Animal Energetics and Temperature Relations

A nimals require fuel, from which they derive chemical energy to perform work and to maintain their molecular and structural integrity. In Chapters 3 and 15, we noted that animals degrade large, organic compounds in a way that permits the transfer of some of their inherent chemical energy to special "energy-rich" molecules (e.g., ATP), which are used to drive endergonic reactions. Thus, animals eventually convert chemical energy of foodstuff molecules into other forms, such as electrical energy, osmotic energy, and contractile energy. All else being equal, the more effectively an animal species utilizes the energy resources of its environment, the better able it is to compete with other species, and hence the more "fit" it is for survival.

Like all other energy-converting machines, animals are less than 100% efficient in their energy conversions. A large fraction of metabolic energy therefore appears as heat, a low-grade form of energy that results as a by-product of the release of free energy during exergonic reactions (see p. 38) or during the conversion of chemical energy to other biologically useful forms of energy such as muscle contraction. This metabolic heat is akin to the waste heat produced by a gasoline engine in converting chemical energy to mechanical work. In some animals, metabolic heat production is sufficient to raise the temperature of the tissues to levels that significantly enhance the rate of chemical reactions. This heat thus serves the same useful purpose as does the waste heat that warms a gasoline engine to a more efficient temperature. In some instances, however, and especially in hot climates, heat production can create problems of excessive body temperature. In cold climates excessive heat loss can lower body temperature to dangerously low levels at which a further drop in temperature leads to still greater loss of body heat, in a vicious circle of reduced metabolic heat production and more cooling.
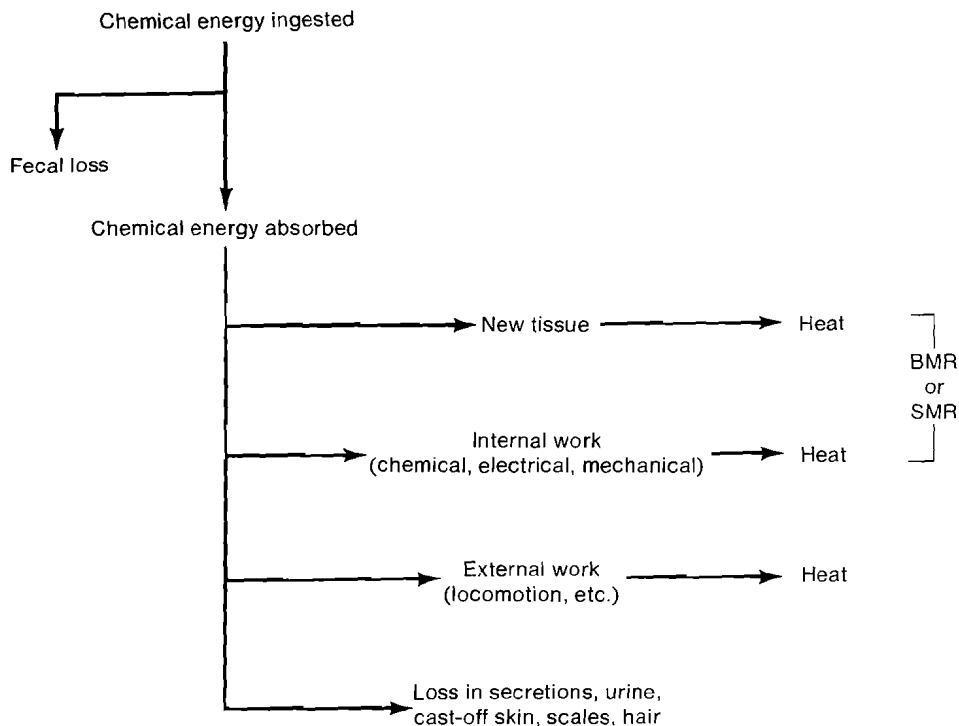
Clearly, the metabolic activity of an animal is closely linked to body temperature. Low body temperatures preclude high metabolic rates because of the temperature dependence of enzymatic reactions, whereas high metabolic rates can lead to overheating and attendant deleterious effects on tissue function. Thus, body temperature is an important parameter in animal function. Some animals elevate their body temperatures continuously above that of the environment, whereas in others body temperature is unregulated or regulated to a lesser extent. Various strategies have evolved to optimize the expenditure or the savings of metabolic energy for various animal life-styles. In this chapter we will consider those factors that influence and are influenced by both metabolic rate and body temperature. In addition, we will consider other aspects of energy metabolism related to body size, locomotion, and temperature regulation.

The Concept of Energy Metabolism

The term *metabolism*, in its broadest sense, embodies the sum total of all the chemical reactions occurring in an organism (see Chapter 3). Metabolic pathways fall into two major categories—*anabolism*, in which simple substances are built up into more complex molecules necessary for the organism, and *catabolism*, in which complex molecules are broken down into simpler ones. Anabolism requires energy and is associated with repair, regeneration, and growth. Although it is difficult to measure anabolic metabolism quantitatively, a positive nitrogen balance (i.e., net incorporation of nitrogen) in an organism is indicative of anabolism. That is, anabolic activity leads to net incorporation through protein synthesis, rather than net loss of nitrogen-containing molecules through excretion. In catabolism, the degradation of complex molecules into simpler ones is accompanied by the release of chemical energy. Some of this energy is stored as high-energy phosphate compounds such as ATP, which are subsequently used to drive cellular activities (see Figure 3-30). Simpler metabolic intermediates such as glucose or lactate serve as energy storage compounds in that they may serve as substrates for additional exergonic reactions (Figure 3-39).

In the absence of external work or storage of chemical energy, all the energy released during metabolic processes appears eventually as heat. This simple fact

Chemical energy ingested

Fecal loss

Chemical energy absorbed

New tissue ⟶ Heat

Internal work
(chemical, electrical, mechanical) ⟶ Heat

BMR
or
SMR

External work
(locomotion, etc.) ⟶ Heat

Loss in secretions, urine,
cast-off skin, scales, hair

16-1 Intake and utilization of chemical energy by an organism. Part of the potential chemical energy ingested is unabsorbed and is degraded by intestinal flora or is passed out in fecal matter. Of the chemical energy absorbed and assimilated in the form of digestion products, some appears directly as heat during exergonic metabolic reactions, while some is either conserved in the anabolic buildup of tissues or utilized for the performance of various kinds of chemical, electrical, or mechanical work. The energy used to synthesize new tissue or produce work within the organism contributes to the basal (BMR) or standard (SMR) metabolic rate.

makes it possible to utilize heat production as an index of *energy metabolism*, providing the organism is in a more-or-less steady state in relation to its environment. The conversion of chemical energy to heat is measured as the *metabolic rate*—heat energy released per unit time. Although heat production is a useful measure of metabolic rate, it is not the only one. More recently, it has been possible to use nuclear magnetic resonance (NMR) to characterize the metabolism of high-energy phosphate groups taking place within the animal body directly.

Measurements of metabolic rates are useful for several reasons. For example, they can be used to calculate the energy requirements of an animal. To survive, an animal must take in as much energy in the form of energy-yielding foodstuff molecules as the total of all the energy that it releases and stores. Measurements of metabolic rate at different ambient (environmental) temperatures will also provide information about the heat-conserving or heat-dissipating mechanisms of an animal. Measurements of metabolic rate during different types of exercise help us understand the energy cost of such activities. How energy-costly, for example, is it simply to stay alive, or to fly, swim, run, or walk a given distance?

The metabolic rate of an animal will, of course, vary with the number and intensity of the activities it performs. These include tissue growth and repair; chem-

ical, osmotic, electrical, and mechanical internal work; external work for locomotion and communication; and loss through secretions, urine, and feces (Figure 16-1). Among the other factors that influence the metabolic rate are environmental temperature, time of day, season of year, age, sex, weight, size, stress, type of food being metabolized, and pregnancy. Consequently, metabolic rates of different animals can be meaningfully compared only under carefully chosen and closely controlled conditions, which we will consider later. First, some essential definitions.

Temperature Classifications of Animals

At first, the thermoregulatory modes of animals were classified according to the stability of body temperatures. When exposed to changing air or water temperatures in the laboratory, *homeotherms* (or *homoiotherms*) can regulate their body temperatures close to a set-point value by producing heat at high rates and by controlling heat production and heat loss (Figure 16-2). In mammals the set point for core body temperature is typically 37° to 38°C, while in birds it is closer to 40°C. Some lower vertebrates and invertebrates can also control their body temperature in this manner, although such control is often limited to periods of activity or rapid growth in these organisms.
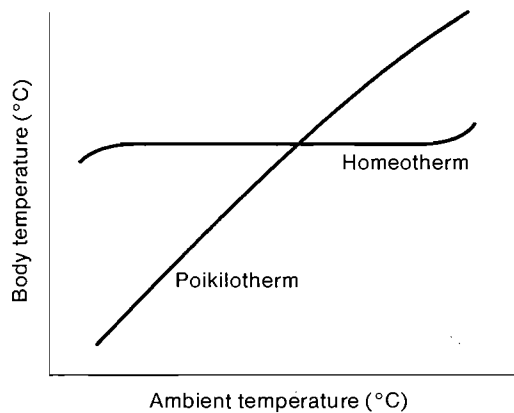
16-2 Generalized relations between body temperature and ambient temperatures in homeotherms and poikilotherms.

Poikilotherms are those animals in which body temperature tends to fluctuate more or less with the ambient temperature when air or water temperatures are varied experimentally. The colloquial terms *warm-blooded* for homeotherms and *cold-blooded* for poikilotherms are unsatisfactory, since many poikilotherms can become quite warm. For example, a locust sustaining flight in the equatorial sun or a lizard exercising at midday in a hot desert may have blood temperatures exceeding those of "hot-blooded" mammals. In brief, then, *homeothermy* and *poikilothermy* are concepts referring to the constancy of body temperature.

All lower vertebrates and invertebrates were at first considered poikilotherms. At the time, all of these animals were considered to lack the high rates of heat production found in birds and mammals. Several difficulties with this dichotomy soon became apparent in the wake of field studies. Some lower vertebrates (e.g., deep-sea fishes) have more stable body temperatures than many higher vertebrates because these fishes live in a stable thermal environment. Many so-called poikilotherms (e.g., lizards) are able to regulate their body temperatures quite well in their natural surroundings by controlling heat exchange with their environment, although this ability is ultimately limited by the availability of heat in the environment. Moreover, numerous birds and mammals were found to allow their body temperature to vary widely, either among various portions of the body or over time.

These inconsistencies necessitated a second classification based on the source of body heat, *endothermic animals* generating it on their own and *ectothermic animals* depending almost entirely on ambient sources of heat. Before proceeding, it should be emphasized that the concepts of homeothermy versus poikilothermy as well as of *endothermy* versus *ectothermy* are idealized extremes, and seldom fully realized conditions. Most organisms are intermediate to these extremes.

Endotherms are animals that generate their own body heat, typically elevating their body temperatures above

ambient temperatures. They produce heat metabolically at high rates, and many have relatively low thermal conductivity (i.e., good insulation), enabling them to conserve heat in spite of a high temperature gradient to the environment. Mammals and birds are examples of animals that regulate their temperatures within relatively narrow limits, and are therefore said to be *homeothermic endotherms*. A few large fish and some flying insects also fit in this category. Because endotherms (all birds and mammals plus many terrestrial lower vertebrates and a number of insects) maintain their body temperatures well above ambient in cold climates, they have access to habitats too cold for most ectotherms. Although most endotherms are well insulated with feathers or fur, they keep warm at considerable metabolic cost, the metabolic rate of an endotherm at rest being at least five times that of an ectotherm of equal size and body temperature.

Ectotherms produce heat metabolically at comparatively low rates. Accordingly, heat exchange with the environment is much more important than metabolic heat production in determining an ectotherm's body temperature. That is, some ectotherms will behave so as to absorb heat from the environment if they have cause to elevate body temperature. Thus, some ectotherms have low rates of metabolic heat production and high *thermal conductivities*—that is, they are poorly insulated. As a result, the heat derived from metabolic processes is quickly lost to the surroundings. On the other hand, the high thermal conductance allows ectotherms to absorb heat readily from their surroundings. If an ectotherm regulates its temperature, as many do, the temperature is adjusted by means other than metabolic heat production. Thus, endothermy and ectothermy are concepts referring primarily to the source of body heat. *Behavioral temperature regulation* is, for the most part, the only type of thermoregulation of which the true ectotherm is capable. Thus, a lizard or a snake may bask in the sun with its body oriented for maximal warming until it achieves a temperature suitable for efficient muscular function. In general, the most effective thermoregulatory action taken by ectotherms is the selection of a suitable *microclimate* in the environment.

Heterotherms are those animals capable of varying degrees of endothermic heat production, but they generally do not regulate body temperature within a narrow range. They may be divided into two groups, regional and temporal heterotherms.

Temporal heterotherms constitute a broad category of animals whose temperatures vary widely over time. Examples are many flying insects, pythons, and some fishes, which can raise their body temperatures well above ambient temperature by virtue of heat generated as a by-product of intense muscular activity. Some insects prepare for flight by exercising their flight muscles for a time to raise their temperatures before takeoff. Monotremes such as *Echidna* are temporal heterotherms (Figure 16-3).
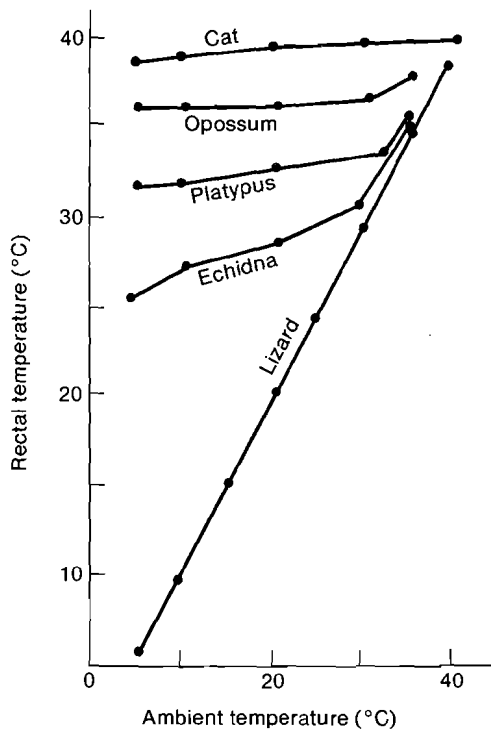
16-3 Relations between body temperature and ambient temperatures in different types of mammals and a lizard. The marsupials and monotremes exhibit temporal heterothermy behavior. [Marshall and Hughes, 1980.]

Certain small mammals and birds, while possessing accurate temperature control mechanisms and thus being basically homeothermic, behave like temporal heterotherms because they allow their body temperatures to undergo daily cyclical fluctuations, having endothermic temperatures during periods of activity and lower temperatures during periods of rest. In hot environments, this flexibility gives certain large animals such as camels the ability to absorb great quantities of heat during the day and to give it off again during the cooler night. Certain tiny endotherms such as hummingbirds must eat frequently to support their high daytime metabolic rate. To avoid running out of energy stores at night when they cannot feed, they enter into a sleeplike torpid state during which they allow the body temperature to drop toward ambient. Even some large endotherms resort to a long winter sleep at reduced body temperature for energy economy (p. 593).

Regional heterotherms are generally poikilotherms, such as certain large teleosts, that can achieve high *core* (i.e., deep-tissue) *temperatures* through muscular activity, while their peripheral tissues and extremities approach the ambient temperature. Examples include mako sharks, tuna, and many flying insects. A special example of regional heterothermy is seen in the scrotums of some mammals, including canines, cattle, and humans, which hold the testes outside the body core so as to keep them at a lower temperature. The scrotum short-

ens in cool air and lengthens as its temperature rises, preventing overheating of the testes, which has a harmful effect on sperm production.

Measurement of Metabolic Rates

The *basal metabolic rate* (*BMR*) is the stable rate of energy metabolism measured in mammals and birds under conditions of minimum environmental and physiological stress, after fasting has temporarily halted digestive and absorptive processes.

Since the body temperature of poikilotherms varies depending on the ambient temperature, and since the minimum metabolic rate varies with the body temperature, it is necessary to measure the equivalent of the BMR at a controlled temperature. For that reason, the *standard metabolic rate* (*SMR*) is defined as an animal's resting and fasting metabolism *at a given body temperature*. Interestingly, the SMR of some ectotherms depends on their previous temperature history, owing to metabolic compensation or thermal acclimation, which is described further on. Both the BMR and the SMR are typically determined with the animal is an unnaturally controlled and quiet state. These measurements are simply baselines against which comparisons can be made both between species and for differing physiological conditions within a given species.

Although the BMR and SMR are useful measurements for baseline comparisons of metabolic rates in different animals, they give little information about the metabolic costs of normal activities carried out by the animals, because the conditions under which the BMR and the SMR are measured differ greatly from natural conditions. The quantity that best describes the metabolic behavior of an animal in its natural state is called its *active metabolic rate*, and represents the average rate of energy utilization as the animal goes about its normal activities. The range of metabolic rates of which an animal is capable is called its *metabolic factorial scope*, or *index of metabolic expansibility*. This is defined as the ratio of the maximum sustained metabolic rate to the BMR or the SMR determined under controlled resting conditions. Factorial scope thus is a dimensionless number (e.g., 10!) that indicates the increase in the amount of energy an animal can expend over and above the amount it expends under resting conditions. Among different animals, it is common for the metabolic rate to increase 10 to 15 times with activity. It should be noted, however, that because sustained activity is powered by aerobic metabolism (see pp. 52–54), this type of measurement defines aerobic scope and does not take into account activity powered briefly by anaerobic processes that build up an oxygen debt (see p. 53).

Metabolic scope has been examined in fishes swimming in flow tanks. Faster swimming can be stimulated by increasing the rate of water flow, and the results indicate that the metabolic scope varies with specimen size. The ratio of active to standard metabolism in salmon, for example, increases from less than 5 in spec-
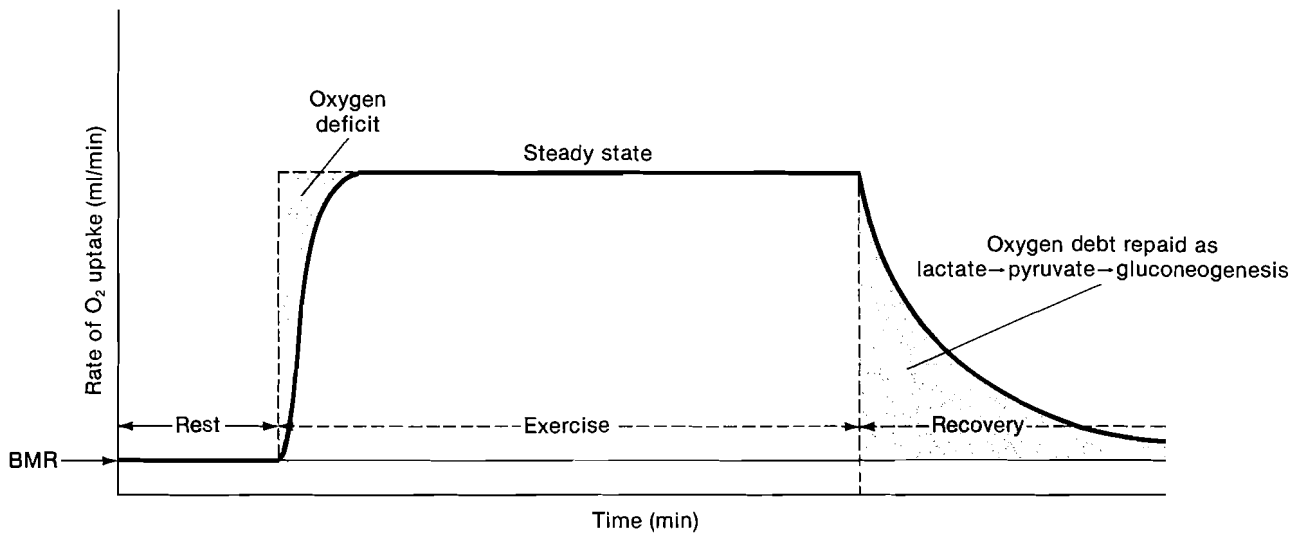
16-4 Following a period of sustained intense activity, active muscle tissue with anaerobic capabilities can build up an "oxygen debt" that is paid off in the form of delayed oxidation of the anaerobic product, lactic acid, that gradually subsides with time. As a result, an elevated metabolic rate continues after cessation of activity, gradually subsiding with time. The initial oxygen deficit represents the utilization of preexisting stores of high-energy phosphagens built up during rest. Replenishment of these stores is included in the repayment of the oxygen debt.

imens weighing 5 g to more than 16 in those weighing 2.5 kg. Flying insects, especially those that sustain high body temperatures during flight, can exhibit ratios of up to 100, probably the highest in the animal kingdom.

Studies on metabolic scope have to contend with certain difficulties. Thus, there may be a significant contribution from anaerobic metabolism (buildup of oxygen debt; see p. 63), especially during short periods of exertion (Figure 16-4). This component may not be detected during short-term measurements, because the aerobic breakdown of anaerobic products can be delayed. For this reason it is best to make measurements of metabolic scope for sustained activity only. White muscles in some vertebrates are specially adapted to develop an oxygen debt through anaerobic metabolism and are therefore particularly suitable for short-term spurts of intense activity. Another practical problem is that any animal's cooperation and motivation are essential for obtaining maximum exertion.

Measurement from Food Intake and Waste Removal

In principle, metabolic rate may be determined from a balance sheet of energy gain and loss. Living organisms obey the laws of energy conservation and transformations that were initially derived for chemical and physical nonliving systems. We could, therefore, in principle determine the metabolic rate of an animal maintaining constant energy content by using the formulation

rate of energy intake

— rate of energy loss per unit time

= metabolic rate

Total energy intake approximates the chemical energy content of ingested food over a given period. Energy loss is the chemical energy that remains in the feces and urine produced by the animal over the same period. The energy content of food and wastes can be obtained from the heat of combustion of these materials in a *bomb calorimeter*. In this method, the material to be tested is dried and placed inside an ignition chamber that in some designs is enveloped in a jacket of water. The material is burned to an ash under its own heat of burning with the aid of oxygen. The heat produced, which is captured in the surrounding water jacket, is determined from the increase in temperature of the known quantity of water.

Not all the energy extracted from food is, however, available for the metabolic needs of the animal. A variable fraction, depending on the type of food, is used up in the process of assimilation, and a correction for this fraction must be made in measurements of energy intake. Measurement errors also occur because (1) energy can be obtained during the period of measurement from an increased utilization of an animal's tissue reserves, and (2) some fraction of the organism's food is generally degraded by microorganisms in the gut. Thus, the balance-sheet approach to energy metabolism not only is cumbersome but also must contend with variables that are difficult to control. Modern studies on energy metabolism generally use the more direct approaches discussed next.

Direct Calorimetry

When no physical work is being performed and no new molecules are being synthesized, all the chemical energy released by an animal in carrying out its metabolic
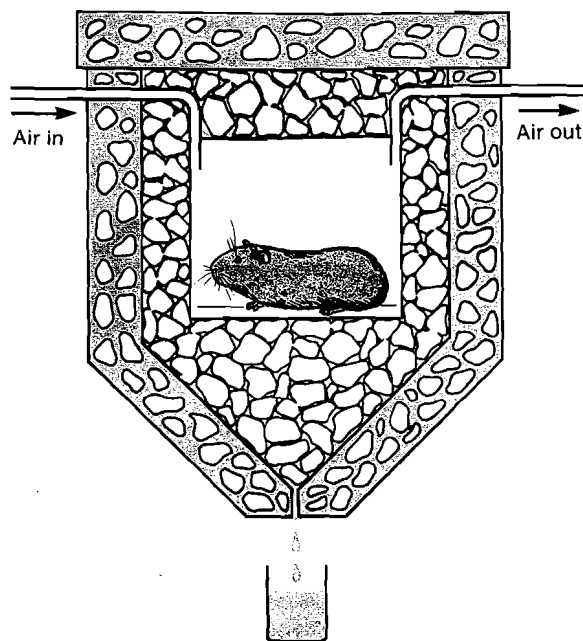
16-5 Lavoisier's ice-jacket calorimeter. The animal's heat production was determined from the quantity of water melted from ice, since 80 kcal of heat melts 1 kg of ice. [Kleiber, 1961.]

functions appears finally as heat. According to *Hess's law* (1840), the total energy released in the breakdown of a fuel to a given set of end products is always the same irrespective of the intermediate chemical steps or pathways utilized. The metabolic rate of an organism is therefore effectively determined by measuring the amount of energy released as heat over a given period. Such measurements are made in a calorimeter, and the method is called *direct calorimetry*. The animal is placed in a well-insulated chamber, and the heat lost by the animal is determined from the rise in temperature of a known mass of water used to trap that heat. The earliest and simplest calorimeter was that devised in the 1780s by Antoine Lavoisier and Pierre de Laplace, in which the heat given off by the animal melted ice packed around the chamber (Figure 16-5). This heat

loss was calculated from the mass of collected water and the latent heat of melting ice. Figure 16-6 shows the essential elements of a modern calorimeter. Water flows through coiled copper pipes in the measuring chamber. The total heat lost by the subject is the sum of the heat gained by the water plus the latent heat present in the water vapor of the expired air and of evaporated skin moisture. To measure this latent heat, the mass of the water vapor is determined by passing the air through sulfuric acid, which absorbs the water. The energy content of each gram of water absorbed is 0.585 kcal, the latent heat of vaporization of water at 20°C. The results are generally reported in calories or kilocalories per hour (Box 16-1).

Direct calorimetry has been used most often with birds and small mammals that have high metabolic rates. With large animals and small animals having low metabolic rates, the precision of the technique may be inadequate. Another disadvantage of direct calorimetry is that the behavior (and therefore metabolism) of the animal is unavoidably altered because of the restrictions imposed by the conditions of the measurement. Though simple in principle, direct calorimetry is rather cumbersome in practice.

Indirect Calorimetry

Indirect calorimetry depends on the measurement of some factor(s) other than heat production related to energy utilization. Oxygen uptake and carbon dioxide production (moles per hour) are the factors commonly used. The energy contained in food molecules becomes available for use by an animal when those molecules or their products are subjected to oxidation, as described in Chapter 3. In aerobic oxidation, the amount of heat produced is related to the quantity of oxygen consumed. *Respirometry* is the measurement of an animal's respiratory exchange. In closed system respirometry, the animal is confined to a closed chamber in which the amount of oxygen consumed and carbon dioxide produced is monitored (Figure 16-6). Oxygen consumption is revealed by serial determinations of the decreasing concentration of oxygen dissolved in the

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Box 16-1   *Energy Units*

The most commonly used unit of measurement of heat is the *calorie* (*cal*), which is defined as the quantity of heat required to raise the temperature of 1 g of water 1°C. This quantity varies slightly with temperature, and so the calorie is more precisely the amount of heat required to raise the temperature of 1 g of water from 14.5° to 15.5°C. A more practical unit is the *kilocalorie* (1 kcal = 1000 cal). The use of calorie and kilocalorie has persisted largely because of their familiarity. However, according to the International System of Units (SI), heat is defined in terms of work, and the unit

of measurement is the *joule* (*J*), the more practical unit being the *kilojoule* (1 kJ = 1000 J). Thus, 1 cal = 4.184 J; 1 kcal = 4.184 kJ. If we assume a respiratory quotient (RQ) of 0.79, which is a typical figure, 1 L of oxygen used in the oxidation of substrate will release 4.8 kcal, or 20.1 kJ, of energy.

Power is energy expended per unit time and is given in *watts* (*W*), with 1 W = 1 J/s. Conversion tables are given in Appendix 3.
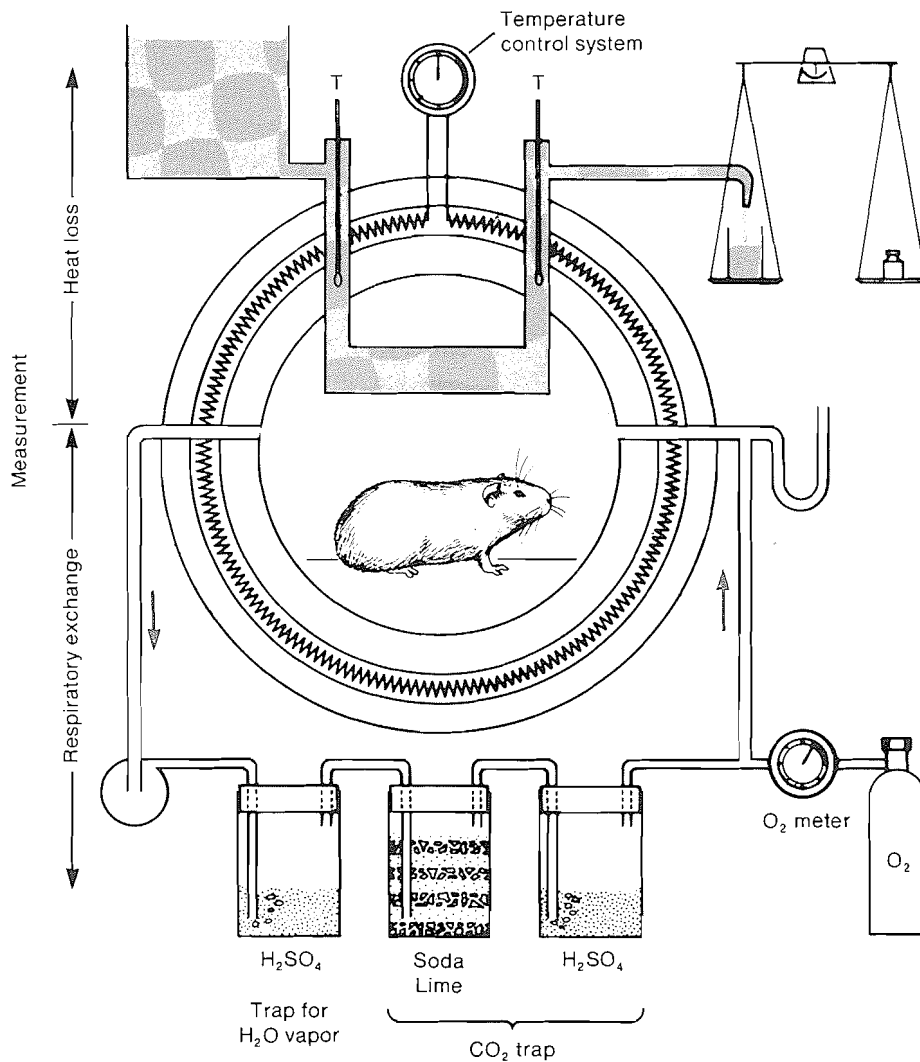
16-6   Atwater–Rosa respiration calorimeter. The animal is confined to an insulated chamber that is kept at a constant temperature. The heat produced by the animal is determined from the heat absorbed by the coolant water (top). T = thermometers. Respiratory exchange is determined by measuring CO_2 and O_2. [Kleiber, 1961.]

water contained in the chamber. These measurements can be obtained very conveniently with the aid of an oxygen electrode and the appropriate electronic circuitry. The partial pressure of oxygen dissolved in the water determines the signal produced in the electrode. In air-breathing animals, O_2 can be measured in the gaseous phase by a mass spectrometer or an electrochemical cell. CO_2 is generally measured with an infrared device. These methods of gas analysis allow mass-flow analytical techniques in which the flow of gas into and out of a chamber is monitored, and the difference in concentrations is used to calculate respiratory exchange. Open system respirometry is also carried out on animals fitted with breathing masks, a method especially useful in wind-tunnel tests of flying animals, because mass air flow would make inflow–outflow comparisons of O_2 and CO_2 inaccurate.

The determination of metabolic rate from O_2 consumption rests on two important assumptions. First, the relevant chemical reactions are assumed to be aerobic. This assumption usually holds for most animals at rest, because energy available from anaerobic reactions is relatively minor except during vigorous activity. However, anaerobiosis is important in animals that live in oxygen-poor environments, as do gut parasites and invertebrates that dwell in deep lake-bottom muds. Oxygen consumption would, of course, be an unreliable index of metabolic rate in such animals. Second, the amount of heat produced (i.e., energy released) when a given volume of oxygen is consumed is assumed to be constant irrespective of the metabolic substrate. This assumption is not precisely true—more heat is produced when 1 L of O_2 is used in the breakdown of carbohydrates than when fats or proteins are the sub-

TABLE 16-1 Heat production and respiratory quotient for the three major foodstuff types.

	Heat production (kcal)			RQ
	Per gram of foodstuff	Per liter of O_2 consumed	Per liter of CO_2 produced	$\dfrac{\text{Liter } CO_2}{\text{Liter } O_2}$
Carbohydrates	4.1	5.05	5.05	1.00
Fats	9.3	4.74	6.67	0.71
Proteins (to urea)	4.2	4.46	5.57	0.80

strate. However, the error involved in this assumption is no greater than about 10%. Unfortunately, it is generally difficult to identify the substrate(s) being oxidized with any precision in correcting for differences in caloric yield.
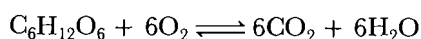
Respiratory Quotient

To translate the amount of oxygen consumed in the oxidation of food into equivalent heat production, we must know the relative amounts of carbon and hydrogen oxidized. The oxidation of hydrogen atoms is hard to determine, however, since metabolic water (i.e., that produced by oxidation of hydrogen atoms available in foodstuffs), together with other water, is lost in the urine and from a variety of body surfaces at a rate that is irregular and determined by unrelated factors such as osmotic stress. It is more practical to measure, along with the O_2 consumed, the amount of carbon converted to CO_2, as explained earlier. The ratio of the volume of CO_2 expired to the volume of O_2 removed from the inspired air within a given time is called the *respiratory quotient (RQ)*:

$$RQ = \frac{\text{rate of } CO_2 \text{ production}}{\text{rate of } O_2 \text{ consumption}} \quad (16\text{-}1)$$

Under resting, steady-state conditions, the RQ is characteristic of the type of foodstuff catabolized—carbohydrate, fat, or protein (Table 16-1)—reflecting the proportions of carbon and hydrogen in the food molecules. The following examples illustrate how the RQ of the major food types may be calculated from a formulation of their oxidation reactions.
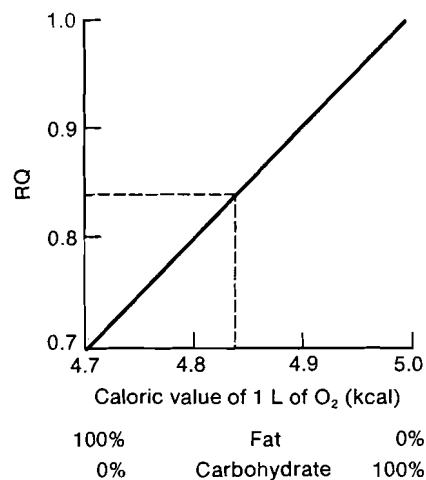
Carbohydrates

The general formula of carbohydrates is $(CH_2O)_n$. During complete oxidation of a carbohydrate, respiratory oxygen is utilized *in effect* only to oxidize the carbon, forming CO_2. Each mole of a carbohydrate upon complete oxidation produces n mol of both H_2O and CO_2 and consumes n mol of O_2. The RQ for carbohydrate oxidation is thus 1. The overall catabolism of glucose, for example, may be formulated as

$$C_6H_{12}O_6 + 6O_2 \rightleftharpoons 6CO_2 + 6H_2O$$

$$RQ = \frac{6 \text{ volumes of } CO_2}{6 \text{ volumes of } O_2}$$

$$= 1.0$$

Caloric value of 1 L of O₂ (kcal)

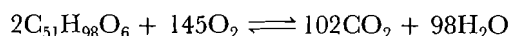| 100%	Fat	0%
0%	Carbohydrate	100%

16-7 Relation between respiratory quotient and caloric value of oxygen. [Hardy, 1979.]

Fats

The RQ characteristic of the oxidation of a fat such as tripalmitin may be calculated as follows:

$$2C_{51}H_{98}O_6 + 145O_2 \rightleftharpoons 102CO_2 + 98H_2O$$

$$RQ = \frac{102 \text{ volumes of } CO_2}{145 \text{ volumes of } O_2}$$

$$= 0.703$$

Since different fats contain different ratios of carbon, hydrogen, and oxygen, they differ slightly in their RQs.

The relations between the caloric value of 1 L of O_2 consumed and the proportions of carbohydrate oxidized are illustrated in Figure 16-7. As the proportion of fat decreases from 100 to 0% and is replaced by carbohydrate, the RQ rises from 0.7 to 1.0, and the caloric value of 1 L of O_2 increases from 4.7 to 5.0 kcal.

Proteins

The RQ characteristic of protein catabolism presents a special problem because proteins are not completely broken down during oxidative metabolism. Some of the oxygen and carbon of the constituent amino acid residues remain combined with nitrogen and are excreted as nitrogenous wastes in urine and feces. In mammals, the excreted end product is urea, $(NH_2)_2CO$, and in birds it is primarily uric acid, $C_5H_4N_4O_2$. To

obtain the RQ, it is therefore necessary to know the amount of ingested protein as well as the amount and kind of nitrogenous wastes excreted. The carbon and hydrogen oxidized during the catabolism of protein typically require 96.7 volumes of O_2 for the production of 77.5 volumes of CO_2, giving an RQ of about 0.80.

It is routinely assumed in making deductions from RQ that (1) the only substances metabolized are carbohydrates, fats, and proteins; (2) no synthesis takes place alongside breakdown; and (3) the amount of CO_2 exhaled in a given time equals the CO_2 produced by the tissues in that interval. These assumptions are not strictly true, so caution must be exercised in using RQ values at rest and in postabsorptive (fasting) states. Under such conditions, protein utilization is negligible, and the animal is considered to be metabolizing only fat and carbohydrate. In Table 16-1 it is seen that the oxidation of 1 g of mixed carbohydrate releases about 4.1 kcal as heat. Further, when 1 L of O_2 is used to oxidize carbohydrate, 5.05 kcal is obtained; the value for fats is 4.75 kcal and for protein (to urea), 4.46 kcal. A fasting aerobic animal presumed to be metabolizing only carbohydrates and fats produces between 4.75 and 5.05 kcal of heat for every liter of oxygen consumed, depending on the proportion of fat to carbohydrate metabolized.

Specific Dynamic Action

A marked increase in metabolism accompanies the processes of digestion and assimilation of food. About 1 h after a meal is eaten, the metabolic rate increases, reaching a peak some 3 h later and remaining above the basal value for several hours in birds and mammals, and up to days in lower vertebrates. Thus, following food intake, an animal's oxygen consumption and heat production increase independently of other activities. Max Rubner reported in 1885 that this increase in heat production differed for each of the classes of foodstuffs, and he gave it the rather awkward name *specific dynamic action* (*SDA*). Its mechanism is not clearly understood, but apparently the work of digestion (and the concomitant increase in metabolism of the tissues of the gastrointestinal tract) is responsible for only a small part of the elevated metabolism. A more likely explanation for this rise in metabolic rate may be that certain organs, such as the liver, expend extra energy to prepare the products of digestion for entry into metabolic pathways. The extra energy consumed by such processes is lost as heat. The magnitude of the increased metabolic rate ranges from 5 to 10% of total energy of ingested carbohydrates and fats and from 25 to 30% for proteins. It is quite important, therefore, that basal metabolism be measured during the postabsorptive state so as to minimize any contribution of the SDA.

Energy Storage

Most animals cannot strike a moment-to-moment balance between food intake and energy expenditure, because they cannot ingest food steadily as they continually expend metabolic energy. As food is taken in, it exceeds immediate energy requirements, and the excess is stored for later use, primarily as fats and carbohydrates. Protein is not an ideal storage material for energy reserves because nitrogen is a relatively scarce commodity and is generally the limiting factor in growth and reproduction; so it would be wasteful to tie up valuable nitrogen in energy reserves. Fat is the most efficient form of energy storage, because oxidation of fat yields 9.56 kcal/g, nearly twice the yield per gram for carbohydrate or protein. This efficiency is of great importance in animals such as migrating birds, in which economy of weight and volume is of the essence. Not only is the energy yield per gram of carbohydrate lower than that of fats, but carbohydrates are stored in a bulky hydrated form, with as much as 4 to 5 g of water required per gram of carbohydrate. Nonetheless, some carbohydrates are important in energy storage. Glycogen, a branched, starchlike carbohydrate polymer, is stored as granules in skeletal muscle fibers and liver cells of vertebrates. Muscle glycogen is converted to glucose for oxidation within the muscle cells during intense activity, and liver glycogen is utilized to maintain blood glucose levels. Glycogen is broken down directly into glucose 6-phosphate, providing fuel for carbohydrate metabolism more directly than does fat.

Body Size and Metabolic Rate

An important physical characteristic of an animal is its size. Increased size introduces changes that are not always simple and proportional. For example, doubling the height of a terrestrial animal while retaining the same body proportions is accompanied by an increase in surface area of four times and an increase in mass of eight times. Certain consequences for the functional anatomy and physiology of the animal are immediately evident. You can carry out a thought experiment by imagining a mouse scaled up to the size of an elephant while retaining its mouselike body proportions. Clearly, the imaginary enlarged mouse has different proportions than the elephant, and its relatively slender legs would probably collapse under the weight of the very massive body. After all, for each doubling in height of the imaginary mouse, the mass increases by a factor of 8 (height cubed) while the cross-sectional area of leg bone increases by a factor of only 4 (height squared).

Similar effects of increased scale are highly significant in many aspects of physiology, such as in metabolic rate. Take, for example, the respiratory requirements faced by a submerged water shrew (which is very tiny) as compared to a submerged whale. Although both whales and water shrews normally submerge, a whale can remain under water, holding its breath, far longer than a shrew. This observation illustrates the general principle that small animals must respire at higher rates than large animals. An inverse relationship, in fact, exists between the rate of O_2 consumption per gram of
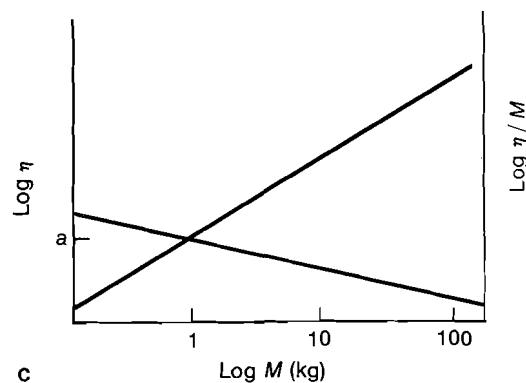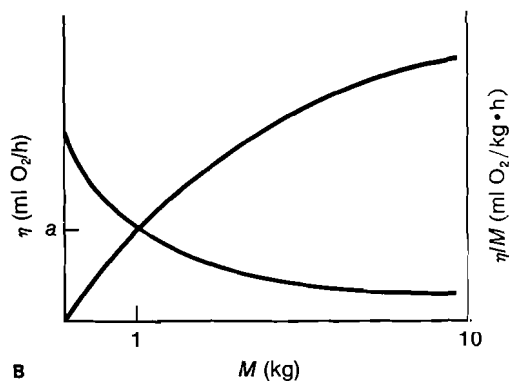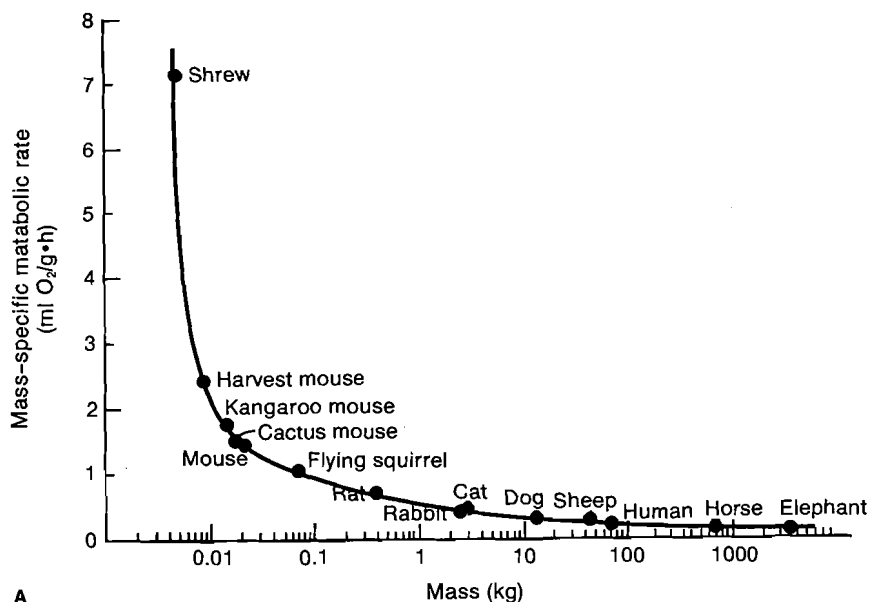
16-8 Relations between body mass (*M*) and metabolic rate at rest (*η*) in mammals. (**A**) The mouse-to-elephant curve, with metabolic intensity given as O_2 consumption per unit mass plotted against body mass. Note the logarithmic scale of body mass. [Schmidt-Nielsen, 1975.] (**B**) Generalized relations between overall metabolic rate and body mass (black curve) and between metabolic intensity and body mass (colored curve). (**C**) Log–log plots of B. The *η* and log *η* plots in B and C cross at *M* = 1 kg. The value of *η* at *M* = 1 kg equals the constant *a*.

body mass and the total mass of the animal. Thus, a 100 g mammal will consume far more than 0.1 the energy per unit mass per unit time than is consumed per unit mass per unit time by a 1000 g mammal. The nonproportionality that exists for BMRs of mammals ranging from very small to very large is illustrated by the well-known "mouse-to-elephant" curve (Table 16-2; Figure 16-8A). A similar relation also holds for other vertebrate groups. Thus, metabolic rate has been found to be a power function of body mass as described by the simple relation

$$\eta = aM^b \qquad (16\text{-}2)$$

in which *η* is the BMR or SMR, *M* is the body mass, *a* is a proportionality coefficient that differs in different species, and *b* is an empirically determined exponent that expresses the rate of change of *η* with change in body mass.

Mass-specific metabolic rate, η/M, also termed *metabolic intensity,* is the metabolic rate of a unit mass of tissue (i.e., milliliters of O_2 consumed per kilogram per hour, ml O_2/kg · h). It is determined by dividing both sides of Equation 16-2 by *M*:

$$\frac{\eta}{M} = \frac{aM^b}{M} = aM^{(b-1)} \qquad (16\text{-}3)$$

This relation is shown in color in Figure 16-8B. To work with straight-line rather than curved plots, it is useful to use a logarithmic form of Equations 16-2 and 16-3. Thus, Equation 16-2 becomes

$$\log \eta = \log a + b(\log M) \qquad (16\text{-}4)$$

and Equation 16-3 becomes

$$\log \frac{\eta}{M} = \log a + (b - 1) \log M \qquad (16\text{-}5)$$

**TABLE 16-2** Oxygen consumption in mammals of various body sizes.

Animal	Body mass (g)	Total O_2 consumption (ml/h)	O_2 consumption per gram (ml/g · h)*
Shrew	4.8	35.5	7.40
Harvest mouse	9.0	22.5	1.50
Kangaroo mouse	15.2	27.3	1.80
Mouse	25	41.0	1.65
Ground squirrel	96	98.8	1.03
Rat	290	250	0.87
Cat	2,500	1,700	0.68
Dog	11,700	3,870	0.33
Sheep	42,700	9,590	0.22
Human	70,000	14,760	0.21
Horse	650,000	71,100	0.11
Elephant	3,833,000	268,000	0.07

*The figures in this column are proportional to metabolic intensity.

Source: Schmidt-Nielsen, 1975.

These are plotted in Figure 16-8C. An important principle illustrated in these hypothetical plots and developed in the following paragraphs is evident in comparing the whole-animal metabolic rate (black plots) and the mass-specific metabolic rate (colored plots). The overall metabolic rate obviously rises with increasing body mass, whereas the mass-specific met-

abolic rate (metabolic rate of a unit mass of tissue) decreases with increasing body mass. This is the point of the mouse-to-elephant plot in Figure 16-8A.

In a large sample of vertebrate species, the value of the exponent *b* lies close to 0.75. This also holds true for invertebrates, and even for various unicellular species (Figure 16-9). An exponential relationship between body size and metabolic rate has attracted the attention of physiologists since it was first recognized over a century ago, and a rational "explanation" for the logarithmic relation between body mass and metabolism has been earnestly sought. An attractive theory was the *surface hypothesis* first proposed by Max Rubner in 1883. He reasoned that the metabolic rate of endotherms should be proportional to body surface area because the rate of heat transfer between two compartments (i.e., warm animal body and cool environment) is proportional, all else being equal, to their area of mutual contact (Box 16-2). The surface area of an object of given density and *isometric shape* (i.e., unvarying proportions) varies as the 0.67 (or 2/3) power of its mass, since mass increases as the cube of linear dimension, whereas surface area increases only as the square. As noted, this relationship holds true for a series of animals of different mass only if body proportions remain constant. This provision is generally satisfied only by adult individuals of different size within a species, since these tend to obey the principle of *isometry*, namely, proportionality of shape regardless of size. In this case it follows, of course, that the surface area must vary as the
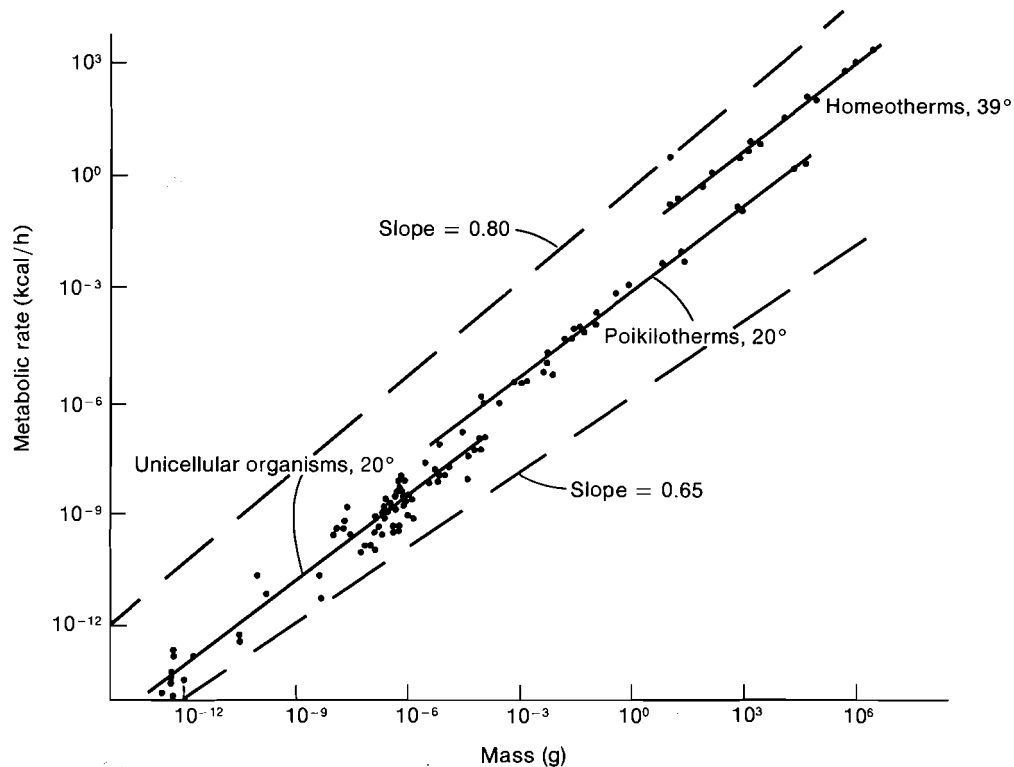
16-9 Minimal metabolic rates of unicellular organisms, poikilotherms, and homeotherms are related to body weight by similar exponents. The solid lines all represent exponents of 0.75. The vertical position of each group on the graph is related to the coefficient *a* in Equation 16-2. [Hemmingsen, 1969.]
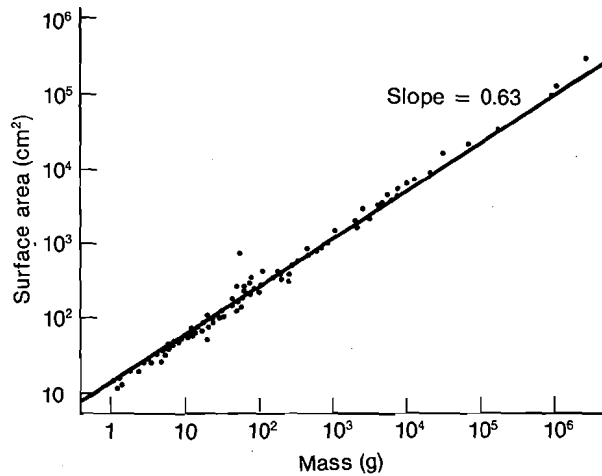
16-10 Body surface area of mammals ranging from mice to whales plotted against body mass. The slope of the line gives an exponent of 0.63 rather than the 0.67 predicted by isometric (i.e., proportional) scaling. [McMahon, 1973.] The allometric (i.e., disproportional) scaling arises from the fact that with increasing species size there is a progressive relative thickening of body parts (i.e., bones, muscles, etc.), so that a large species has relatively less surface area than would be predicted from isometric scaling. Recall the relative proportions of mouse and elephant.

0.67 power of body mass. However, isometry is *not* followed in individuals of different size belonging to related but *different* species. Instead, these tend to follow the principle of *allometry*, namely, systematic changes in body proportions with increasing species size. An example of allometry was alluded to earlier when we compared the proportions of an elephant with those of a mouse. Thus, in comparing surface-to-mass relations in mammals of different species ranging from mice to elephants, surface areas were found to be proportional to the 0.63 power of body mass (Figure 16-10).

The surface hypothesis of Rubner gained support over the years from numerous findings that metabolic rate in homeotherms is *approximately* proportional to body surface area. An especially close correlation can be seen in comparing the metabolic rates of adult guinea pigs (all of the same species), which were found to be proportional to body mass raised to the 0.67 power (Figure 16-11A) or, assuming isometry of shape, proportional to the surface area of the individual. It will be recalled that isometry, and hence a 0.67 power relating surface area to body mass, is characteristic of adult individuals of the same species.

The difference in metabolic intensity between large and small homeotherms may indeed be an adaptation to the more rapid loss of heat from a smaller animal due to surface-to-volume relations, the small animal having more surface area per unit mass. However, in spite of the logical attractiveness of the surface hypothesis, serious questions are raised by several contradictory observations. First, when metabolic rates of individuals of *different* species of mammals are plotted against body mass, the exponent relating metabolic rate

to body mass is found to be approximately 0.75 (Figure 16-11B). The 0.75 power relating metabolic rate to body mass was first discovered by Max Kleiber (1932), and is often referred to as *Kleiber's law*. The exponent 0.75 is significantly higher than that predicted by the surface hypothesis, for it will be recalled that the surface area of mammalian individuals taken from various species of differing size is proportional to the body mass raised to the 0.63 power (Figure 16-10). The difference in the exponents 0.63 and 0.75 is statistically significant (Figure 16-11B). Thus, in comparing different species, the differences in metabolic rate clearly are not in harmony with differences in body surface area.

A second important objection against the surface hypothesis (i.e., that differences in metabolic rate are due to differing rates of heat loss through the body surface) arises from the simple fact that the metabolic rates of ectotherms exhibit nearly the same relations to body mass as the metabolic rates of endotherms (Figure 16-9). There is no self-evident reason why the metabolic rate of ectotherms should be causally related through heat loss to body surface area, since relatively little or no metabolic energy is expended to warm an ectotherm above the ambient temperature, since no net heat flux can occur across the surface of an ectotherm that is in temperature equilibrium with its environment.

In any event, the metabolic rate of a gram of tissue from a small animal is higher than that for a larger animal, which holds for both endotherms and ectotherms. The differences in metabolic intensity of animals of differing sizes show a correlation with the number of mitochondria per unit volume of tissue, and the cells of a small mammal contain more mitochondria and mitochondrial enzymes in a given volume of tissue than do the cells of a large mammal (Figure 16-12). Since the mitochondria are the site of oxidative respiration, this correlation comes as no surprise. However, we are still left with the problem of how metabolic intensity is functionally related to body size.

The question why large animals have lower metabolic rates per volume of tissue than small animals, and the functional reasons for the allometric relationships that exist between metabolic rate (as well as other variables) and animal size are considered in an interesting book by McMahon and Bonner (1983). They point out that the *cross-sectional area* rather than the surface area of the body (or rather of its parts) more closely resembles the scaling of metabolic rate to body mass, for the cross-sectional area of any body part in a series of animals of increasing size should be proportional to the 0.75 power of body mass due to allometric principles that require an elephant's leg to be proportionately thicker than a mouse's leg. It will be recalled that metabolic rate bears the same (0.75) power relationship to body mass in a wide range of animals (Figures 16-9 and 16-11B). Perhaps cross-sectional area and metabolic rate are each independently genetically programmed by selective pressure (i.e., evolution) so as to be adaptively optimal in relation to an animal's size.