

# Energy Metabolism

In 1986 explorers set out to reach the North Pole by dogsled from Ellesmere Island at latitude  $83^\circ$  north. Their objective was to make the journey without 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 sleds needed to be pulled and pushed over numerous ice ridges 20–60 feet high on the way to the pole. Even during progress over level ice fields, the way for the sleds' runners had to be cleared by the explorers often. 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. 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? If you yourself were planning an Arctic expedition, how would you use physiological principles to predict your energy needs and calculate the amount of food to pack on your sleds?

**Energy metabolism**, the subject of this chapter, is the sum of the processes by which animals acquire energy, channel energy into useful functions, and dissipate energy from their bodies. Energy metabolism 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.

## 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 is (see page 11).

The **second law of thermodynamics**, one of the greatest achievements of intellectual history, provides fundamental

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





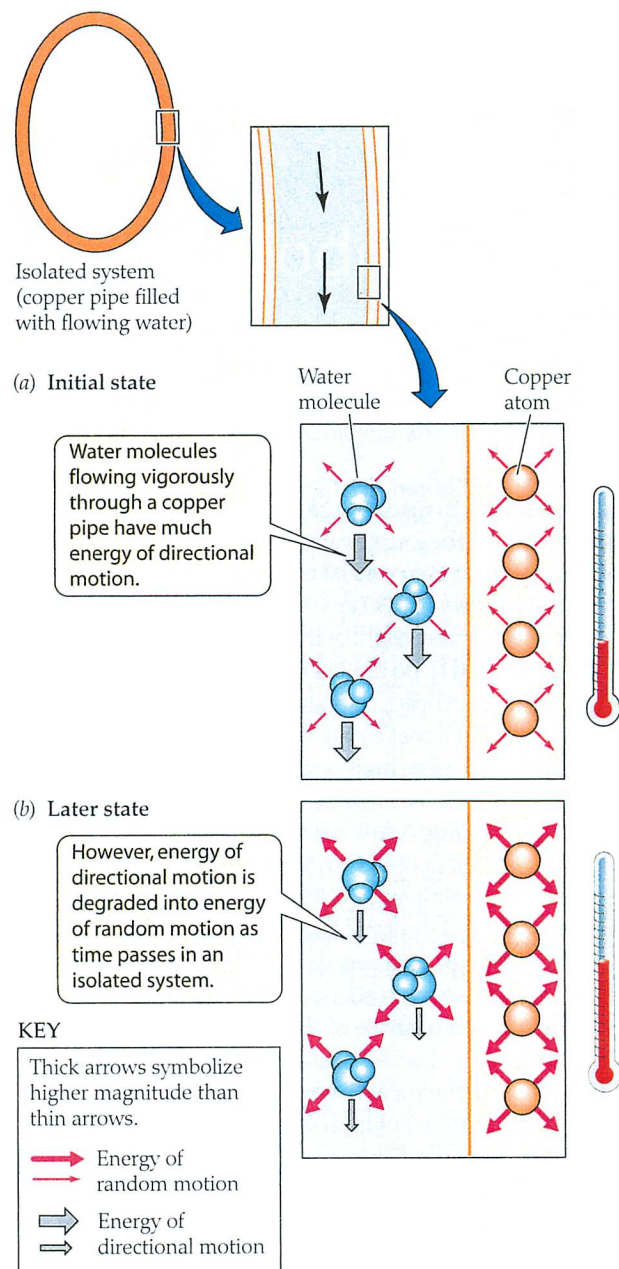
insight into the nature of organized systems. The law applies to **isolated systems**. An isolated system is a part of the material universe that exchanges nothing—neither matter nor energy—with its surroundings. Animals, you will recognize, are not isolated systems. In fact, true isolated systems are 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, being isolated, exchanges no energy or matter with its surroundings. Let’s focus on the motions of atoms and molecules *on an atomic-molecular scale*. Initially, the distribution of atomic-molecular motions in this system is highly nonrandom, because each water molecule is moving in an ordered way in its direction of travel around the loop of pipe (Figure 7.1a). In addition, all of the water molecules—and all of the copper atoms in the walls of the pipe—are also undergoing ceaseless random motions on an atomic-molecular scale.<sup>1</sup>

As time passes in this system, the energy of *directional* motion of the water molecules is gradually transformed into energy of *random* motion (Figure 7.1b). This transformation occurs because each time 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 molecules with which they collide. Over time, the rate of flow of water around the loop of pipe gradually decreases as energy of directional motion is lost in this way. Simultaneously, a gradual increase occurs in the energy of random molecular agitation (heat), and the temperature of the system rises. Eventually, all the energy of directional motion is lost, and the flow of water comes to a halt. At that point the water molecules and copper atoms in the system display only 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 maintain the original order in the 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



**FIGURE 7.1** The second law of thermodynamics in action Energy of directional motion is converted to energy of random motion in this isolated system. This transformation of energy increases the intensity of random motions of both the water molecules and the copper atoms, causing the system temperature to rise.

create order in the system as rapidly as processes within the system tend 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 a 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; eventually, therefore, many molecules 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

<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 within the material substance of the object.



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 separation of positive and negative electrical charges. All cell membranes possess electrical energy because there is charge separation across them (see Figure 5.10). 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 its 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 (nonrandomness), 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. Consider, however, a physical system that has a uniform temperature. The purely random molecular motions that exist throughout such a system cannot do work. 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 10, 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 energy transformation** is defined as follows:

$$\text{Efficiency of energy transformation} = \frac{\text{output of high-grade energy}}{\text{input of high-grade energy}} \quad (7.1)$$

The efficiency of energy transformation is typically much less than 1. For example, when a cell converts chemical-bond energy of 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%—which started as high-grade energy—becomes low-grade energy: heat. When, in turn, a muscle cell uses the chemical-bond energy of ATP to contract, typically a maximum of only 25%–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 (a type of 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%–30%. Even then, 70%–75% of the energy liberated from ATP in the process would become heat inside your body, rather than producing external motion.

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.

<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.



Thus, with each step an animal takes to use the high-grade energy in its food, the resource shrinks, just as each move of the hapless jungle explorer lowers his body farther into the quicksand.

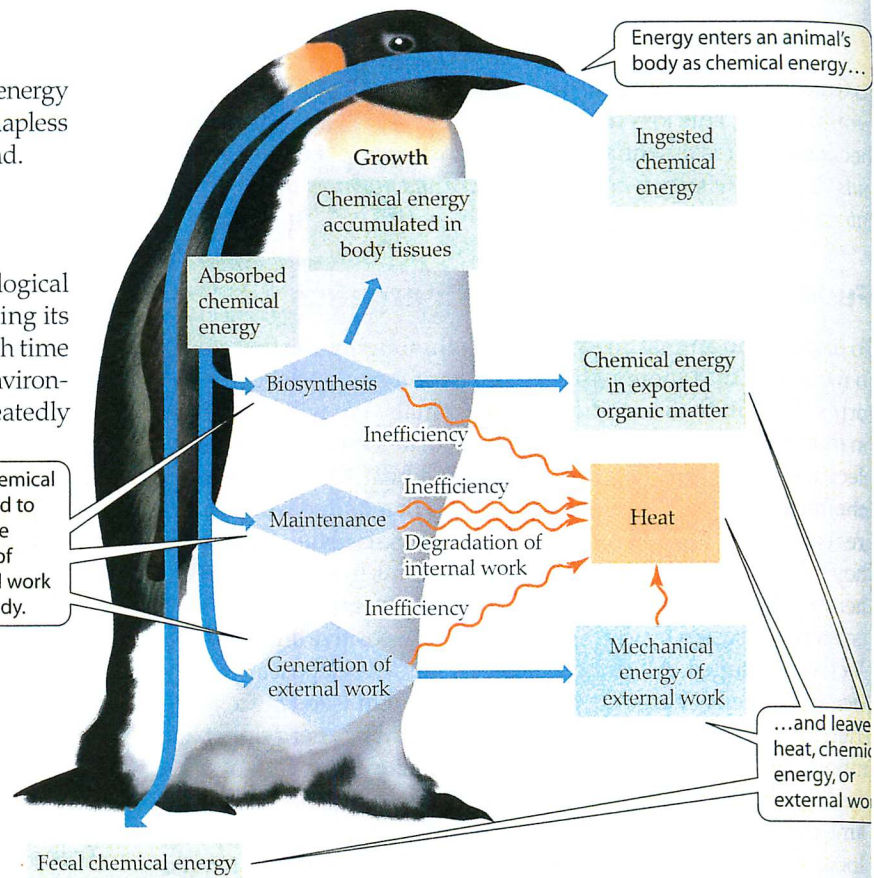
### Animals use energy to perform three major functions

It can be helpful to visualize the energy used for physiological work as a resource that “flows” through an animal during its lifetime (Figure 7.2). From the viewpoint of energetics, each time an animal eats, it gains chemical energy from its external environment. Chemical energy, therefore, enters an animal repeatedly throughout life. This energy, the energy in the chemical bonds of food, is known as the animal’s **ingested chemical energy** or **ingested energy**. Forms of energy derived from the ingested energy later pass back into the external environment.

If we follow ingested energy after it is first taken into an animal’s body, we find that although some of the ingested energy is absorbed, some is not. This distinction parallels the principle—emphasized in Chapter 6—that some chemical compounds in foods can be successfully digested (or fermented) and absorbed into the bloodstream, whereas others cannot. Ingested compounds that an animal is unable to absorb are egested in the feces. The chemical-bond energy in these compounds is known as the animal’s **fecal chemical energy** or **fecal energy** (see Figure 7.2). By contrast, the chemical-bond energy of the organic compounds that are absorbed (or assimilated) is known as the animal’s **absorbed chemical energy** or **absorbed energy** (or **assimilated chemical energy**).<sup>3</sup> The absorbed energy from ingested food is the energy that is distributed to the animal’s living tissues and that therefore is made available to the animal’s cells for use in physiological work.

An animal uses its absorbed chemical energy to carry out three major types of physiological work. As we discuss these, note that Figure 7.2 diagrams many of the points made.

1. **Biosynthesis.** An animal synthesizes its body constituents, such as its proteins and lipids, by use of absorbed energy. As this process—called **biosynthesis**—takes place, some of the absorbed energy that is used *remains in chemical form* because the products of biosynthesis are organic molecules with significant chemical-energy content. During *growth*, chemical energy accumulates in the body in the form of biosynthesized products that are used to assemble new cells and tissues. 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 fasting or starvation; ultimately, all of the chemical energy accumulated in body tissues becomes food for predators or decay organisms when the animal dies. In addition to 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 with
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 as an example. First, the chemical-bond energy of the absorbed food molecules that are used as fuel must be converted into chemical-bond energy of ATP, and energy is lost as heat in the process because of the inefficiency of ATP synthesis discussed previously. Additional energy is then 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, however, in overcoming the viscous resistances that oppose the motion of the blood through the blood vessels. Mechanical work



**FIGURE 7.2** The uses of energy by an animal At death, chemical energy in body tissues becomes ingested energy for other organisms.

<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.



that takes place *inside an animal's body* is termed **internal work**. Several maintenance functions, such as the circulation of the blood and gut motility, are types of internal work. The energy of internal work is 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 drive muscle contraction). However, when external work is performed, 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.* When a bicyclist ascends to the top of a hill, as in **Figure 7.3**, 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. (When the bicyclist later descends, this potential energy of position is converted into mechanical energy [motion downhill] and then to heat.) By contrast, consider horizontal motion. 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 7.2), we see that *all uses of energy by animals generate heat*. All living animals, therefore, produce heat. Because frogs, fish, clams, and other poikilotherms are often cool to the touch, one can get the erroneous impression that they do not produce heat.



**FIGURE 7.3** In this type of external work, some of the energy driving locomotion is converted to potential energy of position. As this bicyclist goes uphill, although much of his mechanical energy of external work becomes heat, a fraction is stored as potential energy because he is propelling the mass of his body and bicycle higher in Earth's gravitational field.

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 they produce (see page 256). Animal heat, which is universal, has been studied for centuries—far longer than most physiological phenomena—and these studies have led to fundamental discoveries about the nature of life (**Box 7.1**).

## BOX 7.1 VIEWS ON ANIMAL HEAT PRODUCTION

**H**eat 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 in a completely opposite way. 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 first 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  $\text{CO}_2$  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 that 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  $\text{O}_2$  use. Not until 1837 did Heinrich Gustav Magnus show that the blood takes  $\text{O}_2$  from the lungs to the rest of the body and returns  $\text{CO}_2$ . 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  $\text{O}_2$ .

The discovery that all tissues use  $\text{O}_2$  and produce heat was one of several lines of thought and investigation that came together in the nineteenth century to give birth to 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, was probably the first person to conceptualize the true nature of animal energy transformations, as described in this chapter.



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 to 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 do animals need to obtain food energy regularly throughout their lives? When an animal ingests and uses totipotent chemical-bond energy, it converts much of the energy in a one-way, irreversible fashion to heat, which is useless for physiological work. Accordingly, as the 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 progressively to heat by plants as well as animals, meaning that new photon energy is required if organic 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.
- 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 to its environment (see Figure 7.2). The energy that an animal converts to heat and external work is defined by physiologists to be **consumed** because that energy is “spent” or “exhausted”: The heat cannot be used at all to do physiological work, and the energy of external work—far from being totipotent—(1) can be used for only a narrowly defined function (the specific external work performed) and (2) soon will itself become heat in most cases.

The *rate* at which an animal consumes energy is its **metabolic rate**. That is, an animal's metabolic rate is the rate at which it converts chemical energy to heat and external work. *Heat is always the dominant component of the metabolic rate*. Accordingly, for simplicity we will sometimes speak of metabolic rates as rates of heat production. Energy is measured in *calories* or *joules*. Metabolic rates, therefore, are expressed in *calories per unit of time* or *watts* (Box 7.2).

## BOX 7.2 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 all other forms 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, an unfortunate system often producing confusion. In the United States, the “calories” listed in formal nutrition labels for foods (see the figure) are kilocalories. To illustrate the sorts of confusion that arise, note in the figure that “calorie” is capitalized at the top of the label but not at the bottom, which would be correct only if the meaning at the top were a unit 1000 times greater than at the bottom. Popular books and periodicals sometimes write “calorie” with a lowercase c when they mean kilocalorie, a

practice that creates three orders of magnitude of ambiguity. 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 of 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 A discusses 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 incandescent light bulb.

| Nutrition Facts                          |     |
|------------------------------------------|-----|
| Serving Size 1 Package (283g)            |     |
| Servings Per Container 1                 |     |
| Amount Per Serving                       |     |
| <b>Calories 270</b> Calories from Fat 20 |     |
| % Daily Value*                           |     |
| Total Fat 2g                             | 3%  |
| Cholesterol less than 5mg                | 1%  |
| Sodium 790mg                             | 33% |
| Total Carbohydrate 52g                   | 17% |
| Dietary Fiber 2g                         | 10% |
| Sugars 5g                                |     |
| Protein 11g                              |     |

\* Percent Daily Values are based on a 2,000 calorie diet.

**A nutrition label for frozen macaroni and cheese sold in the United States** In most parts of the world, energy values are given in unambiguous SI units.



At the start of this chapter, we raised the question of how one could predict the food needs of people and sled dogs during a polar expedition. The *metabolic rates* of the people and dogs are the basis for making this prediction. Knowing the average metabolic rates of the people and dogs, one can calculate how much chemical energy they will need per day and then calculate the total food energy they will require for all the days of their trek.

Speaking broadly, metabolic rates are significant for three principal reasons:

1. An animal's metabolic rate is one of the most important determinants of *how much food it needs*. For an adult, food needs depend almost entirely on metabolic rate.
2. Because every energy-using process that takes place in an animal produces heat, an animal's metabolic rate—its *total rate of heat production*—provides a *quantitative measure of the total activity of all its physiological mechanisms*. An animal's metabolic rate, roughly speaking, represents the animal's *intensity* of living.
3. Ecologically, an animal's metabolic rate measures the *drain the 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 its ecosystem.

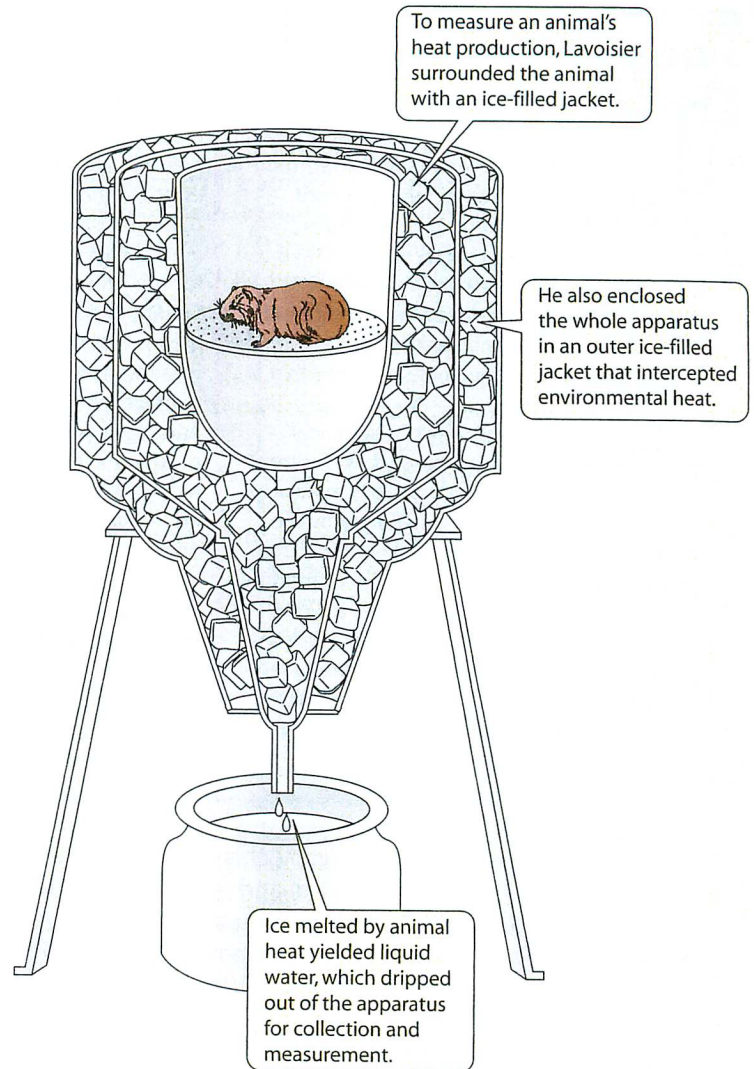
### Direct calorimetry: The metabolic rate of an animal can be measured directly

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 7.3). Although modern direct calorimeters are technically complex instruments, the basic operation of a direct calorimeter is illustrated nicely by the device that Antoine Lavoisier used in the very first measurements of animal heat production (Figure 7.4). The heat produced by the test animal melted ice in an ice-filled jacket surrounding the animal, and Lavoisier collected the melt water over measured periods of time. By knowing the amount of heat required to melt each gram of ice, he was able to calculate the animal's rate of heat output, and thus its metabolic rate.

For measures of metabolic rate by direct calorimetry to be fully accurate, external work—not just heat—sometimes must be considered. If the animal under study is at rest, it is not performing external work; a measurement of heat production alone is then fully sufficient for measuring the animal's metabolic rate. If the animal *is* performing external work, the energy of the external work is often rapidly degraded to heat; this is true, for example, if the animal merely moves around horizontally. In such cases, a measure of heat production includes the energy of external work; again, therefore, a measurement of heat production alone is fully sufficient for measuring the metabolic rate. However, if the test animal is performing external work and some of the energy of its external work fails to be converted to heat because it is stored, that energy must be measured independently and added to heat production to quantify the animal's metabolic rate accurately 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 7.3). Biologists today



**FIGURE 7.4** 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, which prevented the environmental heat from melting the same ice as the animal heat. 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.)

usually measure metabolic rates indirectly because the methods of 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 ( $O_2$ ) 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 oxidation reaction occurring in a test tube. If a mole

<sup>4</sup>Additional methods of indirect calorimetry that are used for active or free-living animals are discussed in Chapter 9.



## BOX 7.3 DIRECT MEASUREMENT VERSUS INDIRECT MEASUREMENT

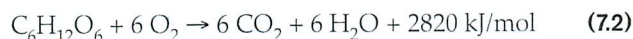
The distinction between *direct* and *indirect* methods of measurement is one of the most fundamental and important concepts in the science of measurement. Direct and indirect methods give results that can be expressed in the same units; a metabolic rate, for example, can be written down in watts whether 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** actually measures the *very properties that are specified by the definition of a trait*. An animal's metabolic rate, for example, is defined to be its rate of production of heat and external work. Thus a direct method of measuring metabolic rate actually measures heat and external work. Direct methods are the *gold standards* of measurement because their results relate unambiguously to the trait being studied.

By contrast, an **indirect method of measurement** actually measures *properties that are different from those specified by the definition of a trait*. The properties that are actually measured 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 crucial 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 indirect regardless of the units in which it is ultimately expressed.

Why is the distinction between direct and indirect methods important? 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 measures something different from what is stated by the definition. The accuracy of an indirect method is assessed by determining how well its results agree with a direct method. Whereas indirect methods often have *practical* advantages, they are usually less accurate than direct ones, at least under certain circumstances. Thus the choice of method involves a compromise. In the measurement of metabolic rate, the indirect methods commonly introduce uncertainties of  $\pm 1\text{--}5\%$  in the results, but they might reduce costs of time and money by tenfold, making them attractive.

of glucose (C<sub>6</sub>H<sub>12</sub>O<sub>6</sub>) is burned completely, chemical stoichiometry dictates that 6 moles of O<sub>2</sub> will be used, and 6 moles of CO<sub>2</sub> 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 per mole (kJ/mol), or 673,000 calories per mole (cal/mol). The following equation therefore applies:



Note that when glucose is oxidized, a fixed proportional relation exists between the amount of heat produced and the amount of O<sub>2</sub> used: 2820 kJ of heat per 6 mol of O<sub>2</sub>. Similarly, a fixed proportional relation exists between heat production and CO<sub>2</sub> production: 2820 kJ per 6 mol of CO<sub>2</sub>. Knowing these relations, if you oxidize an *unknown* quantity of glucose in a test tube and you measure only the amount of O<sub>2</sub> used, or only the amount of CO<sub>2</sub> 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 in the animal are 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 oxidizes glucose to CO<sub>2</sub> and H<sub>2</sub>O, the stoichiometry in Equation 7.2 applies to the animal. Accordingly, if you measure either the animal's O<sub>2</sub> consumption or its CO<sub>2</sub> production, you can calculate the animal's heat production. This is the rationale for estimating animal metabolic rates from rates of respiratory exchange of O<sub>2</sub> and CO<sub>2</sub>.

**Table 7.1** lists conversion factors for calculating the amount of heat generated when a milliliter of O<sub>2</sub> is consumed or a milliliter

of CO<sub>2</sub> is produced.<sup>5</sup> To understand how to use the table, imagine that an animal consumes O<sub>2</sub> at a rate of 10 mL/minute (min), 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 O<sub>2</sub>/min  $\times$  21.1 J/mL O<sub>2</sub> = 211 J/min.

As you can see from Table 7.1, 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<sub>2</sub>

<sup>5</sup>According to universal convention, gas volumes in metabolic studies are expressed at Standard Conditions of Temperature and Pressure (STP). That is the way they are expressed in this chapter and throughout this book. For more information, see Appendix C.

**TABLE 7.1** Ratios of heat production to O<sub>2</sub> consumption, and heat production to 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, STP (see Appendix C).

| Foodstuff             | Heat produced per unit of O <sub>2</sub> consumed (J/mL O <sub>2</sub> ) | Heat produced per unit of 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; the values tabulated here apply to mammals and other animals in which urea is the dominant nitrogenous end product.



consumption (or from CO<sub>2</sub> production) is not a simple, fixed number. Instead, the conversion factor for calculating heat production varies depending on the foodstuffs being oxidized. If animals were to oxidize only glucose, calculating their metabolic rates by measuring their rates of O<sub>2</sub> consumption would be unambiguous, as we have already seen. However, animals oxidize a *variety* of foodstuffs, which yield *different* quantities of heat per unit of volume of O<sub>2</sub> consumed (or CO<sub>2</sub> produced; see Table 7.1). This consideration introduces the possibility of ambiguity or inaccuracy. Returning to our previous example, we saw that if an animal consumes O<sub>2</sub> at a rate of 10 mL O<sub>2</sub>/min, its metabolic rate is 211 J/min (10 mL/min × 21.1 J/mL) if its cells are oxidizing carbohydrates. Its metabolic rate is only 198 J/min, however, if its cells are oxidizing lipids (10 mL/min × 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) unless the investigator knows the exact mixture of foodstuffs that the study animal's cells are oxidizing.

An animal's recent diet often does 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*. One useful index of this sort is obtained by simultaneously measuring both 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. Under many circumstances, *R* and *RQ* are equal, and we limit our discussion here to that straightforward situation.

The value of *R* (and *RQ*) is, in essence, a metabolic signature that reveals the particular sorts of foodstuffs being oxidized by an animal's cells (Table 7.2). If an animal exhibits a value of *R* near 1.0, for example, its cells are likely oxidizing mostly carbohydrates. However, if the 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 7.1 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>.

**TABLE 7.2 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 value listed for proteins 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.

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 measuring 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 about 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. This conversion factor approximates the heat produced by an animal that is assumed to be catabolizing a representative mixture of carbohydrates, lipids, and proteins. Using the representative conversion factor 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 the animal is actually oxidizing only carbohydrates. Because the true conversion factor (for carbohydrates) is 21.1 J/mL O<sub>2</sub>, the investigator will underestimate the metabolic rate by 4.5% by using the approximate factor of 20.2 J/mL O<sub>2</sub>. If the animal is oxidizing only proteins, the true conversion factor (see Table 7.1) is 18.7 J/mL O<sub>2</sub>; thus the investigator will 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 ±5–8% 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 ±5–8% may not be much of a worry.<sup>6</sup>

Among all the methods available to measure metabolic rate, by far the most common approach used today for routine 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 often expressed simply as rates of O<sub>2</sub> consumption. The O<sub>2</sub> consumption method has four notable advantages: Two of these, already mentioned, are its technical ease of accomplishment (Box 7.4) and its relatively small inherent uncertainty under many conditions. A third advantage is that external work does not, in most cases, have to be measured independently when the O<sub>2</sub> consumption method is used. Because the O<sub>2</sub> consumption of an animal is proportional to the ultimate yield of heat from the foodstuffs it aerobically catabolizes, the heat equivalent of any aerobic external work performed by the animal is included in the metabolic rate calculated from its O<sub>2</sub> consumption. The fourth advantage of the O<sub>2</sub> consumption method is that it excludes the metabolism of microbes in the gut (the gut microbiome) because those microbes are anaerobic and do not consume O<sub>2</sub>.

<sup>6</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: ±15–20%. You can see the principal reason in Table 7.1; 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.



## BOX 7.4 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<sub>2</sub> consumption. In **Box Extension 7.4**, you will find illustrations and explanations of the two basic types of respirometry configurations that are used to measure O<sub>2</sub> consumption: (1) *closed* configurations, in which an animal is housed in a fully sealed chamber with a relative fixed volume of nonmoving air and (2) *open* configurations, in which the animal draws its O<sub>2</sub> from an air stream flowing by during measurement.

Regardless of how large and metabolically active the gut microbial populations may be, the method measures just the metabolic rate of the animal tissues.

Related to the points just made, a limitation of the O<sub>2</sub> consumption method—and a vital point to keep in mind—is that an animal's metabolic rate will not be measured accurately if some or all of the animal's tissues are employing anaerobic mechanisms of catabolism to release energy. As discussed in Chapter 8, for example, anaerobic ATP production is used often by skeletal muscles during sudden, highly intense exercise in people and many other sorts of animals. To measure an animal's metabolic rate during anaerobically fueled exercise, one must turn to more-elaborate methods than just measuring O<sub>2</sub> consumption.

**INDIRECT CALORIMETRY BASED ON MATERIAL BALANCE** In addition to 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 one measures the chemical-energy content of *organic materials* entering and leaving an animal's body. This approach, which is widely used in agricultural 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.<sup>7</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 ways other 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.

<sup>7</sup>An instrument known as a *bomb calorimeter* is used to measure the energy values of organic materials. It does this by burning them explosively in pressurized, pure O<sub>2</sub> and measuring the heat evolved.

To use the material-balance method, measurements of ingestion, egestion, and other relevant processes must extend over a substantial period—typically 24 h or more—so that average, steady-state rates of input and output of chemical energy are 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 of average metabolic rates*. To measure minute-by-minute variations in metabolic rate, the methods of choice are those based on respiratory gas exchange or direct calorimetry.

## SUMMARY Metabolic Rate: Meaning and Measurement

- 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. An animal's metabolic rate also provides a quantitative measure of the total activity of all its physiological mechanisms.
- 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

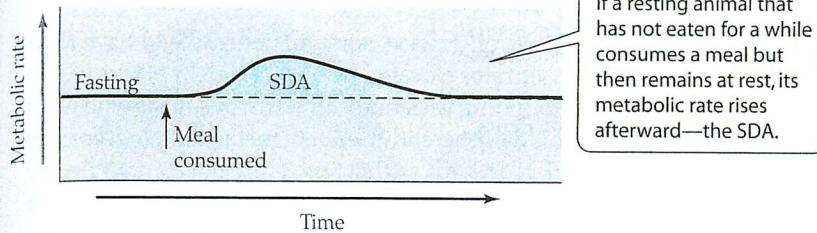
Now that we have discussed how metabolic rates are defined and measured, we can turn our attention to the experiences of animals and the processes within them that influence their metabolic rates. The two factors that typically exert the greatest effects on an animal's metabolic rate are the intensity 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 7.3** provides an overview of many of these factors and identifies where they are discussed in this book.

### Ingestion of food causes metabolic rate to rise

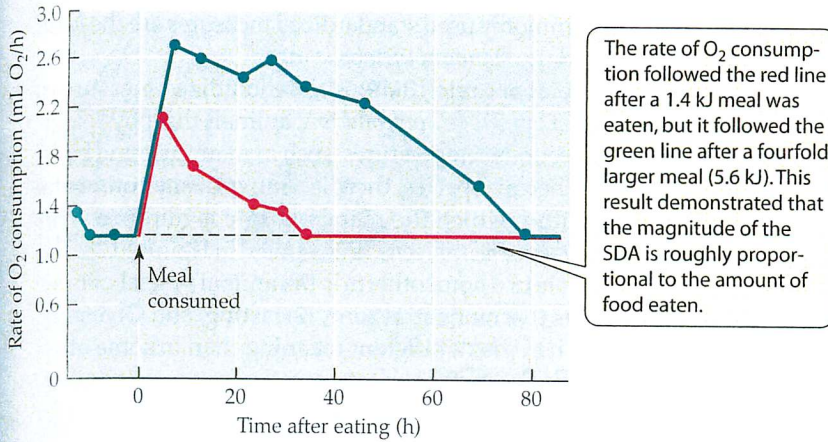
Among the factors that affect metabolic rate, the ingestion of food deserves some extended consideration—even though it is not the most influential factor quantitatively—because it must be taken into account in almost all metabolic studies. Under many circumstances, if an animal has not eaten for a while 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 7.5)**. Although we ourselves may often not notice this process in our day-to-day lives, 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 turkey 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) The concept of SDA



(b) SDA in flatfish



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

**FIGURE 7.5 Specific dynamic action (SDA)** (a) Following a meal, the SDA begins after a delay, which may be up to 1 h. 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 SDA. The timing of the process varies enormously; the SDA might be over in a few hours in a mouse, in 12 h in a cow, and in 1–3 days in a fish. "Fasting" in such studies means the animal has not eaten for long enough that the SDA of the last meal is over. (b) Actual data for predatory flatfish (*Pleuronectes*) fed two different-sized meals of fish meat. The apparent absence of a delay in the beginning of the SDA is an artifact of the sampling schedule: Data were not gathered in the immediate aftermath of feeding, when the delay would have been evident. (b after Jobling 1993.)

background level. Thus the blue area in Figure 7.5a, 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 that occurs 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 (see Figure 7.5b): 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 do lipids or carbohydrates. Traditionally the SDA of a protein meal has been considered to be equivalent to 25%–30% of the total energy value of the meal. Recent research indicates, however, that the percentage (while virtually always high) can vary considerably with prevailing conditions.

**TABLE 7.3** Some factors that affect the metabolic rates of individual animals

| Factor                                               | Response of metabolic rate                                                                                                                                                                                                                  | Chapter(s) where discussed in this book |
|------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------|
| <b>Factors that exert particularly large effects</b> |                                                                                                                                                                                                                                             |                                         |
| Physical activity level (e.g., running speed)        | ↑ with rising activity level                                                                                                                                                                                                                | 8, 9                                    |
| Environmental temperature                            | <i>Mammals and other homeotherms:</i><br>Lowest in thermoneutral zone<br>↑ below thermoneutral zone<br>↑ above thermoneutral zone<br><i>Fish and other poikilotherms:</i><br>↑ with increasing temperature<br>↓ with decreasing temperature | 10                                      |
| <b>Factors that exert smaller effects</b>            |                                                                                                                                                                                                                                             |                                         |
| Ingestion of a meal (particularly protein-rich)      | ↑ for several hours to many hours following ingestion                                                                                                                                                                                       | 7                                       |
| Body size                                            | Weight-specific rate ↑ as size ↓                                                                                                                                                                                                            | 7                                       |
| 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                                                                                                                                                                 | 8, 23                                   |
| Hormonal status                                      | Variable; example: ↑ by excessive thyroid secretions in mammals                                                                                                                                                                             | 16                                      |
| Time of day                                          | Variable; in humans, ↑ in daytime                                                                                                                                                                                                           | 15                                      |
| Salinity of water (aquatic animals)                  | Variable; in osmoregulating marine crabs, ↑ in dilute water                                                                                                                                                                                 | 28                                      |



The mechanism of SDA remains uncertain. Although digestive processes make a contribution, strong evidence exists that the SDA in most animals arises principally *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 associated 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.

In the last 20 years, after a long quiet spell in SDA research, the SDA has been “back in the news” of animal physiology. In some cases, new programs of research have focused on specializations of SDA physiology to particular challenges that animals face. For example, investigators have recently reported evidence that gray seals (*Halichoerus grypus*) dramatically postpone the SDA, compared with terrestrial mammals, when they are engaged in extended bouts of underwater hunting and feeding. In this way, it is argued, the seals prevent the SDA of their protein-rich food (mostly fish) from shortening their dive times by raising their metabolic requirements *during* dives. The postponed SDA occurs after a bout of hunting and feeding has ended. Another striking discovery is the exceptionally great rise in metabolic rate that occurs after feeding in snakes, notably pythons, that undergo long-term fasting, for weeks, from one meal to the next (see Box 6.2).<sup>8</sup>

The SDA is a relatively short-term phenomenon, but sometimes an animal’s diet induces a *semipermanent*, or *chronic*, change in its metabolic rate. Experiments have revealed that if laboratory rats are enticed to eat unusually large amounts of food day after day (as by adding 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 is 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 8 and 10.

## 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 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 h 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. Several 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 10.28. 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 term *fasting* here has a different meaning than in some other contexts. In studies of metabolic rate, **fasting** (or **postabsorptive**) means that a subject’s last meal took place sufficiently long ago for the SDA of the meal to be over.

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. Again, *fasting* signifies that the SDA of the last meal is over. An animal’s standard metabolic rate is specific for its prevailing body temperature; thus, for a given animal there are as many SMRs as there are different body temperatures.

Besides specifying a fasting state, both of the standardized measures of metabolic rate mentioned here call for subjects to be resting. The term *resting* can have somewhat different meanings in different studies because inducing animals to rest is often not simple. Specific 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; when they speak of *standard metabolic rate*, they refer to fish that have been coaxed to truly minimal levels of activity. In human medicine, *resting* means lying down but awake.

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

How does metabolic rate vary with body size within a set of phylogenetically related species? This simple question turns out to have a profoundly important, intricate answer. The study of the relation between metabolic rate and body size is known as the study of **metabolic scaling** or the **metabolism–size relation**.

A comparison between meadow voles and white rhinos provides a revealing starting point for understanding metabolic scaling (Figure 7.6). 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

<sup>8</sup> Although the dramatic post-feeding rise in metabolic rate in pythons and other snakes is considered to be a form of SDA in the literature, its causation may prove not to be entirely typical of SDA as seen in animals in general. When the snakes do not eat for a long time, they deconstruct their digestive apparatus (see Box 6.2). Costs of reconstructing the digestive apparatus are believed to be included in the post-feeding rise in metabolic rate.