40

Basic Principles of Animal Form and Function

▲ **Figure 40.1 How does a jackrabbit keep from overheating?**

KEY CONCEPTS

40.1 Animal form and function are correlated at all levels of organization
40.2 Feedback control maintains the internal environment in many animals
40.3 Homeostatic processes for thermoregulation involve form, function, and behavior
40.4 Energy requirements are related to animal size, activity, and environment

OVERVIEW

Diverse Forms, Common Challenges

The ears of the jackrabbit (*Lepus alleni*) in **Figure 40.1** are thin and remarkably large. They provide this hare with an acute sense of hearing, a primary defense against predators. The ears also help the jackrabbit shed excess heat. Blood flowing through each ear's network of vessels transfers heat to the surrounding air. However, when the air is warmer than the jackrabbit, blood passing through the ears could absorb heat, raising body temperature to a dangerous level. How, then, does a big-eared jackrabbit survive in the midday desert heat? To answer this question, we need to look more closely at the biological form, or **anatomy**, of the animal.

Over the course of its life, a jackrabbit faces the same fundamental challenges as any other animal, whether hydra, hawk, or human. All animals must obtain oxygen and nutrients, fight off infection, and produce offspring. Given that they share these and other basic requirements, why do species vary so enormously in makeup, complexity, organization, and appearance? The answer is adaptation: Natural selection favors those variations in a population that increase relative fitness (see Chapter 23). The solutions to the challenges of survival vary among environments and species, but they frequently result in a close match of form to function.

Because form and function are correlated, examining anatomy often provides clues to **physiology**—biological function. In the case of the jackrabbit, researchers noted that its large, pink-tinged ears turn pale when the air temperature exceeds 40°C (104°F), the normal temperature of the jackrabbit's body. The color change reflects a temporary narrowing of blood vessels in response to a hot environment. With their blood supply reduced, the ears can absorb heat without overheating the rest of the body. When the air cools, blood flow increases, and the large ears again help release excess heat.

In this chapter, we will begin our study of animal form and function by examining the levels of organization in the animal body and the systems for coordinating the activities of distinct body parts. Next, we will use the example of body temperature regulation to illustrate how animals control their internal environment. Finally, we will explore how anatomy and physiology relate to an animal's interactions with the environment and its management of energy use.

CONCEPT **40.1**

Animal form and function are correlated at all levels of organization

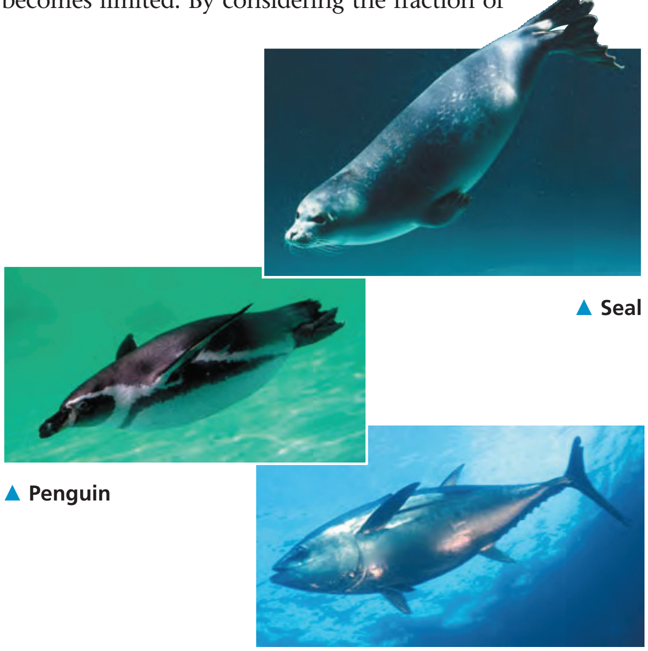
An animal's size and shape are fundamental aspects of form that significantly affect the way the animal interacts with its environment. Although we may refer to size and shape as elements of a "body plan" or "design," this does not imply a process of conscious invention. The body plan of an animal is the result of a pattern of development programmed by the genome, itself the product of millions of years of evolution.

Evolution of Animal Size and Shape

EVOLUTION Many different body plans have arisen during the course of evolution, but these variations fall within certain bounds. Physical laws that govern strength, diffusion, movement, and heat exchange limit the range of animal forms.

As an example of how physical laws constrain evolution, let's consider how some properties of water limit the possible shapes for animals that are fast swimmers. Water is about a thousand times denser than air and also far more viscous. Therefore, any bump on an animal's body surface that causes drag impedes a swimmer more than it would a runner or flyer. Tuna and other fast ray-finned fishes can swim at speeds up to 80 km/hr (50 miles/hour). Sharks, penguins, dolphins, and seals are also fast swimmers. As is apparent in the examples in **Figure 40.2**, such animals share a streamlined body contour: a shape that is fusiform, meaning tapered on both ends. The similar shape found in these speedy vertebrates is an example of convergent evolution (see Chapter 22). Natural selection often results in similar adaptations when diverse organisms face the same environmental challenge, such as overcoming drag during swimming.

Physical laws also influence animal body plans with regard to maximum size. As body dimensions increase, thicker skeletons are required to maintain adequate support. This limitation affects internal skeletons, such as those of vertebrates, as well as external skeletons, such as those of insects and other arthropods. In addition, as bodies increase in size, the muscles required for locomotion must represent an ever-larger fraction of the total body mass. At some point, mobility becomes limited. By considering the fraction of body mass in leg muscles and the effective force such muscles generate, scientists can estimate maximum running speed for a wide range of body plans. Such calculations indicate that the dinosaur *Tyrannosaurus rex*, which stood more than 6 m tall, probably could reach speeds of 30 km/hr (19 miles/hour), about as fast as the fastest humans can run.



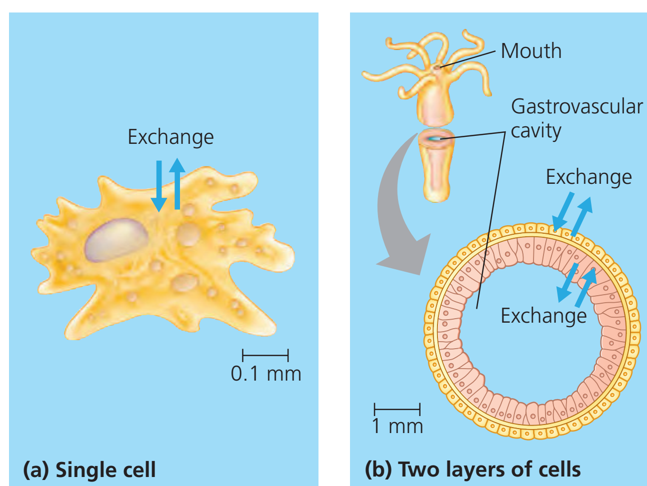
▲ **Figure 40.2 Convergent evolution in fast swimmers.**

Exchange with the Environment

Animals must exchange materials with their environment, and this requirement imposes limitations on their body plans (as it does for all multicellular organisms). Exchange occurs as substances dissolved in an aqueous solution move across the plasma membrane of each cell. The rates of exchange for nutrients, waste products, and gases are proportional to membrane surface area, whereas the amount of material that must be exchanged to sustain life is proportional to cell volume.

The opportunity for exchange depends on the number of cells in an organism's body. A single-celled organism, such as the amoeba in **Figure 40.3a**, has a sufficient membrane surface area in contact with its environment to carry out all necessary exchange. In contrast, an animal is composed of many cells, each with its own plasma membrane across which exchange must occur. A multicellular organization therefore works only if every cell has access to a suitable aqueous environment, either inside or outside the animal's body.

Many animals with a simple internal organization have body plans that enable direct exchange between almost all their cells and the external environment. For example, a pond-dwelling hydra, which has a saclike body plan, has a body wall only two cell layers thick **(Figure 40.3b)**. Because its



▲ **Figure 40.3 Contact with the environment. (a)** In a single-celled organism, such as an amoeba, the entire surface area contacts the environment. **(b)** Although all animals are multicellular, some have a simple organization in which all or nearly all cells contact the environment. For example, a hydra's body consists of two layers of cells. As fluid moves in and out of the hydra's mouth, every body cell can exchange material directly with the aqueous environment.

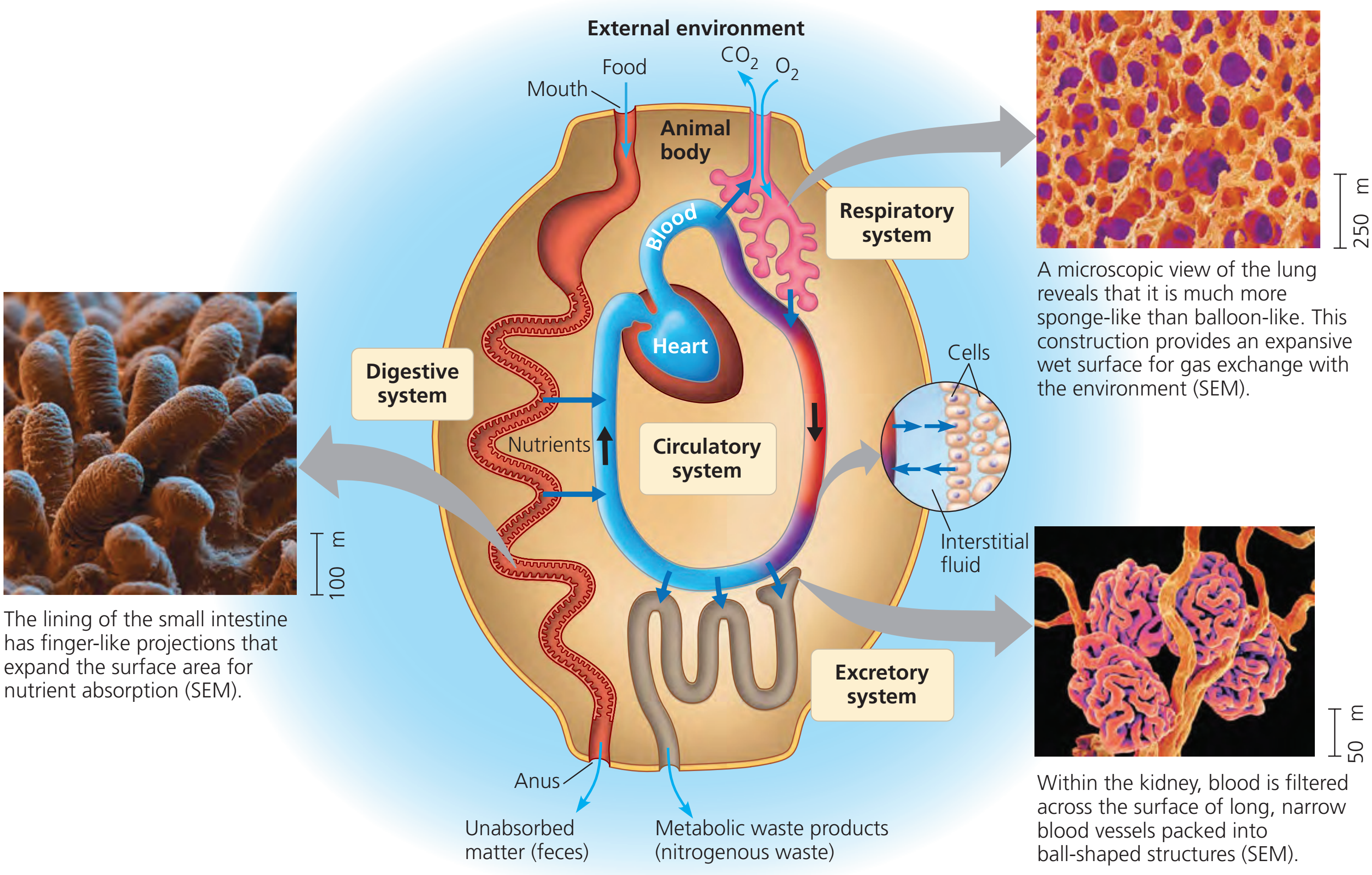
gastrovascular cavity opens to the external environment, both the outer and inner layers of cells are constantly bathed by pond water. Another common body plan that maximizes exposure to the surrounding medium is a flat shape. Consider, for instance, a parasitic tapeworm, which can reach several meters in length (see Figure 33.12). A thin, flat shape places most cells of the worm in direct contact with its particular environment—the nutrient-rich intestinal fluid of a vertebrate host.

The bodies of most animals are composed of compact masses of cells, with an internal organization much more complex than that of a hydra or a tapeworm. For such a body plan, increasing the number of cells decreases the ratio of outer surface area to total volume. As an extreme comparison, the ratio of outer surface to volume for a whale is hundreds of thousands of times smaller than that for a water flea (*Daphnia*). Nevertheless, every cell in the whale must be bathed in fluid and have access to oxygen, nutrients, and other resources. How is this accomplished?

In whales and most other animals, the evolutionary adaptations that enable sufficient exchange with the environment are specialized surfaces that are extensively branched or folded (**Figure 40.4**). In almost all cases, these exchange surfaces lie within the body, an arrangement that protects their delicate tissues from abrasion or dehydration and allows for streamlined body contours. In humans, the internal exchange surfaces of the digestive, respiratory, and circulatory systems each have an area more than 25 times that of the skin.

Internal body fluids link exchange surfaces to body cells. The spaces between cells are filled with fluid, in many animals called **interstitial fluid** (from the Latin for "stand between"). Complex body plans also include a circulatory fluid, such as blood. Exchange between the interstitial fluid and the circulatory fluid enables cells throughout the body to obtain nutrients and get rid of wastes (see Figure 40.4).

Despite the greater challenges of exchange with the environment, complex body plans have distinct benefits over simple



▲ **Figure 40.4 Internal exchange surfaces of complex animals.** This diagram provides an overview of chemical exchange between an animal body and the environment. Most animals have surfaces that are specialized for exchanging chemicals with the surroundings. These exchange surfaces are usually internal but are connected to the environment via openings on the body surface (the mouth, for example). The exchange surfaces are finely branched or folded, giving them a very large area. The digestive, respiratory, and excretory systems all have such exchange surfaces. The circulatory system carries chemicals transported across these surfaces throughout the body.

? *In what sense are exchange surfaces such as the lining of the digestive system both internal and external?*

ones. For example, an external skeleton can protect against predators, and sensory organs can provide detailed information on the animal's surroundings. Internal digestive organs can break down food gradually, controlling the release of stored energy. In addition, specialized filtration systems can adjust the composition of the internal fluid that bathes the animal's body cells. In this way, an animal can maintain a relatively stable internal environment while living in a changeable external environment. A complex body plan is especially advantageous for animals living on land, where the external environment may be highly variable.

Hierarchical Organization of Body Plans

Cells form a functional animal body through their emergent properties. Recall from Chapter 1 that emergent properties arise by way of successive levels of structural and functional organization. Cells are organized into **tissues**, groups of cells with a similar appearance and a common function. Different types of tissues are further organized into functional units called **organs**. (The simplest animals, such as sponges, lack organs or even true tissues.) Groups of organs that work together provide an additional level of organization and coordination and make up an **organ system** (**Table 40.1**). Thus, for example, the skin is an organ of the integumentary system, which protects against infection and helps regulate body temperature.

Many organs contain tissues with distinct physiological roles. In some cases, the roles are different enough that we consider the organ to belong to more than one organ system. The pancreas, for instance, produces enzymes critical to the function of the digestive system and also regulates the level of sugar in the blood as a vital part of the endocrine system.

Just as viewing the body's organization from the "bottom up" (from cells to organ systems) reveals emergent properties, a "top-down" view of the hierarchy reveals the multilayered basis of specialization. Consider the human digestive system: the mouth, pharynx, esophagus, stomach, small and large intestines, accessory organs, and anus. Each organ has specific roles in digestion. One function of the stomach, for example, is to initiate the breakdown of proteins. This process requires a churning motion powered by stomach muscles, as well as digestive juices secreted by the stomach lining. Producing digestive juices, in turn, requires highly specialized cell types: One cell type secretes a protein-digesting enzyme, a second generates concentrated hydrochloric acid, and a third produces mucus, which protects the stomach lining.

The specialized and complex organ systems of animals are built from a limited set of cell and tissue types. For example, lungs and blood vessels have distinct functions but are lined by tissues that are of the same basic type and that therefore share many properties.

There are four main types of animal tissues: epithelial, connective, muscle, and nervous. **Figure 40.5**, on the next three pages, explores the structure and function of each type. In later chapters, we'll discuss how the tissues described here contribute to the functions of each organ system.

Table 40.1 Organ Systems in Mammals

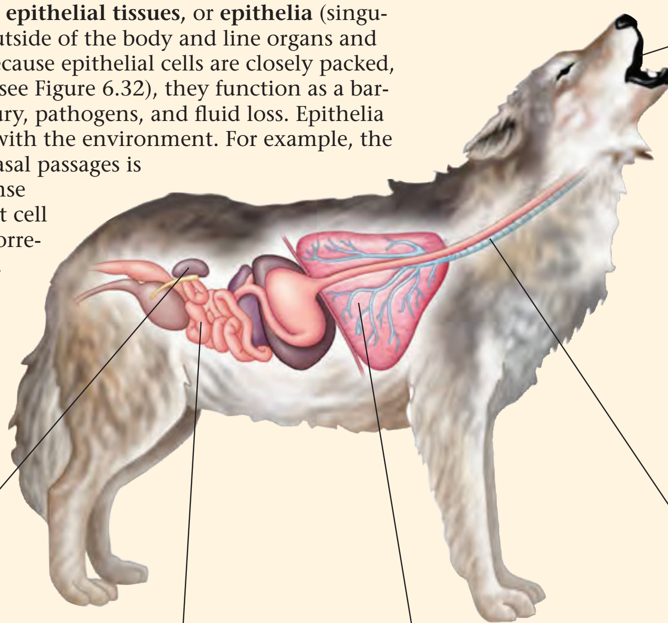
Organ System	Main Components	Main Functions
Digestive	Mouth, pharynx, esophagus, stomach, intestines, liver, pancreas, anus	Food processing (ingestion, digestion, absorption, elimination)
Circulatory	Heart, blood vessels, blood	Internal distribution of materials
Respiratory	Lungs, trachea, other breathing tubes	Gas exchange (uptake of oxygen; disposal of carbon dioxide)
Immune and lymphatic	Bone marrow, lymph nodes, thymus, spleen, lymph vessels, white blood cells	Body defense (fighting infections and cancer)
Excretory	Kidneys, ureters, urinary bladder, urethra	Disposal of metabolic wastes; regulation of osmotic balance of blood
Endocrine	Pituitary, thyroid, pancreas, adrenal, and other hormone-secreting glands	Coordination of body activities (such as digestion and metabolism)
Reproductive	Ovaries or testes and associated organs	Reproduction
Nervous	Brain, spinal cord, nerves, sensory organs	Coordination of body activities; detection of stimuli and formulation of responses to them
Integumentary	Skin and its derivatives (such as hair, claws, skin glands)	Protection against mechanical injury, infection, dehydration; thermoregulation
Skeletal	Skeleton (bones, tendons, ligaments, cartilage)	Body support, protection of internal organs, movement
Muscular	Skeletal muscles	Locomotion and other movement

▼ **Figure 40.5**

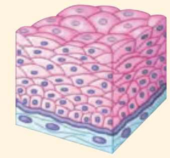
Exploring Structure and Function in Animal Tissues

Epithelial Tissue

Occurring as sheets of cells, **epithelial tissues**, or **epithelia** (singular, *epithelium*), cover the outside of the body and line organs and cavities within the body. Because epithelial cells are closely packed, often with tight junctions (see Figure 6.32), they function as a barrier against mechanical injury, pathogens, and fluid loss. Epithelia also form active interfaces with the environment. For example, the epithelium that lines the nasal passages is crucial for olfaction, the sense of smell. Note how different cell shapes and arrangements correlate with distinct functions.



Stratified squamous epithelium

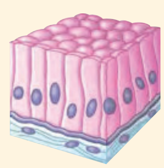


A stratified squamous epithelium is multilayered and regenerates rapidly. New cells formed by division near the basal lamina (see micrograph below) push outward, replacing cells that are sloughed off. This epithelium is commonly found on surfaces subject to abrasion, such as the outer skin and the linings of the mouth, anus, and vagina.

Cuboidal epithelium

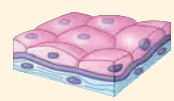
Cuboidal epithelium, with dice-shaped cells specialized for secretion, makes up the epithelium of kidney tubules and many glands, including the thyroid gland and salivary glands.

Simple columnar epithelium



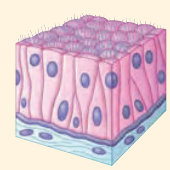
The large, brick-shaped cells of simple columnar epithelia are often found where secretion or active absorption is important. For example, a simple columnar epithelium lines the intestines, secreting digestive juices and absorbing nutrients.

Simple squamous epithelium

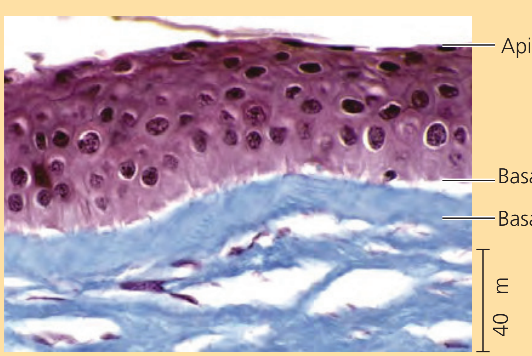


The single layer of platelike cells that form a simple squamous epithelium functions in the exchange of material by diffusion. This type of epithelium, which is thin and leaky, lines blood vessels and the air sacs of the lungs, where diffusion of nutrients and gases is critical.

Pseudostratified columnar epithelium



A pseudostratified epithelium consists of a single layer of cells varying in height. In many vertebrates, a pseudostratified epithelium of ciliated cells forms a mucous membrane that lines portions of the respiratory tract. The beating cilia sweep the film of mucus along the surface.



Polarity of epithelia

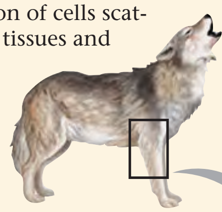
All epithelia are polarized, meaning that they have two different sides. The *apical* surface faces the lumen (cavity) or outside of the organ and is therefore exposed to fluid or air. Specialized projections often cover this surface. For example, the apical surface of the epithelium lining the small intestine is covered with microvilli, projections that increase the surface area available for absorbing nutrients. The opposite side of each epithelium is the *basal* surface. The basal surface is attached to a *basal lamina,* a dense mat of extracellular matrix that separates the epithelium from the underlying tissue.

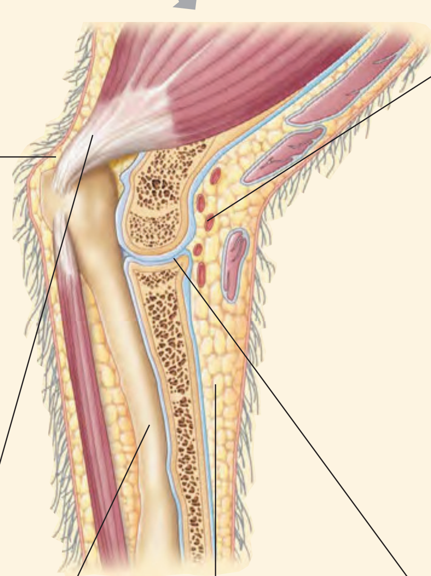
(All photos in figure are LMs.)

Connective Tissue

Connective tissue, consisting of a sparse population of cells scattered through an extracellular matrix, holds many tissues and organs together and in place. The matrix generally consists of a web of fibers embedded in a liquid, jellylike, or solid foundation. Within the matrix are numerous cells called **fibroblasts,** which secrete fiber proteins, and **macrophages,** which engulf foreign particles and any cell debris by phagocytosis (see Chapter 6).

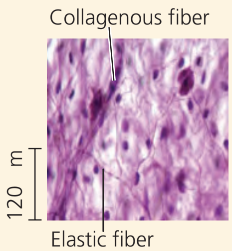
Connective tissue fibers are of three kinds: *Collagenous fibers* provide strength and flexibility, *reticular fibers* join connective tissue to adjacent tissues, and *elastic fibers* make tissues elastic. If you pinch a fold of tissue on the back of your hand, the collagenous and reticular fibers prevent the skin from being pulled far from the bone, whereas the elastic fibers restore the skin to its original shape when you release your grip. Different mixtures of fibers and foundation form the major types of connective tissue shown below.





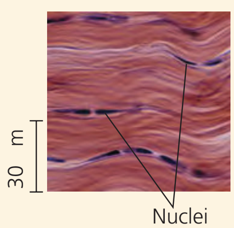
Loose connective tissue

The most widespread connective tissue in the vertebrate body is *loose connective tissue,* which binds epithelia to underlying tissues and holds organs in place. Loose connective tissue gets its name from the loose weave of its fibers, which include all three types. It is found in the skin and throughout the body.



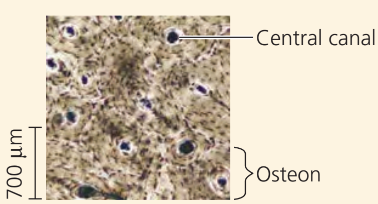
Fibrous connective tissue

Fibrous connective tissue is dense with collagenous fibers. It is found in **tendons**, which attach muscles to bones, and in **ligaments**, which connect bones at joints.



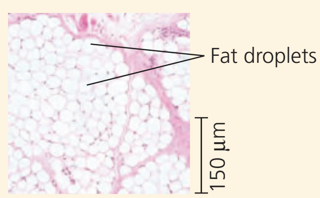
Bone

The skeleton of most vertebrates is made of **bone**, a mineralized connective tissue. Bone-forming cells called *osteoblasts* deposit a matrix of collagen. Calcium, magnesium, and phosphate ions combine into a hard mineral within the matrix. The microscopic structure of hard mammalian bone consists of repeating units called *osteons*. Each osteon has concentric layers of the mineralized matrix, which are deposited around a central canal containing blood vessels and nerves.



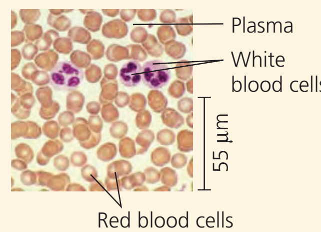
Adipose tissue

Adipose tissue is a specialized loose connective tissue that stores fat in adipose cells distributed throughout its matrix. Adipose tissue pads and insulates the body and stores fuel as fat molecules (see Figure 4.6). Each adipose cell contains a large fat droplet that swells when fat is stored and shrinks when the body uses that fat as fuel.



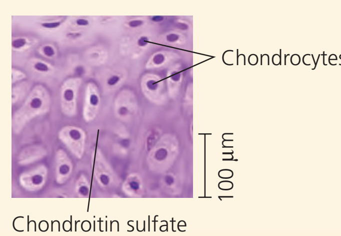
Blood

Blood has a liquid extracellular matrix called plasma, which consists of water, salts, and dissolved proteins. Suspended in plasma are erythrocytes (red blood cells), leukocytes (white blood cells), and cell fragments called platelets. Red cells carry oxygen, white cells function in defense, and platelets aid in blood clotting.



Cartilage

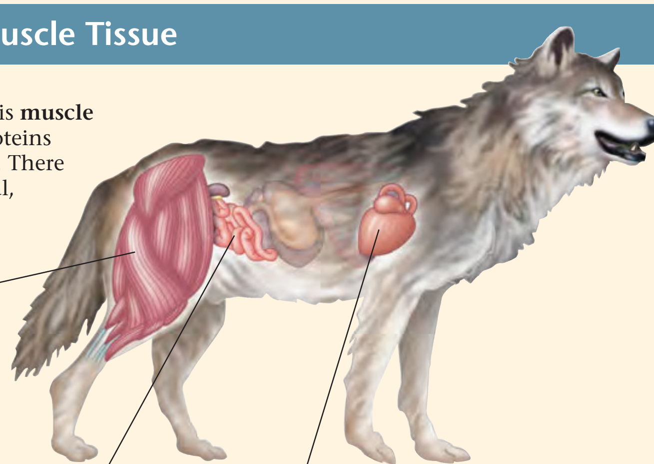
Cartilage contains collagenous fibers embedded in a rubbery protein-carbohydrate complex called chondroitin sulfate. Cells called *chondrocytes* secrete the collagen and chondroitin sulfate, which together make cartilage a strong yet flexible support material. The skeletons of many vertebrate embryos contain cartilage that is replaced by bone as the embryo matures. Cartilage remains in some locations, such as the disks that act as cushions between vertebrae.



Exploring Structure and Function in Animal Tissues

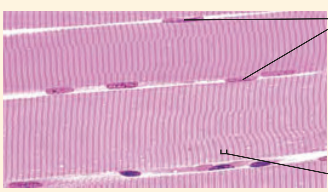
Muscle Tissue

The tissue responsible for nearly all types of body movement is **muscle tissue**. All muscle cells consist of filaments containing the proteins actin and myosin, which together enable muscles to contract. There are three types of muscle tissue in the vertebrate body: skeletal, smooth, and cardiac.



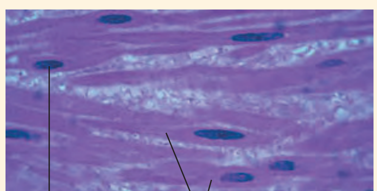
Skeletal muscle

Attached to bones by tendons, **skeletal muscle**, or *striated muscle,* is responsible for voluntary movements. Skeletal muscle consists of bundles of long cells called muscle fibers. During development, skeletal muscle fibers form by the fusion of many cells, resulting in multiple nuclei in each muscle cell or fiber. The arrangement of contractile units, or sarcomeres, along the fibers gives the cells a striped (striated) appearance. In adult mammals, building muscle increases the size but not the number of muscle fibers.



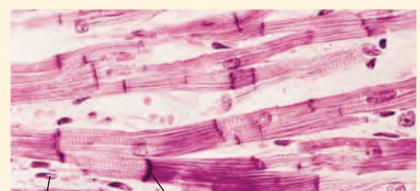
Smooth muscle

Smooth muscle, which lacks striations, is found in the walls of the digestive tract, urinary bladder, arteries, and other internal organs. The cells are spindle-shaped. Smooth muscles are responsible for involuntary body activities, such as churning of the stomach and constriction of arteries.



Cardiac muscle

Cardiac muscle forms the contractile wall of the heart. It is striated like skeletal muscle and has similar contractile properties. Unlike skeletal muscle, however, cardiac muscle has fibers that interconnect via intercalated disks, which relay signals from cell to cell and help synchronize heart contraction.

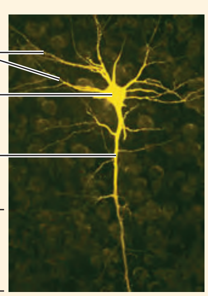


Nervous Tissue

Nervous tissue functions in the receipt, processing, and transmission of information. Nervous tissue contains **neurons**, or nerve cells, which transmit nerve impulses, as well as support cells called **glial cells,** or simply **glia.** In many animals, a concentration of nervous tissue forms a brain, an information-processing center.

Neurons

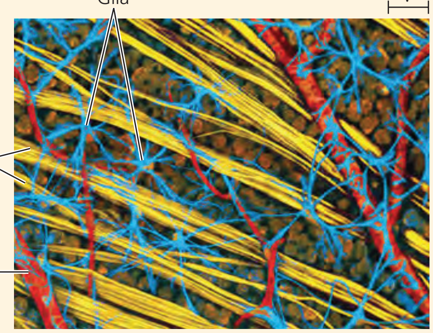
Neurons are the basic units of the nervous system. A neuron receives nerve impulses from other neurons via its cell body and multiple extensions called dendrites. Neurons transmit impulses to neurons, muscles, or other cells via extensions called axons, which are often bundled together into nerves.



(Fluorescent LM)

Glia

The various types of glia help nourish, insulate, and replenish neurons, and in some cases, modulate neuron function.



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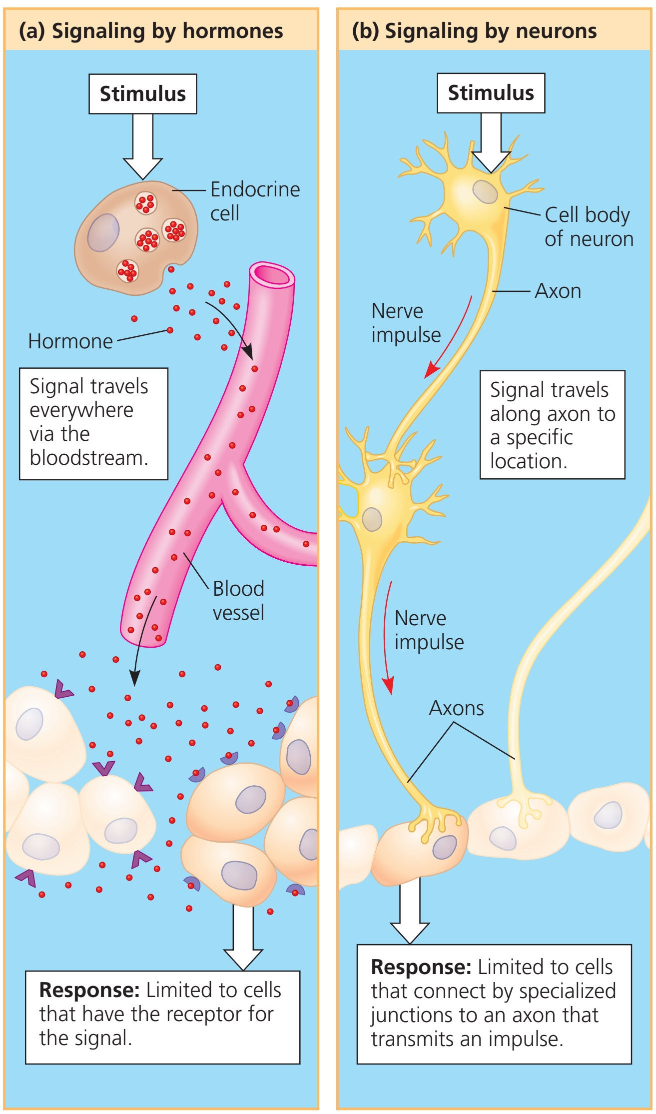
Coordination and Control

An animal's tissues, organs, and organ systems must act in concert with one another. For example, during long dives, the harbor seal in Figure 40.2 slows its heart rate, collapses its lungs, and lowers its body temperature while propelling itself forward with its hind flippers. Coordinating activity across an animal's body in this way requires communication between different locations in the body. What signals are used? How do the signals move within the body? There are two sets of answers to these questions, reflecting the two major systems for controlling and coordinating responses to stimuli **(Figure 40.6)**.

In the endocrine system, signaling molecules released into the bloodstream by endocrine cells reach all locations in the body. In the nervous system, neurons transmit signals, called nerve impulses, between specific locations in the body. In each system, the type of pathway used is the same regardless of whether the signal reaches across the length of the body or ends up just a few cell diameters away.

▼ **Figure 40.6 Signaling in the endocrine and nervous systems**



The signaling molecules broadcast throughout the body by the endocrine system are called **hormones**. Different hormones cause distinct effects, and only cells that have receptors for a particular hormone respond **(Figure 40.6a)**. Depending on which cells have receptors for that hormone, the hormone may have an effect in just a single location or in sites throughout the body. For example, only cells of the thyroid gland have the receptor for thyroid-stimulating hormone (TSH). Upon binding TSH, thyroid cells release thyroid hormone, which acts directly on cells in nearly every tissue to increase oxygen consumption and heat production.

Hormones are relatively slow acting. It takes many seconds for TSH and other hormones to be released into the bloodstream and carried throughout the body. The effects of hormones are often long-lasting, however, because hormones remain in the bloodstream for seconds, minutes, or even hours.

In the nervous system, signals are not broadcast throughout the entire body. Instead, each nerve impulse travels to specific target cells along dedicated communication lines consisting mainly of axons **(Figure 40.6b)**. Four types of cells can receive nerve impulses: other neurons, muscle cells, endocrine cells, and exocrine cells. Unlike the endocrine system, the nervous system conveys information by the *pathway* the signal takes. For example, a person can distinguish different musical notes because each note's frequency activates different neurons connecting the ear to the brain.

Communication in the nervous system usually involves more than one type of signal. Nerve impulses travel along axons, sometimes over long distances, as changes in voltage. But in many cases, passing information from one neuron to another involves very short-range chemical signals. Overall, transmission is extremely fast; nerve impulses take only a fraction of a second to reach the target and last only a fraction of a second.

Because the two major communication systems of the body differ in signal type, transmission, speed, and duration, they are adapted to different functions. The endocrine system is well suited for coordinating gradual changes that affect the entire body, such as growth and development, reproduction, metabolic processes, and digestion. The nervous system is well suited for directing immediate and rapid responses to the environment, especially in controlling fast locomotion and behavior.

Although the functions of the endocrine and nervous systems are distinct, the two systems often work in close coordination. Both contribute to maintaining a stable internal environment, our next topic of discussion.

CONCEPT CHECK 40.1

1. What properties are shared by all types of epithelia?
2. In cool weather, jackrabbits sometimes flatten their ears against their body. What advantage and disadvantage do you think this body posture offers for survival?
3. **WHAT IF?** Suppose you are standing at the edge of a cliff and suddenly slip—you barely manage to keep your balance and avoid falling. As your heart races, you feel a burst of energy, due in part to a surge of blood into dilated (widened) vessels in your muscles and an upward spike in the level of glucose in your blood. Why might you expect that this "fight-or-flight" response requires both the nervous and endocrine systems?

For suggested answers, see Appendix A.

CONCEPT 40.2

Feedback control maintains the internal environment in many animals

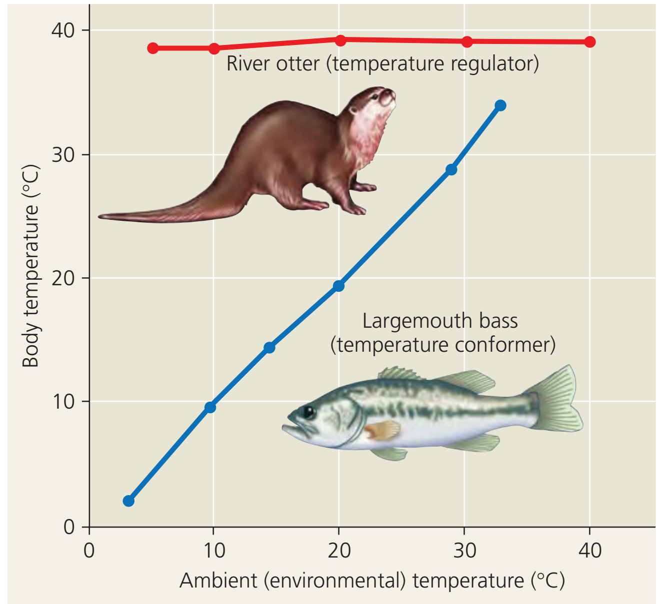
Imagine that your body temperature soared every time you took a hot shower or drank a freshly brewed cup of coffee. Managing the state of the internal environment is a major challenge for the animal body. Faced with environmental fluctuations, animals manage their internal environment by either regulating or conforming.

Regulating and Conforming

An animal is said to be a **regulator** for a particular environmental variable if it uses internal mechanisms to control internal change in the face of external fluctuation. The river otter in **Figure 40.7** is a regulator for temperature, keeping its body at a temperature that is largely independent of that of the water in which it swims.

An animal is said to be a **conformer** for a particular environmental variable if it allows its internal condition to change in accordance with external changes in the variable. The largemouth bass in Figure 40.7 conforms to the temperature of the lake it inhabits. As the water warms or cools, so does the body of the bass. Some animals conform to more constant environments. For example, many marine invertebrates, such as spider crabs of the genus *Libinia*, let their internal solute concentration conform to the relatively stable solute concentration (salinity) of their ocean environment.

Regulating and conforming represent extremes on a continuum. An animal may regulate some internal conditions while allowing others to conform to the environment. For example, even though the bass conforms to the temperature of the surrounding water, the solute concentration in its blood and interstitial fluid differs from the solute concentration of the fresh water in which it lives. This difference occurs because the fish's anatomy and physiology enable it to regulate internal changes in solute concentration. (You will learn more about the mechanisms of this regulation in Chapter 44.)



▲ **Figure 40.7 The relationship between body and environmental temperatures in an aquatic temperature regulator and an aquatic temperature conformer.** The river otter regulates its body temperature, keeping it stable across a wide range of environmental temperatures. The largemouth bass, meanwhile, allows its internal environment to conform to the water temperature.

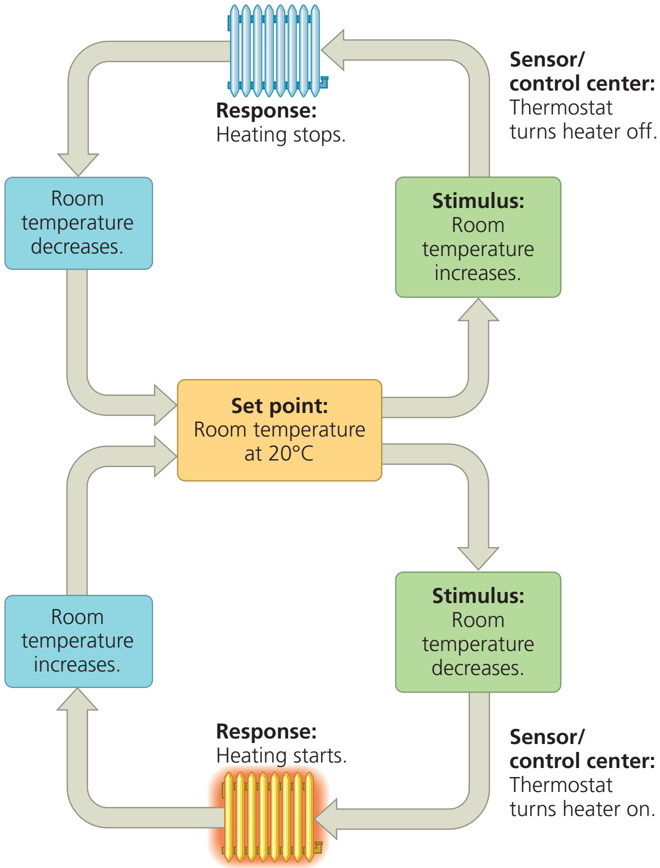
Homeostasis

The steady body temperature of a river otter and the stable concentration of solutes in a freshwater bass are examples of **homeostasis**, which means "steady state," referring to the maintenance of internal balance. In achieving homeostasis, animals maintain a relatively constant internal environment even when the external environment changes significantly.

Like many animals, humans exhibit homeostasis for a range of physical and chemical properties. For example, the human body maintains a fairly constant temperature of about 37°C (98.6°F) and a pH of the blood and interstitial fluid within 0.1 pH unit of 7.4. The body also regulates the concentration of glucose in the bloodstream so that it remains predominantly in the range of 70–110 mg of glucose per 100 mL of blood.

Mechanisms of Homeostasis

Before exploring homeostasis in animals, let's first consider a nonliving example: the regulation of room temperature



▲ **Figure 40.8 A nonliving example of temperature regulation: control of room temperature.** Regulating room temperature depends on a control center (a thermostat) that detects temperature change and activates mechanisms that reverse that change.

WHAT IF? *How would adding an air conditioner to the system contribute to homeostasis?*

(Figure 40.8). Let's assume you want to keep a room at 20°C (68°F), a comfortable temperature for normal activity. You adjust a control device—the thermostat—to 20°C and allow a thermometer in the thermostat to monitor temperature. If the room temperature falls below 20°C, the thermostat responds by turning on a radiator, furnace, or other heater. Heat is produced until the room reaches 20°C, at which point the thermostat switches off the heater. Whenever the temperature in the room again drifts below 20°C, the thermostat activates another heating cycle.

Like a home heating system, an animal achieves homeostasis by maintaining a variable, such as body temperature or solute concentration, at or near a particular value, or **set point**. Fluctuations in the variable above or below the set point serve as the **stimulus** detected by a receptor, or **sensor**. Upon receiving a signal from the sensor, a *control center* generates output that triggers a **response**, a physiological activity that helps return the variable to the set point. In the home heating example, a drop in temperature below the set point acts as a stimulus, the thermostat serves as the sensor and control center, and the heater produces the response.

Feedback Control in Homeostasis

Like the regulatory circuit shown in Figure 40.8, homeostasis in animals relies largely on **negative feedback**, a control mechanism that reduces, or "damps," the stimulus. For example, when you exercise vigorously, you produce heat, which increases body temperature. Your nervous system detects this increase and triggers sweating. As you sweat, the evaporation of moisture from your skin cools your body, helping return your body temperature to its set point.

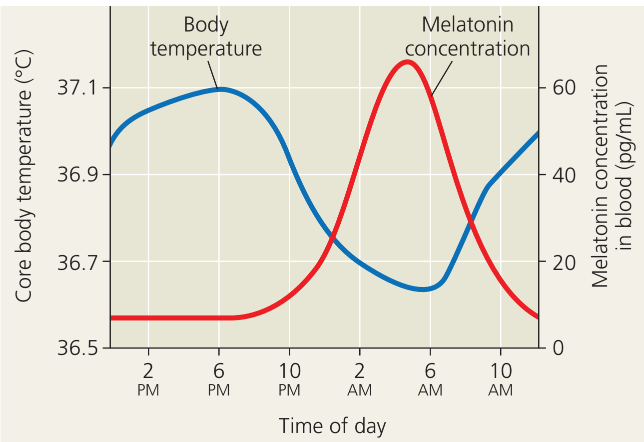
Homeostasis is a dynamic equilibrium, the interplay between external factors that tend to change the internal environment and internal control mechanisms that oppose such changes. Note that physiological responses to stimuli are not instantaneous, just as switching on a furnace does not immediately warm a room. As a result, homeostasis moderates but doesn't eliminate changes in the internal environment. Additional fluctuation occurs if a variable has a *normal range*—an upper and lower limit—rather than a single set point. This is equivalent to a heating system that begins producing heat when the room temperature drops to 19°C (66°F) and stops heating when the temperature reaches 21°C (70°F). Regardless of whether there is a set point or a normal range, homeostasis is enhanced by adaptations that reduce fluctuations, such as insulation in the case of temperature and physiological buffers in the case of pH.

Unlike negative feedback, **positive feedback** is a control mechanism that amplifies rather than reduces the stimulus (see Figure 1.13). Positive-feedback loops in animals do not play a major role in homeostasis, but instead help drive processes to completion. During childbirth, for instance, the pressure of the baby's head against receptors near the opening of the mother's uterus stimulates the uterus to contract. These contractions result in greater pressure against the opening of the uterus, heightening the contractions and thereby causing even greater pressure, until the baby is born.

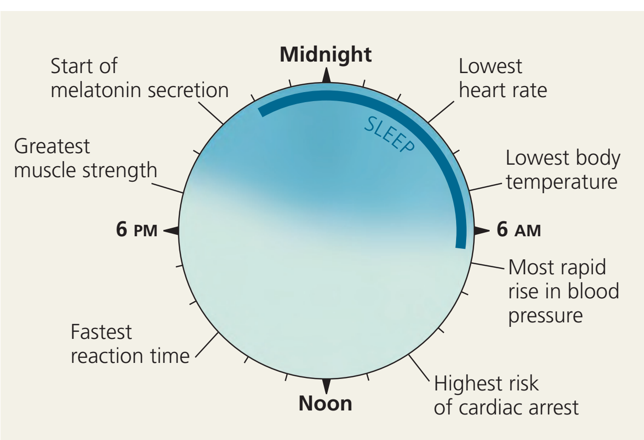
Alterations in Homeostasis

The set points and normal ranges for homeostasis can change under various circumstances. In fact, *regulated changes* in the internal environment are essential to normal body functions. Some regulated changes are associated with a particular stage in life, such as the radical shift in hormone balance that occurs during puberty. Other regulated changes are cyclic, such as the variation in hormone levels responsible for a woman's menstrual cycle (see Figure 46.14).

In all animals (and plants, too), certain cyclic alterations in metabolism reflect a **circadian rhythm**, a set of physiological changes that occur roughly every 24 hours. For example, your body temperature typically undergoes a cyclic rise and fall of more than 0.6°C (1°F) in every 24-hour period. Remarkably, a biological clock maintains this rhythm even when variations in human activity, room temperature, and light levels are minimized **(Figure 40.9a)**. A circadian rhythm is thus intrinsic to the body, although the biological clock is normally coordinated with the cycle of light and darkness in the environment **(Figure 40.9b)**. For example, the hormone melatonin is secreted at night, and more is released during the longer nights of winter. External stimuli can reset the biological clock, but the effect is not immediate. That is why flying across several time zones results in jet lag, a mismatch between the circadian rhythm and local environment that persists until the clock fully resets.



(a) Variation in core body temperature and melatonin concentration in blood. Researchers measured these two variables in resting but awake volunteers in an isolation chamber with constant temperature and low light. (Melatonin is a hormone that appears to be involved in sleep/wake cycles; see Chapter 45.)



(b) The human circadian clock. Metabolic activities undergo daily cycles in response to the circadian clock. As illustrated for a typical individual who rises early in the morning, eats lunch around noon, and sleeps at night, this variation in metabolism is apparent both day and night.

▲ **Figure 40.9 Human circadian rhythm.**

One way in which the normal range of homeostasis may change is through **acclimatization**, the gradual process by which an animal adjusts to changes in its external environment. For example, when an elk or other mammal moves up into the mountains from sea level, physiological changes that occur over several days facilitate activity at the higher elevations. The lower oxygen concentration in the air stimulates the animal to breathe more rapidly and deeply. It therefore loses more CO_2 through exhalation, raising blood pH above its set point. As the animal acclimatizes, changes in kidney function result in excretion of more alkaline urine, returning blood pH to its normal range. Other changes during acclimatization to a higher altitude include increased production of red blood cells, which carry oxygen. Note that acclimatization, a temporary change during an animal's lifetime, should not be confused with adaptation, a process of change in a population brought about by natural selection acting over many generations.

CONCEPT CHECK 40.2

1. **MAKE CONNECTIONS** Figure 8.21 (p. 160) illustrates feedback inhibition in an enzyme-catalyzed biosynthetic process. How does this type of negative feedback differ from that in thermoregulation?
2. If you were deciding where to put the thermostat in a house, what factors would govern your decision? How do these factors relate to the fact that many homeostatic control sensors in humans are located in the brain?
3. **MAKE CONNECTIONS** Like animals, cyanobacteria have a circadian rhythm. By analyzing the genes that maintain biological clocks, scientists were able to conclude that the 24-hour rhythms of humans and cyanobacteria reflect convergent evolution (see Concept 26.2, pp. 540–541). What evidence would have supported this conclusion? Explain.

For suggested answers, see Appendix A.

CONCEPT 40.3

Homeostatic processes for thermoregulation involve form, function, and behavior

In this section, we will examine the regulation of body temperature as an example of how form and function work together in regulating an animal's internal environment. Later chapters in this unit will discuss other physiological systems involved in maintaining homeostasis.

Thermoregulation is the process by which animals maintain an internal temperature within a tolerable range. Thermoregulation is critical to survival because most biochemical and physiological processes are very sensitive to changes in body temperature. For every 10°C (18°F) decrease in temperature, the rates of most enzyme-mediated reactions decrease two- to threefold. Increases in temperature speed up reactions but cause some proteins to become less active. For instance, the oxygen carrier molecule hemoglobin becomes less effective at binding oxygen as temperature increases. Membranes can also change fluidity, becoming increasingly fluid or rigid as temperatures rise or fall, respectively.

Each animal species has an optimal temperature range. Thermoregulation helps maintain body temperature within that optimal range, enabling cells to function effectively even as the external temperature fluctuates.

Endothermy and Ectothermy

Internal metabolism and the external environment are the sources of heat for thermoregulation. Birds and mammals are mainly **endothermic**, meaning that they are warmed mostly by heat generated by metabolism. A few nonavian reptiles, some fishes, and many insect species are also mainly endothermic. In contrast, amphibians, lizards, snakes, turtles, many fishes, and most invertebrates are mainly **ectothermic**, meaning that they gain most of their heat from external sources.

Animals that are mainly endothermic are referred to as endotherms; those that are mainly ectothermic are known as ectotherms. Keep in mind, though, that endothermy and ectothermy are not mutually exclusive modes of thermoregulation. For example, a bird is mainly endothermic, but it may warm itself in the sun on a cold morning, much as an ectothermic lizard does.

Endotherms can maintain a stable body temperature even in the face of large fluctuations in the environmental temperature. For example, few ectotherms are active in the below-freezing weather that prevails during winter over much of Earth's surface, but many endotherms function very well in these conditions **(Figure 40.10a)**. In a cold environment, an endotherm generates enough heat to keep its body substantially warmer than its surroundings. In a hot environment, endothermic vertebrates have mechanisms for cooling their bodies, enabling them to withstand heat loads that are intolerable for most ectotherms.

Because their heat source is largely environmental, ectotherms generally need to consume much less food than endotherms of equivalent size—an advantage if food supplies are limited. Ectotherms also usually tolerate larger fluctuations in their internal temperature. Although ectotherms do not generate enough heat for thermoregulation, many adjust body temperature by behavioral means, such as seeking out shade or basking in the sun **(Figure 40.10b)**. Overall, ectothermy is an effective and successful strategy in most environments, as shown by the abundance and diversity of ectothermic animals.

(a) A walrus, an endotherm

(b) A lizard, an ectotherm

▲ **Figure 40.10 Endothermy and ectothermy.**

Variation in Body Temperature

Animals can have either a variable or a constant body temperature. An animal whose body temperature varies with its environment is called a *poikilotherm* (from the Greek *poikilos*, varied). In contrast, a *homeotherm* has a relatively constant body temperature. For example, the largemouth bass is a poikilotherm, and the river otter is a homeotherm (see Figure 40.7).

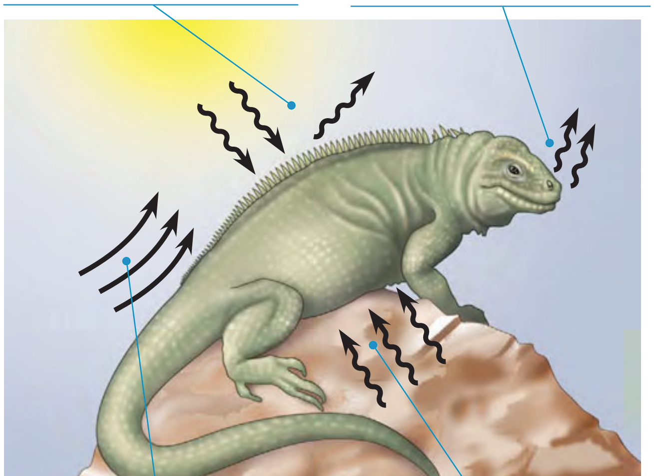
From the descriptions of ectotherms and endotherms, it might seem that all ectotherms are poikilothermic and all endotherms are homeothermic. In fact, there is no fixed relationship between the source of heat and the stability of body temperature. For example, many ectothermic marine fishes and invertebrates inhabit waters with such stable temperatures that their body temperature varies less than that of endotherms such as humans and other mammals. Conversely, the body temperature of a few endotherms varies considerably. For example, bats and hummingbirds may periodically enter an inactive state in which they maintain a lower body temperature.

It is a common misconception that ectotherms are "cold-blooded" and endotherms are "warm-blooded." Ectotherms do not necessarily have low body temperatures. In fact, when sitting in the sun, many ectothermic lizards have higher body temperatures than mammals. Thus, the terms *cold-blooded* and *warm-blooded* are misleading and are avoided in scientific communication.

Balancing Heat Loss and Gain

Thermoregulation depends on an animal's ability to control the exchange of heat with its environment. Any organism, like any object, exchanges heat by four physical processes: radiation, evaporation, convection, and conduction. **Figure 40.11** distinguishes these processes, which account for the flow of heat both within an organism and between an organism and its external environment. Note that heat is always transferred from an object of higher temperature to one of lower temperature.

The essence of thermoregulation is maintaining rates of heat gain that equal rates of heat loss. Animals do this through mechanisms that either reduce heat exchange overall or favor heat exchange in a particular direction. In mammals, several of these mechanisms involve the **integumentary system**, the outer covering of the body, consisting of the skin, hair, and nails (claws or hooves in some species).



▲ **Figure 40.11 Heat exchange between an organism and its environment.**

Insulation

A major thermoregulatory adaptation in mammals and birds is insulation, which reduces the flow of heat between an animal and its environment. Sources of insulation include hair, feathers, and layers of fat formed by adipose tissue.

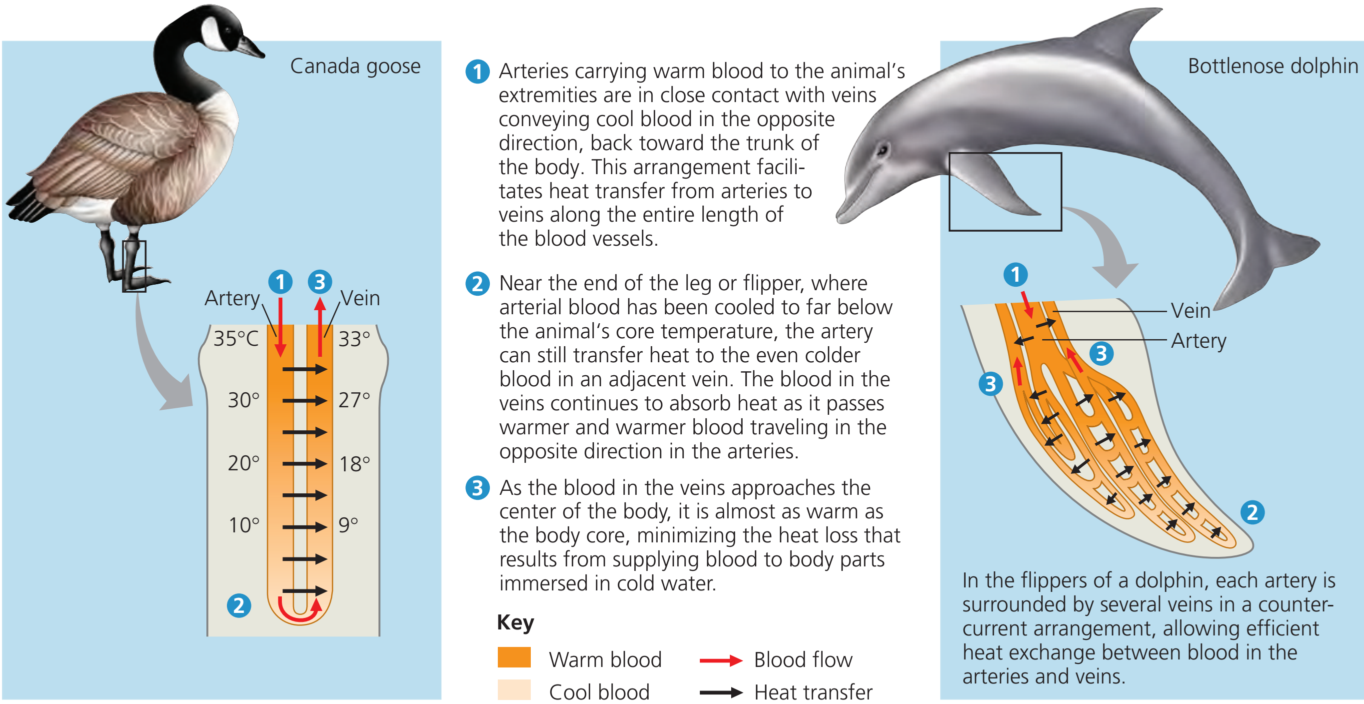
Many animals that rely on insulation to reduce overall heat exchange also adjust their insulating layers to help thermoregulate. Most land mammals and birds, for example, react to cold by raising their fur or feathers. This action traps a thicker layer of air, thereby increasing the insulating power of the fur or feather layer. To repel water that would reduce the insulating capacity of feathers or fur, some animals secrete oily substances, such as the oils that birds apply to their feathers during preening. Lacking feathers or fur, humans must rely primarily on fat for insulation. "Goose bumps" are a vestige of hair raising inherited from our furry ancestors.

Insulation is particularly important for marine mammals, such as whales and walruses. These animals swim in water colder than their body core, and many species spend at least part of the year in nearly freezing polar seas. The problem of thermoregulation is made worse by the fact that the transfer of heat to water occurs 50 to 100 times more rapidly than heat transfer to air. Just under their skin, marine mammals have a very thick layer of insulating fat called blubber. The insulation that blubber provides is so effective that marine mammals can maintain body core temperatures of about 36–38°C (97–100°F) without requiring much more energy from food than land mammals of similar size.

Circulatory Adaptations

Circulatory systems provide a major route for heat flow between the interior and exterior of the body. Adaptations that regulate the extent of blood flow near the body surface or that trap heat within the body core play a significant role in thermoregulation.

In response to changes in the temperature of their surroundings, many animals alter the amount of blood (and hence heat) flowing between their body core and their skin. Nerve signals that relax the muscles of the vessel walls result in *vasodilation*, a widening of superficial blood vessels (those near the body surface). As a consequence of the increase in vessel diameter, blood flow in the skin increases. In endotherms, vasodilation usually warms the skin and increases the transfer of body heat to the environment by radiation, conduction, and convection (see Figure 40.11). The reverse process, *vasoconstriction*, reduces blood flow and heat transfer by decreasing the diameter of superficial vessels. It is vasoconstriction in blood vessels of the ear that allows the jackrabbit shown in Figure 40.1 to avoid overheating on hot desert days.



▲ **Figure 40.12 Countercurrent heat exchangers.** A countercurrent exchange system traps heat in the body core, thus reducing heat loss from the extremities, particularly when they are immersed in cold water or in contact with ice or snow. In essence, heat in the arterial blood emerging from the body core is transferred directly to the returning venous blood instead of being lost to the environment.

Like endotherms, some ectotherms control heat exchange by regulating blood flow. For example, when the marine iguana of the Galápagos Islands swims in the cold ocean, its superficial blood vessels undergo vasoconstriction. This process routes more blood to the central core of the iguana's body, conserving body heat.

In many birds and mammals, reducing heat loss from the body relies on **countercurrent exchange**, the transfer of heat (or solutes) between fluids that are flowing in opposite directions. In a countercurrent heat exchanger, arteries and veins are located adjacent to each other **(Figure 40.12)**. As warm blood moves from the body core in the arteries, it transfers heat to the colder blood returning from the extremities in the veins. Because blood flows through the arteries and veins in opposite directions, heat is transferred along the entire length of the exchanger, maximizing the rate of heat exchange.

Certain sharks, fishes, and insects also use countercurrent heat exchange. Although most sharks and fishes are temperature conformers, countercurrent heat exchangers are found in some large, powerful swimmers, including great white sharks, bluefin tuna, and swordfish. By keeping the main swimming muscles several degrees warmer than tissues near the animal's surface, this adaptation enables the vigorous, sustained activity that is characteristic of these animals. Similarly, many endothermic insects (bumblebees, honeybees, and some moths) have a countercurrent exchanger that helps maintain a high temperature in their thorax, where flight muscles are located.

In controlling heat gain and loss, some species regulate the extent of blood flow to the countercurrent exchanger. By allowing blood to pass through the heat exchanger or diverting it to other blood vessels, these animals alter the rate of heat loss as their physiological state or environment changes. For example, insects flying in hot weather run the risk of overheating because of the large amount of heat produced by working flight muscles. In some species, the countercurrent mechanism can be "shut down," allowing muscle-produced heat to be lost from the thorax to the abdomen and then to the environment.

Cooling by Evaporative Heat Loss

Many mammals and birds live in places where thermoregulation requires cooling as well as warming. If the environmental temperature is above their body temperature, animals gain heat from the environment as well as from metabolism, and evaporation is the only way to keep body temperature from rising. Terrestrial animals lose water by evaporation from their skin and respiratory surfaces. Water absorbs considerable heat when it evaporates (see Chapter 3); this heat is carried away from the body surface with the water vapor.

Some animals have adaptations that can greatly augment the cooling effect of evaporation. Panting is important in birds and many mammals. Some birds have a pouch richly supplied with blood vessels in the floor of the mouth; fluttering the pouch increases evaporation. Pigeons, for example, can use this adaptation to keep their body temperature close to 40°C (104°F) in air temperatures as high as 60°C (140°F), as long as they have sufficient water. Sweating or bathing moistens the skin and enhances evaporative cooling. Many terrestrial mammals have sweat glands that are controlled by the nervous system.

Behavioral Responses

Both endotherms and ectotherms control body temperature through behavioral responses to changes in the environment. Many ectotherms maintain a nearly constant body temperature by engaging in relatively simple behaviors. More extreme behavioral adaptations in some animals include hibernation or migration to a more suitable climate.

All amphibians and most reptiles other than birds are ectothermic. Therefore, these organisms control body temperature mainly by behavior. When cold, they seek warm places, orienting themselves toward heat sources and expanding the portion of their body surface exposed to the heat source (see Figure 40.10b). When hot, they move to cool areas or turn in another direction.

Many terrestrial invertebrates can adjust internal temperature by the same behavioral mechanisms used by vertebrate ectotherms. The desert locust *(Schistocerca gregaria)*, for example, must reach a certain temperature to become active, and on cold days it orients itself in a direction that maximizes the absorption of sunlight. Other terrestrial invertebrates have certain postures that enable them to maximize or minimize their absorption of heat from the sun **(Figure 40.13)**.

Honeybees use a thermoregulatory mechanism that depends on social behavior. In cold weather, they increase heat production and huddle together, thereby retaining heat. Individuals move between the cooler outer edges of the cluster and the warmer center, thus circulating and distributing the heat. Even when huddling, honeybees must expend considerable energy to keep warm during long periods of cold weather. (This is the main function of storing large quantities of fuel in the hive in the form of honey.) In hot weather, honeybees cool the hive by transporting water to the hive and fanning with their wings, promoting evaporation and convection. Thus, a colony of honeybees uses many of the mechanisms of thermoregulation seen in individual organisms.

▶ Figure 40.13 Thermoregulatory behavior in a dragonfly. This dragonfly's "obelisk" posture is an adaptation that minimizes the amount of body surface exposed to the sun. This posture helps reduce heat gain by radiation.

Adjusting Metabolic Heat Production

Because endotherms generally maintain a body temperature considerably higher than that of the environment, they must counteract continual heat loss. Endotherms can vary heat production—*thermogenesis*—to match changing rates of heat loss. Thermogenesis is increased by such muscle activity as moving or shivering. For example, shivering helps chickadees (genus *Poecile*), birds with a body mass of only 20 g, remain active and hold their body temperature nearly constant at 40°C (104°F) in environmental temperatures as low as −40°C (−40°F), as long as they have adequate food.

In some mammals, certain hormones can cause mitochondria to increase their metabolic activity and produce heat instead of ATP. This process, called *nonshivering thermogenesis,* takes place throughout the body; some mammals also have a tissue called *brown fat* in their neck and between their shoulders that is specialized for rapid heat production. (In human infants, brown fat represents about 5% of total body weight. In 2009, brown fat was found for the first time in human adults, with greater amounts being detected when outdoor temperatures were lower.) Through shivering and nonshivering thermogenesis, mammals and birds in cold environments can increase their metabolic heat production by as much as five to ten times the levels that occur in warm conditions.

A few large reptiles become endothermic in particular circumstances. In the early 1960s, Herndon Dowling documented this phenomenon for a female Burmese python (*Python molurus bivittatus*). Placing temperature-recording devices along the snake's coils, Dowling found that the snake maintained a body temperature roughly 6°C (11°F) above that of the surrounding air during the month when she was incubating eggs. Where did the heat come from? Further studies by Dowling and colleagues showed that pythons, like mammals and birds, can raise their body temperature through shivering **(Figure 40.14)**. These and other findings have led to new insights into thermoregulation in reptiles and have contributed to the idea, still under debate, that certain groups of Mesozoic dinosaurs were endothermic (see Chapter 34).

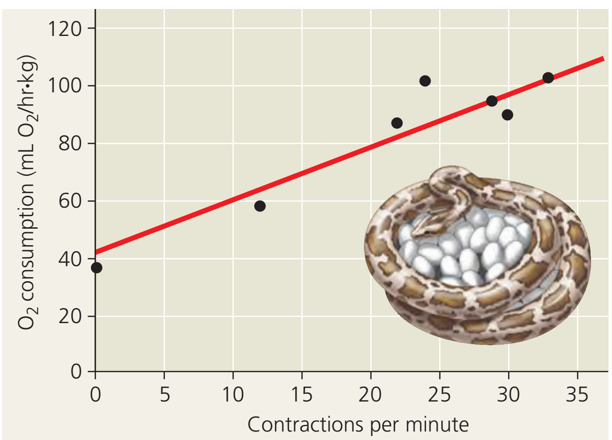
As mentioned earlier, many species of flying insects, such as bees and moths, are endothermic—the smallest of all endotherms. The capacity of such endothermic insects to elevate

▼ **Figure 40.14** **INQUIRY**

How does a Burmese python generate heat while incubating eggs?

EXPERIMENT Herndon Dowling, graduate student Allen Vinegar, and the student's research supervisor, Victor Hutchison, at the Bronx Zoo in New York, observed that when a female Burmese python incubated eggs by wrapping her body around them, she raised her body temperature and frequently contracted the muscles in her coils. To learn if the contractions were elevating her body temperature, they placed the python and her eggs in a chamber. As they varied the chamber's temperature, they monitored the python's muscle contractions as well as her oxygen uptake, a measure of her rate of cellular respiration.

RESULTS The python's oxygen consumption increased when the temperature in the chamber decreased. Her oxygen consumption also increased with the rate of muscle contraction.

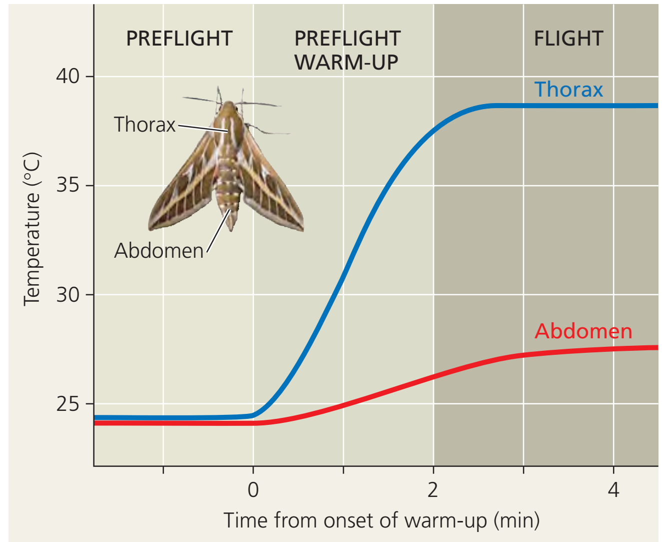


CONCLUSION Because oxygen consumption generates heat through cellular respiration and increases linearly with the rate of muscle contraction, the researchers concluded that the muscle contractions, a form of shivering, were the source of the Burmese python's elevated body temperature.

SOURCE V. H. Hutchison, H. G. Dowling, and A. Vinegar, Thermoregulation in a brooding female Indian python, *Python molurus bivittatus*, *Science* 151:694–696 (1966).

WHAT IF? Suppose you varied air temperature and measured oxygen consumption for a female Burmese python without a clutch of eggs. Since she would not show shivering behavior, how would you expect the snake's oxygen consumption to vary with environmental temperature?

body temperature depends on powerful flight muscles, which generate large amounts of heat when contracting. Many endothermic insects warm up by shivering before taking off. As they contract their flight muscles in synchrony, only slight wing movements occur, but considerable heat is produced. Chemical reactions, and hence cellular respiration, speed up in the warmed-up flight "motors," enabling these insects to fly even when the air is cold **(Figure 40.15)**.



▲ **Figure 40.15** **Preflight warm-up in the hawkmoth.** The hawkmoth (*Manduca sexta*) is one of many insect species that use a shivering-like mechanism for preflight warm-up of thoracic flight muscles. Warming up helps these muscles produce enough power to let the animal take off. Once the moth is airborne, flight muscle activity maintains a high thoracic temperature.

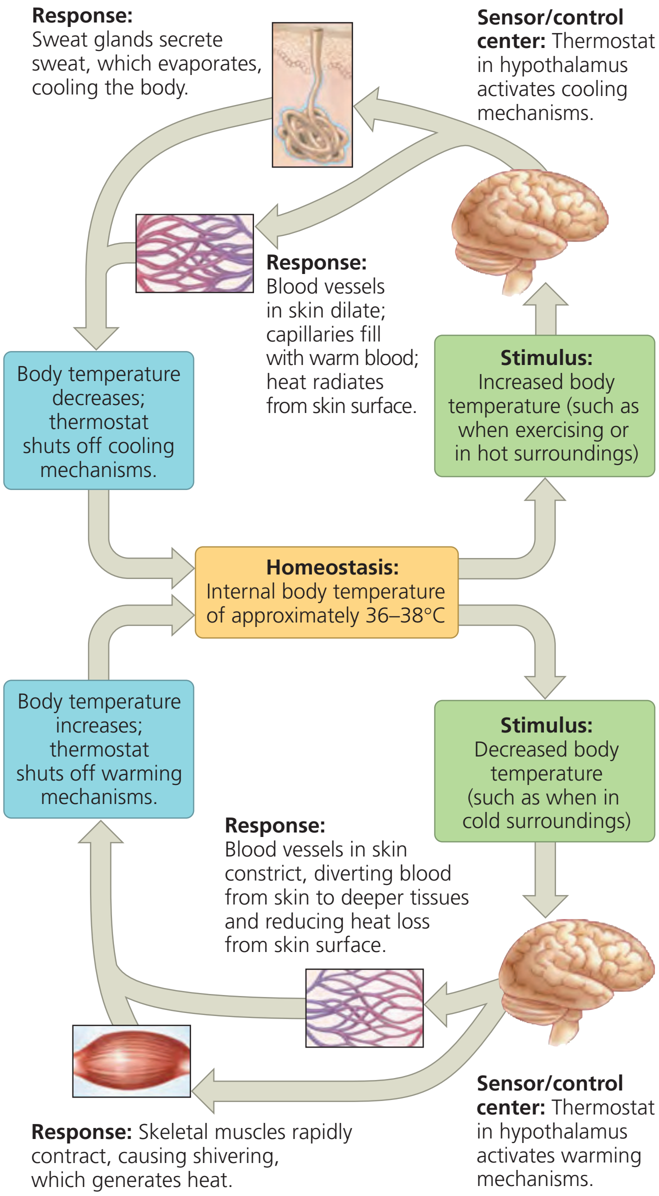
Acclimatization in Thermoregulation

Acclimatization contributes to thermoregulation in many animal species. In birds and mammals, acclimatization to seasonal temperature changes often includes adjusting insulation—growing a thicker coat of fur in the winter and shedding it in the summer, for example. These changes help endotherms keep a constant body temperature year-round.

Acclimatization in ectotherms often includes adjustments at the cellular level. Cells may produce variants of enzymes that have the same function but different optimal temperatures. Also, the proportions of saturated and unsaturated lipids in membranes may change; unsaturated lipids help keep membranes fluid at lower temperatures (see Figure 7.5). Some ectotherms that experience subzero body temperatures protect themselves by producing "antifreeze" compounds that prevent ice formation in their cells. In the Arctic Ocean and Southern (Antarctic) Ocean, these compounds enable certain fishes to survive in water as cold as −2°C (28°F), below the freezing point of unprotected body fluids (about −1°C, or 30°F).

Physiological Thermostats and Fever

The regulation of body temperature in humans and other mammals is brought about by a complex system based on feedback mechanisms. The sensors for thermoregulation are concentrated in a brain region called the **hypothalamus**. A group of nerve cells in the hypothalamus functions as a thermostat, responding to body temperatures outside a normal range by activating mechanisms that promote heat loss



▲ **Figure 40.16 The thermostatic function of the hypothalamus in human thermoregulation.**

or gain **(Figure 40.16)**. Warm receptors signal the hypothalamic thermostat when temperatures increase; cold receptors signal when temperatures decrease. (Because the same blood vessel supplies the hypothalamus and ears, an ear thermometer records the temperature detected by the hypothalamic thermostat.) At body temperatures below the normal range, the thermostat inhibits heat loss mechanisms and activates heat-saving ones, such as vasoconstriction and the raising of fur, while stimulating heat-generating mechanisms (shivering and nonshivering thermogenesis). In response to elevated body temperature, the thermostat shuts down heat retention mechanisms and promotes cooling the body by vasodilation, sweating, or panting.

In the course of certain bacterial and viral infections, mammals and birds develop fever, an elevated body temperature. A variety of experiments have shown that fever reflects an increase in the set point for the biological thermostat. For example, artificially raising the temperature of the hypothalamus in an infected animal reduces fever in the rest of the body!

Although only endotherms develop fever, lizards exhibit a related response. When infected with certain bacteria, the desert iguana (*Dipsosaurus dorsalis*) seeks a warmer environment and then maintains a body temperature that is elevated by 2–4°C (4–7°F). Similar observations in fishes, amphibians, and even cockroaches indicate that this response to certain infections is a common feature of many animal species.

Having explored thermoregulation in depth, we'll now consider some other energy-consuming processes and the different ways that animals allocate, use, and conserve energy.

CONCEPT CHECK 40.3

1. What mode of heat exchange is involved in "wind chill," when moving air feels colder than still air at the same temperature? Explain.
2. Flowers differ in how much sunlight they absorb. Why might this matter to a hummingbird seeking nectar on a cool morning?
3. **WHAT IF?** Suppose at the end of a hard run on a hot day you find that there are no drinks left in the cooler. If, out of desperation, you dunk your head into the cooler, how might the ice-cold water affect the rate at which your body temperature returns to normal?

For suggested answers, see Appendix A.

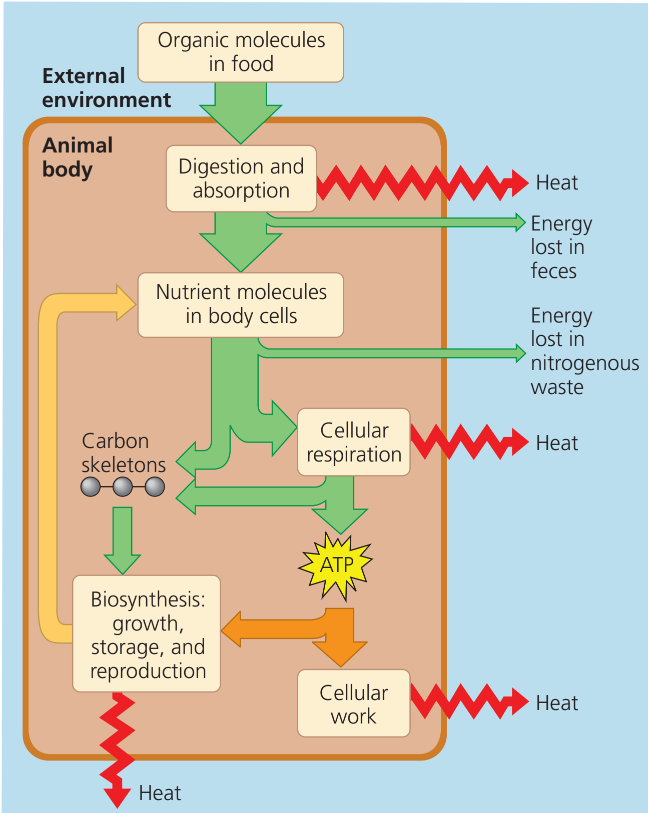
CONCEPT 40.4

Energy requirements are related to animal size, activity, and environment

One of the unifying themes of biology introduced in Chapter 1 is that life requires energy transfer and transformation. Like other organisms, animals use chemical energy for growth, repair, activity, and reproduction. The overall flow and transformation of energy in an animal—its **bioenergetics**—determines nutritional needs and is related to the animal's size, activity, and environment.

Energy Allocation and Use

As we have discussed in other chapters, organisms can be classified by how they obtain chemical energy. Most autotrophs, such as plants, use light energy to build energy-rich organic molecules and then use those organic molecules for fuel. Most heterotrophs, such as animals, must obtain their chemical



▲ **Figure 40.17 Bioenergetics of an animal: an overview.**

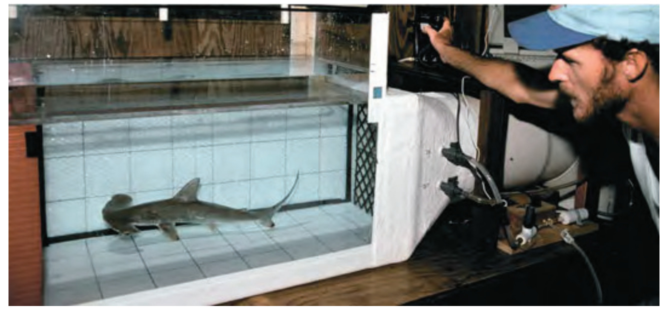
MAKE CONNECTIONS *Review the idea of energy coupling in Concept 8.3 (pp. 149–151). Then use that idea to explain why heat is produced in the absorption of nutrients, in cellular respiration, and in the synthesis of biopolymers.*

energy from food, which contains organic molecules synthesized by other organisms.

Animals use chemical energy harvested from the food they eat to fuel metabolism and activity **(Figure 40.17)**. Food is digested by enzymatic hydrolysis (see Figure 5.2b), and nutrients are absorbed by body cells. Most nutrient molecules are used to generate ATP. ATP produced by cellular respiration and fermentation powers cellular work, enabling cells, organs, and organ systems to perform the functions that keep an animal alive. Energy in the form of ATP is also used in biosynthesis, which is needed for body growth and repair, synthesis of storage material such as fat, and production of gametes. The production and use of ATP generates heat, which the animal eventually gives off to its surroundings.

Quantifying Energy Use

How much of the total energy an animal obtains from food does it need just to stay alive? How much energy must be expended to walk, run, swim, or fly from one place to another? What fraction of the energy intake is used for reproduction? Physiologists answer such questions by measuring the rate at



▲ **Figure 40.18 Measuring the rate of oxygen consumption by a swimming shark.** A researcher monitors the drop in oxygen level in the recirculating water of a juvenile hammerhead's tank.

which an animal uses chemical energy and how this rate changes in different circumstances.

The amount of energy an animal uses in a unit of time is called its **metabolic rate**—the sum of all the energy used in biochemical reactions over a given time interval. Energy is measured in joules (J) or in calories (cal) and kilocalories (kcal). (A kilocalorie equals 1,000 calories, or 4,184 joules. The unit Calorie, with a capital C, as used by many nutritionists, is actually a kilocalorie.)

Metabolic rate can be determined in several ways. Because nearly all of the chemical energy used in cellular respiration eventually appears as heat, metabolic rate can be measured by monitoring an animal's rate of heat loss. For this approach, researchers use a calorimeter, which is a closed, insulated chamber equipped with a device that records an animal's heat loss. Metabolic rate can also be determined from the amount of oxygen consumed or carbon dioxide produced by an animal's cellular respiration **(Figure 40.18)**. To calculate metabolic rate over longer periods, researchers record the rate of food consumption, the energy content of the food (about 4.5–5 kcal per gram of protein or carbohydrate and about 9 kcal per gram of fat), and the chemical energy lost in waste products (feces and nitrogenous waste).

Minimum Metabolic Rate and Thermoregulation

Animals must maintain a minimum metabolic rate for basic functions such as cell maintenance, breathing, and heartbeat. Researchers measure this minimum metabolic rate differently for endotherms and ectotherms. The minimum metabolic rate of a nongrowing endotherm that is at rest, has an empty stomach, and is not experiencing stress is called the **basal metabolic rate (BMR)**. BMR is measured under a "comfortable" temperature range—a range that requires no generation or shedding of heat above the minimum. The minimum metabolic rate of ectotherms is determined at a specific temperature because changes in the environmental temperature alter body temperature and therefore metabolic rate. The metabolic rate of a fasting, nonstressed ectotherm at rest at a particular temperature is called its **standard metabolic rate (SMR)**.

Comparisons of minimum metabolic rates reveal that endothermy and ectothermy have different energy costs. The BMR for humans averages 1,600–1,800 kcal per day for adult males and 1,300–1,500 kcal per day for adult females. These BMRs are about equivalent to the rate of energy use by a 75-watt light bulb. In contrast, the SMR of an American alligator is only about 60 kcal per day at 20°C (68°F). Since this represents less than $\frac{1}{20}$ the energy used by a comparably sized adult human, the lower energetic requirement of ectothermy is readily apparent.

Influences on Metabolic Rate

Metabolic rate is affected by many factors besides whether the animal is an endotherm or an ectotherm. Some key factors are age, sex, size, activity, temperature, and nutrition. Here we'll examine the effects of size and activity.

Size and Metabolic Rate

Larger animals have more body mass and therefore require more chemical energy. Remarkably, the relationship between overall metabolic rate and body mass is constant across a wide range of sizes and forms, as illustrated for various mammals in **Figure 40.19a**. In fact, for even more varied organisms ranging in size from bacteria to blue whales, metabolic rate remains roughly proportional to body mass to the three-quarter power ($m^{3/4}$). Scientists are still researching the basis of this relationship, which applies to ectotherms as well as endotherms.

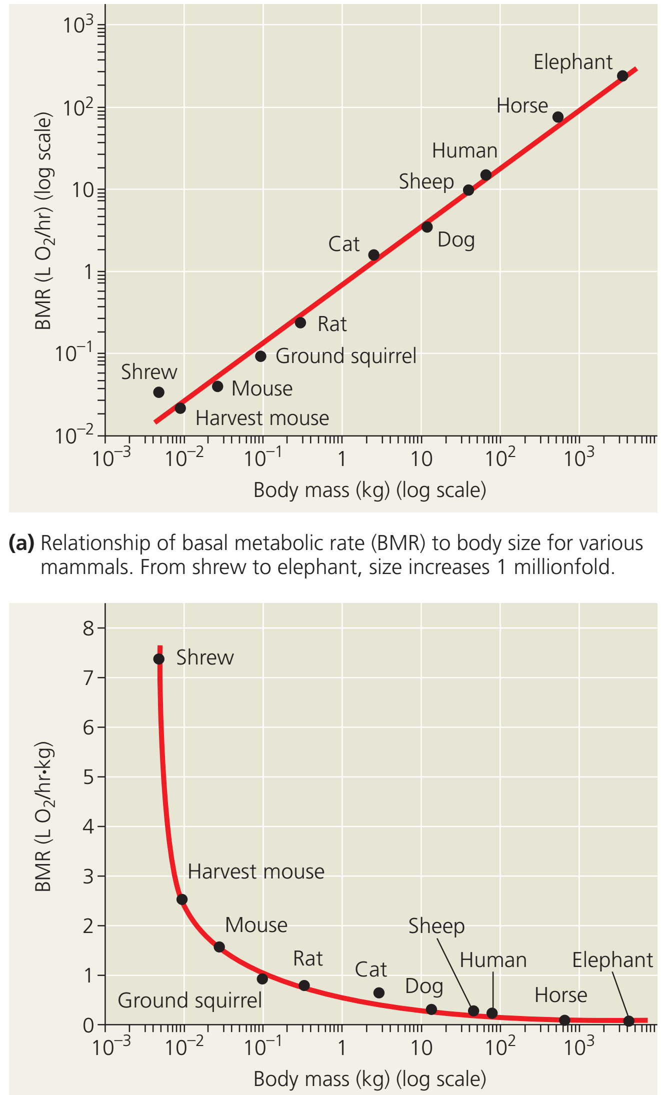
The relationship of metabolic rate to size profoundly affects energy consumption by body cells and tissues. As shown in **Figure 40.19b**, the energy it takes to maintain each gram of body mass is inversely related to body size. Each gram of a mouse, for instance, requires about 20 times as many calories as a gram of an elephant, even though the whole elephant uses far more calories than the whole mouse. The smaller animal's higher metabolic rate per gram demands a higher rate of oxygen delivery. Correlated with its higher metabolic rate per gram, the smaller animal has a higher breathing rate, blood volume (relative to its size), and heart rate. Also, it must eat much more food per unit of body mass.

Bioenergetic considerations associated with body size provide a clear example of how trade-offs shape the evolution of body plans. As body size becomes smaller, each gram of tissue increases in energy cost. As body size increases, energy costs per gram of tissue decrease, but an ever-larger fraction of body tissue is required for exchange, support, and locomotion.

Activity and Metabolic Rate

For both ectotherms and endotherms, activity greatly affects metabolic rate. Even a person reading quietly at a desk or an insect twitching its wings consumes energy beyond the BMR or SMR. Maximum metabolic rates (the highest rates of ATP use) occur during peak activity, such as lifting heavy weights, sprinting, or high-speed swimming. In general, the maximum metabolic rate an animal can sustain is inversely related to the duration of activity.

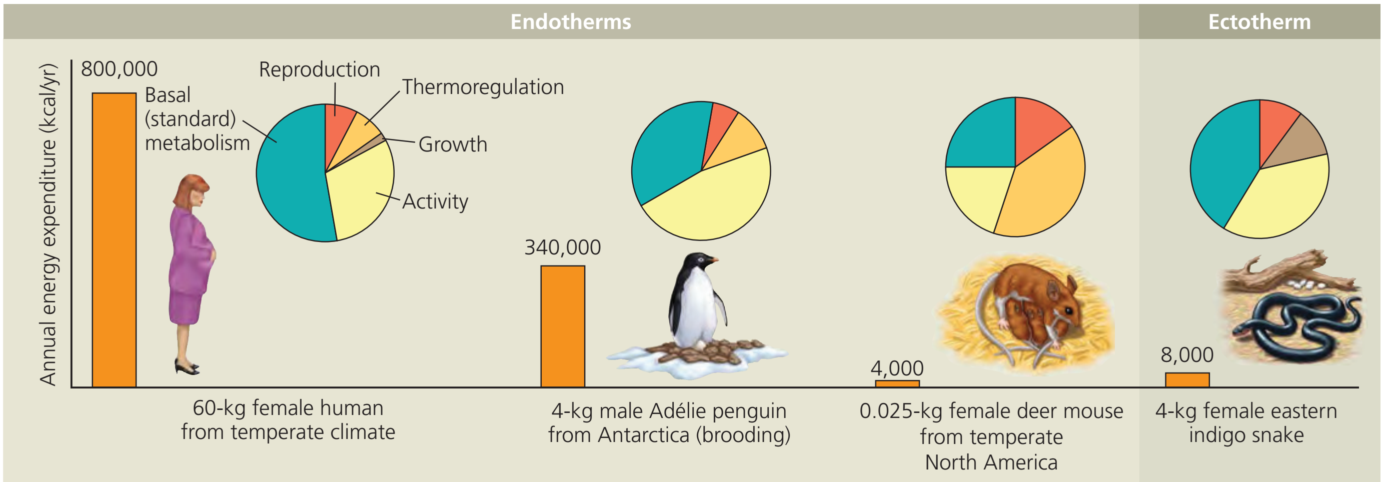
For most terrestrial animals, the average daily rate of energy consumption is 2 to 4 times BMR (for endotherms) or SMR (for ectotherms). Humans in most developed countries have an unusually low average daily metabolic rate of about 1.5 times BMR—an indication of their relatively sedentary lifestyles.



(a) Relationship of basal metabolic rate (BMR) to body size for various mammals. From shrew to elephant, size increases 1 millionfold.

(b) Relationship of BMR per kilogram of body mass to body size for the same mammals as in (a).

▲ **Figure 40.19 The relationship of metabolic rate to body size.**



▲ **Figure 40.20 Energy budgets for four animals.** The slices of the pie charts indicate annual energy expenditures for various functions.

Energy Budgets

As we have seen, the ways in which animals use the chemical energy of food depend on environment, behavior, size, and thermoregulation. To understand how these influences affect bioenergetics in animal bodies, let's consider typical annual energy "budgets" of four terrestrial vertebrates varying in size and thermoregulatory strategy: a 60-kg female human, a 4-kg male Adélie penguin, a 25-g (0.025-kg) female deer mouse, and a 4-kg female eastern indigo snake **(Figure 40.20)**. Reproduction is included in these energy budgets because it can greatly influence energy allocation and is critical to species survival.

The female human, an endothermic mammal, spends the largest fraction of her annual energy budget for BMR and comparatively less for activity and thermoregulation. The small amount of growth, about 1%, is equivalent to adding about 1 kg of body fat or 5–6 kg of other tissues. (Growth is not shown in the budgets for the penguin and deer mouse because these animals don't typically gain weight year to year after they are adults.) The cost of nine months of pregnancy and several months of breast-feeding is only 5–8% of the mother's energy requirements for a year.

A male penguin spends the largest fraction of his energy for activity because he must swim to catch food. Being well insulated and fairly large, he has relatively low costs of thermoregulation in spite of living in the cold Antarctic. His reproductive costs, about 6% of annual energy expenditures, come mainly from incubating eggs (brooding) and bringing food to his chicks.

Despite living in a temperate climate, the female deer mouse spends a large fraction of her energy budget for temperature regulation. Because of the high surface-to-volume ratio that goes with small size, deer mice lose body heat rapidly and must constantly generate metabolic heat to maintain body temperature.

In contrast with these endothermic animals, the ectothermic snake has no thermoregulation costs. Like most snakes, she grows continuously throughout her life. In the example in Figure 40.20, the snake adds about 750 g of new body tissue in a year. She also produces about 650 g of eggs. The snake's economical ectothermic strategy is revealed by her very low energy expenditure, only $1/40$ the energy expended by the similarly sized endothermic penguin.

For all the animals in Figure 40.20, locomotion and other activities are a major part of the energy budget. Some animals can conserve energy by temporarily decreasing their activity to a very low level, a process we will consider next.

Torpor and Energy Conservation

Despite their many adaptations for homeostasis, animals may encounter conditions that severely challenge their abilities to balance their heat, energy, and materials budgets. For example, at certain times of the day or year, their surroundings may be extremely hot or cold, or food may be unavailable. **Torpor**, a physiological state of decreased activity and metabolism, is an adaptation that enables animals to save energy while avoiding difficult and dangerous conditions.

Many small mammals and birds exhibit a daily torpor that seems to be adapted to feeding patterns. For instance, some bats feed at night and go into torpor in daylight. Chickadees and hummingbirds feed during the day and often go into torpor on cold nights; the body temperature of chickadees drops as much as 10°C (18°F) at night, and the temperature of hummingbirds can fall 25°C (45°F) or more. All endotherms that exhibit daily torpor are relatively small; when active, they have high metabolic rates and thus very high rates of energy consumption.

Hibernation is long-term torpor that is an adaptation to winter cold and food scarcity. When a mammal enters hibernation, its body temperature declines as its body's thermostat is turned down. The temperature reduction may be dramatic: Some hibernating mammals cool to as low as 1–2°C (34–36°F), and at least one, the Arctic ground squirrel (*Spermophilus parryii*), can enter a supercooled (unfrozen) state in which its body temperature dips below 0°C (32°F). Periodically, perhaps every two weeks or so, hibernating animals undergo arousal, raising their body temperature and becoming active briefly before resuming hibernation. Nevertheless, the energy savings from hibernation are huge: Metabolic rates during hibernation can be 20 times lower than if the animal attempted to maintain normal body temperatures of 36–38°C (97–100°F). As a result, hibernators such as the ground squirrel can survive through the winter on limited supplies of energy stored in the body tissues or as food cached in a burrow. Similarly, the slow metabolism and inactivity of *estivation*, or summer torpor, enables animals to survive long periods of high temperatures and scarce water supplies.

What happens to the circadian rhythm in hibernating animals? In the past, some researchers have reported detecting daily biological rhythms in hibernating animals. However, in some cases the animals were probably in a state of torpor, from which they could readily arouse, rather than "deep" hibernation. Recently, a group of researchers in France addressed this question in a different way, examining the machinery of the biological clock rather than the rhythms it controls **(Figure 40.21)**. Working with the European hamster, they found that molecular components of the clock stopped oscillating during hibernation. These findings support the hypothesis that the circadian clock ceases operation during hibernation, at least in this species.

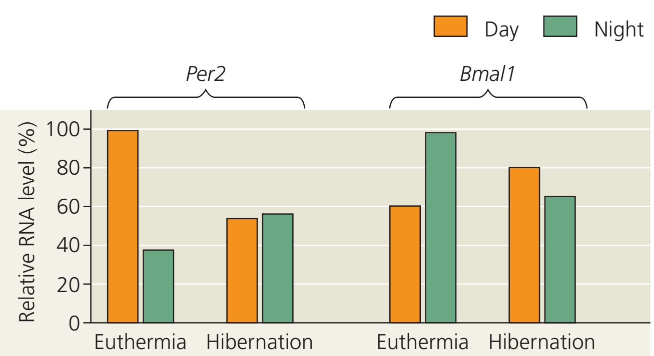
From discussing body shape to considering energy conservation, this chapter has focused on the whole animal. We surveyed common tissue types that make up organs and organ systems. We also investigated how body plans provide for exchange of materials with the environment, how some animals maintain a constant internal environment, and how size and activity affect metabolic rate. For much of the rest of this unit, we'll explore how specialized organs and organ systems enable animals to meet the basic challenges of life.

▼ Figure 40.21 **INQUIRY**

What happens to the circadian clock during hibernation?

EXPERIMENT To determine whether the 24-hour biological clock continues to run during hibernation, Paul Pévet and colleagues at the University of Louis Pasteur in Strasbourg, France, studied molecular components of the circadian clock in the European hamster (*Cricetus cricetus*). The researchers measured RNA levels for two clock genes—*Per2* and *Bmal1*—during normal activity (euthermia) and during hibernation in constant darkness. The RNA samples were obtained from the suprachiasmatic nuclei (SCN), a pair of structures in the mammalian brain that control circadian rhythms.

RESULTS



CONCLUSION Hibernation disrupted circadian variation in the hamster's clock gene RNA levels. Further experiments demonstrated that this disruption was not simply due to the dark environment during hibernation, since for nonhibernating animals RNA levels during a darkened daytime were the same as in daylight. The researchers concluded that the biological clock stops running in hibernating European hamsters and, perhaps, in other hibernators as well.

SOURCE F. G. Revel et al., The circadian clock stops ticking during deep hibernation in the European hamster, *Proceedings of the National Academy of Sciences USA* 104:13816–13820 (2007).

WHAT IF? Suppose you discovered a new hamster gene and found that the levels of RNA for this gene were constant during hibernation. What could you conclude about the day and night RNA levels for this gene during euthermia?

CONCEPT CHECK 40.4

1. If a mouse and a small lizard of the same mass (both at rest) were placed in experimental chambers under identical environmental conditions, which animal would consume oxygen at a higher rate? Explain.
2. Which animal must eat a larger proportion of its weight in food each day: a house cat or an African lion caged in a zoo? Explain.
3. **WHAT IF?** If you monitored energy allocation in the penguin in Figure 40.20 for just a few months instead of an entire year, you might find the "growth" category to be a significant part of the pie chart. Given that adult penguins don't grow from year to year, how would you explain this finding?

For suggested answers, see Appendix A.

40 CHAPTER REVIEW

SUMMARY OF KEY CONCEPTS

CONCEPT 40.1

Animal form and function are correlated at all levels of organization (pp. 852–860)

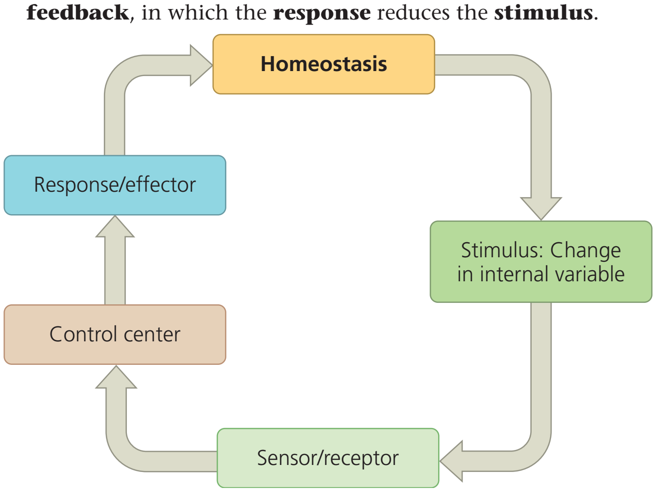
- Physical laws constrain the evolution of an animal's size and shape. These constraints contribute to convergent evolution, the similar but independent adaptations of different species to a common environmental challenge.
- Each animal cell must have access to an aqueous environment. Simple two-layered sacs and flat shapes maximize exposure to the surrounding medium. More complex body plans have highly folded internal surfaces specialized for exchanging materials.
- In the hierarchical organization of animal bodies, groups of cells with a common structure and function make up **tissues**. Different tissues make up **organs**, which together make up **organ systems**. Animal tissues fall into four main groups, each with distinct functions. **Epithelial tissue** forms active interfaces with the environment on external and internal surfaces of the body. **Connective tissue** binds and supports other tissues. **Muscle tissue** contracts, moving the parts of the body. **Nervous tissue** transmits nerve impulses throughout the body.
- The endocrine and nervous systems are the two means of communication between different locations in the body. The endocrine system broadcasts signaling molecules called **hormones** everywhere via the bloodstream, but only certain cells are responsive to each hormone. The nervous system uses dedicated cellular circuits involving electrical and chemical signals to send information to specific locations.

? *For a large animal, what challenges would a spherical shape pose for carrying out exchange with the environment?*

CONCEPT 40.2

Feedback control maintains the internal environment in many animals (pp. 860–862)

- Faced with environmental fluctuations, animals *regulate* (control) certain internal variables while allowing other internal variables to *conform* to (correspond to) external changes. **Homeostasis** is the maintenance of a steady state despite internal and external changes.
- Homeostatic mechanisms are usually based on **negative feedback**, in which the **response** reduces the **stimulus**.



In contrast, **positive feedback** involves amplification of a stimulus by the response and often brings about a change in state, such as the transition from pregnancy to childbirth.
- Regulated change in the internal environment is essential to normal function. **Circadian rhythms** are daily fluctuations in metabolism and behavior tuned to the cycles of light and dark in the environment. Other environmental changes may trigger **acclimatization**, a temporary shift in the steady state.

? *Is it accurate to define homeostasis as a constant internal environment? Explain.*

CONCEPT 40.3

Homeostatic processes for thermoregulation involve form, function, and behavior (pp. 862–868)

- An animal maintains its internal temperature within a tolerable range by **thermoregulation**. **Endotherms** are warmed mostly by heat generated by metabolism. **Ectotherms** get most of their heat from external sources. Endothermy requires a greater expenditure of energy. Body temperature may vary with environmental temperature, as in *poikilotherms*, or be relatively constant, as in *homeotherms*.
- In thermoregulation, physiological and behavioral adjustments balance heat gain and loss, which occur through **radiation**, **evaporation**, **convection**, and **conduction**. Insulation and **countercurrent exchange** reduce heat loss, whereas panting, sweating, and bathing increase evaporation, cooling the body. Both ectotherms and endotherms adjust their rate of heat exchange with their surroundings by vasodilation or vasoconstriction and by behavioral responses.
- Many mammals and birds adjust their amount of body insulation in response to changes in environmental temperature. Ectotherms undergo a variety of changes at the cellular level to acclimatize to shifts in temperature.
- The **hypothalamus** acts as the thermostat in mammalian regulation of body temperature. Fever reflects a resetting of this thermostat to a higher set point in response to infection.

? *Given that humans thermoregulate, explain why your skin is cooler than your body core.*

CONCEPT 40.4

Energy requirements are related to animal size, activity, and environment (pp. 868–872)

- Animals obtain chemical energy from food, storing it for short-term use in ATP. The total amount of energy used in a unit of time defines an animal's **metabolic rate**. Metabolic rates are generally higher for endotherms than for ectotherms.
- Under similar conditions and for animals of the same size, the **basal metabolic rate** of endotherms is substantially higher than the **standard metabolic rate** of ectotherms. Minimum metabolic rate per gram is inversely related to body size among similar animals. Animals allocate energy for basal (or standard) metabolism, activity, homeostasis, growth, and reproduction.
- **Torpor**, a state of decreased activity and metabolism, conserves energy during environmental extremes. Animals may enter torpor during sleep periods (daily torpor), in winter (**hibernation**), or in summer (estivation).

? *Most hibernators are small. After reviewing Figure 40.19, suggest an explanation for this observation.*

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

1. The body tissue that consists largely of material located outside of cells is
   a. epithelial tissue.
   b. connective tissue.
   c. skeletal muscle.
   d. smooth muscle.
   e. nervous tissue.

2. Which of the following would increase the rate of heat exchange between an animal and its environment?
   a. feathers or fur
   b. vasoconstriction
   c. wind blowing across the body surface
   d. countercurrent heat exchanger
   e. blubber or fat layer

3. Consider the energy budgets for a human, an elephant, a penguin, a mouse, and a snake. The __________ would have the highest total annual energy expenditure, and the __________ would have the highest energy expenditure per unit mass.
   a. elephant; mouse
   b. elephant; human
   c. human; penguin
   d. mouse; snake
   e. penguin; mouse

LEVEL 2: APPLICATION/ANALYSIS

4. Compared with a smaller cell, a larger cell of the same shape has
   a. less surface area.
   b. less surface area per unit of volume.
   c. the same surface-to-volume ratio.
   d. a smaller average distance between its mitochondria and the external source of oxygen.
   e. a smaller cytoplasm-to-nucleus ratio.

5. An animal's inputs of energy and materials would exceed its outputs
   a. if the animal is an endotherm, which must always take in more energy because of its high metabolic rate.
   b. if it is actively foraging for food.
   c. if it is hibernating.
   d. if it is growing and increasing its mass.
   e. never; homeostasis makes these energy and material budgets always balance.

6. You are studying a large tropical reptile that has a high and relatively stable body temperature. How would you determine whether this animal is an endotherm or an ectotherm?
   a. You know from its high and stable body temperature that it must be an endotherm.
   b. You know that it is an ectotherm because it is not a bird or mammal.
   c. You subject this reptile to various temperatures in the lab and find that its body temperature and metabolic rate change with the ambient temperature. You conclude that it is an ectotherm.
   d. You note that its environment has a high and stable temperature. Because its body temperature matches the environmental temperature, you conclude that it is an ectotherm.
   e. You measure the metabolic rate of the reptile, and because it is higher than that of a related species that lives in temperate forests, you conclude that this reptile is an endotherm and its relative is an ectotherm.

7. Which of the following animals uses the largest percentage of its energy budget for homeostatic regulation?
   a. a hydra
   b. a marine jelly (an invertebrate)
   c. a snake in a temperate forest
   d. a desert insect
   e. a desert bird

8. **DRAW IT** Draw a model of the control circuit(s) required for driving an automobile at a fairly constant speed over a hilly road. Indicate each feature that represents a sensor, stimulus, or response.

LEVEL 3: SYNTHESIS/EVALUATION

9. **EVOLUTION CONNECTION**
   In 1847, the German biologist Christian Bergmann noted that mammals and birds living at higher latitudes (farther from the equator) are on average larger and bulkier than related species found at lower latitudes. Suggest an evolutionary hypothesis to explain this observation.

10. **SCIENTIFIC INQUIRY**
    Eastern tent caterpillars (*Malacosoma americanum*) live in large groups in silk nests, or tents, which they build in trees. They are among the first insects to be active in early spring, when daily temperature fluctuates from freezing to very hot. Over the course of a day, they display striking differences in behavior: Early in the morning, they rest in a tightly packed group on the tent's east-facing surface. In midafternoon, they are on its undersurface, each caterpillar hanging by a few of its legs. Propose a hypothesis to explain this behavior. How could you test it?

11. **SCIENCE, TECHNOLOGY, AND SOCIETY**
    Medical researchers are investigating artificial substitutes for various human tissues. Why might artificial blood or skin be useful? What characteristics would these substitutes need in order to function well in the body? Why do real tissues work better? Why not use the real tissues if they work better? What other artificial tissues might be useful? What problems do you anticipate in developing and applying them?

12. **WRITE ABOUT A THEME**
    Feedback Regulation In a short essay (about 100–150 words) focusing on feedback control in thermoregulation, explain why shivering is likely during the onset of a fever.

For selected answers, see Appendix A.