporation more or less advantageous than another for a particular animal. We will therefore examine the characteristic features of each method.

In humans, sweating carries virtually the entire burden of increased evaporation. Evaporation from the body surface is an effective way of cooling, and in the absence of fur the water can evaporate readily. However, several furred mammals, in particular those of large body size, such as cattle, large antelopes, and camels, also depend mainly on sweating for evaporation. The camel in particular has a thick fur, but evaporation is not much impeded because in a desert atmosphere the air is very dry and the sweat evaporates so rapidly that some observers have reported that camels do not sweat at all. In contrast, a number of smaller ungulates – sheep, goats, and many small gazelles – evaporate mostly by panting. Those carnivores that have been studied also pant.

The third method, salivation and licking, is common in a fairly large number of Australian marsupials, including the large kangaroos, and can also be found in some rodents, including the ordinary laboratory rat. The salivation-and-licking method is not very effective and seems to be used primarily as an emergency measure when the body temperature threatens to approach a lethal level. The importance of salivation can be demonstrated in rats by removal of the major salivary glands. The rats are then much less tolerant of high air temperatures, and when they are exposed to a heat load their body temperature increases faster and to higher levels (Hainsworth 1967).

In addition to being less effective than sweating and panting, salivation and licking are less widespread, and we shall not discuss the method further. Instead, we shall compare sweating and panting and see what possible advantages and disadvantages each method may have.

Birds, in contrast to mammals, have no sweat glands. They increase evaporation either by panting or by a rapid oscillation of the thin floor of the mouth and upper part of the throat, a mechanism known as *gular flutter*. Either mechanism seems to be an effective means of cooling, for birds may use one or the other or often a combination of both (Bartholomew et al. 1968).

An obvious difference between panting and sweating is that the panting animal provides its own air flow over the moist surfaces, thus facilitating evaporation. In this regard the sweating animal is not so well off. Another difference is that the sweat (at least in humans) contains considerable amounts of salt, and a heavily sweating human may lose enough salt in the sweat to become salt-deficient. This is the reason for the recommendation that we should increase the intake of sodium chloride when sweating is excessive in very hot situations. Panting animals, in contrast, do not lose any of the electrolytes secreted from glands in the nose and the mouth (unless the saliva actually drips to the ground) and are thus better off in this regard as well.

Panting has two obvious disadvantages. One is that increased ventilation easily causes an excessive loss of carbon dioxide from the lungs, which can result in severe alkalosis; the other is that increased ventilation requires muscular work, which in turn increases the heat production and thus adds to the heat load. The tendency to develop alkalosis can in part be counteracted by shifting to a more shallow respiration (smaller tidal volume) at an increased frequency, so that the increased ventilation takes place mostly in the dead space of the upper respiratory tract. Nevertheless, heavily panting animals regularly become severely alkalotic, and thus they do not utilize fully the possibility of restricting the ventilation to the dead space (Hales and Findlay 1968).

The increased work of breathing during panting would be a considerable disadvantage were it not for the interesting fact that the muscular work, and thus heat production, can be greatly reduced by taking advantage of the elastic properties of the respiratory system. When a dog begins to pant, its respiration tends to shift rather suddenly from a frequency of about 30 to 40 respirations per minute to a relatively constant high level of about 300 to 400. A dog subjected to a moderate heat load does not pant at intermediate frequencies; instead, it pants for brief periods at the high frequency, alternating with periods of normal slow respiration.

The meaning of this becomes clear when we realize that the entire respiratory system is elastic and has a natural frequency of oscillation, like other elastic bodies. That is, on inhalation, much of the muscular work goes into stretching elastic elements, which on exhalation bounce back again, like a tennis ball bouncing. To keep the respiratory system oscillating at its natural frequency (the *resonant frequency*) requires only a small muscular effort. As a consequence, the heat production of the respiratory muscles is small, adding only little to the heat load (Crawford 1962).

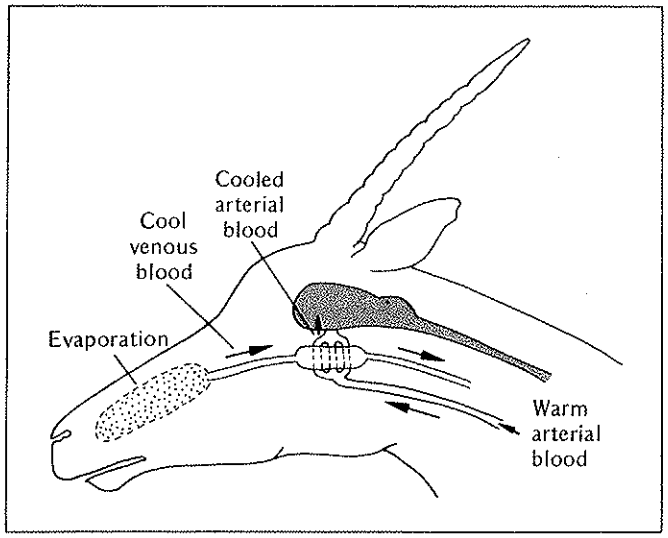
It has been estimated that if panting were to take place without the benefit of a resonant elastic system, the increased muscular effort of breathing at the high frequency of panting would generate more heat than the total heat that can be dissipated by panting. Apparently, birds can also pant at a resonant frequency, thus achieving the same benefits as mammals (Crawford and Kampe 1971).

Although we recognize some characteristic functional differences between panting and sweating, we do not have a clear picture of why one method or the other is used. Many animals use both methods, and this may indicate that both have valuable characteristics we do not yet fully appreciate.

Brain temperature. The greatest advantage of panting may be that an animal under sudden heat stress, such as a fast-running African gazelle pursued by a predator, can reach a high body core temperature and yet keep the brain, the most heat-sensitive organ, at a lower temperature. This may, at first glance, seem impossible, for the brain is supplied with arterial blood at a high flow rate. It is achieved as follows (see Figure 7.23).

In gazelles and other ungulates, most of the blood to the brain flows in the external carotid artery, which at the base of the skull divides into hundreds of small arteries, which then rejoin before passing into the brain. These small arteries lie in a large sinus of venous blood that comes from the walls of the nasal passages where it has been cooled. The blood that flows through these small arteries is

FIGURE 7.23 The brain of a gazelle can be kept at a lower temperature than the body core because the arterial blood, before it reaches the brain, passes in small arteries through a pool of cooler venous blood that drains from the nasal region, where evaporation takes place. [Taylor 1972]



therefore cooled before it enters the skull, and as a result the brain temperature may be 2 or 3°C lower than the blood in the carotid artery and the body core.

Such temperature differences have been measured in the small East African gazelle, Thomson's gazelle, which weighs about 15 to 20 kg. When it ran for 5 minutes at a speed of 40 km per hour, a rapid buildup of body heat caused the arterial blood temperature to increase from a normal 39 to 44°C. The brain temperature did not even reach 41°C, which is a safe level (Taylor and Lyman 1972). It would be difficult to design a cooling system that can keep the entire body from heating up when an animal runs in hot surroundings at a speed that may require a 40-fold increase in metabolic rate, but by selective cooling of the blood to the brain the most serious hazard of overheating is avoided.

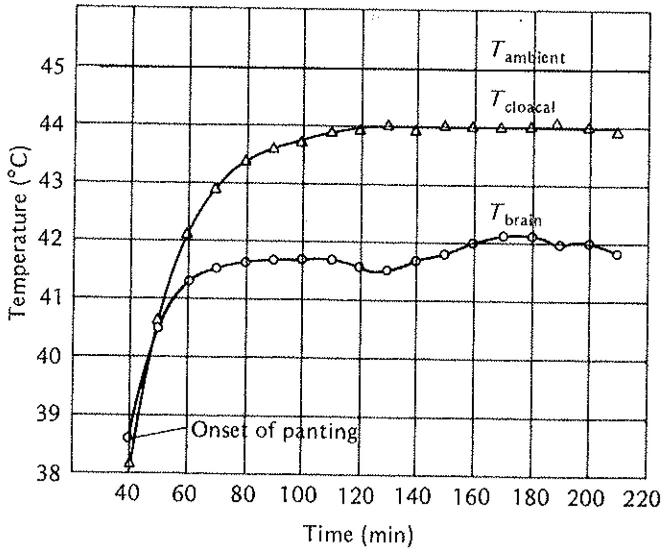
Similar cooling of blood to the brain has been observed in a number of domestic ungulates, and it may be a fairly common mechanism in animals that pant. We could surmise that the existence of a brain-cooling mechanism is unlikely in humans because we do not pant, and sweating and cooling take place over the entire body surface. This conclusion is too hasty, however. It appears that selective cooling of the brain can result with the aid of venous blood returning from facial skin via the ophthalmic vein to the cavernous sinus, where a cooling of arterial blood ascending to the brain can take place (Cabanac 1986).

It has been known for many years that some reptiles, when they are exposed to a severe heat stress, increase their respiration frequencies and breathe with open mouth, a situation reminiscent of panting. It has been difficult to establish with certainty that this increased respiration, which does increase respiratory evaporation, plays any major role in heat regulation. The amount of water evaporated does not suffice to keep the animals substantially cooler than the environment, and the mechanism therefore seems to be no more than a rudiment of panting found in birds and mammals. However, in view of the ability of mammals to cool the brain selectively, the panting of lizards can better be understood.

In a desert lizard, the chuckawalla (*Sauromalus obesus*), panting is of marginal importance in the overall heat balance. When the ambient temperature is kept at 45°C, the body is barely cooler (44.1°C), but the brain remains at 42.3°C, or nearly 3°C below the ambient temperature. If a chuckawalla is moved from a room at 15°C to 45°C, the brain and cloacal temperatures initially increase rapidly (Figure 7.24), but as these temperatures reach 41 to 42°C, the brain temperature stabilizes at this level, while the cloacal temperature continues to rise until it nearly reaches the ambient temperature.

In the chuckawalla the carotid arteries run very close to the surface of the pharynx, so close that they are visible through the open mouth of the animal. As the arteries pass right under the moist surfaces where evaporation takes place, the blood is cooled before it enters the brain. This is again an example of an animal that is able to maintain dif-

FIGURE 7.24 When the lizard *Sauromalus* is moved from 15 °C to 45 °C, cloacal and brain temperatures increase rapidly. As these temperatures reach about 41 °C, they separate and the brain remains about 2 °C below the cloacal temperature and 3 °C below the air temperature. [Crawford 1972]



ferent parts of its body at different, well-regulated temperatures.

TORPOR AND HIBERNATION

Maintaining the body temperature in the cold at a cost of a several-fold increase in metabolic rate is expensive. Small animals have high metabolic rates to begin with, and a further increase may be too expensive when food is scarce or unavailable. The easy way out, and the only logical solution, is to give up the struggle to keep warm and let the body temperature drop. This not only eliminates the increased cost of keeping warm, but cold tissues use less fuel and the energy reserves last longer. This, in essence, is what hibernation is all about.*

Many mammals and a few birds hibernate regularly each winter. This means that the body temperature drops almost to the level of the surroundings. Metabolic rate, heart rate, respiration, and many other functions are greatly reduced; and the animal is torpid and shows little response to external stimuli such as noise or being touched. With active life virtually suspended, the animal can survive a long winter. Before entering into a period of hibernation, most hibernators also become very fat (i.e., they deposit large fuel reserves). Without the burden of keeping warm, the reserves can last for extended periods of unfavorable conditions.

Most animals that hibernate are small. This makes sense, for their high metabolic rates require a high food intake. Thus, many rodents – hamsters, pocket mice, dormice – hibernate. Insect eaters at high latitudes can find little food in winter, and bats and insectivores (e.g., hedgehogs) could not possibly manage without hibernation. Hibernators are also found among Australian marsupials, such as the pygmy possum (Bartholomew and Hudson 1962). Hibernating birds include hummingbirds, the smallest of all birds, the insect-eating swifts, and some mouse birds (*Colius*, an African genus).

It is not easy to give a completely satisfactory definition of the term *hibernation.* In physiology the word refers to a torpid condition with a substantial drop in metabolic rate. Thus, bears may sleep during much of the winter, but most physiologists say that they are not true hibernators. Their body temperature drops only a few degrees, they show only a moderate drop in metabolic rate and other physiological functions, and the females often give birth to the cubs during the winter. In other words, the bear does not conform to what a physiologist customarily considers true hibernation.

Another term, *estivation* (Latin *aestas* = summer), refers to inactivity during the summer and is even less well defined. It may be applied to snails that become dormant and inactive in response to drought, or it may refer to ground squirrels that during the hottest months disappear into their burrows and remain inactive. The Columbian ground squirrel begins to estivate in the hot month of August, but then it remains inactive throughout

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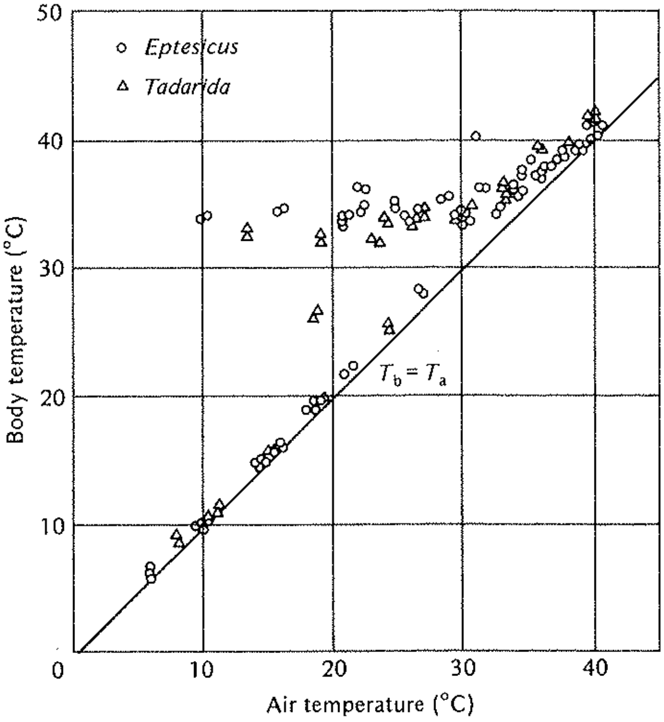
*The word hibernation (from Latin *hiberna* = winter) is also used to designate an overwintering, inactive stage of poikilothermic animals such as insects or snails.

the autumn and winter and does not appear again until the following May. Does it estivate or hibernate, and when does one condition change into the other? The fact is that no clear physiological distinction can be made between the two states. Furthermore, many animals, such as bats and hummingbirds, undergo daily periods of torpor with decreased body temperature and metabolic rate. Their physiological state is then quite similar to hibernation, although it lasts only for hours instead of weeks or months.

Because we lack precise definitions and there are no sharp lines between these different states, we will treat torpor and hibernation as one coherent physiological phenomenon.

It was earlier believed that hibernation and torpor result from a failure of temperature regulation in the cold and express some kind of "primitive" condition or poor physiological control. It is quite clear, however, that hibernation is not attributable to inadequate temperature regulation; it is a well-regulated physiological state, and the superficial similarity between a hibernating mammal and a cold-blooded animal (say, a lizard or frog) is misleading. We shall find that hibernation can in no way be considered a physiological failure.

FIGURE 7.25 The body temperatures of two species of North American bats. At low air temperature these bats may be either active with normal body temperatures about 34 °C or torpid with body temperatures near the air temperature. [Herreid and Schmidt-Nielsen 1966]



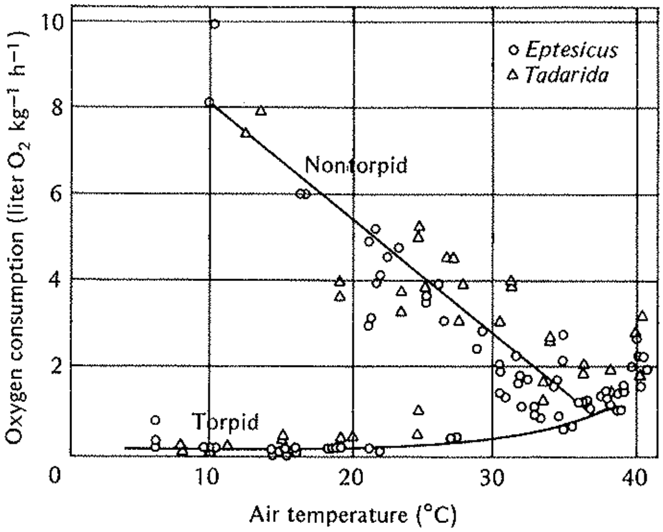
Body temperature and oxygen consumption

Bats are among the animals that may have daily periods of torpor and may also hibernate for longer periods. If exposed to low ambient temperature, bats may respond in one of two different characteristic ways. This is illustrated in Figure 7.25, which shows measured body temperatures of two North American bat species. At temperatures below about 30°C these bats can be either torpid and have body temperatures within a degree or two of the air temperature, or they can be metabolically active with normal body temperatures between 32 and 36°C. Even at air temperatures below 10°C, these bats may be either active or torpid.

The two bats are of similar size. The larger, the big brown bat (*Eptesicus fuscus*), which weighs about 16 g, ranges over most of the United States; and at least in the northern part of its range it hibernates. The smaller species, the Mexican free-tailed bat (*Tadarida mexicana*), weighs about 10 g; it inhabits the hot, dry southwestern United States and Mexico, and in winter in migrates southward and is not known to hibernate.

The response to low temperature of these two species is amazingly similar, although in nature one hibernates and the other does not. The oxygen consumption of those individuals that maintain a high body temperature at low air temperature shows the typical homeothermic pattern. As ambient temperature decreases, the cost of keeping warm is reflected in the increased oxygen consumption, which is at a minimum at about 35°C (Figure 7.26). Those individuals that become torpid, however, have very low metabolic rates. At 15°C, for example, the dif-

FIGURE 7.26 The oxygen consumption of active bats increases with decreasing air temperature; the oxygen consumption of torpid bats drops to a small fraction of the active rate (same bat species as in Figure 7.25). [Herreid and Schmidt-Nielsen 1966]



ference in oxygen consumption between an active and a torpid bat is about 40-fold. The torpid bat thus uses fuel at a rate only one-fortieth the rate of the active bat, and its fat reserves would last 40 times as long.

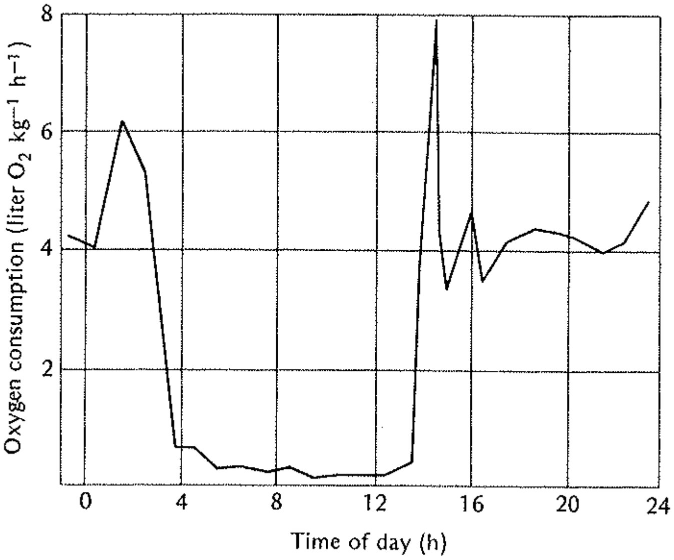
The amount of energy that can be saved by going into torpor has been more carefully analyzed by Tucker (1965a,b, 1966). The oxygen consumption during torpor is easily determined, but in addition, the energy cost required to rewarm the animal at the end of a period of torpor must be included in the cost. Tucker studied the California pocket mouse (*Perognathus californicus*) and found that for a short period of torpor the energy cost of reheating was a substantial part of the total cost.

The pocket mouse weighs about 20 g and readily becomes torpid at any ambient temperature between 15 and 32°C. Below 15°C the normal torpid state is disrupted and the animals usually cannot arouse on their own; in other words, if cooled below 15°C they are unable to produce enough metabolic heat to get the rewarming cycle started.

Pocket mice enter torpor much more readily if their food ration is restricted. With a gradual restriction of the food supply, longer and longer periods are spent in torpor. In this way a pocket mouse can maintain its body weight on a food ration that is about one-third of what it normally consumes when it remains active. A characteristic curve for the oxygen consumption of a pocket mouse on a restricted food ration is given in Figure 7.27. This particular individual received 1.5 g seed per day, and on this ration it was torpid for about 9 hours out of every 24. Although the food ration was less than half of what the animal would normally need if it remained active, it maintained a constant body weight.

When an animal goes into torpor, what happens first? Does heat loss first increase, the body temperature therefore drop, and the metabolic rate as a consequence decrease, thus accelerating the temperature drop? Or does the animal decrease its metabolic rate, the body temperature therefore begin

FIGURE 7.27 Oxygen consumption over a 24-hour period of a pocket mouse kept on a restricted food ration of 1.5 g seeds per day. During 9 hours the animal was torpid and had a very low rate of oxygen consumption followed by a peak as it returned to the active state. Air temperature was 15 °C. [Tucker 1965a]



to drop, the temperature drop causing a further decrease in heat production, and so on?

With information about heat production and heat loss during all stages of the torpor cycle, this question can be answered. The conclusion is that entry into torpor can result simply from a cessation of any thermoregulatory increase in metabolism at air temperatures below the lower critical temperature (about 32.5°C in the pocket mouse). At any temperature below this point, a decrease in metabolic rate to the thermoneutral resting level alone will, without change in conductance, lead to a decrease in body temperature. In other words, there is no need for a special mechanism to increase the heat loss. As the body temperature begins to fall, metabolism decreases and the pocket mouse slides into torpor with a further drop in heat production and body temperature.

Arousal can take place at any temperature above 15°C if the animal changes to maximum heat production at that temperature, which is about 10 to 15 times the minimum oxygen consumption at the same temperature. Arousal is thus an active process that requires a considerable expenditure of energy for a considerable period until the body temperature has reached normal.

If a pocket mouse goes into torpor at 15°C and immediately arouses again, does it save any energy, or does rewarming cost too much? The decline in body temperature takes about 2 hours, and the total oxygen consumption during this period is 0.7 ml O_2 per gram. If arousal follows immediately, normal body temperature is reached in 0.9 hour at a cost of 5.8 ml O_2 per gram. Entering into torpor and then immediately arousing therefore costs a total of 6.5 ml O_2 per gram in 2.9 hours. The cost of maintaining normal body temperature for the same period of time at 15°C ambient temperature would be 11.9 ml O_2 per gram. This period of torpor thus consumes only 55% of the energy required to keep warm for the same period of time (Tucker 1965b).

Remaining in torpor for longer periods, for example, 10 hours, is even more favorable for the animal. We must now add to the previously calculated cost of entry and arousal the cost of 7.1 hours at 15°C, which is 1.2 ml O_2 per gram, giving a total for a 10-hour cycle, including entry and arousal, of 7.7 ml O_2 per gram. This is less than 20% of the cost of maintaining normal body temperature for 10 hours, which at 15°C would be over 40 ml O_2 per gram.

We can see that in all these cases the cost of arousal is the major part of the cost of the torpor cycle. For the 10-hour period of torpor the cost of arousal alone is 75% of the total energy expenditure for the period.

The widespread occurrence of torpidity as a response to unfavorable conditions suggests that this ability is a very fundamental trait. Animals that can enter torpor include the egg-laying echidna (the spiny anteater, *Tachyglossus aculeatus*), which is only remotely related to modern mammals. The echidna is normally an excellent temperature regulator in the cold and can maintain its normal body temperature at freezing temperatures (Schmidt-Nielsen et al. 1966). However, when it is without food and kept at 5°C, it readily becomes torpid. The heart rate decreases from about 70 to 7 beats per minute, and the body temperature remains about +5.5°C. In this state the oxygen consumption of the echidna is about 0.03 ml O_2 g^{-1} h^{-1}, roughly one-tenth its normal resting oxygen consumption (Augee and Ealey 1968).

Control mechanisms

Torpor and hibernation are under accurate physiological control. We have just seen how the duration of the daily torpor of a pocket mouse is adjusted to the food ration and the need for energy savings. Obviously, not only must entry into torpor be controlled, but the duration of the cycle and the arousal process must be accurately regulated.

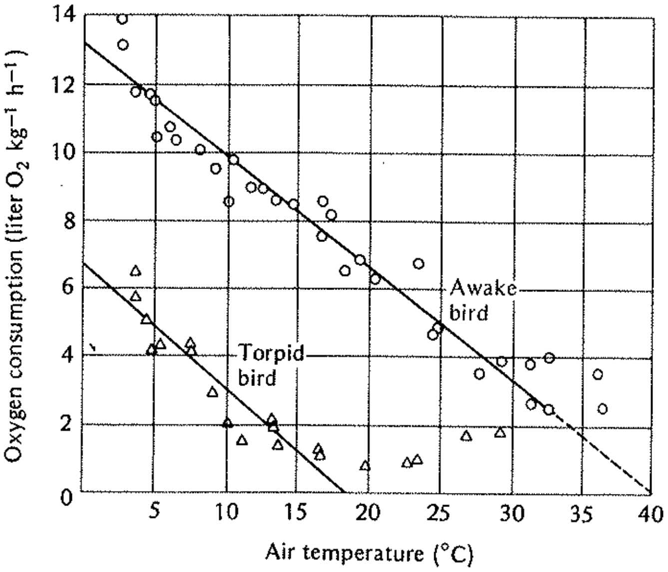
In nature the beginning of the hibernation cycle is usually associated with the time of the year, but it is not necessarily induced by low temperature or lack of adequate food. The yearly cycle of hibernation is influenced by the duration of the daily light cycle and is associated with endocrine cycles. For example, it is often impossible to induce even a good hibernator to begin a cycle of torpor during early summer and especially during the reproductive period.

The torpid animal with its low body temperature seems quite passive; it cannot perform coordinated movements, and it hardly responds to sensory stimuli. Superficially it resembles a cold-blooded animal that has been chilled. All of us have experienced how our fingers become numb when the hands are cold; this is because nerve conduction ceases at temperatures below some 10 to 15°C, and we sense nothing. (The reason we can still move our cold fingers is that the appropriate muscles are located above the hand in the lower part of the arm.)

If the nerves of a hibernator became inoperative at lower temperatures, the nervous system could not remain coordinated at, say, 5°C. Yet respiration and many other functions continue in a well-coordinated fashion although at a lower rate. If the ambient temperature decreases toward or below freezing, some hibernators die. Others, however, respond in one of two ways, leaving no doubt about the integrity of the central nervous system. Either they arouse and return to the fully active condition, or they resist the decrease in body temperature by a regulated increase in heat production, keeping the body temperature at some low level, say +5°C.

Such a well-regulated heat production does indeed require a well-coordinated central nervous system. For example, the European hedgehog maintains its body temperature at +5 to +6°C as the ambient temperature decreases to below freezing. This prevents freezing damage and at the same time saves fuel, for it eliminates the need of going through an expensive complete arousal and the cost of then maintaining the high body temperature of the active state. For a hibernator that may be exposed to freezing temperatures several times during winter, such repeated arousals might prove too expensive; maintaining a low body temperature, just sufficient to keep from freezing, is far more economical.

FIGURE 7.28 Oxygen consumption of the tropical hummingbird *Eulampis*. In the awake *Eulampis* oxygen consumption increases linearly with decreasing temperature. In the torpid *Eulampis* oxygen consumption drops to a low level, but if the air temperature goes below 18 °C, the animal produces more heat and maintains its body temperature at 18 to 20 °C without arousing from torpor. [Hainsworth and Wolf 1970]



A similar well-regulated state of torpor has been observed in the West Indian hummingbird, *Eulampis jugularis*, which like other hummingbirds readily becomes torpid. The temperature of *Eulampis*, when torpid, approaches air temperature, but if the air temperature falls below 18°C, *Eulampis* resists a further fall and maintains its body temperature constant at 18 to 20°C. Below this point the heat production must therefore be increased (Figure 7.28), and the increase must be linearly related to the drop in the ambient temperature.

Eulampis is particularly interesting because it is a clear case of torpidity in a tropical warm-blooded animal, and this shows that torpidity is not restricted to animals from cold climates. Also, the well-regulated metabolic rate at two different levels of body temperature certainly shows that torpor in no way is a failure of the process of thermoregulation. Another interesting aspect is that the overall thermal conductance (the slope of the metabolic regression line) is the same in torpid and in normal nontorpid hummingbirds.

Arousal

The rewarming during arousal, as we have seen, is metabolically the most expensive part of the torpor cycle. The arousing animal displays violent shivering and muscle contractions and apparently uses fuel at a maximal rate. However, not only the muscles but also a particular kind of tissue, known as *brown fat,* is important in the rewarming process.

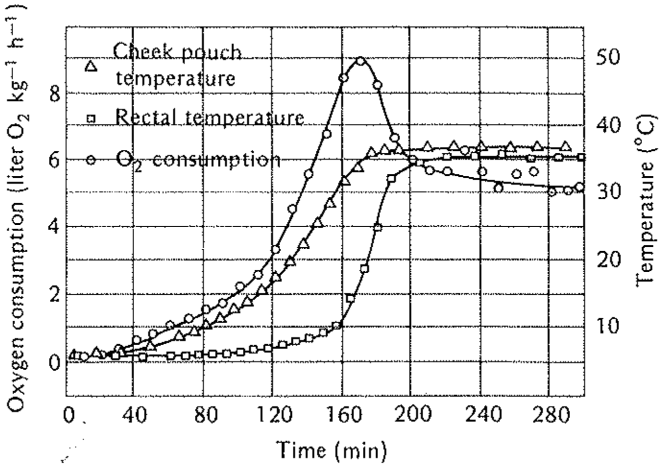
Brown fat is found in smaller and larger patches along the neck and especially between the shoulders. The cells are filled with fat, but in contrast to ordinary white fat cells, they are packed with large mitochondria that give the brown fat its characteristic color. The tissue has a rich blood supply and is innervated by sympathetic nerves.

In the cells of brown fat the mitochondrial respiration is uncoupled from the mechanism of ATP synthesis so that the energy of oxidation is dissipated as heat instead of being used for ATP synthesis. A special protein with a molecular weight of 32 000, known as *thermogenin,* is responsible for the uncoupling. As a result fat is oxidized and heat produced at an extremely high rate. The cells use the stored fat, but can also utilize substrates supplied with the blood (Himms-Hagen 1985). The heat production is turned on by noradrenalin or by nervous stimulation.

Brown fat is found in all hibernating mammals, but it also occurs in many newborn mammals, including humans, in whom its importance is to produce heat and maintain body temperature. In most adult mammals the brown fat has been lost, but in hibernators it remains prominent. During arousal large amounts of heat are produced in the brown fat, and because the venous blood returns directly to the heart, this essential organ is heated rapidly.

It is characteristic of an arousing hibernator that the temperature is not the same throughout the body; the rewarming is far from uniform. Figure 7.29 shows temperatures recorded separately in the cheek pouch and in the rectum of an arousing hamster. The anterior part of the body, which contains vital organs such as heart and brain, warms much more rapidly than the posterior part. Rewarming of the heart is not only essential but must be an initial step, for the heart is needed to provide circulation and oxygen for all the other organs. The major masses of brown fat are also located in the anterior part of the body. The records show that not until the anterior portion of the body has reached near-normal temperatures does the posterior part enter into the reheating process. At this moment, when the entire body rapidly attains normal temperature, there is a peak in the oxygen consumption, which afterward declines and settles at a normal level.

FIGURE 7.29 The temperature increase in a hamster arousing from hibernation proceeds more rapidly in the anterior part of the body (cheek pouch temperature) and more slowly in the posterior part (rectal temperature). [Lyman 1948]



The uneven temperature increase in the various parts of the body leads to an inevitable conclusion: During the early stages of arousal the blood flow is directed almost exclusively to the vital organs in the anterior part of the body, and not until these have been rewarmed does circulation increase substantially in the posterior parts as well.

The blood flow to the various organs can be followed by means of radioactive tracers, and such studies have shown that the skeletal muscles in the anterior part of arousing animals receive more than 16 times as much blood as in an awake, nonhibernating individual. This confirms that the muscles are highly involved in the increased heat production.

During early arousal the muscles in the hind part of the animal receive only one-tenth as much blood as in the front part. The brown fat, however, receives even more blood than the most active muscles, implicating this tissue in heat production during arousal. As could be expected, the digestive tract, in particular the small intestine, is among the tissues that receive the least blood during arousal (Johansen 1961).

It is perplexing that brown adipose tissue, which is so important for mammalian hibernators, appears to be absent from a number of birds that regularly hibernate, such as hummingbirds, swifts, and nighthawks (Johnston 1971).

BODY TEMPERATURE IN "COLD-BLOODED" ANIMALS

Birds and mammals are traditionally known as warm-blooded, the term cold-blooded being used for all other animals. However poor the term is, it is well established and convenient, and we will use it, for no better single word is available that is both complete and accurate.

Most cold-blooded animals are more or less at the mercy of their environment in regard to the body temperatures they attain. However, some so-called cold-blooded animals can and indeed do stay warmer than the medium in which they live, whether it be air or water. What they can achieve in this regard is governed by simple physical principles, although some of the solutions seem quite ingenious.

Let us return to the heat balance equation on page 253 and rearrange the terms with only the term for heat storage (H_s) on the left side. On the right side are the total heat production (H_{tot}) and heat exchange by radiation (H_r), by conduction and convection (H_c), and by evaporation (H_e). If the body temperature is higher than the surrounding medium, the terms for conduction (H_c) and evaporation (H_e) will signify heat losses and be negative. The equation can therefore be written:

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

If the goal is to increase the body temperature, we must see what the animal can do to maximize heat storage (H_s).

Aquatic animals

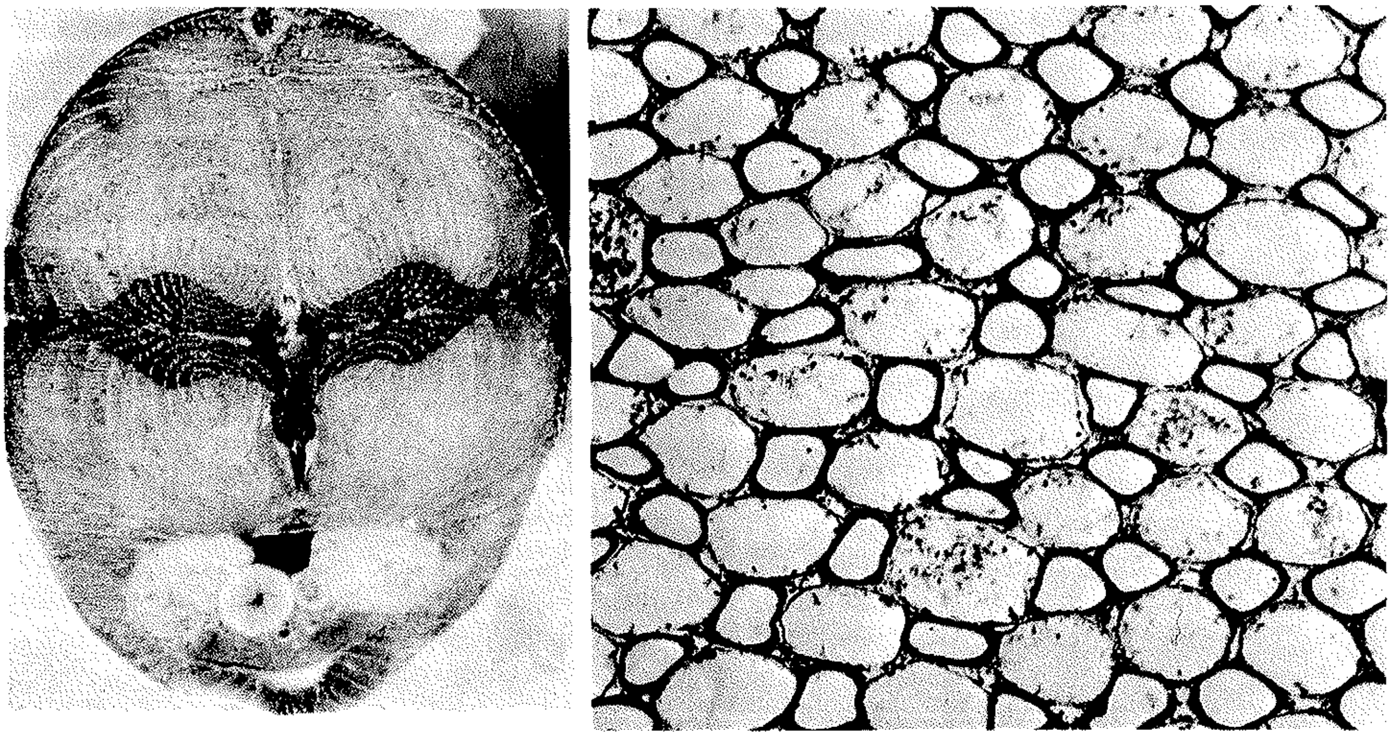
For an aquatic animal the situation is simple, for in water there is no evaporation and no significant radiation source (infrared radiation is rapidly absorbed in water). This leaves the equation: $H_s = H_{tot} - H_c$. Only two parameters can be manipulated in order to increase heat storage: Either total heat production must be increased, or conductive heat loss must be minimized.

Because of the high thermal conductivity and high heat capacity of water, a small animal loses heat rapidly and has no chance of attaining a body temperature very different from the medium. Even if it has a high level of heat production (metabolic rate), it needs oxygen to sustain this heat production.

Here is where the heat problem comes in. A high rate of oxygen uptake requires a large gill surface and blood for oxygen transport. As the blood flows through the gills, it is inevitably cooled to water temperature. The gill membrane, which must be thin enough to permit passage of oxygen, provides virtually no barrier to heat loss. The blood is therefore cooled to water temperature, and it is impossible for the animal to attain a high temperature unless a heat exchanger is placed between the gills and the tissues.

This solution is used by some large, fast-swimming fish (e.g., tunas and sharks) to achieve independent control of the temperature in limited parts of the body. They have heat exchangers that permit them to maintain high temperatures in their

HEAT EXCHANGER Cross section of a 2-kg skipjack tuna (*Katsuwonis pelamis*) shows how this powerful swimming machine consists mostly of muscle (left). The red muscle, which is maintained at high temperature, appears nearly black in the photo. In some tunas the heat exchanger is located laterally, but in the skipjack the main heat exchanger is located just below the vertebral column, almost exactly in dead center of the photo. A cross section of the vascular heat exchanger (right) shows a roughly equal number of arteries and veins. The arteries (smaller and thick-walled) are interspersed with veins (larger and thin-walled). The diameter of the arteries is about 0.04 mm and of the veins 0.08 mm, and their length is about 10 mm. [Courtesy of E. D. Stevens, University of Guelph, Ontario]



swimming muscles, independent of the water in which they swim.

The heat exchangers that supply the swimming muscles of the tuna are, in principle, similar to the countercurrent heat exchangers in the whale flipper, but anatomically they are somewhat differently arranged. In the ordinary fish the swimming muscles are supplied with blood from the large dorsal aorta that runs along the vertebral column and sends branches out to the periphery. In the tuna the pattern is different.

The blood vessels that supply the dark red muscles (which the tuna uses for steady cruising) run along the side of the fish just under the skin. From these major vessels come many parallel fine blood vessels that form a slab in which arteries are densely interspersed between veins running in the opposite direction (Figure 7.30). This puts the cold end of the heat exchanger at the surface of the fish and the warm end deep in the muscles.

The arterial blood from the gills is at water temperature, and as this blood runs in the fine arteries between the veins, it picks up heat from the venous blood that comes from the muscles. Heat exchange is facilitated by the small diameter of the vessels, about 0.1 mm. When the venous blood has reached the larger veins under the skin, it has lost its heat, which is returned to the muscle via the arterial blood.

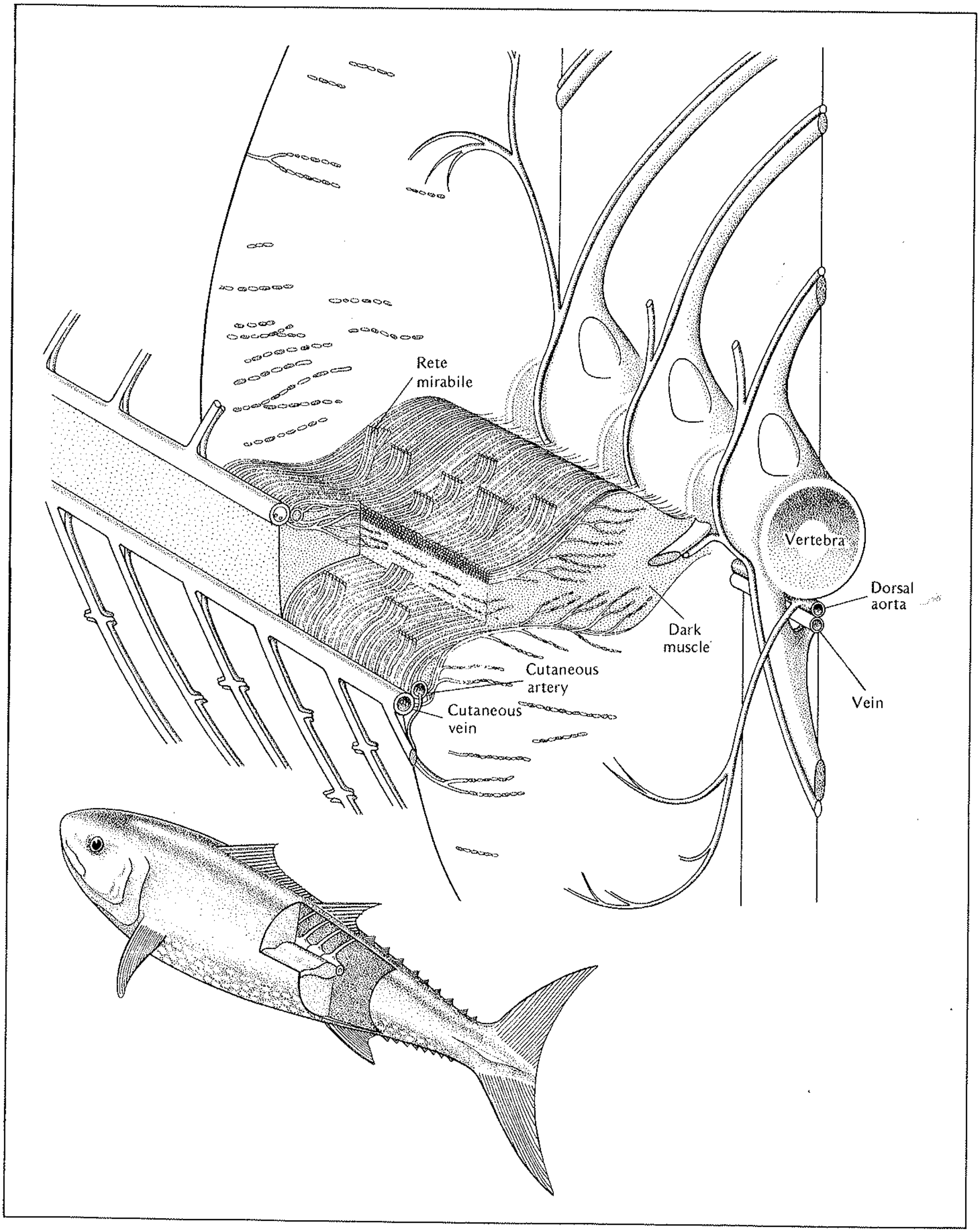

Rete
mirabile
Vertebra
Dorsal
aorta
Dark
muscle
Vein
Cutaneous
artery
Cutaneous
vein

FIGURE 7.30 The blood supply to the swimming muscle of the tuna comes through a heat exchanger, which is arranged so that these muscles retain a high temperature, although the arterial blood is at water temperature. A network of blood vessels arranged in this way is known as a *rete mirabile*, meaning "wonderful net." [Carey and Teal 1966]

As a result, the tuna can maintain muscle temperatures as much as 14°C warmer than the water in which it swims.

The advantage of keeping the swimming muscles warm is that high temperature increases their power output.* A high power output gives the tuna a high swimming speed relatively independent of water temperature, and this in turn enables the tuna to pursue successfully prey that otherwise swims too fast to be caught, such as pelagic fish (e.g., mackerel) or squid. The greatest advantage is probably that it makes the tuna relatively independent of abrupt changes in water temperature as it moves rapidly between the surface and deeper cold water.

Several of the large sharks, but by no means all of them, have similar heat exchangers that permit their muscles to be kept considerably warmer than the water in which they swim (Carey et al. 1971).

The tuna enjoys an additional advantage from the substantial temperature differences between various parts of the body. Separate heat exchangers permit the digestive organs and the liver to be kept at a high temperature. The high power output of the muscles requires a high rate of fuel supply, and this puts a premium on a rapid rate of digestion, which is most readily achieved by a high temperature in the digestive tract (Carey et al. 1984).

Swordfish and the closely related marlins and sailfish have the remarkable ability to keep eyes and brain warm, again by using countercurrent heat exchangers to prevent the loss of heat. These predatory fish have some of the largest eyes of any animal. A large swordfish has eyes the size of grapefruit, which undoubtedly is helpful when it pursues prey in deep cold water where the light is minimal.

In these fish it is not the eye and brain that produce the large amounts of heat; the heat is produced in a special organ that is derived from one of the eye muscles. The organ has lost all contractile characteristics but has extensive systems of membranes that correspond to what in muscle cells is known as the sarcoplastic reticulum (Block 1986). The uncoupling of the ATP synthesis seems to be associated with an increased flux of Ca^{++} ions across these membranes (Block 1987).

Similar eye and brain heater organs are found also in some of the large sharks, the porbeagle and the mako sharks (Block and Carey 1985).

Let us now compare the warm-bodied fish with marine mammals and consider the main differences and similarities between them. Seals and whales have heavily insulated surfaces (blubber); heat loss from the extremities is reduced by heat exchangers; and most important, they are air breathers whose blood escapes being cooled to water temperature at the respiratory surface. The warm-bodied fish, in contrast, would gain no advantage from a better surface insulation, for all the arterial blood coming from the gills is already at water temperature. They do achieve independent temperature control in limited parts of the body by strategic location of efficient heat exchangers that help retain locally produced heat.

Terrestrial animals

The heat balance of terrestrial animals includes all the terms listed in the equation on page 253. To raise the body temperature (i.e., to increase heat storage), it is important to reduce evaporation and heat loss by conduction and to maximize heat gain

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*The force exerted by a contracting muscle is relatively independent of temperature, and the work performed in a single contraction (work = force × distance) is therefore also temperature-independent. However, at higher temperature the muscle contracts faster, and because the number of contractions per unit time increases, the power output (work per unit time) increases accordingly.

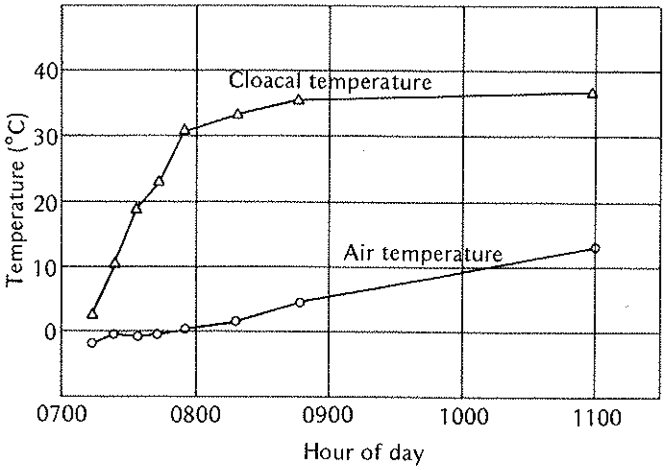
by radiation and metabolic heat production. The only commonly available radiation source is the sun, and in the absence of solar radiation, metabolic heat production is the only way to increase the heat gain. Of course, external and internal sources of heat (i.e., sun and metabolism), can be used simultaneously, but it is more economical to use an external source rather than body fuel.

Solar radiation is used especially by insects and reptiles. To increase the amount of radiant energy absorbed, these animals depend both on their color and on their orientation relative to the sun. Many reptiles can change their color by dispersion or contraction of black pigment cells in their skin. Because about half the solar radiation energy is in the visible light, a dark skin substantially increases the amount of solar energy that is absorbed rather than reflected. The absorption in the near infrared is not much affected by color change, for the animal surface is already close to being "black" in this range of the spectrum.

The other way of increasing heat gain from solar radiation is to increase the exposed area. This is done by orienting the body at right angles to the direction of the sun's rays and by spreading the legs and flattening the body. In this way a lizard can attain a temperature much higher than the surrounding air. When a suitable temperature has been reached, further heating is avoided by lightening the skin color and changing the orientation to a posture more parallel to the sun's rays, and eventually by moving into shade. The temperature of the substratum is also important, for a cool lizard can place itself in close contact with a warm rock and thereby increase its heat gain.

The temperature a lizard can attain by warming itself in the sun can be spectacular. In the mountains of Peru, at an altitude of 4000 m where the air temperature is low even in summer, the lizard *Liolaemus* remains active and comes out at temperatures below freezing. One lizard that weighed 108 g was tethered in the sun in the morning while the air temperature was still at −2°C. Within the next hour the air temperature increased to +1.5°C, but the cloacal temperature of the lizard had increased from +2.5°C to 33°C (Figure 7.31). The lizard's body temperature was 30°C higher than the air temperature, allowing it to be active in the near-freezing surroundings.

FIGURE 7.31 The Peruvian mountain lizard *Liolaemus* comes out in the morning while the air temperature is still below freezing and, by exposing itself to the sun, rapidly heats up to a body temperature that permits full activity. [Data from Pearson 1954]



Once the lizard is warm, its body temperature remains more or less constant around 35°C, while the air temperature slowly continues to rise. This is achieved because the lizard reduces the amount of absorbed solar energy by changing posture, so that it maintains its *preferred body temperature*, also known as the *eccritic temperature.*

It is, of course, important for the animal to heat up rapidly and become fully active as fast as possible. However, when the animal moves out of the sun, retarding the inevitable cooling would be an advantage. Can the lizard do anything to increase the rate of heating and decrease the rate of cooling? The heating of the body core can be accelerated by increasing the circulation to the heated skin area, but what about retarding cooling?

This question has been studied in several species of lizards. It is of particular importance to the Galápagos marine iguana, which feeds in water where

FIGURE 7.32 Heating and cooling rates of the Galápagos marine iguana (body weight 652 g) when immersed in water (open triangles) or in air (open circles). The initial temperature difference between animal and medium (ΔT) was, in all cases, 20 °C. [Bartholomew and Lasiewski 1965]

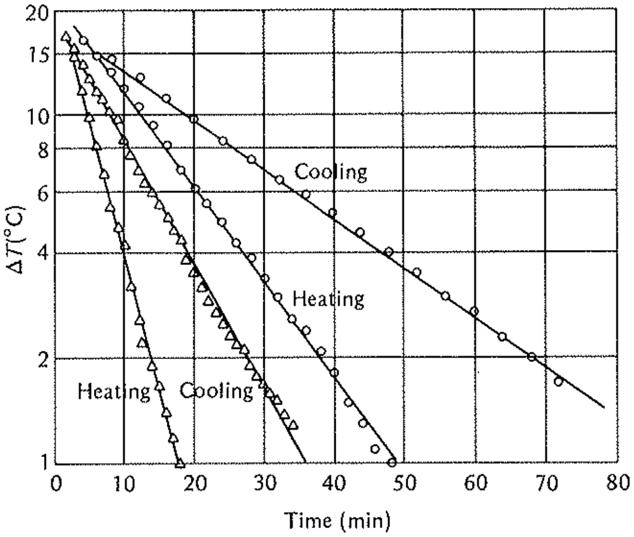
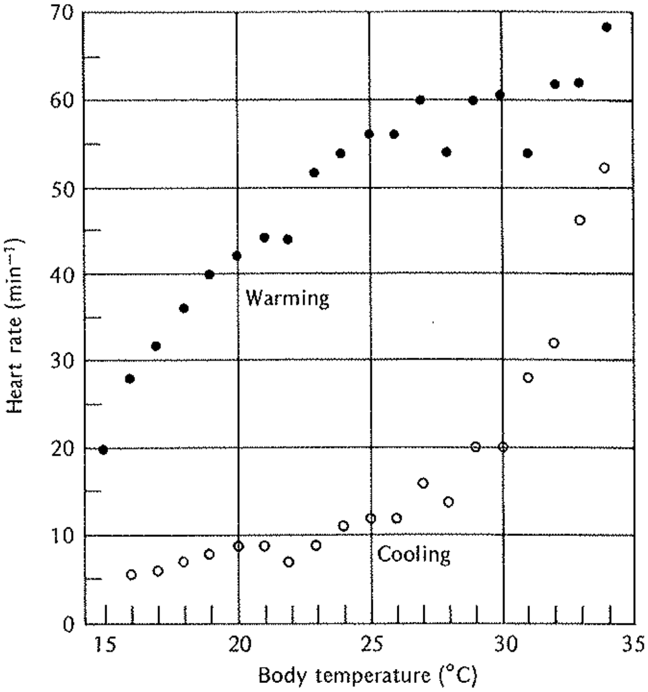


FIGURE 7.33 The heart rate of a soft-shelled turtle weighing 650 g. The heart rate, measured at any given body temperature, was much higher if the turtle was being heated than if it was undergoing cooling. The animal was in water during both heating and cooling. [Smith et al. 1981]



the temperature is 22 to 27°C. When it is out of water, the animal sits on the rocks near the surf where it can warm itself in the sun. When it enters the water to feed on the seaweed, its temperature drops toward that of the water, which is below the eccritic temperature. It would be advantageous for the marine iguana to reduce its rate of cooling while in water, and thus extend the period during which it can feed actively and move fast enough to escape predators. Conversely, after leaving the sea, it would be advantageous to heat up as rapidly as possible.

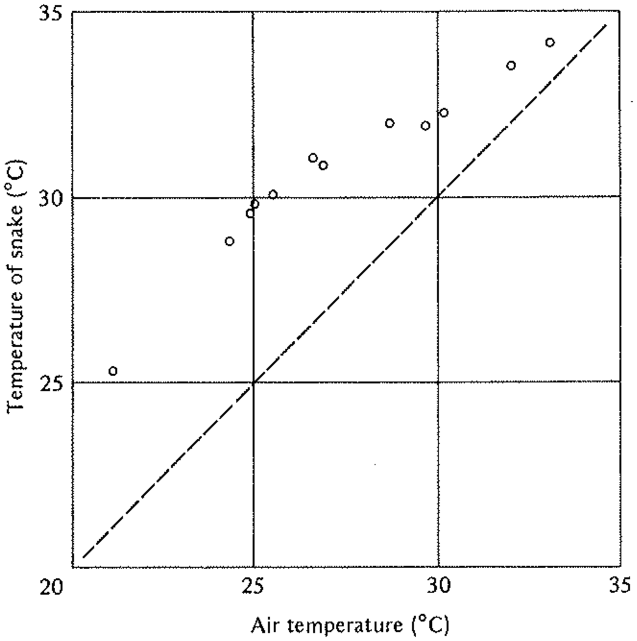
A comparison of the rates of heating and cooling for the marine iguana shows that heating rates are about twice as high as cooling rates, both in air and in water (Figure 7.32). When a cold animal is immersed in water that is 20°C above body temperature, the heating is twice as fast as the cooling when a warm animal is immersed in water 20°C below its body temperature. In air both rates are lower, but again, heating is about twice as fast as cooling at the same temperature differential.

The different rates of heating and cooling can best be explained by changes in circulation in the skin. During heating, the heart rate is high and increases with body temperature, but in an iguana being cooled the heart rate drops to half of what it otherwise is at the same body temperature.

For blood flow to be effective in control of heat exchange, it must occur in a region of the body where the resistance to heat flow is relatively high, and in an environment where the external resistance to heat exchange is relatively low. This means that control of heat exchange should be especially effective in water (Turner 1987).

A soft-shelled turtle (*Trionyx spinifer*) when kept in water showed very different responses of the heart rate to heating and to cooling (Figure 7.33). During heating the heart rate increased with increasing

FIGURE 7.34 A brooding female python while incubating a clutch of eggs keeps her body temperature above that of the surroundings by strong muscular contractions reminiscent of shivering in mammals. The diagonal line indicates equality between the snake's temperature and air temperature. [Vinegar et al. 1970]



body temperature, and during cooling the heart rate dropped rapidly to very low values, thus reducing circulation and retarding heat loss (Smith et al. 1981).

Many reptiles habitually bask in the sun. Both tortoises and snakes, and even the most aquatic reptiles, crocodiles, can often be seen sunning themselves at the edge of the water.

Internal heat production (i.e., metabolic rate) can also be used to attain a high body temperature. It has been reported that some female snakes maintain a high body temperature while incubating their eggs. This has been observed in the New York Zoological Park, where a 2.7-m long female python started incubating a clutch of 23 eggs. She coiled herself around the eggs, and temperatures were measured with thermocouples placed between the tightly appressed coils of the snake. As the air temperature was lowered, the animal increased her rate of oxygen consumption and kept her body temperature at 4 to 5°C above the air (Figure 7.34).

The increase in oxygen consumption of the brooding snake seemed to be caused by strong contractions of the body musculature, reminiscent of the shivering of mammals. At 25.5°C the oxygen consumption was 9.3 times higher than during the nonbrooding period. When the temperature was decreased further to 21°C, the animal seemed unable to increase her metabolic rate further, for her temperature fell and there was a drop in the oxygen consumption. After 30 days of incubation the animal had decreased in weight from 14.3 kg to 10.3 kg, a decrease of nearly 30%, supposedly attributable to the fuel consumption needed to keep warm (Hutchison et al. 1966).

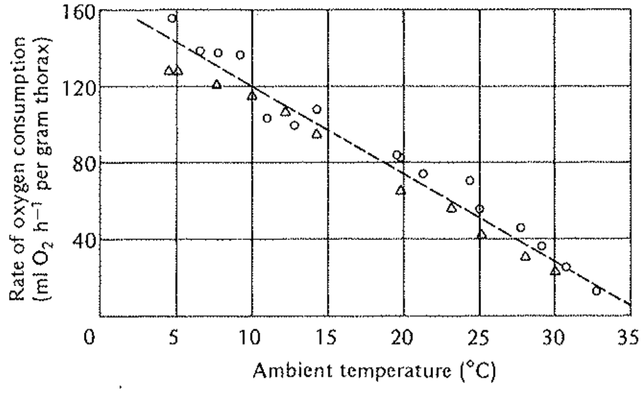
Flying insects

Most insects become increasingly sluggish and are unable to fly at low temperatures. Some insects, however, can warm up their flight muscles and be active in quite cold air. The flight muscles are located in the thorax and can produce large amounts of heat by a process similar to shivering in vertebrates. Heating of the flight muscles before takeoff occurs mainly in large insects such as locusts, large moths, butterflies, and bumblebees, and also in wasps and bees that are strong and rapid fliers.

A bumblebee must have a thoracic temperature of at least 29 to 30°C before it is able to fly (Heinrich 1972). If the flight muscles are at lower temperature, their speed of contraction is too slow to support flight, which requires a wing-beat frequency of 130 Hz.

The maintenance of a high thoracic temperature enables the bumblebee to forage for nectar at temperatures as low as 5°C. However, remaining warm on a continuous basis is not feasible unless the bee can find food at a rate at least equal to the rate at which fuel is consumed. A bumblebee weighing 0.5 g may have an oxygen consumption of 50 ml

FIGURE 7.35 The rate of oxygen consumption of two bumblebee queens (*Bombus vosnesenskii*) during periods of uninterrupted incubation. The weight of the thorax, which contains the muscles that produce essentially all the heat, is about 0.2 g; the total body weight of a queen may be around 0.5 g, but varies with the contents of the honey stomach. [Heinrich 1974]

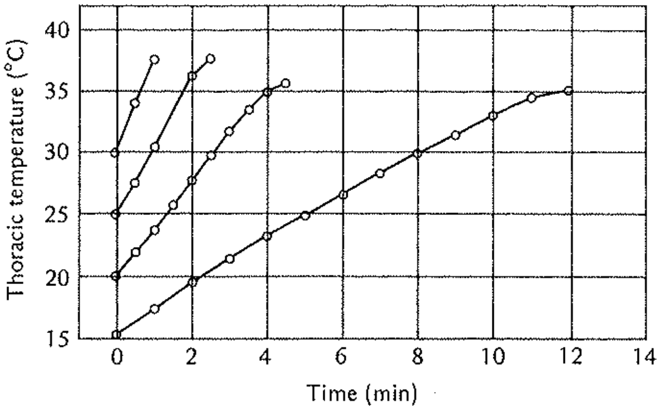


O_2 per hour (100 liter O_2 kg^{-1} h^{-1}), which corresponds to the use of 60 mg sugar. This investment in fuel may be worthwhile, for at low temperature the competition for the available food supply is reduced because many other nectar-feeding insects are inactive.

The advantage of a small body size, relative to mammals, is not only that warmup can be achieved rapidly, but also that cooling is rapid. Therefore, the body temperature can easily be adjusted to the energy supplies, and the insect can choose to keep warm only when the energy supplies warrant the expense; in other words, it can be utterly opportunistic about being "warm-blooded."

The thermoregulation in bumblebees extends to the incubation of their brood. An incubating queen keeps her abdomen in close contact with the brood clump and regulates her abdominal temperature at 31 to 36°C, which helps maintain the brood at a relatively high temperature. Even at an air temperature as low as 5°C, the brood can be maintained nearly 20 °C higher by the incubating queen. The oxygen consumption of the incubating queen increases linearly at lower temperature, so that her

FIGURE 7.36 The increase in thoracic temperature of the sphinx moth (*Manduca sexta*) proceeds more rapidly when the initial temperature of the animal is higher. [Heinrich and Bartholomew 1971]



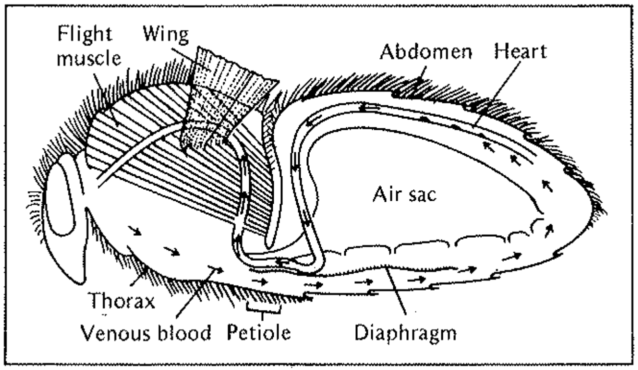
metabolic curve (Figure 7.35) resembles those we saw for mammals (e.g., Figure 7.7).

Another insect that has been carefully studied in regard to thermoregulation is the sphinx moth, *Manduca sexta* (whose larva is the tobacco hornworm). Sphinx moths are fairly large and weigh between 2 and 3 g. They feed on nectar while hovering in front of a flower, much like a hummingbird. Because they are nocturnal, they often fly at quite low air temperatures, and flight would be impossible unless they could heat themselves.

Hovering flight requires a muscle temperature of at least 35 °C; nevertheless, sphinx moths can fly and feed when the air temperature is as low as 10 °C. This is possible through preflight heating of the thorax. The lower the initial temperature, the lower the rate of heating (Figure 7.36). During the warmup the animal seems to shiver as the wings vibrate lightly.

The heat is generated by contraction of the wing muscles, and the reason that the wings do not flap is that the muscles for upstroke and downstroke contract simultaneously, rather than alternately as in flight. We might expect that the warmup should progress faster and faster as the temperature of the moth increases, for more heat can be produced at higher temperatures. However, as the insect be-

FIGURE 7.37 The flight muscles of honeybees and bumblebees are supplied with blood from the heart, which is located in the abdomen. A countercurrent arrangement in the petiole serves to retain heat in the flight muscles. When, at high air temperature, the bee needs to dissipate excess heat, the countercurrent arrangement is circumvented by alternating the flows in the artery and in the returning venous channel, thus eliminating countercurrent exchange. [Heinrich 1976]



comes warmer, the rate of heat loss to the air also increases, and for this reason the temperature curves in Figure 7.36 appear as more or less straight lines.

The thorax of the moth is covered by long, furry scales. This helps retain the generated heat in the thorax during the warmup. In free flight the sphinx moth maintains its thoracic temperature at about 40 to 41 °C over a wide range of air temperatures, but because of the high rate of heat production in the flight muscles, it must be able to increase the rate of heat loss to keep the temperature from rising even higher. This is achieved through an increased circulation of blood between the thorax and the abdomen.

Heat loss from the abdomen is facilitated by its larger surface and a smaller amount of surface insulation. If we tie off the large dorsal blood vessel leading from the heart (located in the abdomen) so that the flight muscles cannot be cooled, the moth rapidly overheats and cannot continue to fly even at an air temperature of 23 °C. The cause could, of course, be that the blood supply to the muscles is necessary for supplying fuel. However, a simple experiment can answer this objection. If the scales are removed from the thorax of a moth with ligated circulation, the heat loss is sufficiently improved to enable the animal to fly again (Heinrich 1970).

Bumblebees also depend on cooling from the abdomen when they need to dump excess heat from the flight muscles in the thorax. At low air temperatures, however, the problem is to retain heat, and this is aided by a countercurrent exchange system (Figure 7.37). The main blood vessel to the thorax passes from the heart (in the abdomen) through the thin stem, the petiole, that connects to the thorax. Blood that returns from the flight muscles to the abdomen flows through the petiole in the opposite direction in a closely apposed space. This arrangement forms a typical countercurrent heat exchanger, which serves to retain heat in the thorax.

At higher air temperatures, heat must be dissipated rather than retained. The thin petiole has no alternate route for the returning blood to bypass the exchanger; the blood must run in the one available pathway. The only way to block heat exchange is therefore to separate the two flows in time, so that the flow alternates between arterial and venous blood.

The respiratory movements help in the following way. When the abdomen distends during inhalation, venous blood is pulled into the abdomen, and when the bee exhales, the abdomen is compressed and arterial blood is pushed into the thorax. The increased arterial pressure causes the artery in the petiole to expand, flattening and blocking the venous channel while the arterial blood flows, thus blocking the heat exchanger (Heinrich 1976).

Honeybees regulate not only their own individual temperature, but that of the entire colony as well. In summer the temperature of a beehive is maintained at about 35 °C and fluctuates very little. This provides the colony with an optimum temperature for development of the brood. Rapid reproduction permits a fast buildup of the population during the most favorable season, and an optimal temperature for the brood is therefore ecologically highly desirable.

If the beehive temperature rises above the regulated level, the bees spread droplets of water over the comb, and evaporation is aided by air currents created by a large number of bees fanning their wings. Below 30 °C bees do not usually consume any water, but at higher temperatures their water intake increases enormously as water is used for cooling (Free and Spencer-Booth 1958).

At low outside temperatures the bees cluster together and maintain a temperature within the cluster of about 20 to 30 °C. The temperature at the center of the cluster is the highest, and it appears that the bees at the periphery force their way into the center where it is warmer, thus exposing others to the outside. The core temperature of the cluster is regulated between 18 and 32 °C at outside air temperatures ranging as low as −17 °C. In fact, there is a tendency for the cluster temperature to be higher at the very lowest ambient temperatures. For each 5 °C drop in the outside air temperature, the cluster temperature increases by about 1 °C (Southwick and Mugaas 1971). In this way a cluster of bees behaves much like a single large organism that maintains a well-regulated high temperature at external temperature conditions that would rapidly kill individual bees.

At low air temperatures the oxygen consumption and heat exchange in clusters of bees change with the size of the cluster, similar to what we have seen about body size in mammals. In a study of honey bee clusters between 5 and 1200 g, the specific rate of oxygen consumption (ml O_2 g^{-1} h^{-1}) was related to "body" (cluster) size by the relation:

$$\dot{V}_{O2} = 22.7\, M_b^{-0.48}$$

For mammals the specific rate of oxygen consumption is related to body size by the exponent −0.27. Thus, the advantage for bees to congregate in large clusters in the cold is very substantial indeed, and for very small clusters the demand on fuel is too great to be feasible during winter (Southwick 1985).

We have now discussed the temperature relations of animals, and in this last chapter we have seen how important water can be in maintaining proper temperature conditions. We shall now move on to a more detailed treatment of this important substance and its physiological role.

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