

# 5 Energy Metabolism

In 1986 explorers set out to reach the North Pole by dogsled from Ellesmere Island at latitude 83° north. Their objective was to make the journey without any resupply along the way and thus to reenact the famous expedition by Admiral Robert Peary in 1909. Each of the modern explorers' sleds was huge—16 feet (5 m) long, and loaded with 1400 pounds (630 kg) of material. Of the two-thirds of a ton on each sled, most was food for people and dogs. Most of the weight of the food, moreover, was required to meet energy needs; if the only food materials that had needed to be hauled were vitamins, minerals, amino acids, and other sources of chemical building blocks for biosynthesis, the pile of food on each sled would have been much smaller. Two people's needs for energy were to be met by the supplies on each sled. The sled needed to be pulled and pushed over numerous ice ridges 20 to 60 feet high on the way to the pole. Even during progress over level ice fields, the way for the sled's runners needed often to be cleared by manpower. A team of sled dogs had to be maintained and fed to do most of the hauling. A trek to the North Pole by dogsled would be immeasurably easier if there were no need for food energy for people and dogs. The need for energy is equally consequential in the natural world. Animals regularly risk their lives to obtain energy, or die because they did not obtain enough.

Why do animals need energy? Even if the answer to that question seems obvious, why do animals need new inputs of energy on a regular basis? Why do people typically need new food energy every day, for instance? Why not take in an adequate amount of energy early in life and simply reuse it, over and over, for the rest of life? These are some of the key questions addressed in this chapter.

Other questions to be discussed are more practical. If you were planning an Arctic expedition, how would you use physiological principles to predict the energy needs of you and your companions? Knowing the energy needs of your team, how would you calculate the amount of food to pack on your sleds? The food on the sleds of the North Pole explorers was rich in fats and oils; the meat they carried, for instance, was a 50:50 mix of ground beef and lard (pure fat). Why did they emphasize lipids?

Energy metabolism, the subject of this chapter, is the sum of the processes by which energy is acquired, transformed, channeled into useful functions, and dissipated. It consists of two subsets of processes mentioned in Chapter 2: *catabolic processes* that break down organic molecules to release energy and *anabolic processes* that use energy to construct molecules.

**The burden of food** A trek to the North Pole from the nearest land requires hundreds of pounds of food to be hauled per explorer, to supply energy for the explorers and their dogs.



## Why Animals Need Energy: The Second Law of Thermodynamics

Animals are *organized* or *ordered* systems. As we saw in discussing the dynamic state of body constituents in Chapter 1, the atoms composing an animal's body are routinely exchanged with atoms in the environment. The *organization* of atoms in the body persists, however, even as particular atoms come and go. As this observation suggests, organization is a far more fundamental feature of animals than their material construction (see page 10).

The second law of thermodynamics, one of the greatest achievements of intellectual history, provides fundamental insight into the nature of organized systems. The law applies to isolated systems. An isolated system is a part of the material universe that exchanges nothing—neither matter nor energy—with its surroundings. Animals, you will recognize, are not isolated systems. In fact, true isolated systems are difficult to create even in the highly controlled setting of a physics laboratory. Thus the concept of an isolated system is largely an abstraction. Nonetheless, we can gain insight into animal energetics by analyzing isolated systems. The second law of thermodynamics states that *if an isolated system undergoes internal change, the direction of the change is always toward greater disorder*.

A corollary of the second law is that order can be maintained or increased within a system only if the system is *not* isolated. If “energy” is permitted to enter a system from the outside, order may be maintained or increased within the system. Energy is defined in the field of mechanics to be the capacity to do mechanical work, measured as the product of force and distance. A broader definition that is often more useful for biologists is that *energy is the capacity to increase order*.

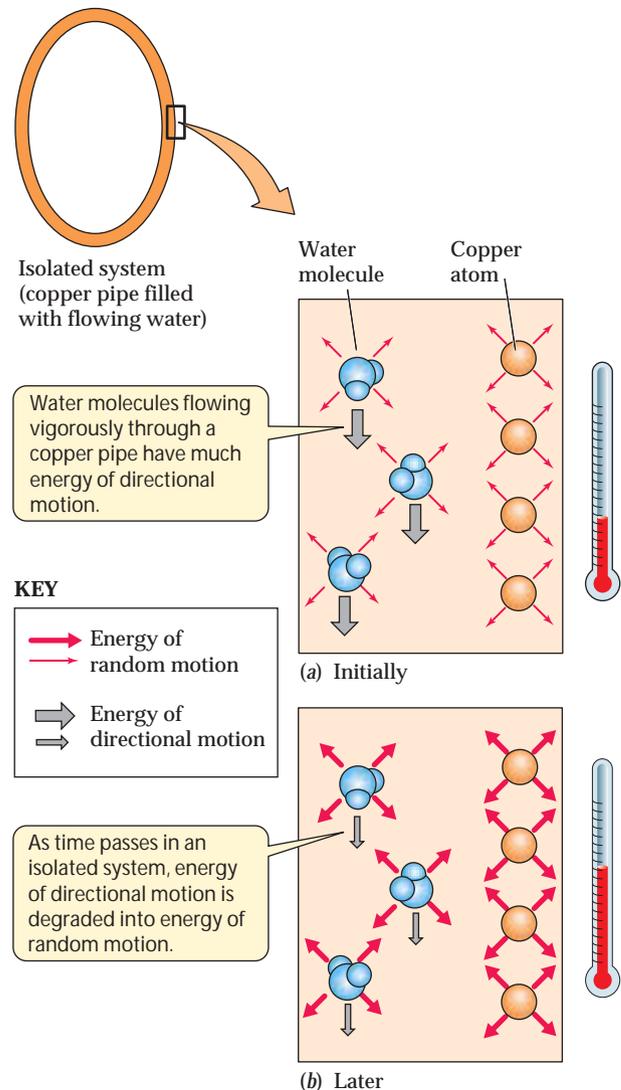
To illustrate the second law of thermodynamics, let's examine an isolated system that consists of a closed loop of copper pipe filled with water, with the water initially flowing around and around in the loop. We need not know how the water started moving; it is enough to know that the loop of pipe has water flowing in it and that the loop exchanges no energy or matter with its surroundings. Focus on the motions of atoms and molecules *on an atomic-molecular scale*. The distribution of atomic-molecular motions in the system we have described is highly nonrandom initially, because each water molecule is moving in an ordered way in its direction of travel around the loop of pipe (Figure 5.1a). In addition, all of the water molecules—and all of the copper atoms in the wall of the pipe—undergo ceaseless random motions on an atomic-molecular scale.<sup>1</sup>

Over time, the energy of *directional* motion of the water molecules is gradually transformed to energy of *random* motion (Figure 5.1b). The energy changes in this manner because when water molecules collide with copper atoms or other water molecules, some of their energy of directional motion is transferred in such a way as to increase the intensity of random motions of the atoms and mole-

cules with which they collide. Consequently, as time passes, the rate of flow of water around the pipe diminishes. The energy of nonrandom flow is translated into random molecular agitation (heat), and the temperature of the system rises. Eventually, the flow of water ceases. At that point all the water molecules and copper atoms in the system display merely random motions, and the original order in the system (the directional motion of water molecules) is entirely degraded to disorder. This inevitable outcome represents the second law of thermodynamics in action.

The only way to keep the water flowing, and thus to maintain the original order in our water-filled loop of pipe, would be to convert the system into an open system, a system that is *not* isolated. If there were a pump in the loop of pipe, and if electricity were provided to the pump from outside, the initial nonrandom state could be sustained indefinitely. That is, an energy input to the system could cre-

<sup>1</sup> Random atomic-molecular motions are a universal property of matter that is at a temperature above absolute zero. In fact, the *temperature* of an object is a measure of the intensity of these motions in an object.



**Figure 5.1 The second law of thermodynamics in action** Energy of directional motion is converted to energy of random motion as time passes from an initial time (a) to a later time (b) in an isolated system. This transformation of energy increases the intensity of the random motions of both the water molecules and the copper atoms in the system, causing the system temperature to rise.

ate order in the system as rapidly as processes within the system tended to diminish order.

In terms of their thermodynamics, animals must function as open systems. Without an energy input, the blood coursing through an animal's circulatory system will slow to a halt, just as the water in the loop of pipe does when there is no energy supplied from outside. Without an energy input, vital molecules in an animal's tissues will become more disorganized, as by spontaneously breaking down; thus eventually they will lose their critical structural and functional properties. Without an energy input, positive and negative ions will distribute themselves randomly across an animal's cell membranes; this randomization of electrical charges, among other things, will make nerve impulses impossible. The second law of thermodynamics dictates that if an animal were required to function as an isolated system, all forms of order within its body would decay. This loss of order would eventually kill the animal because order is essential for life. *Animals require energy from the outside because energy is necessary to create and maintain their essential internal organization.*

## Fundamentals of Animal Energetics

To understand animal energetics more thoroughly, the first step is to recognize that energy exists in different *forms*, and the various forms differ in their significance for animals. We will focus here on four forms of energy of particular importance: chemical energy, electrical energy, mechanical energy, and heat. Chemical energy (chemical-bond energy) is energy liberated or required when atoms are rearranged into new configurations. Animals obtain the energy they need to stay alive by reconfiguring atoms in food molecules, thereby liberating chemical energy. Electrical energy is energy that a system possesses by virtue of the separation of positive and negative electrical charges. All cell membranes possess electrical energy because there is charge separation across them, as we saw in Chapter 3. There are two forms of energy of motion (kinetic energy) that are important for animals. One, mechanical energy, is energy of *organized* motion in which many molecules move simultaneously in the same direction. The motion of a moving arm, or that of circulating blood, provides an example. Heat, often called molecular kinetic energy, is the energy of *random atomic-molecular* motion. Heat is the energy that matter possesses by virtue of the ceaseless, random motions of all the atoms and molecules of which it is composed.<sup>2</sup>

### The forms of energy vary in their capacity for physiological work

Although, by definition, all forms of energy are capable of doing work in one context or another, all forms of energy are *not equally* capable of doing physiological work in animals. Physiological work is any process carried out by an animal that increases order. For example, an animal does physiological work when it synthesizes

macromolecules such as proteins, generates electrical or chemical gradients by actively transporting solutes across cell membranes, or contracts muscles to move materials inside or outside its body (or set its whole body in motion).

How do the forms of energy that we have mentioned—chemical energy, electrical energy, mechanical energy, and heat—differ in their ability to do physiological work? Animals can use chemical energy (directly or indirectly) to do *all* forms of physiological work; hence, for animals, chemical energy is *totipotent* (*toti*, “all”; *potent*, “powerful”). Animals use electrical and mechanical energy to accomplish some forms of physiological work, but neither form of energy is totipotent. For example, animals use electrical energy to set ions in motion and mechanical energy to pump blood, but they cannot use either form of energy to synthesize proteins. Finally, *animals cannot use heat to do any form of physiological work.*

This last point is important. According to thermodynamics, a system can convert heat to work only if there is a temperature difference between one part of the system and another. Temperature is a measure of the intensity of random atomic-molecular motions. If the intensity of random motions differs from one place to another within a system, this difference represents a form of order, and the system can be used as a machine to convert heat to work; the high temperatures in the cylinders of an internal combustion engine, for example, permit heat from the burning of fuel to be converted into mechanical energy that propels a car. The purely random molecular motions that exist throughout a physical system at a uniform temperature cannot do work, however. Within cells—the relevant functional systems of organisms—temperature differences from place to place are very small and transient, when they exist at all. Hence, cells cannot in theory use heat to do physiological work, and biological experiments confirm that they cannot. Heat is hardly unimportant to animals; as discussed later in this chapter and in Chapter 8, inputs of heat influence animal metabolic rates and affect the abilities of macromolecules such as proteins to carry out their functions. However, heat has no importance as a source of energy for physiological work because heat cannot do work in organisms.

The forms of energy are placed into two categories based on their ability to do physiological work. High-grade energy can do physiological work; chemical, electrical, and mechanical energy are included in this category. Low-grade energy—heat—cannot do physiological work. When we say that animals degrade energy, we mean that they transform it from a high-grade form to heat.

### Transformations of high-grade energy are always inefficient

When organisms transform energy from one high-grade form to another high-grade form, the transformation is always incomplete, and some energy is degraded to heat. The efficiency of an energy transformation is defined as follows:

$$\text{Efficiency of energy transformation} = \frac{\text{output of high-grade energy}}{\text{input of high-grade energy}} \quad (5.1)$$

The efficiency of energy transformation is typically much less than 1. For example, when a cell converts chemical-bond energy of

<sup>2</sup> The study of forms of energy is part of thermodynamics. Some specialists in thermodynamics emphasize energy transfer. For them, heat and mechanical work are not forms of energy, but rather *heating* and *working* are processes that *transfer* energy.

glucose into chemical-bond energy of adenosine triphosphate (ATP), at most only about 70% of the energy released from glucose is incorporated into bonds of ATP; the other 30% is lost as heat. When, in turn, a muscle cell uses the chemical-bond energy of ATP to contract, typically a maximum of only 25% to 30% of the energy liberated from the ATP appears as energy of muscular motion; again, the remainder is lost as heat. The contraction efficiency of muscles in fact depends on the type of work they are doing. If you plant one of your feet on a wall and use your leg muscles to push your foot steadily against the wall (isometric exercise), no motion occurs, and the muscles' efficiency in producing motion is zero. If you ride an exercise bike, however, the efficiency of your leg muscles in producing external motion might be as high as 25% to 30%. Even then, 70% to 75% of the energy liberated from ATP in the process would become heat inside your body.

You may be familiar with the Hollywood image of a jungle explorer caught in quicksand. The victim sinks deeper every time he moves. In certain ways an animal's use of food energy is analogous to this image. To make use of the chemical energy from a meal, an animal *must* transform the energy, usually in multiple steps. Each step, however, robs the energy of part of its value because energy transformations are always inefficient and degrade energy to heat. Thus, with each step an animal takes to use the chemical energy in its food, the

resource shrinks, just as each move of the hapless jungle explorer lowers his body further into the quicksand.

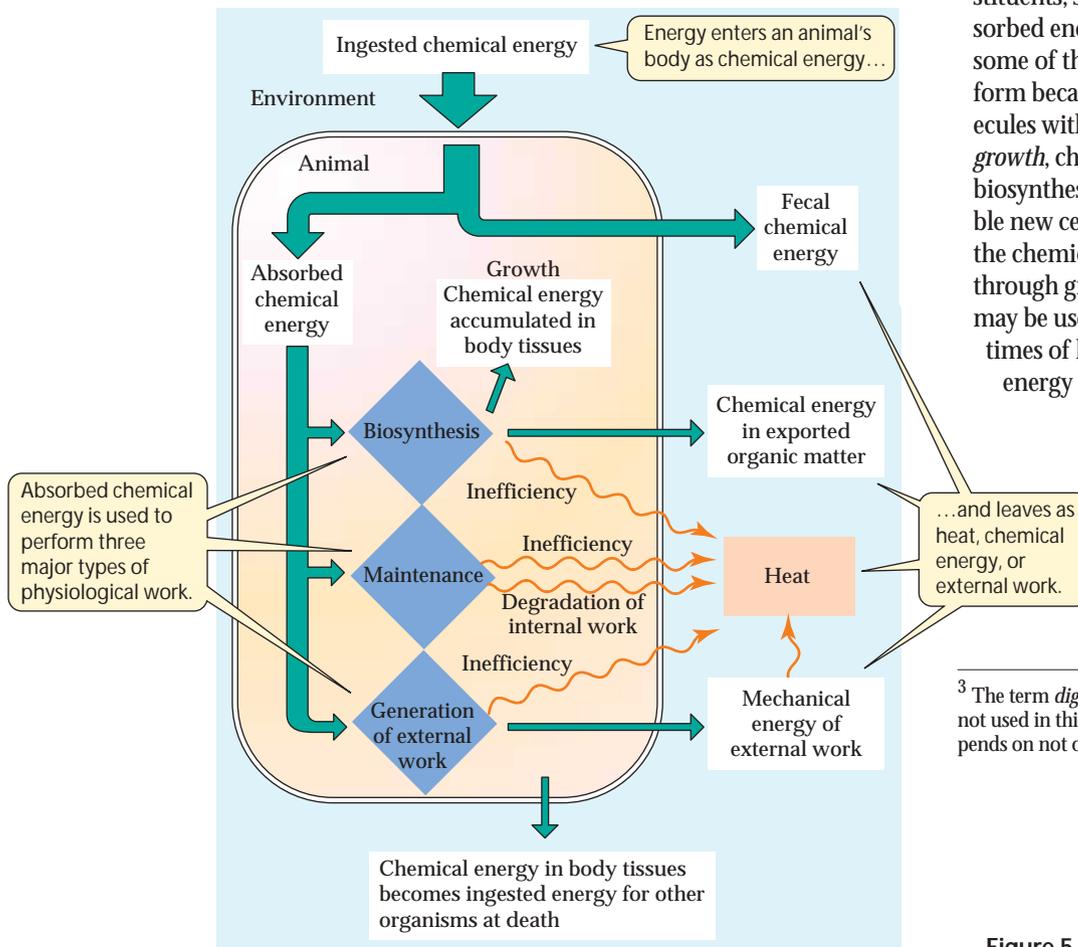
### Animals use energy to perform three major functions

It is helpful to visualize the energy used for physiological work as a resource that “flows” through an animal during its lifetime. Chemical energy enters the animal from the external environment (Figure 5.2). Then forms of energy derived from the chemical energy pass back into the external environment. This flow of energy begins as ingested chemical energy (also termed ingested energy), the energy present in the chemical bonds of an animal's food. Some of this ingested energy is not absorbed because following digestion it remains in chemical structures that the animal is unable to absorb. This portion of the energy never really enters the animal's tissues and is egested in the feces. The egested chemical-bond energy is known as the animal's fecal chemical energy (fecal energy). The remainder of the ingested energy is taken into the living tissues of the animal. The chemical-bond energy of the organic compounds that are absorbed or assimilated is known as the animal's absorbed chemical energy (absorbed energy) or assimilated chemical energy.<sup>3</sup> It is the energy available for the performance of physiological work by the animal's cells.

An animal uses its absorbed chemical energy to carry out three major tasks:

1. **Biosynthesis.** An animal synthesizes its body constituents, such as its proteins and lipids, using absorbed energy. In this process, called biosynthesis, some of the absorbed energy remains in chemical form because the products of biosynthesis are molecules with chemical-energy content. During *growth*, chemical energy accumulates in the body as biosynthesized products, which are used to assemble new cells and tissues (see Figure 5.2). Some of the chemical energy accumulated in body tissues through growth (e.g., the chemical energy of fat) may be used by an animal as food energy during times of hunger or starvation; ultimately, all of the energy accumulated in body tissues becomes

food for predators or decay organisms when the animal dies. Besides contributing to tissues during growth, biosynthesis also produces *organic compounds that are exported from the body during an animal's life*, taking chemical-bond energy



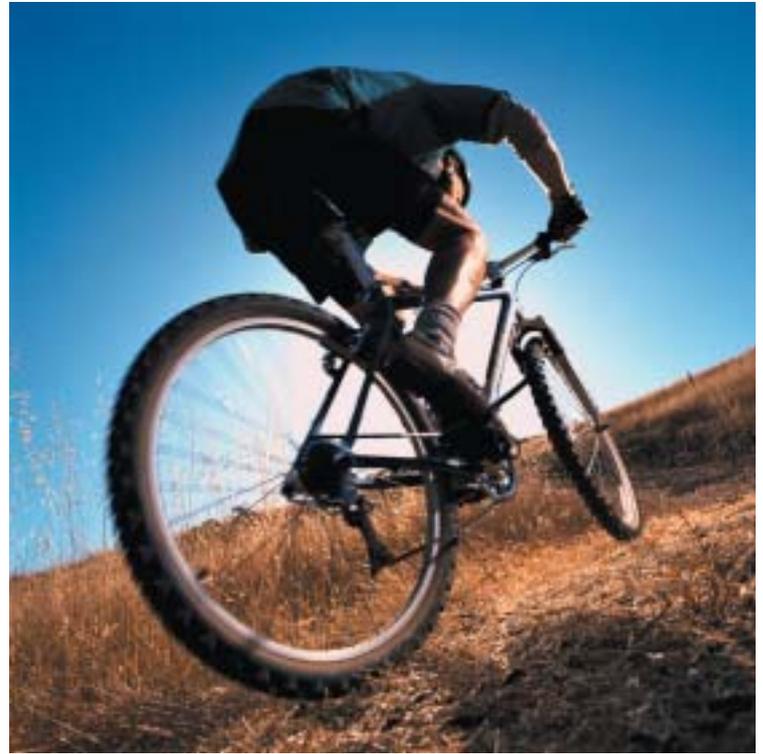
<sup>3</sup> The term *digestible energy* is widely used as a synonym, but it is not used in this book because the absorbed chemical energy depends on not only digestive but also absorptive processes.

Figure 5.2 The uses of energy by an animal

with them. Gametes, milk, mucoid secretions, sloughed skin or hair, and shed exoskeletons are just a few of the organic products that animals synthesize and lose to the environment during their lives. Whether biosynthesis yields growth or exported organic products, this form of physiological work typically involves elaborate biochemical pathways requiring many steps. Heat is produced during biosynthesis because each step is inevitably inefficient.

2. *Maintenance.* An animal's maintenance functions are all the processes that maintain the integrity of its body; examples include circulation, respiration, nervous coordination, gut motility, and tissue repair. With only trivial exceptions, *the energy used for maintenance is degraded entirely to heat within the body.* To see why, consider the circulation of the blood. First, the chemical-bond energy of the absorbed food molecules that are used as fuel is converted into chemical-bond energy of ATP, and energy is lost as heat in the process because of the inefficiency of the conversion. Additional energy is lost as heat when the energy of ATP is used to drive contraction of the heart muscle. Finally, a small fraction of the chemical-bond energy originally obtained from food molecules appears as mechanical energy in the motion of the blood ejected from the heart. Even that mechanical energy is degraded to heat within the body, in overcoming the viscous resistances that oppose motion of the blood through the blood vessels. Mechanical work that takes place inside an animal's body is termed *internal work*. Several maintenance functions, such as the circulation of the blood, are kinds of internal work. The energy of internal work is entirely (or almost entirely) degraded to heat within the body.
3. *Generation of external work.* Animals perform external work when they apply mechanical forces to objects outside their bodies. A mouse running across a field and a bicyclist ascending a hill, for example, are performing external work using their leg muscles. Much of the absorbed chemical energy used to fuel external work is degraded to heat within the body (e.g., in using ATP to set muscles in motion). When external work is performed, however, some energy leaves the body as mechanical energy transmitted to the environment. The fate of that energy depends on whether it is stored. *Energy of external work is stored if it is converted into increased potential energy of position.* As a bicyclist ascends to the top of a hill, part of his energy of external work is stored as increased potential energy of position because his body and bike move to a higher position in Earth's gravitational field (Figure 5.3). When he later descends, this potential energy of position is converted into mechanical energy (the motion of his body and the bike downhill) and then to heat. On the other hand, if a mouse scurries a *horizontal* distance across a field—or a person bicycles along a horizontal road—no energy is stored in repositioning the body relative to gravity, and the mechanical energy transmitted to the environment is entirely, and quickly, degraded to heat in overcoming resistances to motion.

Reviewing the flow of energy through an animal's body (see Figure 5.2), we can see that all uses of energy by animals generate heat. Thus, all living animals produce heat. Because frogs, fish, clams, and other poikilotherms are often cool to the touch, one can get the er-



**Figure 5.3** The energy driving upward locomotion is converted into heat and potential energy of position. As this bicyclist goes uphill, much of his mechanical energy of external work becomes heat, but a fraction is stored as potential energy because he is propelling the mass of his body and bicycle higher in Earth's gravitational field.

roneous impression that they do not produce heat. However, such animals are cool not because they fail to produce heat, but because their rates of heat production are so low and their bodies are so slightly insulated that they are not warmed by the heat that they produce (see page 219). Animal heat, which is universal, has been studied for centuries, leading to fundamental discoveries about the nature of life (Box 5.1).

Another point to stress as we conclude our discussion of energy flow through animals is that the conversion of chemical-bond energy to heat is one-way: No animal or other living creature is able to convert heat back to chemical-bond energy or any other form of high-grade energy. Thus, energy is not recycled within individual animals or within the biosphere as a whole. This principle provides the answer to a key question we asked at the start of this chapter—namely, why animals need to obtain food energy regularly throughout their lives. When an animal ingests and uses totipotent chemical-bond energy, it converts much of it in a one-way, irreversible fashion to heat, which is useless for physiological work. Thus, as an animal uses the chemical-bond energy from a meal, it inevitably develops a need to eat again to acquire new chemical-bond energy. The biosphere as a whole requires a continuing input of high-grade photon energy from the sun for much the same reason. The photon energy captured in bonds of organic compounds by photosynthesis is converted to heat by plants as well as animals, meaning that new photon energy is required if organ-

## BOX 5.1 Views on Animal Heat Production

Heat is an inevitable *by-product* of the use of high-grade, chemical-bond energy to create and maintain the vital organization of living organisms. Interestingly, from the time of Aristotle until the nineteenth century, the significance of heat was generally viewed quite oppositely. Far from being a by-product, heat was usually seen as a primary source of life, a vital force that endowed many parts of organisms with their living attributes. This “vital heat” was thought to differ from the heat of a fire. It was believed to originate exclusively in the heart, lungs, or blood and to suffuse the rest of the body. When William Harvey described the circulation of the blood in the early seventeenth century, one of the principal roles attributed to the newfound circulation was transport of “vital heat” from tissues where it was produced to other tissues, which it animated.

The old view of animal heat began to change at about the time of the American Revolution, when Antoine Lavoisier, in France, showed that the ratio of heat production to CO<sub>2</sub> production was about the same for a guinea pig as for burning charcoal. From this and other evidence, Lavoisier and the Englishman Adair Crawford argued that animal respiration is a slow form of combustion, and animal heat is the same as the heat produced by fire. Still, for several more decades, all animal heat was believed to originate in the lungs, and the lungs were thought to be the exclusive site of O<sub>2</sub> utilization. Not until 1837 did Heinrich Gustav Magnus show that the blood takes O<sub>2</sub> from the lungs to the rest of the body and returns CO<sub>2</sub>. Evidence for the all-important concept that tissues throughout the body make heat came a decade later when Hermann von

Helmholtz demonstrated that muscular contraction liberates heat. In 1872, Eduard Pflüger presented evidence that all tissues consume O<sub>2</sub>.

The discovery that all tissues use O<sub>2</sub> and produce heat was one of several lines of thought and investigation that came together in the nineteenth century to spawn our modern understanding of animal energetics. Other important developments were the flowering of the science of thermodynamics (sparked by the Industrial Revolution) and profound changes in the understanding of energy. In the 1840s, Julius Robert von Mayer in Germany and James Joule in England developed the seminal concept that heat, motion, electricity, and so on are all forms of one thing: energy. Mayer, a physician, conceptualized clearly for the first time the nature of animal energy transformations described in this chapter.

ic compounds are to continue to be available. The heat that all organisms collectively make is radiated from Earth into outer space.

### Summary: Fundamentals of Animal Energetics

- Forms of energy vary in their capacity to do physiological work. Chemical-bond energy is totipotent for animals. Electrical and mechanical energy can do certain types of physiological work but are not totipotent. Heat cannot perform physiological work of any kind.
- Animals use their absorbed chemical energy for three major functions: biosynthesis, maintenance, and generation of external work. Biosynthesis, which preserves some of the absorbed energy in the form of chemical energy, includes both growth and the synthesis of organic materials that are exported from the body during an individual's life.
- Some energy is degraded to heat (low-grade energy) whenever one high-grade form of energy is transformed to another. Energy transformations are always inefficient.
- Energy is not recycled, either in individual animals or in the biosphere as a whole.
- Animals take in chemical-bond energy and put out heat, chemical-bond energy, and external work.

### Metabolic Rate: Meaning and Measurement

We have seen that an animal takes in chemical energy in its food, and in the process of living it releases chemical energy, heat, and external work. The energy converted to heat and external work is defined by physiologists to be consumed, because an animal cannot use that energy to do additional physiological work. An animal's

metabolic rate is its *rate of energy consumption*: the rate at which it converts chemical energy to heat and external work. Energy is measured in *calories* or *joules*, and metabolic rates are expressed in *calories per unit time* or *watts* (Box 5.2). Heat is always the main component of the metabolic rate.

You will recall that at the start of this chapter, we wondered how it is possible to predict the food needs of people and sled dogs during a polar expedition. Their metabolic rates are the basis for making this prediction because once you know their daily energy consumption, you can estimate the total energy that the explorers and their dogs will need over the days of their trek. Speaking broadly, metabolic rates are significant for three reasons:

1. An animal's metabolic rate is a principal determinant of how much food it needs.
2. An animal's metabolic rate provides a quantitative measurement of the *total activity* of all its physiological mechanisms, because every energy-using process contributes heat. The metabolic rate, roughly speaking, represents an animal's *intensity* of living.
3. Ecologically, the metabolic rate measures the drain an animal places on the physiologically useful energy supplies of its ecosystem because the metabolic rate is the pace at which the animal degrades the chemical energy of organic compounds in the ecosystem.

**Direct calorimetry:** The metabolic rate of an animal can be measured directly

Physiologists sometimes measure metabolic rates directly using a direct calorimeter, a device that measures the rate at which heat leaves an animal's body (Box 5.3). Modern direct calorimeters are technically complex instruments. The basic operation of a direct calorimeter is illustrated nicely, however, by the relatively simple device that Antoine Lavoisier used in the first measurements of animal heat production (Figure 5.4). The heat leaving the test animal melted the sur-

## BOX 5.2 Units of Measure for Energy and Metabolic Rates

The traditional unit of measure for energy is the **calorie (cal)**, which is the amount of heat needed to raise the temperature of 1 g of water by 1°C. Although the calorie is defined as a quantity of heat, it can be used as a unit of measure for motion, electricity, or any other form of energy because the forms of energy bear strict equivalencies to each other. A **kilocalorie (kcal)** is 1000 cal. Sometimes the kilocalorie is written *Calorie*, with a capital C. (Popular books and periodicals sometimes write *calorie* with a

lowercase c when they mean kilocalorie, an unfortunate practice that can create three orders of magnitude of confusion.) If energy is expressed in calories or kilocalories, then *rates* of energy exchange or transformation—such as metabolic rates—are expressed in calories or kilocalories *per unit time*.

The fundamental unit of measure for energy in the SI system of units is the **joule (J)**, named in honor of James Joule. Appendix B (The Système International and Other Units of Measure) dis-

cusses the derivation of the joule from the SI base units. A **watt (W)**, which is equivalent to 1 joule/second (J/s), is the fundamental SI unit for rates of energy exchange or transformation.

One calorie is equivalent to 4.186 J, a relation that permits the interconversion of units in the calorie and SI systems. For example, as you sit quietly reading this page, your body is likely producing heat at a rate near 23 cal/s, equivalent to  $23 \times 4.186 = 96$  J/s, or 96 W. That is, you are producing heat about as rapidly as a 100-W light bulb.

rounding ice, and Lavoisier collected the meltwater over measured periods of time. By knowing the amount of heat required to melt each gram of ice, he could calculate the animal's rate of heat output, and thus its metabolic rate.

Sometimes, to carry out direct calorimetry, one must also measure external work, the second component of metabolic rate. If an animal under study is at rest, no external work is being performed; thus a measurement of heat production alone encompasses a resting animal's entire metabolic rate. When external work *is* being performed, the energy of the external work is often rapidly degraded to heat (as in the case discussed earlier of a mouse scurrying over a horizontal surface). In such cases, a measure of heat production includes the

energy of external work, so heat production remains a sufficient determination of metabolic rate. If some energy of external work fails to be converted to heat because it is stored, however, that energy must be measured independently and added to heat production to quantify an animal's metabolic rate by direct calorimetry.

**Indirect calorimetry: Animal metabolic rates are usually measured indirectly**

Indirect calorimetry measures an animal's metabolic rate by means other than quantifying heat and work (see Box 5.3). Biologists today usually measure metabolic rates indirectly because the methods of

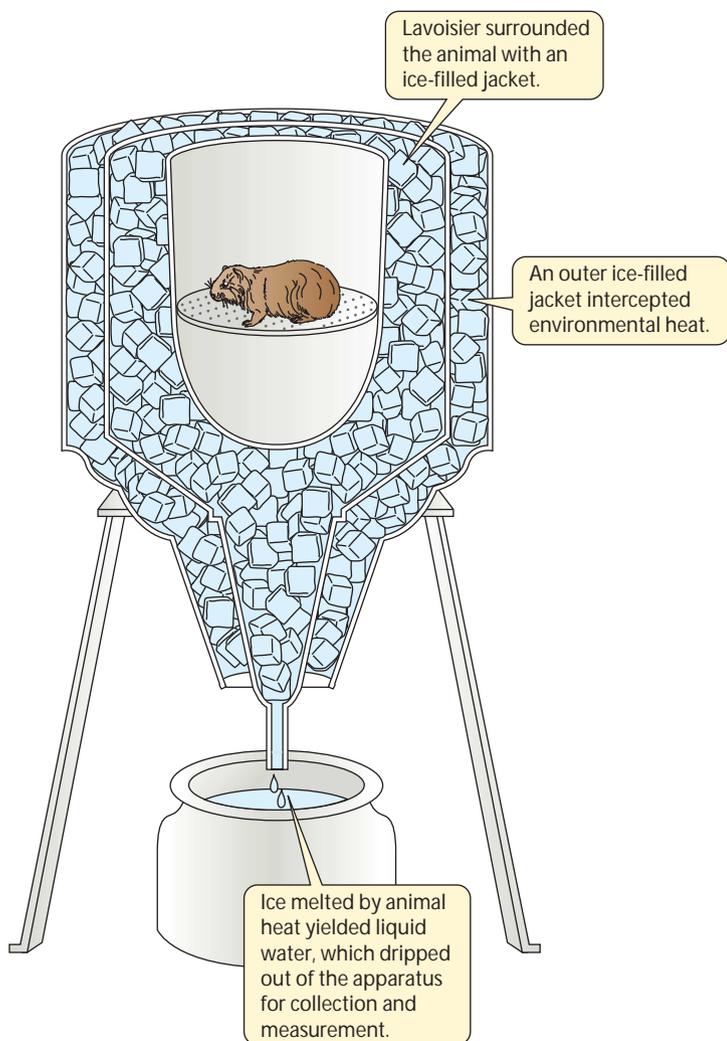
## BOX 5.3 Direct Measurement versus Indirect Measurement

An investigator who wants to measure a particular trait of an animal or environment must decide whether to use a *direct* or *indirect* method of measurement. The distinction between direct and indirect methods is very important and yet can seem subtle at first. The two types of measurement give results that can be expressed in the same units; a metabolic rate, for example, can be written down in watts whether it is measured directly or indirectly. The distinction between direct and indirect methods is in the property that is *actually measured*.

Rigorously speaking, any physiological trait is *defined* by specific properties. A direct method of measurement records the *very same properties specified by the definition of a trait*. An animal's metabolic rate, for example, is defined as its rate of production of heat and external work. Thus a direct method of measuring metabolic rate actually quantifies heat and external work. Direct methods are the gold standards of measurement because their results relate unambiguously to the trait being studied.

On the other hand, an indirect method of measurement records *properties different from those specified by the definition of a trait*. The properties that are actually measured and quantified by an indirect method serve as "stand-ins" or "proxies" for the properties that define the trait. For instance, some indirect methods for measuring metabolic rate record O<sub>2</sub> consumption. Researchers use such methods because O<sub>2</sub> consumption is relatively easy to measure and often closely reflects an animal's rate of production of heat and external work. After measuring the amount of O<sub>2</sub> consumed per unit of time, researchers often convert the amount of O<sub>2</sub> to calories or joules, units of energy. It is important to understand that the act of converting the measurement results does not change the nature of the measurement method. A measure of metabolic rate obtained by recording O<sub>2</sub> consumption is an indirect measure regardless of the units in which it is ultimately expressed.

Why does the distinction between direct and indirect methods matter? A direct method, if carried out carefully with suitable instruments, *must* provide information of the sort desired because it measures exactly what the definition specifies. An indirect method, however, may introduce errors regardless of how carefully it is carried out, because it is measuring something different from what is stated by the definition. Why, then, are indirect methods ever used? As the example of O<sub>2</sub> consumption illustrates, indirect methods often have practical advantages; they may be cheaper or easier than direct methods. The accuracy of an indirect method must be judged by how well its results agree with a direct method. Indirect methods are usually less accurate than direct ones, at least under certain circumstances, so the choice of method involves a compromise. In the measurement of metabolic rate, the indirect methods commonly introduce uncertainties of 1% to 5% in the results, but they might reduce costs of time and money by tenfold, making them attractive.



**Figure 5.4 Lavoisier's direct calorimeter** Heat from the general environment must be excluded from measurement of animal heat. In Lavoisier's device, heat entering from the air surrounding the calorimeter was intercepted by an outer ice-filled jacket. Modern direct calorimeters, although they measure heat in a different way and more precisely, still reflect the fundamental design considerations that Lavoisier introduced. (After Lavoisier 1862.)

indirect calorimetry are cheaper and easier than those of modern, sophisticated direct calorimetry. Here we consider two methods of indirect calorimetry: (1) measuring an animal's rate of respiratory gas exchange with its environment (termed *respirometry*) and (2) measuring the chemical-energy content of the organic matter that enters and leaves an animal's body (the *material-balance method*).<sup>4</sup>

**INDIRECT CALORIMETRY BASED ON RESPIRATORY GAS EXCHANGE** An animal's rate of oxygen consumption provides a convenient and readily measured estimate of its metabolic rate. To understand the use of  $O_2$  consumption for this purpose, consider first an oxida-

tion reaction occurring in a test tube. If a mole of glucose ( $C_6H_{12}O_6$ ) is burned completely, chemical stoichiometry dictates that 6 moles of  $O_2$  will be used, and 6 moles of  $CO_2$  will be produced. The reaction will also release heat, known as *heat of combustion*. For glucose, the heat of combustion during complete oxidation is about 2820 kilojoules (kJ), or 673,000 calories (cal), per mole (mol). The following equation applies:



Note that when glucose is oxidized, a fixed proportional relation prevails between the amount of heat produced and the amount of  $O_2$  used: 2820 kJ of heat per 6 mol of  $O_2$ . Similarly, a proportional relation exists between heat production and  $CO_2$  production: 2820 kJ per 6 mol of  $CO_2$ . Knowing these relations, if you oxidize an *unknown* quantity of glucose in a test tube and you measure only the amount of  $O_2$  used or the amount of  $CO_2$  produced, you can calculate the exact amount of heat produced.

When an animal metabolically oxidizes glucose (or any other chemical substance), if the chemical end products are the same in the animal as in a test tube, then the stoichiometric relations that prevail among heat production,  $O_2$  consumption, and  $CO_2$  production in the animal will be the same as those in the test tube. This important principle, established by Max Rubner and Wilbur Atwater in the 1890s, is true even though the *intermediate* steps of the metabolic oxidation reactions in an animal differ from the intermediate steps of test-tube oxidation. Because of this principle, if an animal were to oxidize glucose to  $CO_2$  and  $H_2O$  and you were to measure either the animal's  $O_2$  consumption or its  $CO_2$  production in the process, you could calculate the animal's heat production, just as you could calculate heat production in the test tube discussed earlier. This is the rationale for estimating animal metabolic rates from rates of respiratory exchange of  $O_2$  and  $CO_2$ .

Table 5.1 provides conversion factors for calculating the amount of heat generated when a milliliter of  $O_2$  is consumed or a milliliter of  $CO_2$  is produced.<sup>5</sup> To understand how to use the table, imagine that an animal consumes  $O_2$  at a rate of 10 mL/minute, and suppose you know that the animal's cells are oxidizing only glucose (a carbohydrate). The animal's metabolic rate would then be 10 mL/minute  $\times$  21.1 J/mL = 211 J/minute.

As you can see from Table 5.1, problems can arise in the use of respiratory gas exchange to measure metabolic rates because the correct conversion factor for calculating heat production from  $O_2$  consumption or  $CO_2$  production is not a simple, fixed number. Instead, the conversion factor varies depending on the foodstuffs being oxidized. If animals oxidize only glucose, calculating their metabolic rates by measuring their rates of  $O_2$  consumption is unambiguous, as we have already seen. However, animals oxidize a variety of foodstuffs, which yield different quantities of heat per unit volume of  $O_2$  consumed or  $CO_2$  produced (see Table 5.1). This consideration introduces the possibility of ambiguity or inaccuracy. Returning to our previous example, we saw that if an animal consumes  $O_2$  at a rate of 10 mL/minute, its metabolic rate is 211 J/minute (10 mL/minute  $\times$

<sup>4</sup> Additional methods of indirect calorimetry that are used for active or free-living animals are discussed in Chapter 7.

<sup>5</sup> It is a universal convention in metabolic studies to express gas volumes at standard conditions of temperature and pressure (STP), and that is the way they are expressed here. For more information, see Appendix D: Gases at Standard Temperature and Pressure.

**TABLE 5.1 Ratios of heat production to O<sub>2</sub> consumption and CO<sub>2</sub> production during the aerobic catabolism of carbohydrates, lipids, and proteins** Values given are for representative mixtures of each of the three foodstuffs. Gas volumes are at standard conditions of temperature and pressure (see Appendix D: Gases at Standard Temperature and Pressure).

Foodstuff	Heat produced per unit O <sub>2</sub> consumed (J/mL O <sub>2</sub> )	Heat produced per unit CO <sub>2</sub> produced (J/mL CO <sub>2</sub> )
Carbohydrates	21.1	21.1
Lipids	19.8	27.9
Proteins <sup>a</sup>	18.7	23.3

Source: After Brown and Brengelmann 1965.

<sup>a</sup> For proteins, values depend on the metabolic disposition of nitrogen; those tabulated apply to mammals and other animals in which urea is the dominant nitrogenous end product.

21.1 J/mL) if its cells are oxidizing carbohydrates. Its metabolic rate is only 198 J/minute, however, if its cells are oxidizing lipids (10 mL/minute × 19.8 J/mL). Hence an investigator cannot calculate metabolic rate (the rate of heat production) exactly from measurements of O<sub>2</sub> consumption or CO<sub>2</sub> production without knowing the exact mixture of foodstuffs that the study animal's cells are oxidizing.

An animal's recent diet may not provide accurate insight into the foodstuffs its cells are oxidizing, because animals store and interconvert foodstuffs. We can determine the foodstuffs that cells are oxidizing only by looking at indices of *cellular function*. We can obtain one useful index of cellular function by simultaneously measuring CO<sub>2</sub> production and O<sub>2</sub> consumption and taking their ratio:

$$\frac{\text{moles of CO}_2 \text{ produced per unit time}}{\text{moles of O}_2 \text{ consumed per unit time}}$$

This ratio is called the respiratory exchange ratio (*R*) when measured at the respiratory organs (e.g., lungs); it is called the respiratory quotient (*RQ*) when measured at the level of the cells.<sup>6</sup> Under many circumstances, *R* and *RQ* are equal, and we limit ourselves here to that straightforward situation. The *R* and *RQ* values provide a signature of the particular sorts of foodstuffs being oxidized by an animal's cells (Table 5.2). If an animal exhibits a value of *R* near 1.0, for example, its cells are likely oxidizing mostly carbohydrates. On the other hand, if an animal's *R* value is near 0.7, its cells are likely catabolizing mostly lipids. An *R* or *RQ* value near 1.0 or 0.7 strongly suggests which conversion factor from Table 5.1 should be used to calculate an animal's metabolic rate from its O<sub>2</sub> consumption. Specifically, an *R* value near 1.0 suggests use of the carbohydrate factor, 21.1 J/mL O<sub>2</sub>, whereas an *R* value near 0.7 suggests use of the lipid factor, 19.8 J/mL O<sub>2</sub>.

Unfortunately, *R* values that are not close to 1.0 or 0.7 are often difficult to interpret. For example, if an animal has an *R* value of 0.8, a researcher cannot simply conclude that its cells are catabolizing proteins, because the catabolism of a mixture of carbohydrates and

lipids (or of all three foodstuffs) could also produce an *R* value of 0.8. The potential for ambiguity stems from the fact that although three unknowns exist (the proportions of the three foodstuffs being oxidized), the *R* or *RQ* value encompasses only two knowns (O<sub>2</sub> consumption and CO<sub>2</sub> production). The ambiguity can be resolved, but only by the measurement of additional indices of cellular function besides O<sub>2</sub> consumption and CO<sub>2</sub> production.

Investigators often sidestep the uncertainty concerning foodstuffs by using a “representative” conversion factor of 20.2 J/mL O<sub>2</sub> (4.8 cal/mL O<sub>2</sub>) to calculate an animal's metabolic rate from its O<sub>2</sub> consumption. The representative factor approximates the heat produced by an animal that is assumed to be catabolizing a representative mixture of carbohydrates, lipids, and proteins. Using a representative factor of 20.2 J/mL O<sub>2</sub> to calculate metabolic rate does not do away with the uncertainty we have been discussing. To illustrate, suppose that an investigator uses the conversion factor of 20.2 J/mL O<sub>2</sub> but that the animal was actually oxidizing only carbohydrates. Because the true conversion factor (for carbohydrates) is 21.1 J/mL O<sub>2</sub>, the investigator would underestimate the metabolic rate by 4.5% by using the approximate factor of 20.2 J/mL O<sub>2</sub>. If the animal were oxidizing only proteins, the true conversion factor (according to Table 5.1) would be 18.7 J/mL O<sub>2</sub>; thus the investigator would overestimate the metabolic rate by 8% by using the approximate factor. The use of the representative conversion factor is a “good news, bad news” situation. The bad news is that the metabolic rate can be misestimated by ±5% to 8% if one ignores the foodstuff question and simply multiplies the O<sub>2</sub> consumption by the representative conversion factor to calculate metabolic rate. The good news is that the use of this conversion factor is convenient, and for many purposes an error of ±5% to 8% may not be much of a worry.<sup>7</sup>

Among all the methods available to measure metabolic rates, the most common approach used today for routine metabolic rate studies is to measure the rate of O<sub>2</sub> consumption—nothing more—and “live with” the relatively small potential errors that are inherent in the method. Metabolic rates, in fact, are very often expressed simply

<sup>7</sup> If one measures only CO<sub>2</sub> production and calculates metabolic rate with a representative conversion factor, the potential error is much greater: ±15% to 20%. You can see the principal reason in Table 5.1; namely, the relationship between CO<sub>2</sub> production and heat production depends very strongly on foodstuff. Because of the large potential error, CO<sub>2</sub> production—measured by itself—is hardly ever used as an indirect measure of metabolic rate in laboratory studies.

**TABLE 5.2 Respiratory exchange ratios (*R* values) during the aerobic catabolism of carbohydrates, lipids, and proteins** Respiratory quotients (*RQ* values) are equal in steady state.

Foodstuff	Respiratory exchange ratio
Carbohydrates	1.0
Lipids	0.71
Proteins	0.83 <sup>a</sup>

Source: After Kleiber 1975.

<sup>a</sup> The protein *R* value is for animals such as mammals in which urea is the dominant nitrogenous end product. Different values apply to animals that produce ammonia or uric acid as their principal nitrogenous end product.

<sup>6</sup> To calculate *R* or *RQ*, one can divide the *volume* of CO<sub>2</sub> produced per unit time by the *volume* of O<sub>2</sub> consumed per unit time. This is true because all gases occupy essentially the same volume per mole under given conditions (that value is approximately 22.4 L per mole at standard conditions of temperature and pressure).

as rates of  $O_2$  consumption. Besides its technical ease of accomplishment (Box 5.4) and relatively small inherent uncertainty, a third advantage of using  $O_2$  consumption to measure metabolic rate is that external work by an animal need never be measured independently when this method is used. Because the  $O_2$  consumption of an animal is proportional to the ultimate yield of heat from the foodstuffs it catabolizes, the heat equivalent of any external work performed by the animal is included in the metabolic rate computed from its  $O_2$  consumption. An important point to keep in mind about the  $O_2$  consumption method, however, is that  $O_2$  consumption reflects only

*aerobic* catabolism. Thus, if part or all of an animal's catabolism is anaerobic, one must turn to alternative methods, such as direct calorimetry, to measure metabolic rate (see Chapter 6).

**INDIRECT CALORIMETRY BASED ON MATERIAL BALANCE** Besides methods based on respiratory gas exchange, the second most commonly used approach for measuring animal metabolic rates today is a type of indirect calorimetry in which investigators measure the chemical-energy content of *organic materials* entering and leaving an animal's body. This approach, which is widely used in agricul-

## BOX 5.4 Respirometry

**R**espirometry is the process of measuring an animal's gas exchange with its environment. The devices used are called *respirometers*. For studies of metabolic rate, the most common type of respirometry is the measurement of an animal's rate of  $O_2$  consumption. Two basic respirometry configurations are used: *closed* and *open*.

In **closed respirometry** (Figure A), air does not flow through the animal chamber during measurement. The principal practical challenge with closed respirometry is to prevent temperature-induced changes in gas volume from confounding the results. This problem is solved in the closed respirometer shown in Figure A by connecting

Figure A A closed respirometer

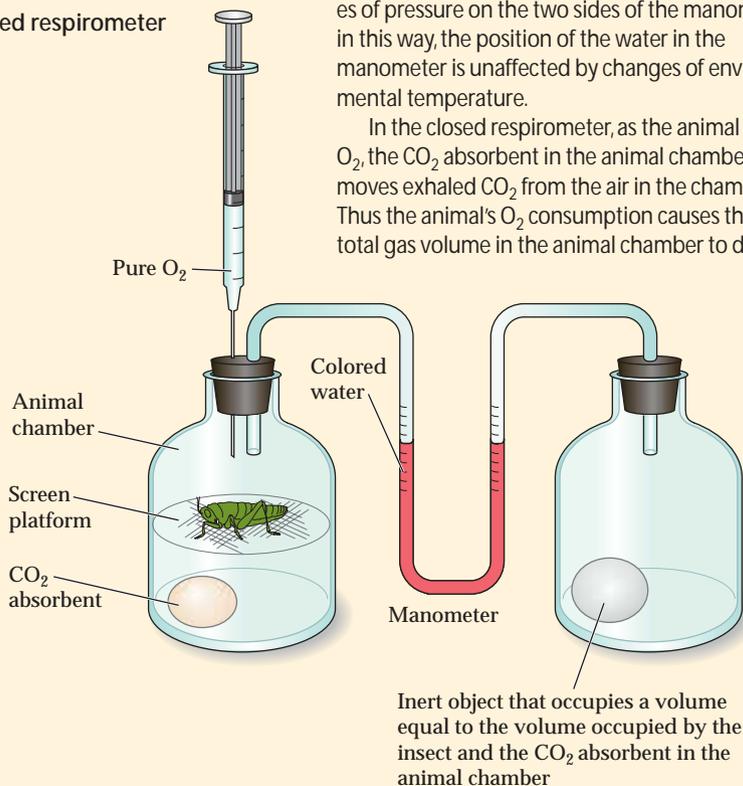
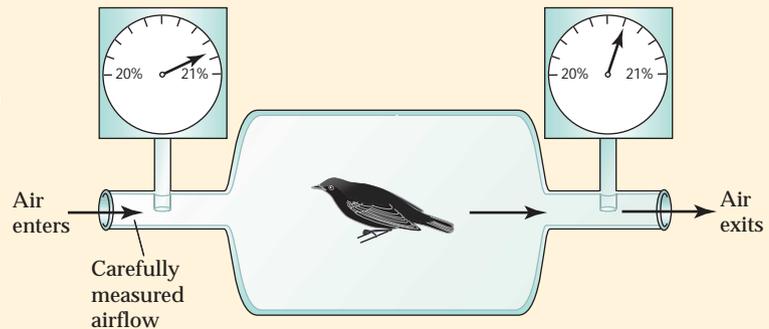


Figure B An open respirometer



two identical chambers to either side of a *manometer*, a device that measures gas-pressure differences (the U-shaped tube filled with water in Figure A). If the environmental temperature changes, the gas pressure within both chambers rises equally, exerting equal and opposite increases of pressure on the two sides of the manometer; in this way, the position of the water in the manometer is unaffected by changes of environmental temperature.

In the closed respirometer, as the animal uses  $O_2$ , the  $CO_2$  absorbent in the animal chamber removes exhaled  $CO_2$  from the air in the chamber. Thus the animal's  $O_2$  consumption causes the total gas volume in the animal chamber to de-

crease relative to that in the other (animal-free) chamber; this decrease in the gas volume in the animal chamber causes the water in the manometer to shift, rising higher in the left arm than the right. At timed intervals, enough pure  $O_2$  is injected from the syringe into the animal chamber to make the manometer return exactly to the initial, unshifted position shown in Figure A. The amount of  $O_2$  injected at any one moment in this procedure must equal the amount of  $O_2$  that the animal consumed during the interval of time preceding the injection. By measuring the  $O_2$  injected and knowing the length of the preceding time interval, a researcher can calculate the animal's  $O_2$  use per unit of time.

In **open respirometry** (Figure B), air flows through the animal chamber (or through a mask worn by the animal) during the measurement of  $O_2$  consumption. The rate of airflow is measured as carefully as possible. A precision  $O_2$  meter, typically using an electrochemical or paramagnetic cell for  $O_2$  detection, measures the  $O_2$  concentration of the flowing air just before the air enters the animal chamber and just afterward. The researcher calculates the animal's rate of  $O_2$  consumption by taking account of the volume of air passing through the chamber per unit of time and the amount of  $O_2$  extracted from each unit volume. Although open respirometry requires the use of far more costly equipment than closed respirometry does, it permits continuous, minute-by-minute (even instantaneous) monitoring of an animal's rate of  $O_2$  consumption.

tural production research, is described as the study of material balance. To apply the method, one measures the chemical-energy content of all the food an animal eats over a period of time, as well as the chemical-energy content of the feces and urine eliminated over the same period of time.<sup>8</sup> Subtracting the energy content of the excreta from that of the food then gives an estimate of the animal's metabolic rate. The logic of the method is straightforward: Any energy that an animal ingests as chemical energy, but does not void as chemical energy, must be consumed.

Complications arise if the animal under study is increasing or decreasing its biomass. If, for example, an animal is growing and thus increasing the chemical-energy content of its body, some of the chemical energy ingested but not voided is nonetheless not consumed; an estimate of this quantity must enter the calculation of metabolic rate. Another type of complication is that chemical energy may enter or leave an animal's body in other ways than in food, feces, and urine. For instance, an animal could lose chemical energy by shedding feathers or secreting mucus. For the material-balance method to be applied, the chemical-energy content of *all* significant inputs and outputs of organic material must be measured.

To use the material-balance method, measurements of ingestion, egestion, and other relevant processes must extend over a substantial period of time—typically 24 hours or more—so that average, steady-state rates of input and output of chemical energy will be quantified. The metabolic rate calculated from the method is the animal's average rate over the entire study period. Thus the material-balance method is suited only for *long-term measurements*

<sup>8</sup> An instrument known as a *bomb calorimeter* is used to measure the energy values of the organic materials. It does this by burning them in pressurized, pure O<sub>2</sub> and measuring the heat evolved.

*of average metabolic rates.* To measure minute-to-minute variations in metabolic rate, the methods of choice are those based on respiratory gas exchange or direct calorimetry.

### Summary: Metabolic Rate

- An animal's metabolic rate is the rate at which it converts chemical energy into heat and external work.
- Metabolic rate is important because it helps determine the amount of food an animal needs, and therefore the food energy that the animal removes from its ecosystem. Metabolic rate also measures an animal's intensity of existence.
- An animal's rate of O<sub>2</sub> consumption is the most common measure of metabolic rate. Metabolic rates can also be measured by direct calorimetry or studies of material balance.

### Factors That Affect Metabolic Rates

Now that we have discussed how metabolic rates are defined and measured, we can turn our attention to the experiences of animals and the processes within them that influence their metabolic rates. The two factors that typically exert the greatest effects on an animal's metabolic rate are the intensity of its physical activity (e.g., speed of running) and the temperature of its environment. Other factors that commonly influence animal metabolic rates include the ingestion of food, age, gender, time of day, body size, reproductive condition, hormonal state, psychological stress, and for aquatic animals, the salinity of the ambient water. [Table 5.3](#) provides an overview of many of these factors and identifies where they are discussed in this book.

**TABLE 5.3** Some factors that affect the metabolic rates of individual animals

Factor	Response of metabolic rate	Chapter(s) where discussed in this book
<b>Exerting largest effects</b>		
Physical activity level (e.g., running speed)	↑ with rising activity level	6, 7
Environmental temperature	<i>Mammals and other homeotherms:</i> Lowest in thermoneutral zone ↑ below thermoneutral zone ↑ above thermoneutral zone <i>Fish and other poikilotherms:</i> ↑ with increasing temperature ↓ with decreasing temperature	8
<b>Exerting smaller effects</b>		
Ingestion of a meal (particularly protein-rich)	↑ for several to many hours following ingestion	5
Body size	Weight-specific rate ↑ as size ↓	5
Age	Variable; in humans, weight-specific rate ↑ to puberty, then ↓	
Gender	Variable; in humans, ↑ in male	
Environmental O <sub>2</sub> level	Often ↓ as O <sub>2</sub> ↓ below a threshold, not affected above threshold	6, 21
Hormonal status	Variable; example: ↑ by excessive thyroid secretions in mammals	14
Time of day	Variable; in humans, ↑ in daytime	10
Salinity of water (aquatic animals)	Variable; in osmoregulating marine crabs, ↑ in dilute water	26

### Ingestion of food causes metabolic rate to rise

Among the factors that affect metabolic rate, the ingestion of food deserves some extended consideration, even though it is not the most influential factor quantitatively, because it must be taken into account in almost all metabolic studies. Under many circumstances, if an animal has been fasting and then consumes food, its metabolic rate temporarily increases following the meal *even though all other conditions are kept constant*. This increase in metabolic rate caused by food ingestion is known as specific dynamic action (SDA), the calorigenic effect of ingested food, or the heat increment of feeding (Figure 5.5). We may often not notice this process in our day-to-day lives, but it is very apparent at certain times. Think back, for example, to a festive holiday dinner when everyone ate lots of high-protein food such as poultry or other meat. After such a meal, people may feel so warm that they remove sweaters and loosen neckties or scarves. The reason for the sense of excessive warmth is the SDA of the ingested protein. The occurrence of SDA means that a certain portion of the energy available from a meal is degraded to heat in processing the meal; only the remaining portion of the energy is available for subsequent physiological uses.

The *magnitude* of the SDA following a meal is the total *excess* metabolic heat production induced by the meal, integrated from the time metabolism first rises to the time that it falls back to the background level. Thus the blue area in Figure 5.5a, showing the integrated difference between the actual metabolic rate after a meal and the metabolic rate that would have prevailed without eating, represents the magnitude of the SDA. The magnitude of the SDA occurring after a meal of a particular type of food tends to be roughly proportional to the amount of food eaten, for given animals under given conditions (Figure 5.5b). Doubling the amount of food eaten tends approximately to double the SDA. Protein foods exhibit much higher SDAs, in proportion to the amount eaten, than lipids or carbohydrates. Although traditionally the SDA of a protein meal has been considered rather dogmatically to be equivalent to 25% to 30% of the total energy value of the meal, recent research indicates that the percentage (while high) varies with prevailing conditions.

The mechanism of SDA remains uncertain. Although digestive processes make a contribution, strong evidence exists that the SDA arises mainly *after the absorption* of digestive products from the gastrointestinal tract, as a consequence of cellular processing of the absorbed organic compounds. An important cause of the SDA asso-

ciated with protein meals, for example, is believed to be the energy expenditure required to synthesize nitrogenous waste products (e.g., urea in mammals) to dispose of nitrogen from excess amino acids.

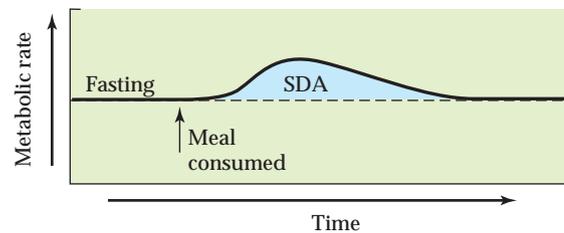
The SDA is a relatively short-term phenomenon, but sometimes an animal's diet induces a *semipermanent*, or *chronic*, change in its metabolic rate. This effect was discovered only about 20 years ago. Experiments revealed that if laboratory rats are enticed to eat unusually large amounts of food day after day (as by the addition of sweets to their food), some individuals do not fatten, because their metabolic rates chronically rise, turning the excess food energy into heat. The long-term increase in metabolic rate induced by persistent overeating was dubbed *diet-induced thermogenesis* (DIT). Research on DIT has been intense ever since its discovery because DIT is an anti-obesity process of potential human importance. The relation between DIT and SDA is confused at present. We say more about DIT in Chapters 6 and 8.

### Basal Metabolic Rate and Standard Metabolic Rate

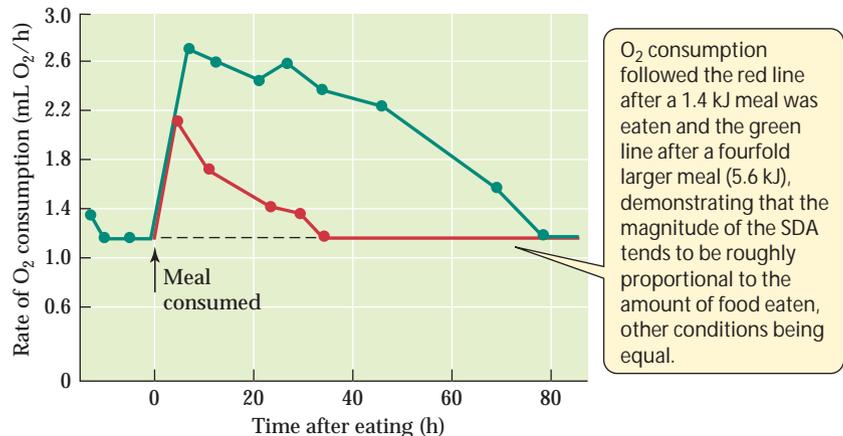
Physiologists, ecologists, and other biologists often wish to compare metabolic rates. A physician, for example, might want to know how the metabolic rate of a particular patient compares with the average metabolic rate of all people of similar age, because some diseases are distinguished by abnormal rates of energy consumption. An ecologist might want to compare the metabolic rates of two species in an

**Figure 5.5 Specific dynamic action** (a) A resting, fasting animal is fed at the time marked and then remains at rest. The SDA begins after a delay, which may be up to an hour. The solid line shows the animal's actual metabolic rate. The dashed line depicts what the rate would have been, had the meal not been eaten. The area shaded blue is the magnitude of the specific dynamic action (SDA). There is enormous variation in the timing of this process; the SDA might be over in a few hours in a mouse, in 12 hours in a cow, and in 1 to 3 days in a fish. (b) Actual data for predatory flatfish (*Pleuronectes*) fed two different-sized meals of fish meat. (b after Jobling 1993.)

(a) The concept of SDA



(b) SDA in flatfish



attempt to learn which species is more likely to place high demands for food on an ecosystem.

In making comparisons, it is often important to standardize factors that could confound results. For example, physicians typically standardize food ingestion during diagnostic metabolic studies by having patients fast for at least 12 hours prior to measurements of their metabolic rates; otherwise, some patients would have their measured metabolic rates elevated by SDA, whereas others would not, creating confounding variation. Similarly, biologists who want to know if species have inherently different metabolic rates typically standardize physical activity, so that results are not confounded by having the individuals of one species walking around while those of the other rest during measurement. A number of standardized measures of metabolic rate have been defined to facilitate valid comparisons. The two most commonly used standardized measures are the *basal metabolic rate* and the *standard metabolic rate*.

The basal metabolic rate (BMR) is a standardized measure of metabolic rate that applies to *homeotherms*, animals that physiologically regulate their body temperatures, such as mammals and birds. For each homeothermic species, there is a range of environmental temperatures within which the metabolic rate is minimal. This range, called the *thermoneutral zone*, is illustrated in Figure 8.22. The basal metabolic rate of a homeotherm is the animal's metabolic rate while it is (1) in its thermoneutral zone, (2) fasting, and (3) resting.

The concept of standard metabolic rate (SMR) applies to *poikilotherms* (*ectotherms*), animals that allow their body temperatures to fluctuate freely with variations in environmental temperature, such as amphibians, molluscs, and most fish. The standard metabolic rate is the metabolic rate of a poikilothermic animal while it is (1) fasting and (2) resting. The SMR is specific for the prevailing body temperature; thus there are as many SMRs as there are different body temperatures.

Both of the standardized measures of metabolic rate mentioned here call for subjects to be fasting and resting. In studies of metabolic rate, the term fasting (or postabsorptive) has a specific meaning—namely, that a subject's last meal took place long enough ago for the SDA of the meal to be over. The term *resting* can have somewhat different meanings in different studies because inducing animals to rest is often not simple. Different levels of rest are formally recognized in some subdisciplines of physiology. Fish physiologists, for instance, often use the term routine metabolic rate to refer to metabolic rates of reasonably quiet fish exhibiting only small, spontaneous movements and reserve *standard metabolic rate* to describe fish that have been coaxed to a truly minimal level of activity.

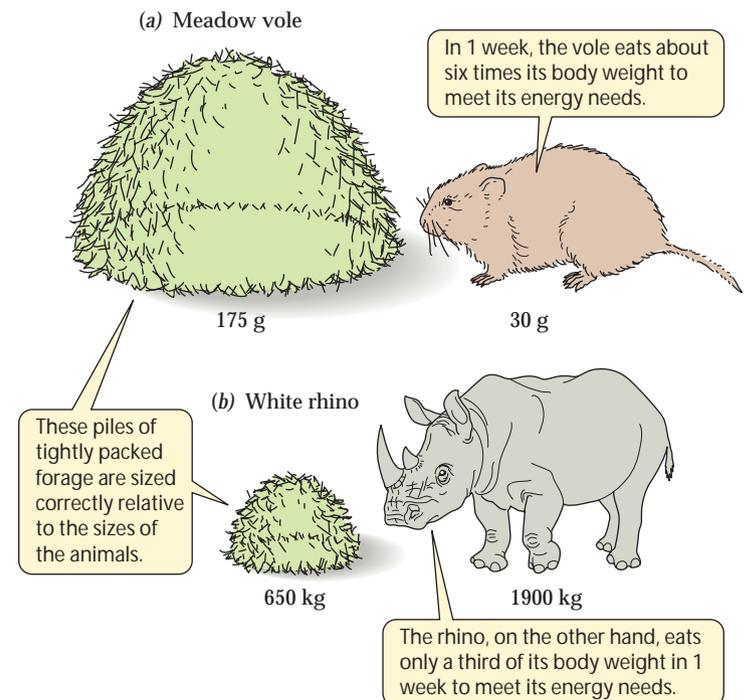
## The Relation between Metabolic Rate and Body Size

How does metabolic rate vary with body size within sets of phylogenetically related species? This simple question turns out to have an intricate and profoundly important answer. A comparison between meadow voles and white rhinos provides a revealing starting point for understanding the relation between metabolic rate and body size. Both of these species are mammals, and both eat similar foods, being “pure grazers” that eat little else besides grassland plants. They are

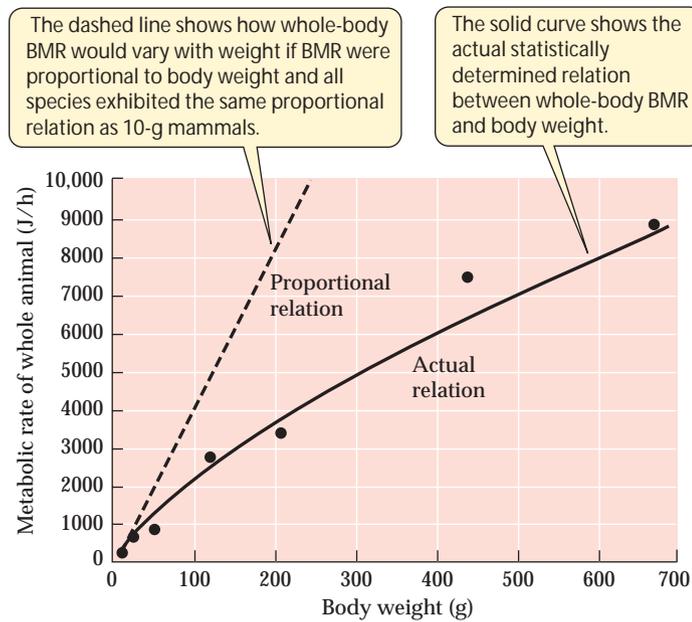
very different in body size, however. An interesting way to gain insight into the effect of their different body sizes on their metabolic rates is to compare how much food they must eat to meet their metabolic needs. If we pile up all the grass that a vole and a rhino must eat in a week under similar measurement conditions, we find, not surprisingly, that the rhino requires more food than the vole. However, a week's pile of food for the vole is larger than the vole itself, whereas the pile for the rhino is much smaller than the rhino (Figure 5.6). This disparity indicates that *the energy needs of the species are not proportional to their respective body sizes*.

### Resting metabolic rate is an allometric function of body weight in related species

To fully understand the relation between metabolic rate and body size, it is important to compare large numbers of related species, not just two. The BMRs of over 600 species of placental mammals have been measured. When all these BMRs are plotted against the body weights of the species, statistics can be used to draw the best-fitted line through the data (see Appendix E: Fitting Lines to Data). From this sort of analysis, physiologists have discovered that the pattern we have observed in comparing voles and rhinos is in fact a general pattern that applies across the full range of mammalian body sizes. Although the total BMR of species of placental mammals increases with body weight, it does not increase in proportion to weight. Instead, the total BMR increases less than proportionally with body



**Figure 5.6** The effect of body size on weekly food requirements. Both species—(a) the 30-g meadow vole (*Microtus pennsylvanicus*) and (b) the 1900-kg white rhino (*Ceratotherium simum*)—are grazers. (Calculated from Golley 1960 and Owen-Smith 1988, assuming 70% moisture content in the forage.)

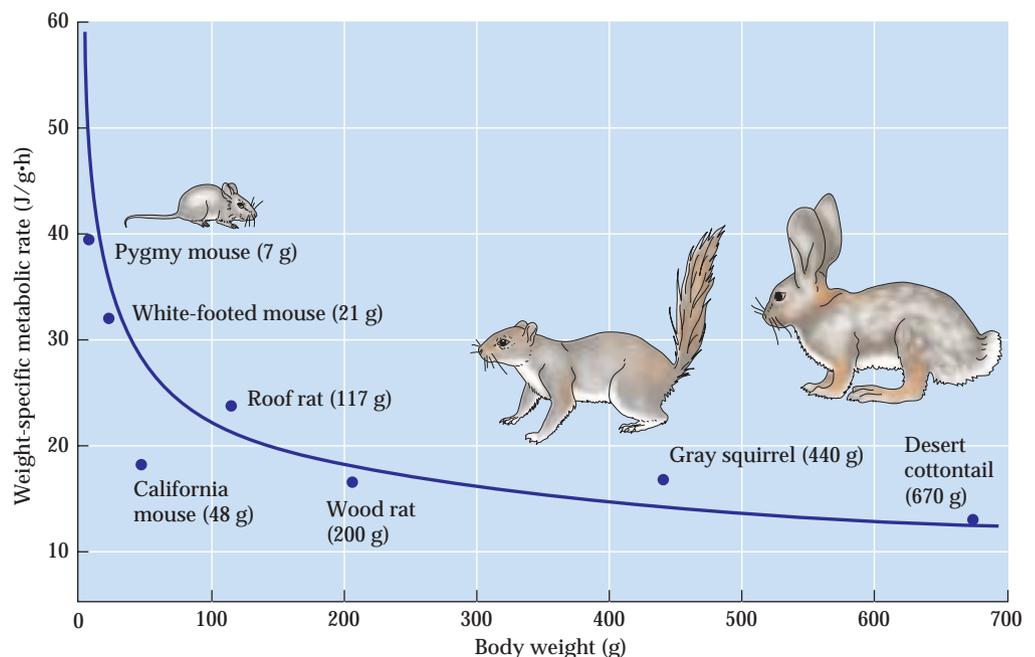


**Figure 5.7 BMR as a function of body weight in various species of placental mammals** The curve showing the actual relation is statistically fitted to data for all sizes of mammals, although this plot includes body weights up to only 700 g. The points are data for seven North American species (see Figure 5.8 for identifications), illustrating that although the statistical line runs through the data, individual species do not necessarily fall right on the line. (After Hayssen and Lacy 1985.)

weight (Figure 5.7). Consider, for example, that an average 10-g species of placental mammal exhibits a total BMR of about 400 J/hour. If the BMR increased in proportion to body size, a 100-g species would have a total BMR of 4000 J/hour. In actuality, the average total BMR of a 100-g species is much less, about 2200 J/hour. This quantitative trend persists through the entire range of mammalian weights. For instance, the average BMR of a 400-g species of placental mammal is only about 2.7 times higher than that of a 100-g species, not 4 times higher.

An alternative way to examine the relation between metabolic rate and body weight is to calculate the metabolic rate *per unit of body weight*, termed the weight-specific metabolic rate, and plot it as a

**Figure 5.8 Weight-specific BMR as a function of body weight in various species of placental mammals** The x axis (body weight) and animals are the same as in Figure 5.7, but here the BMRs (y axis) are expressed per gram of body weight. Small mammals have higher weight-specific BMRs than big ones. (After Hayssen and Lacy 1985.)



function of body weight. Figure 5.8 presents the data points and curve from Figure 5.7 in this new way. This representation illustrates that the weight-specific BMR of mammals decreases as weight increases. Under basal conditions, a 670-g desert cottontail rabbit produces only about 40% as much metabolic heat per gram as a 21-g white-footed mouse. These trends become even more dramatic if we examine mammals still larger than those represented in Figure 5.8. A 70-kg human produces about 10% as much heat per gram as the mouse; and a 4000-kg elephant, about 5% as much. The basal energy expenditure of a gram of mammalian tissue is far lower if it is a gram of elephant than a gram of mouse!

Suppose that instead of mammals, we look at many species of fish of different body weights—or many species of crustaceans of different sizes. Do poikilothermic animals (ones having variable body temperatures) exhibit the same sorts of relations between metabolic rate and body size? Yes, for phylogenetically related poikilothermic species of different body sizes, the standard metabolic rate (SMR) at a particular body temperature usually varies with body size in the same basic pattern as seen in mammals. The total SMR increases with body weight, but it increases less than proportionally. Thus the weight-specific SMR decreases as body weight increases.

The patterns we are discussing are of such great generality that a single type of equation describes the relation between resting metabolic rate and body weight within most groups of related species. If  $M$  symbolizes the total (whole-animal) BMR or SMR, and  $W$  symbolizes body weight, then usually

$$M = aW^b \quad (5.3)$$

where  $a$  and  $b$  are constants. The constants in the equation are determined statistically. To determine  $a$  and  $b$  for placental mammals, for example, researchers begin by tabulating the total BMR and the body weight for as many species as possible. The raw information used for the process, in other words, is a series of points on  $M, W$  co-

ordinates, such as those plotted on the graph in Figure 5.7. The researchers then use a statistical algorithm to fit an equation of the form  $M = aW^b$  as closely as possible to the data points. Such a statistical procedure calculates the values of  $a$  and  $b$  that make the equation match the data points as closely as possible (see Appendix E: Fitting Lines to Data).

Note that the values of  $a$  and  $b$  depend not only on the animal group being studied but also on the particular data used. Thus if two researchers independently investigated mammals using data for different sets of species, they would obtain slightly different values of  $a$  and  $b$ .

If  $b$  equaled 1.0, Equation 5.3 would become  $M = aW$ , a proportional relation. However,  $b$  is almost always less than 1.0. If  $b$  is not 1.0, an equation like Equation 5.3 (having the general form  $Y = aX^b$ ) is nonproportional and is known as an allometric equation.<sup>9</sup> Resting metabolic rate (BMR or SMR) is said to be an allometric function of body weight because the relation between metabolic rate and weight follows the form of the allometric equation.

Biologists have discovered that the exponent  $b$  in the allometric relation between metabolic rate and body weight exhibits an impressive consistency in its value from one phylogenetic group to another.<sup>10</sup> The value of  $b$  for the resting metabolic rates of diverse groups of animals is usually about 0.7. This is true of mammals, fish, crustaceans, and most other animal groups. Most commonly,  $b$  is between 0.65 and 0.75; it is nearly always between 0.6 and 0.9. Universal biological principles seem to be at work in determining  $b$ .

Unlike the value of  $b$ , the value of  $a$  is not at all consistent from one phylogenetic group to another. From Equation 5.3, you can see that  $M = a$  when  $W = 1$ . Thus,  $a$  is the metabolic rate of a 1-gram animal (real or theoretical) in the phylogenetic group under consideration. Some phylogenetic groups (e.g., mammals) have intrinsically much higher metabolic rates than others (e.g., fish) and thus also have much higher values of  $a$ .

What is the mathematical relation between *weight-specific* resting metabolic rate and body weight? This relation is easily derived if both sides of Equation 5.3 are divided by  $W$ , yielding

$$M/W = aW^{(b-1)} \quad (5.4)$$

The expression  $M/W$  is the weight-specific BMR or SMR, and you can see that it is an allometric function of  $W$ . The value of  $a$  is the same as in Equation 5.3, but the exponent in Equation 5.4 is  $(b - 1)$ . Because  $b$  is usually about 0.7, the exponent here is usually about  $-0.3$ . The negative value of  $(b - 1)$  signifies what we have already said; namely, weight-specific resting metabolic rate *decreases* with increasing body weight. Four examples of Equation 5.4, fitted to four different groups of vertebrates, are presented in Figure 5.9. Note the similarity of the exponents but the differences in  $a$ , signifying different metabolic intensities in the four types of animals.

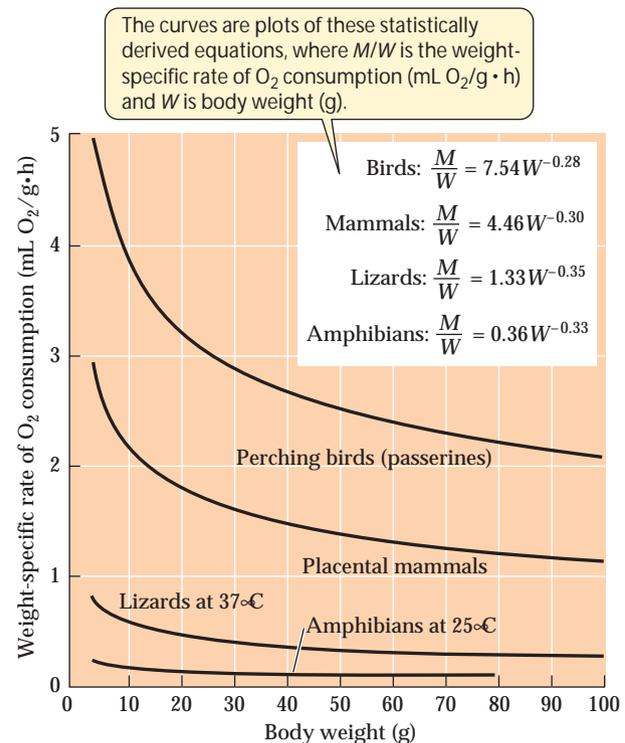
A useful property of Equations 5.3 and 5.4 is that they are linear equations when plotted on log-log coordinates (see Appendix G: Exponential and Allometric Equations). For example, taking the logarithm of both sides of Equation 5.3 yields

$$\log M = \log a + b \log W \quad (5.5)$$

Note that the dependent variable in Equation 5.5 ( $\log M$ ) equals a constant ( $\log a$ ) plus the independent variable ( $\log W$ ) multiplied by another constant ( $b$ ). This means that Equation 5.5 describes a straight line. Thus a plot of  $\log M$  as a function of  $\log W$  is linear, and similarly, a plot of  $\log M/W$  against  $\log W$  is linear. Data relating metabolic rate to weight are nearly always graphed on a log-log plot, as exemplified by Figure 5.10. An advantage of logarithmic axes is that they can accommodate very wide ranges of values. Figure 5.10a, for instance, permits species of mammals ranging in weight from 77 g to almost 200,000 g to be analyzed together on one graph.

The metabolic rate of active animals is often also an allometric function of body weight

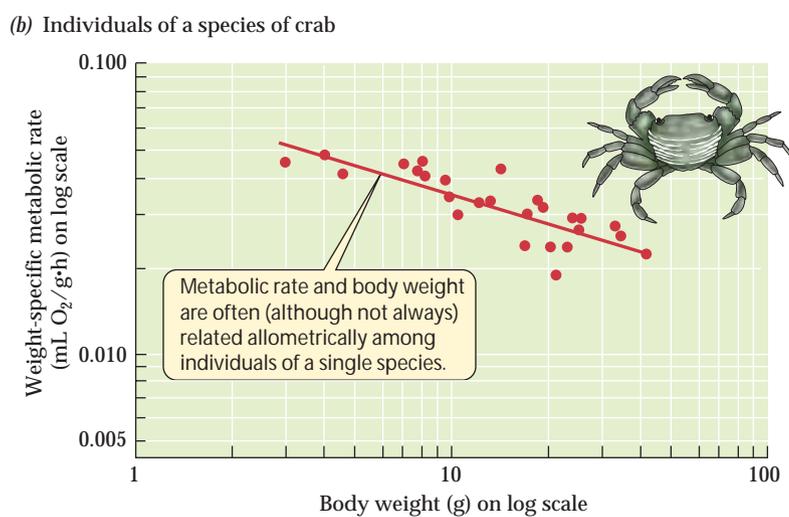
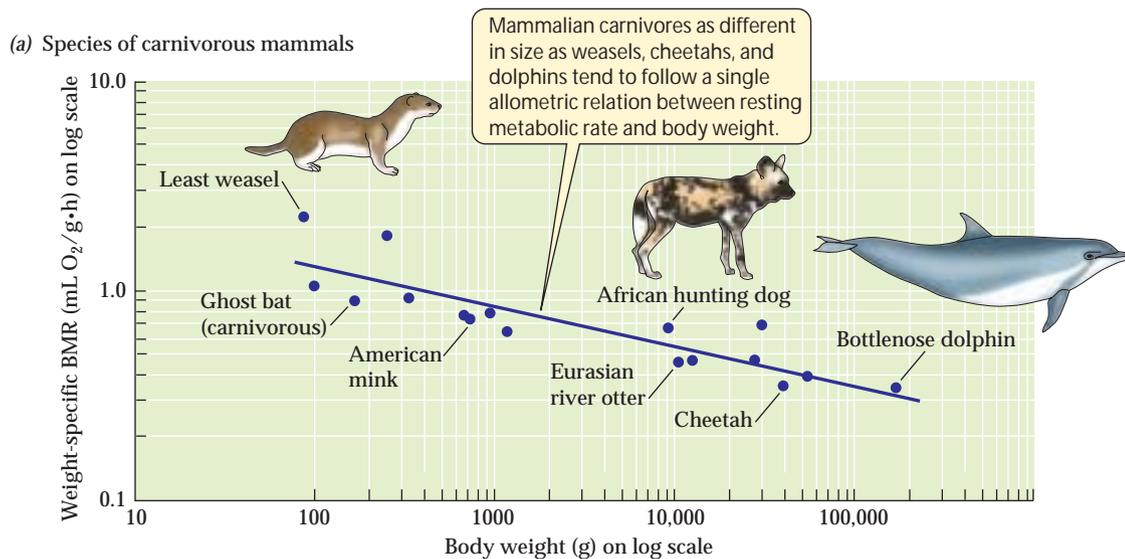
Sustained vigorous physical activity causes an animal's rate of aerobic metabolism to reach a maximum. How does the maximal rate of aerobic metabolism compare to the resting metabolic rate, and how does it vary with body weight within sets of phylogenetically related



**Figure 5.9 Weight-specific metabolic rate as a function of body weight in four groups of vertebrates** The lines for birds and mammals show BMR. The line for lizards shows the SMR when the lizards are at the same body temperature as placental mammals, 37°C. The line for amphibians shows the SMR in temperate-zone anurans and salamanders at a body temperature of 25°C. The lines are based on the statistically derived equations shown, where  $M/W$  is weight-specific rate of  $O_2$  consumption ( $\text{mL } O_2/\text{g} \cdot \text{h}$ ) and  $W$  is body weight (g). (Sources for equations: birds, Lasiewski and Dawson 1967; mammals, Hayssen and Lacy 1985; lizards, Templeton 1970; amphibians, Whitford 1973.)

<sup>9</sup> This form of equation is discussed in Appendix G: Exponential and Allometric Equations.

<sup>10</sup> The exponent  $b$  is dimensionless and thus has no units of measure.



**Figure 5.10 Metabolic rate and body weight are related linearly on log–log coordinates** (a) Weight-specific BMR as a function of body weight for mammalian species that eat primarily vertebrate flesh, plotted on log–log coordinates. The points represent individual species; the line is statistically fitted to them. (b) A log–log plot of weight-specific metabolic rate as a function of body weight in a common Pacific shore crab (*Pachygrapsus crassipes*) at a body temperature of 16°C. Each point represents a particular individual. The line is statistically fitted to the points. See Appendix F (Logarithms) for the axis layouts. (a after McNab 1986; b after Roberts 1957.)

species? A useful rule of thumb in vertebrates and some groups of invertebrates is that the exercise-induced maximal aerobic metabolic rate tends to be about ten times higher than the resting metabolic rate (BMR or SMR). Usually the maximal aerobic metabolic rate ( $M_{\max}$ ) is an allometric function of body weight:  $M_{\max} = a'W^{b'}$ , where  $a'$  and  $b'$  are the constants that apply in the case of maximal metabolic rate. The value of  $a'$  for the maximal metabolic rate tends to be roughly ten times the value of  $a$  for the resting metabolic rate (corresponding to the tenfold difference we noted). The exponent  $b'$  for the maximal metabolic rate is usually similar to  $b$ , the exponent for resting metabolic rate. However,  $b'$  and  $b$  clearly differ a bit in mammals and some other groups that can be analyzed in close detail using available data; in placental mammals, for example, whereas the exponent for resting metabolic rate is about 0.7, that for maximal metabolic rate is about 0.85. The difference in exponents is noteworthy because it has theoretical significance, as we will soon discuss.

What about the *average* metabolic rates of animals living in nature? Animals in nature sometimes rest and sometimes are active. Recognizing that both resting metabolic rate and maximal aerobic metabolic rate are typically allometric functions of body weight, we might expect that *average daily* metabolic rate is also an allometric

function of weight within sets of phylogenetically related animals. It is.<sup>11</sup>

### The metabolic rate–body weight relation has important physiological and ecological implications

The allometric relation between metabolic rate and body weight suggests that different-sized, but related, species are likely to differ in how well their cells and tissues are endowed with mitochondria and other components of the aerobic catabolic apparatus. Cellular properties indeed often vary allometrically with body size. In animals as diverse as mammals and fish, for example, the skeletal muscles of small species have more mitochondria per unit of tissue than those of large species. The density of mitochondria varies allometrically with body weight, paralleling the relation between weight-specific metabolic rate and weight.

Because the breathing and circulatory systems are responsible for delivering the O<sub>2</sub> consumed by the tissues, you might predict that

<sup>11</sup> Chapter 7 discusses methods used to measure the average daily metabolic rates of free-living animals.

**TABLE 5.4** Resting heart rate, and heart size relative to body weight, in seven species of mammals

Species and average body weight	Resting heart rate (beats/min) <sup>a</sup>	Heart weight per unit body weight (g/kg) <sup>b</sup>
African elephant (4100 kg)	40	5.5
Horse (420 kg)	47	7.5
Human (69 kg)	70	5.2
Domestic dog (19 kg)	105	9.2
Domestic cat (3 kg)	179	4.1
Roof rat (0.34 kg)	340	2.9
Lab mouse (0.03 kg)	580	4.0

Source: After Seymour and Blaylock 2000.

<sup>a</sup> According to the source of these data, the statistical relation between resting heart rate (*RHR*) and body weight (*W*) in mammals is  $RHR \text{ (beats/min)} = 227W^{-0.23}$ , where *W* is in kilograms.

<sup>b</sup> Although heart weight per unit body weight varies, it shows little or no consistent relation to body size.

key features of respiratory and circulatory physiology are also allometrically related to body size within sets of related species. If such predictions made millionaires, you would be one!

The resting heart rate in placental mammals, to cite one example, varies with body weight in almost exactly the same functional relation as weight-specific BMR, small species having far higher heart rates than large ones (Table 5.4). This pattern makes sense in view of the fact that statistically, all mammals have about the same size of heart in relation to their body size. Small mammals require more O<sub>2</sub> per gram of body weight than large ones, but their hearts are no bigger relative to their body size than the hearts of large mammals. Thus the hearts of small mammals must beat faster than those of large mammals for O<sub>2</sub> to be delivered at a greater rate per unit of body weight. Various species of mammals also have about the same size of lungs in relation to body size. Thus, by much the same logic, small mammals must breathe more rapidly than large ones. Whereas humans, for example, breathe about 12 times per minute when resting, mice breathe about 100 times per minute. The metabolism–weight relation pervades almost every aspect of an animal's physiology.

Numerous ecological and practical implications also arise from the allometric relation between metabolic rate and body weight. We have already seen in our initial comparison of voles and rhinos that within sets of phylogenetically related animals, small-bodied species typically require food at a greater rate per unit of body weight than large-bodied species (see Figure 5.6). Ecologically, the uninitiated might expect that the basal food requirements of 3500 mice, each weighing 20 g (total weight 70,000 g), would place no greater demands on a woodland ecosystem than a single 70,000-g deer would. Because the weight-specific BMR of a 20-g mouse is about eight times greater than that of a deer, however, the total basal food requirement of only about 440 mice is equivalent to that of a single deer.

When whole ecosystems are analyzed, ecologists sometimes observe that the allometric relation between metabolic rate and body weight has a significant structuring effect. Consider, for example, the woodland savannahs of eastern and southern Africa. These ecosystems are among the marvels of life on Earth, in part because they

support such an extreme diversity of coexisting antelopes and other medium-sized to large mammalian herbivores (Figure 5.11). From aerial surveys of major national parks in Africa, we know the average numbers of many herbivore species per square kilometer. Multiplying numbers by body weights, we can calculate the average population biomass per square kilometer of each species. Population biomass per square kilometer turns out to be a regular function of body size; for example, whereas all the warthogs (a relatively small species) living per square kilometer together weigh about 95 kg, the zebras in a square kilometer collectively weigh 460 kg, and the elephants weigh 1250 kg (Table 5.5). Metabolic allometry, while not the only factor at work, helps explain this trend, because each kilogram of a large-bodied species requires less food than each kilogram of a small-bodied species.

The allometric relation between metabolic rate and body size also means that related small and large species process foreign chemicals differently. Small species, for instance, tend to be more prone to accumulating environmental pollutants. Because the small species eat food and breathe air at greater rates per unit of body weight than their larger counterparts, they tend to receive greater weight-specific doses of food-borne and airborne toxins such as pesticides; the toxins may then accumulate more readily to high concentrations in their tissues. On the other hand, the high weight-specific metabolic rates of small species also mean that small animals tend to catabolize or excrete some substances faster per unit weight than related larger animals. One practical consequence of this fact is that small species may require relatively high doses of a veterinary drug per unit weight to achieve and sustain the drug's intended effect.



**Figure 5.11** Herbivores of different body sizes coexisting on an African grassland. Species vary in population biomass in a way that depends in part on body size and metabolic allometry.

**TABLE 5.5 Biomasses of populations of selected herbivores living in mixed communities in African national parks** Species are listed in order of increasing individual size. These species were chosen for listing because they are statistically about average in population biomass for their body sizes.

Species	Average biomass of whole population per square kilometer (kg/km <sup>2</sup> )	Average individual body weight (kg)
Oribi ( <i>Ourebia ourebi</i> )	44	13
Gray duiker ( <i>Sylvicapra grimmia</i> )	62	16
Gray rhebok ( <i>Pelea capreolus</i> )	105	25
Warthog ( <i>Phacochoerus aethiopicus</i> )	95	69
Waterbuck ( <i>Kobus ellipsiprymnus</i> )	155	210
Greater kudu ( <i>Tragelaphus strepsiceros</i> )	200	215
Plains zebra ( <i>Equus burchelli</i> )	460	275
White rhino ( <i>Ceratotherium simum</i> )	2400	1900
African elephant ( <i>Loxodonta africana</i> )	1250	3900

Source: After Owen-Smith 1988.

### The explanation for allometric metabolism–weight relations remains unknown

The fact that  $b$ , the allometric exponent, is often about 0.7 in widely diverse sorts of animals is profoundly intriguing. The exponent, in fact, is often about 0.7 in both microbes and plants! For a century, some of the greatest minds in biology have grappled with the questions of *why* metabolic rate and body weight are related allometrically and *why* the allometric exponent so consistently assumes the value it does. Great minds have been drawn to these questions because of a conviction that the allometries are manifestations of fundamental—and possibly universal—organizing principles of life. There is as yet, however, no consensus about how to explain the allometries.

Eighty years ago, the problem seemed solved. Physiologists thought they then understood the reasons for not only the allometric relation between metabolic rate and weight, but also the particular value of  $b$ . The theory offered at that time has been reinvented by every generation of biologists because it seems so “obvious.” Thus an understanding of the theory’s flaws remains important even today. At the time the theory first appeared in the early twentieth century, all the data on metabolism–weight relations were on mammals, and mammals therefore dominated thinking about the subject. During that period, Max Rubner articulated an explanatory theory that is still known as *Rubner’s surface “law.”*

Euclidean geometry provides the starting point for understanding this “law” that is not a law. Recall from your study of geometry that the surface area  $s$  of a sphere is proportional to the square of  $r$ , the sphere’s radius:  $s \propto r^2$ . The volume  $v$  of a sphere, however, is proportional to the cube of the radius:  $v \propto r^3$ . From the rules of exponents, we can write  $r^2 = (r^3)^{2/3}$ . Thus,  $s \propto (r^3)^{2/3}$ ; and substituting  $v$  for  $r^3$ , we get

$$s \propto v^{2/3} \quad (5.6)$$

In words, as spheres increase in size, their surface area increases only as the two-thirds power of their volume, signifying that the increase

in surface area is less than proportional to that in volume. Thus, big spheres have less surface area per unit of volume (or weight) than little spheres. Similar relationships hold true for all sets of geometrically similar objects. Whether you consider cubes, cylinders, hearts, or whole animals, as the objects within a geometrically similar set become larger, the area of the outside surface is expected to increase approximately as the two-thirds power of volume, and the ratio of outside-surface area to volume declines.

Rubner’s surface “law” stated that the BMR of a mammal is proportional to its body-surface area<sup>12</sup> and that the allometric relation between BMR and body weight is a corollary of this proportionality. Rubner’s explanation of the allometric relation rested on four logical steps:

1. Mammals maintain high, relatively constant body temperatures (near 37°C) and thus tend to lose heat to the environment when studied at their moneutral environmental temperatures.
2. Because heat is lost across the outer body surfaces, the rate of heat loss from a mammal is approximately proportional to the animal’s body-surface area.
3. Small mammals have more surface area per unit of weight than large mammals and thus lose heat more rapidly per unit of weight.
4. Heat lost must be replaced metabolically for a mammal to stay warm. Thus, small mammals must produce heat at a greater rate per unit of weight than large ones.

The surface “law” as just outlined can hardly be faulted as a thought exercise. Why, then, do most physiologists today believe that it is not the correct mechanistic explanation of the allometric relation between BMR and body weight? The answer is that data contradict the “law” in two respects. First, although the surface “law” predicts an allometric exponent,  $b$ , equal to about 0.67 ( $\frac{2}{3}$ ), most physiologists who have estimated values of  $b$  have concluded that  $b$  is statistically higher than 0.67 to a significant degree. Second, by now we realize, as emphasized in this chapter, that poikilothermic animals—such as crabs, fish, and frogs—display allometric relations between metabolic rate and body weight (see Figures 5.9 and 5.10). Rubner’s “law” cannot possibly explain these relations in poikilotherms because the reasoning behind the “law” applies only to animals that warm their bodies to elevated, regulated temperatures using metabolic heat production. Since the surface “law” cannot explain the allometric relations in the vast majority of animals, it seems unlikely to be the correct explanation even for mammals.

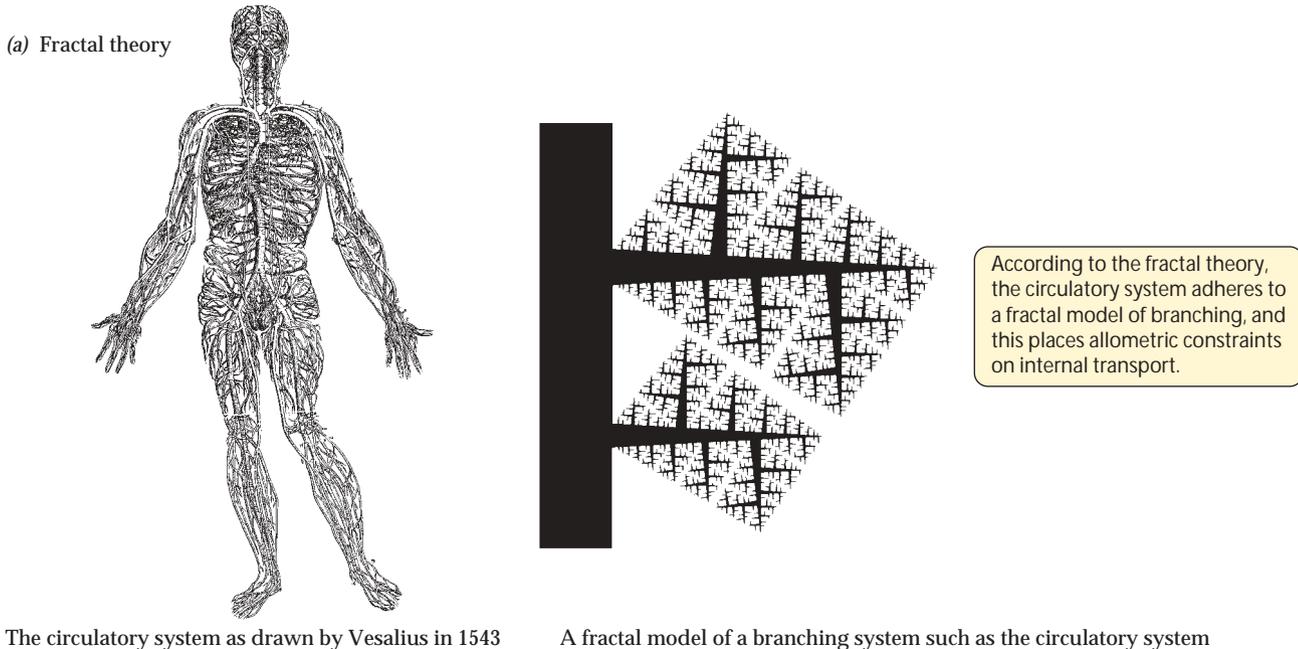
Since the time in the mid-twentieth century when the surface “law” started to be rejected by most physiologists, a number of alternative hypotheses have been put forward. Most have attracted little enthusiasm. Just recently, however, a renewed flurry of interest in the

<sup>12</sup> A modern holdover of the early emphasis on body-surface area is that surface areas are employed to calculate certain sorts of critical variables in the contemporary practice of medicine. In breast cancer chemotherapy, for example, the doses of chemotherapeutic agents administered to a woman are calculated from her body-surface area.

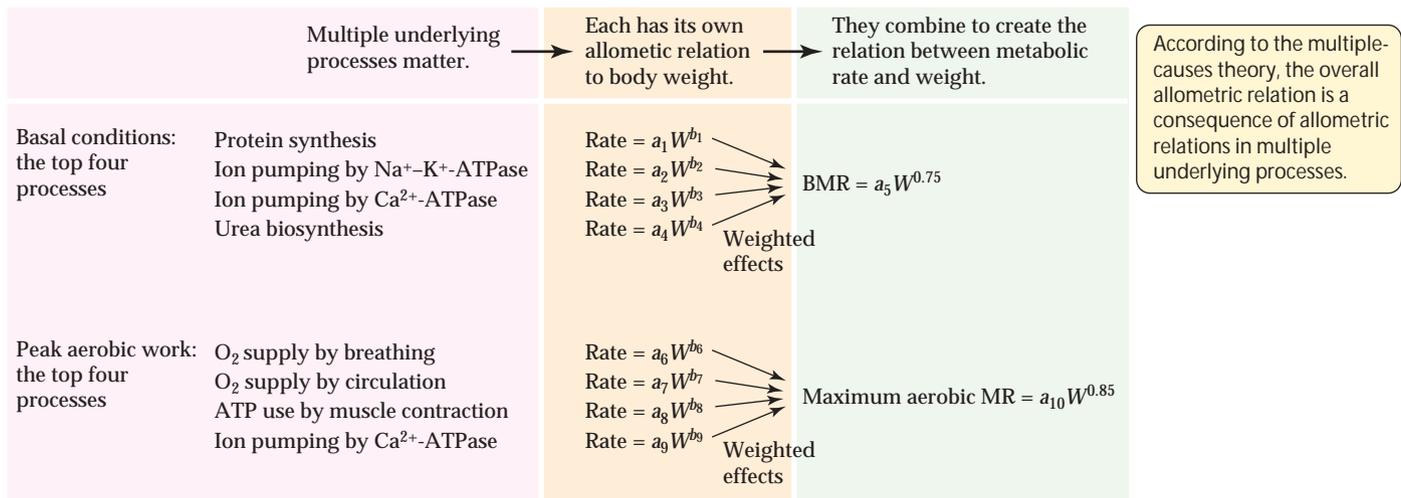
allometric relations between metabolic rate and body size has developed because of the publication in prominent journals of two new theories explaining the relations.

One of the new theories is based on the mathematics of *fractal geometry*. According to this theory, the allometric relations observed between metabolic rate and body weight occur because key internal

transport systems of animals, such as their blood vascular systems, branch according to fractal-geometric principles (Figure 5.12a). The internal transport of O<sub>2</sub> and metabolic fuels is critical for metabolism. This theory stresses that in fractally structured transport systems, *rates* of transport are constrained in distinctive ways by the geometry. The theory is based on complex computer models of in-



(b) Multiple-causes theory



**Figure 5.12 Two contemporary theories to explain the allometric relation between metabolic rate and body weight** (a) The fractal theory argues that with the invention of fractal geometry by Benoit Mandelbrot in about 1980, it is now possible to understand properly the constraints faced by internal transport systems, which are argued to branch according to fractal-geometric principles. These constraints, it is theorized, help give rise to allometric relations between metabolic rate and body size. Fractal systems, as you can see in the example shown, are “self-similar” at multiple scales in that the patterns of branching of fine elements are miniatures of the patterns of branching of large elements. (b) The multiple-causes theory argues that the over-

all allometric relation between metabolic rate and body weight arises from the interplay of allometric relations in multiple processes that underlie an animal's metabolic rate. The theory is illustrated here with information on placental mammals. Because the key processes that underlie metabolism shift with an animal's metabolic intensity, the multiple-causes theory predicts that the allometric relation between BMR and body weight differs in *b* as well as *a* from the relation between maximum aerobic metabolic rate and body weight. (Left drawing in a from Vesalius's *De Humani Corporis Fabrica*, 1543, as reproduced in Saunders and O'Malley 1950; right drawing after Mandelbrot 1983. *b* after Darveau et al. 2002.)

ternal transport that examine how the constraints of fractal geometry interact with evolutionary selection pressures to maintain optimized transport capabilities as animals evolve different body sizes. This theory, championed by people like Geoffrey West and James Brown, predicts that an allometric exponent of  $0.75$  ( $\frac{3}{4}$ ) will occur almost universally—not just in animals but also in plants—because of the fundamental fractal nature of transport systems.

The second major contemporary theory is different from all other theories ever put forth in that it is a *multiple-causes* theory. Rubner's theory and the fractal theory exemplify single-cause theories; each postulates that a single property accounts for allometric relations.<sup>13</sup> The multiple-causes theory, argued by people like Peter Hochachka and Raul Suarez, is based on modern hierarchical models of how biochemical processes in metabolism are controlled. According to these control models, the rate of any major process depends on an interaction of the rates of multiple underlying processes (Figure 5.12b). For example, the rate of resting metabolism depends on at least four underlying rates: (1) the rate at which ATP is used to replace proteins that break down, (2) the rate at which  $\text{Na}^+ - \text{K}^+$ -ATPase in cells throughout the body uses ATP to pump ions, (3) the rate at which  $\text{Ca}^{2+}$ -ATPase uses ATP, and (4) the rate at which ATP is used to synthesize nitrogenous waste molecules. *Each* of these underlying rates exhibits its own allometric relation to body size. According to the multiple-causes theory, the rates of all the relevant underlying processes interact in a quantitatively defined way—some processes having greater effect than others—to determine the overall relation between metabolic rate and body size.

An important attribute of the control models used in the multiple-causes theory is that the models openly recognize and stress that changing circumstances often result in shifts in the relative importance of underlying processes. For example, the models recognize and stress that when mammals exercise near peak intensity, the maximum capability of the circulatory system to deliver  $\text{O}_2$  takes on great importance, even though it has little importance at rest (when peak circulatory function is not required). Because such shifts in the importance of underlying processes are recognized in the multiple-causes theory, the theory (unlike single-cause theories) can account for shifts in the allometric exponent under different conditions. For example, earlier we noted that the allometric exponent differs in exercising and resting mammals. The multiple-causes theory can account for this phenomenon (see Figure 5.12b).

### Summary: The Relation between Metabolic Rate and Body Size

- BMR, SMR, and other measures of resting metabolic rate are allometric functions of body weight within phylogenetically related groups of animals ( $M = aW^b$ , where  $b$  is usually about 0.7). Small-bodied species tend to have higher weight-specific metabolic rates than related large-bodied species, an effect so great that the weight-specific BMR is 20 times higher in mice than in elephants, for example.

- The maximal aerobic metabolic rate also tends to be an allometric function of body weight in sets of related species, but sometimes the allometric exponent for maximal metabolic rate differs from that for resting metabolic rate.
- The allometric relation between metabolic rate and weight exerts important effects on the organization and structure of both individual animals and ecosystems. Heart rates, breathing rates, mitochondrial densities, and dozens of other features of individual animals are allometric functions of body weight within sets of phylogenetically related species. In ecosystems, population biomasses and other features of community organization may vary allometrically with individual body size.
- Scientists are not agreed on the explanation for the allometric relations between metabolic rate and body weight. Rubner's surface "law," based on heat loss from homeothermic animals, does not provide a satisfactory explanation. The newest theories are based on fractal geometry and multiple causes.

## Energetics of Food and Growth

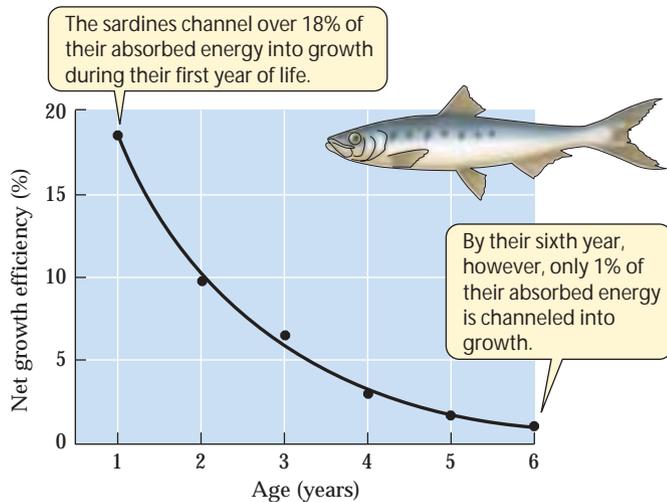
Food and growth are important topics in animal energetics, aptly discussed together because one animal's growth is another's food. A consequential attribute of foods as energy sources is that lipids are at least twice as high as proteins or carbohydrates in their energy density—that is, their energy value per unit weight (see Table 4.2). We asked at the start of this chapter why polar explorers carry lipid-rich foods, such as meat mixed with pure lard. If they are going to pull, push, and lift their food for many miles before they eat it, they should choose food that provides a lot of energy per kilogram transported. Similarly, migrating animals often take advantage of the high energy density of lipids by carrying their fuel as body fat.

A key question about any food in relation to an animal is how well the animal can digest the food and absorb the products of digestion. Recall that the energetic efficiency of a process is the output of high-grade energy expressed as a proportion of input (see Equation 5.1). When digestion and absorption are the functions of interest, the output of high-grade energy is the absorbed energy, whereas the input is the ingested energy (see Figure 5.2). Thus,

$$\text{Energy absorption efficiency} = \frac{\text{absorbed energy}}{\text{ingested energy}} \quad (5.7)$$

This efficiency matters because the absorbed energy is the energy actually available to an animal for use in its metabolism. To illustrate the application of the concept of absorption efficiency, consider the processing of ingested cellulose by people and ruminants. Because people cannot digest cellulose, they cannot absorb it, and their absorption efficiency for the compound is essentially 0%; if they eat only cellulose, they starve. Ruminants such as cows, in contrast, commonly achieve about 50% absorption efficiency for cellulose because their rumen microbes ferment cellulose into compounds that the animals can absorb; thus, ruminants are able to use about half of the energy available from cellulose in their own metabolism. This example illustrates how the physiology of digestion and absorption, discussed in Chapter 4, bears on the physiology of energy.

<sup>13</sup> For Rubner, heat loss through surfaces was the single overriding property that gave rise to allometric relations. According to the fractal theory, allometric relations arise from the fractal branching of internal transport systems.



**Figure 5.13** Net growth efficiency during each year of life in Pacific sardines (*Sardinops sagax*) When their populations are thriving, these fish are a major food source for seals, predatory fish, birds, and humans. (After Lasker 1970.)

Growing animals accumulate chemical-bond energy in their bodies (by adding tissue consisting of organic molecules). When growth is the energy input–output process of interest, the output of high-grade energy is the chemical-bond energy of added tissue, whereas the input is food energy. Two types of growth efficiency, termed gross growth efficiency and net growth efficiency, are defined on the basis of whether the food energy is expressed as the ingested energy or the absorbed energy:

$$\text{Gross growth efficiency} = \frac{\text{chemical-bond energy of tissue added in net fashion by growth}}{\text{ingested energy}} \quad (5.8)$$

$$\text{Net growth efficiency} = \frac{\text{chemical-bond energy of tissue added in net fashion by growth}}{\text{absorbed energy}} \quad (5.9)$$

The growth efficiency of animals (gross or net) typically declines with age (Figure 5.13). Besides being of interest in the analysis of energy flow in ecological communities, growth efficiencies are of great concern in agriculture and aquaculture because they affect the amount of product (such as meat) that is obtained in return for the investment in food to feed farmed or cultured animals. In the production of broiler chickens, for example, the birds are slaughtered at just 2 to 3 months of age because at that point they are large enough to be meaty but their growth efficiency—their growth in return for feed provided—is declining.<sup>14</sup>

## Conclusion: Energy as the Common Currency of Life

Energy features in virtually every biological process and in many inanimate processes as well. It is a factor in animal growth, body

maintenance, migration, photosynthesis, building construction, automobile operation, ecosystem degradation, and war.

When scientists attempt to analyze complex systems—from individual animals to whole ecosystems or even the whole biosphere—they inevitably come up with long lists of processes that they must take into account. The study of individual processes may be straightforward, but the step of integrating knowledge of numerous processes is usually not. One of the greatest challenges in the integrated study of complex systems is to find a common set of units of measure—a “common currency”—in which all the operative processes can be expressed so that they can be compared, added, or multiplied.

Energy is probably the single most promising common currency. In the study of an individual animal, for example, processes as diverse as growth, running, nerve conduction, blood circulation, tissue repair, and thermoregulation can all be expressed in units of energy. Thus their costs can be summed to estimate a total cost of life for the individual, and the impact of a whole population on an ecosystem can be determined by multiplication of the cost per individual by the number of individuals present. Few, if any, other properties come close to energy in their potential to serve as common currencies in this way.

## POSTSCRIPT:

### The Energy Cost of Mental Effort

Not the least of the energy costs of analyzing complex systems is the cost of operating our brain. This cost has some most interesting and unexpected properties, however. From studies of tissue metabolic rates, we know that the human brain accounts for about 20% of resting metabolic rate; loosely put, a fifth of our food is for our brain when we are at rest. This cost resembles an “idling” cost; the energy is expended whether we subjectively feel we are doing hard mental labor or not. The prominent physiologist Francis Benedict (1870–1957) wanted to know how much, exactly, the brain’s energy needs increase with mental “effort.” So, of course, he recruited a group of college students to find out. He told the students on one occasion to sit for tens of minutes keeping their minds as blank as possible. Then he had them spend an equal amount of time working mental arithmetic problems at a fevered pace. Measures of their metabolic rates under the two conditions indicated that the increase in energy consumption caused by an hour of hard mental effort is slight, equivalent to the energy of half a peanut! Thus the brain’s high costs are largely steady costs, and thinking hard is not a way to stay slim.

## Study Questions

- Assuming that 10 people plan to trek 500 miles to the North Pole, outline the steps you would take to calculate the amount of food they should pack, taking into account the number of sled dogs needed and the food needed for the dogs.
- Suppose you use a tire pump to inflate a tire on a bicycle. The elevated pressure created in the tire represents a form of potential energy because the release of the pressure can do mechanical work (such as making a pinwheel turn). The potential energy in the tire is derived from chemical-bond energy in your food. Trace the energy from the time it enters your mouth at a meal until it ends up in the tire, identifying losses of energy as heat along the way.

<sup>14</sup> Feed accounts for 60% to 75% of a farmer’s costs.

3. Define *absorbed energy* (*assimilated energy*). Then list the major categories of use of absorbed energy, and specify the fate of energy used in each category. Explain rigorously why heat is a fate of energy used in any and all categories.
4. Small animals tend to expire sooner than related large ones if forced to live on stored supplies. For instance, suppose you have a mouse and a dog that both start with body stores of fat equal to 20% of body weight. Explain why the mouse would be likely to die sooner if these animals could not find any food and thus had to live on their fat reserves. Which one would die sooner if they were trapped underwater and had only their stores of O<sub>2</sub> to live on while trying to escape?
5. Suppose that over a period of 4 hours, a dog was observed to consume 20 L of O<sub>2</sub> and produce 14 L of CO<sub>2</sub>. Making use of Tables 5.1 and 5.2, estimate the dog's total heat production over the 4 hours. Explain why Table 5.2 is relevant to your calculation.
6. Poultry scientists are doing research on the design of diets that are nutritionally complete for chickens but minimize the SDA. These scientists believe that such diets would be particularly helpful to the poultry industry in southern states during the heat of summer. Why might this be true?
7. Before Mayer and Joule came along (see Box 5.1), people were well aware that if a person cranked a drill or the like, heat appeared. For instance, the drilling of the bores of cannons was legendary for the heat produced. However, heat per se was believed to be neither created nor destroyed, and thus no one thought that the motion associated with drilling *turned into* heat. Mayer and Joule go down in history in part because they demonstrated the real relation between motion and heat. Suppose that you were alive in the early nineteenth century and, like Mayer and Joule, you hypothesized that animal motion could turn into heat. Design an experiment that would provide a rigorous test of your hypothesis.
8. Suppose you are measuring the metabolic rate of a young, growing cow by using the material-balance method. What procedures could you use to take account of the cow's growth, so that you measure a correct metabolic rate?
9. Suppose you have measured the average rate of O<sub>2</sub> consumption of two groups of laboratory rats that are identical, except that one group was injected with a hormone that is being tested to see if it affects metabolic rate. If the hormone-treated group has a rate of O<sub>2</sub> consumption 5% higher than the other, there are physiological reasons why you cannot conclude that the hormone has changed the metabolic rate. Explain, referring to Table 5.1. According to the table, what might the hormone have done to change the rate of O<sub>2</sub> consumption without changing the metabolic rate?
10. Only eight species of existing land mammals grow to adult body weights over 1000 kg (1 megagram). All are herbivores that employ fermentative digestion. These "megaherbivores" are the two species of elephants, the four species of rhinos, the hippo, and the giraffe. What are the metabolic pros and cons of such large size? Can you suggest why no terrestrial carnivores achieve such large size?
11. If there are many species of herbivores in a grassland ecosystem, and if the species as populations are equally competitive in acquiring food, predict  $b$  in the following allometric equation: population biomass per square kilometer =  $aW^b$ , where  $W$  is individual body weight. Do the data in Table 5.5 follow your equation? What hypotheses are suggested by the comparison?

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- See also references in Appendix A.*