CHAPTER

32 The Internal Environment of Animals: Organization and Regulation

▲ **Figure 32.1** How do long legs help this scavenger survive in the scorching desert heat?

KEY CONCEPTS

32.1 Animal form and function are correlated at all levels of organization

32.2 The endocrine and nervous systems act individually and together in regulating animal physiology

32.3 Feedback control maintains the internal environment in many animals

32.4 A shared system mediates osmoregulation and excretion in many animals

32.5 The mammalian kidney's ability to conserve water is a key terrestrial adaptation

Diverse Forms, Common Challenges

The desert ant (*Cataglyphis*) in **Figure 32.1** scavenges insects that have succumbed to the daytime heat of the Sahara Desert. To gather corpses for feeding, the ant must forage when surface temperatures on the sunbaked sand exceed 60°C (140°F), well above the thermal limit for virtually all animals. How does the desert ant survive these conditions? To address this question, we need to consider the relationship of **anatomy**, or biological form, to species survival.

Over the course of its life, an ant faces the same fundamental challenges as any other animal, whether hydra, hawk, or human. All animals must obtain nutrients and oxygen, 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 Concept 21.4). The evolutionary adaptations that enable 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 desert ant, researchers noted that its stilt-like legs are disproportionately long, elevating the rest of the ant 4 mm above the sand. At this height, the ant's body is exposed to a temperature 6°C lower than that at ground level. The ant's long legs also facilitate rapid locomotion: Researchers have found that desert ants can run as fast as 1 m/sec, close to the top speed recorded for a running arthropod. Speedy sprinting minimizes the time that the ant is exposed to the sun. Thus, the long legs of the desert ant are adaptations that allow it to be active during the heat of the day, when competition for food and the risk of predation are lowest.

We will begin our study of animal form and function by examining the organization of cells and tissues in the animal body, the systems for coordinating the activities of different body parts, and the general means by which animals control their internal environment. We then apply these ideas to two challenges of particular relevance for desert animals: regulating body temperature and maintaining proper balance of body salts and water.

CONCEPT 32.1

Animal form and function are correlated at all levels of organization

For animals, as for other multicellular organisms, having many cells facilitates specialization. For example, a hard outer covering helps protect against predators, and large muscles facilitate rapid escape. In a multicellular body, the immediate environment of most cells is the internal body fluid. Control systems that regulate the composition of this solution allow the animal to maintain a relatively stable internal environment, even if the external environment is variable. To understand how these control systems operate, we first need to explore the layers of organization that characterize animal bodies.

Cells form a working animal body through their emergent properties, which arise from 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, providing an additional level of organization and coordination, make up an **organ system** **(Table 32.1)**. Thus, for example, the skin is an organ of the *integumentary system*, which protects against infection and helps regulate body temperature.

Many organs have more than one physiological role. If the roles are distinct enough, 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, but 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—each organ has specific roles. In the case of the stomach, one role is to initiate protein breakdown. 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 different functions but are lined by tissues that are of the same basic type and that therefore share many properties. Animal tissues are commonly grouped into four main types: epithelial, connective, muscle, and nervous **(Figure 32.2)**.

As you read in Unit Five, plants also have a hierarchical organization. Although plant anatomy and animal anatomy differ, they are adapted to a shared set of challenges, as shown in **Figure 32.3**.

CONCEPT CHECK 32.1

1. What properties do all types of epithelia share?
2. Suggest why a disease that damages connective tissue is likely to affect most of the body's organs.

For suggested answers, see Appendix A.

Table 32.1 Organ Systems in Mammals

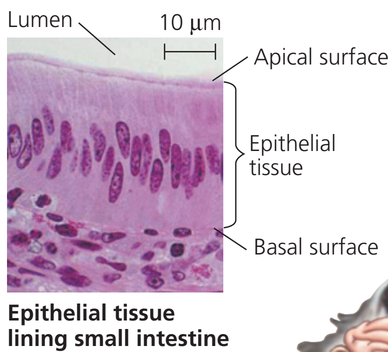
Organ System	Main Components	Main Functions
Digestive	Mouth, pharynx, esophagus, stomach, intestines, liver, pancreas, anus	Food processing (ingestion, digestion, absorption, elimination)
Circulatory	Heart, blood vessels, blood	Internal distribution of materials
Respiratory	Lungs, trachea, other breathing 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 virally induced cancers)
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, sweat 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 32.2 Exploring Structure and Function in Animal Tissues

Epithelial Tissue

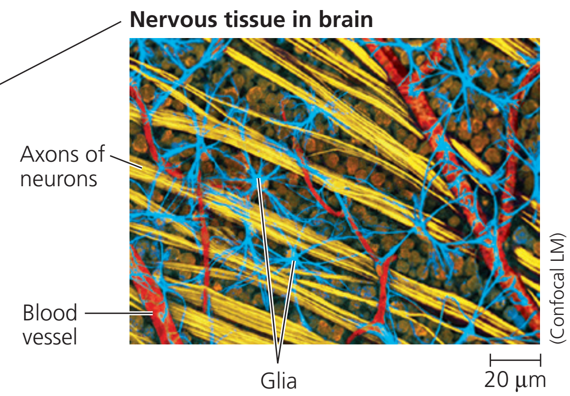
Occurring as sheets of closely packed cells, **epithelial tissue** covers the outside of the body and lines organs and cavities. Epithelial tissue functions as a barrier against mechanical injury, pathogens, and fluid loss. It also forms active interfaces with the environment. For example, the **epithelium** (plural, epithelia) that lines the intestines secretes digestive juices and absorbs nutrients.

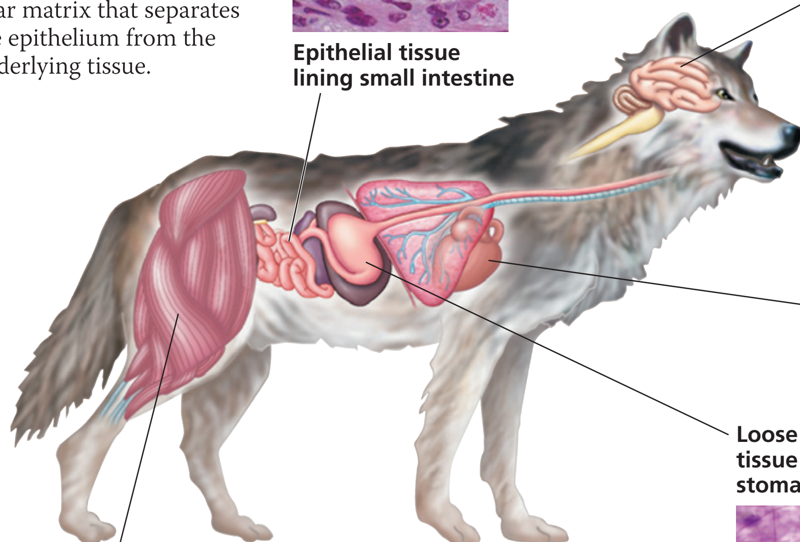
All epithelia are polarized, meaning that they have two different sides. The *apical* surface faces the lumen (cavity) or outside of the organ and is therefore exposed to fluid or air. The basal surface is attached to a *basal lamina*, a dense mat of extracellular matrix that separates the epithelium from the underlying tissue.

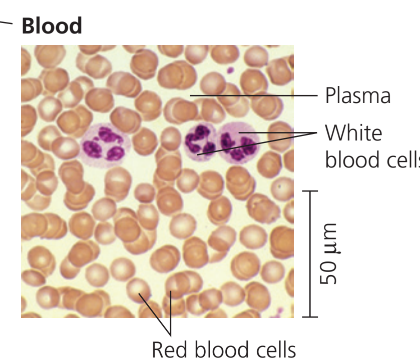


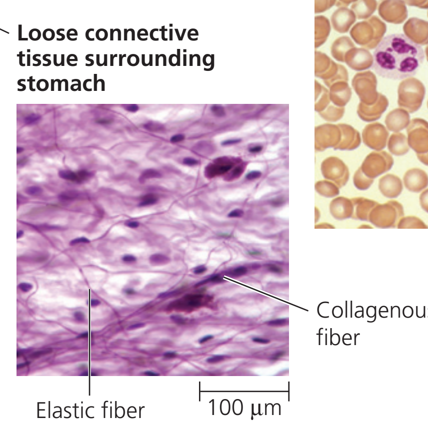
Nervous Tissue

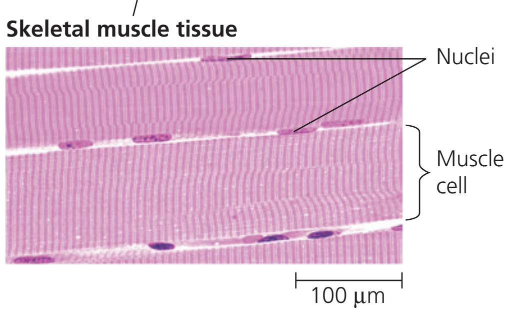
Nervous tissue functions in the receipt, processing, and transmission of information. Specialized cells called **neurons** are the basic units of the nervous system. A neuron receives nerve impulses from other neurons via its cell body and multiple extensions called dendrites. Neurons transmit impulses to neurons, muscles, or other cells via extensions called axons, which are often bundled together into nerves. Nervous tissue also contains support cells called **glial cells**, or simply **glia**. The various types of glia help nourish, insulate, and replenish neurons and in some cases modulate neuron function. In many animals, a concentration of nervous tissue forms a brain, an information-processing center.











(All photos in the figure are LMs)

Muscle Tissue

Vertebrates have three types of **muscle tissue**: skeletal, cardiac, and smooth. All muscle cells consist of filaments containing the proteins actin and myosin, which together enable muscles to contract. Attached to bones by tendons, **skeletal muscle**, or striated muscle, is responsible for voluntary movements. The arrangement of contractile units along the cells gives them a striped (striated) appearance. Cardiac muscle, which is also striated, forms the contractile wall of the heart. Smooth muscle, which lacks striations and has spindle-shaped cells, is found in the walls of many internal organs. Smooth muscles are responsible for involuntary activities, such as churning of the stomach and constriction of arteries.

Muscle Tissue

Connective tissue consists of cells scattered through an extracellular matrix, often forming a web of fibers embedded in a liquid, jellylike, or solid foundation. Within the matrix are cells called *fibroblasts*, which secrete collagen and other matrix proteins, and *macrophages*, which engulf foreign particles and cell debris.

In vertebrates, the many forms of connective tissue include loose connective tissue, which holds skin and other organs in place; fibrous connective tissue, found in tendons and ligaments; adipose tissue, which stores fat; blood, which consists of cells and cell fragments suspended in a liquid called plasma; cartilage, which provides flexible support in the spine and elsewhere; and bone, a hard mineral of calcium, magnesium, and phosphate ions in a matrix of collagen.

▼ **Figure 32.3**

MAKE CONNECTIONS

Life Challenges and Solutions in Plants and Animals

Multicellular organisms face a common set of challenges. Comparing the solutions that have evolved in plants and animals reveals both unity (shared elements) and diversity (distinct features) across these two lineages.

Nutritional Mode

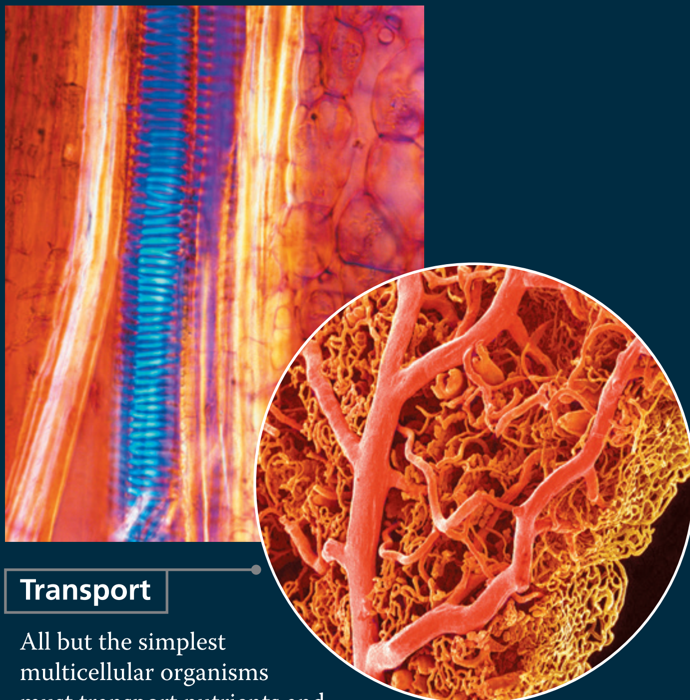
All living things must obtain energy and carbon from the environment to grow, survive, and reproduce. Plants are autotrophs, obtaining their energy through photosynthesis and their carbon from inorganic sources, whereas animals are heterotrophs, obtaining their energy and carbon from food. Evolutionary adaptations in plants and animals support these different nutritional modes. The broad surface of many leaves (left) enhances light capture for photosynthesis. When hunting, a bobcat relies on stealth, speed, and sharp claws (right). (See Figure 29.2 and Figure 33.14.)

Environmental Response

All forms of life must detect and respond appropriately to conditions in their environment. Specialized organs sense environmental signals. For example, the floral head of a sunflower (left) and an insect's eyes (right) both contain photoreceptors that detect light. Environmental signals activate specific receptor proteins, triggering signal transduction pathways that initiate cellular responses coordinated by chemical and electrical communication. (See Figure 31.12 and Figure 38.26.)

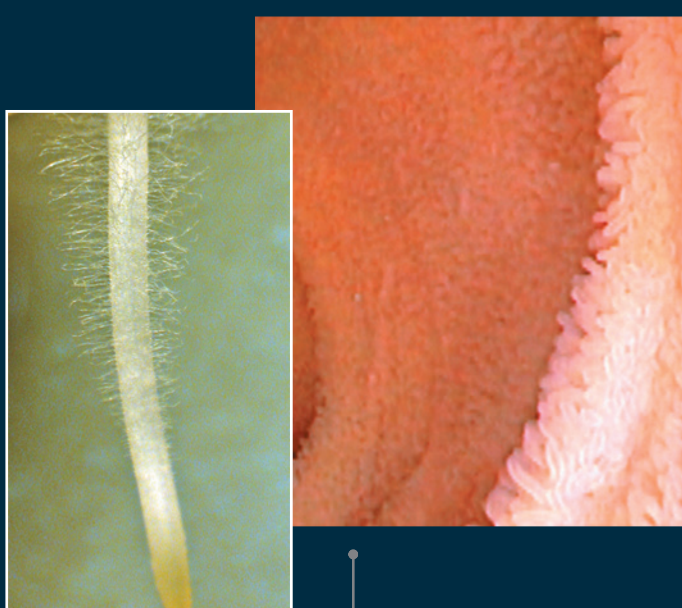
Growth and Regulation

The growth and physiology of both plants and animals are regulated by hormones. In plants, hormones may act in a local area or be transported in the body. They control growth patterns, flowering, fruit development, and more (left). In animals, hormones circulate throughout the body and act in specific target tissues, controlling homeostatic processes and developmental events such as molting (below). (See Table 31.1 and Figure 33.19.)



Transport

All but the simplest multicellular organisms must transport nutrients and waste products between locations in the body. A system of tubelike vessels is the common evolutionary solution, while the mechanism of circulation varies. Plants harness solar energy to transport water, minerals, and sugars through specialized tubes (left). In animals, a pump (heart) moves circulatory fluid through vessels (right). (See Figure 28.9 and Figure 34.3.)

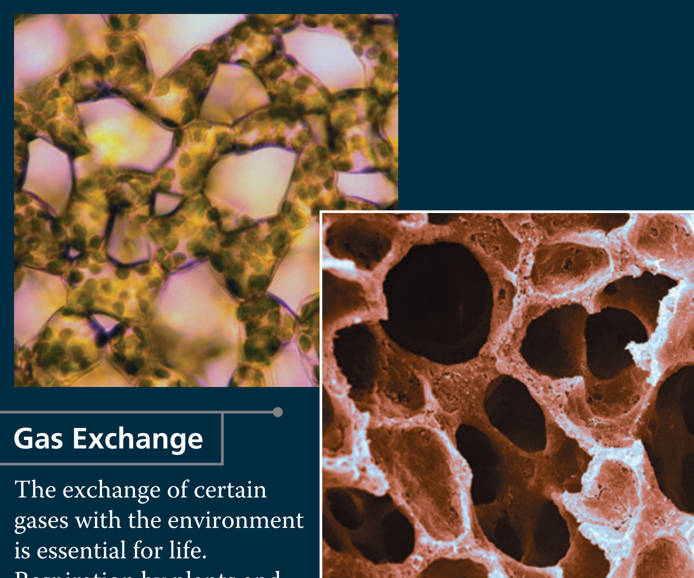


Absorption

Organisms need to absorb nutrients. The root hairs of plants (left) and the villi (projections) that line the intestines of vertebrates (right) increase the surface area available for absorption. (See Figure 28.4 and Figure 33.10.)

Reproduction

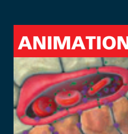
In sexual reproduction, specialized tissues and structures produce and exchange gametes. Offspring are generally supplied with nutritional stores that facilitate rapid growth and development. For example, seeds (left) have stored food reserves that supply energy to the young seedling, while milk provides sustenance for juvenile mammals (right). (See Figure 30.8 and Figure 32.7.)



Gas Exchange

The exchange of certain gases with the environment is essential for life. Respiration by plants and animals requires taking up oxygen (O_2) and releasing carbon dioxide (CO_2). In photosynthesis, net exchange occurs in the opposite direction: CO_2 uptake and O_2 release. In both plants and animals, highly convoluted surfaces that increase the area available for gas exchange have evolved, such as the spongy mesophyll of leaves (left) and the alveoli of lungs (right). (See Figure 28.17 and Figure 34.20.)

MAKE CONNECTIONS *Compare the adaptations that enable plants and animals to respond to the challenges of living in hot and cold environments. See Concepts 31.3 and 32.3.*



Visit the Study Area in **MasteringBiology** for the BioFlix® 3-D Animations on Water Transport in Plants (Chapter 29), Homeostasis: Regulating Blood Sugar (Chapter 33), and Gas Exchange (Chapter 34).

CONCEPT 32.2

The endocrine and nervous systems act individually and together in regulating animal physiology

For an animal's tissues and organ systems to perform their specialized functions effectively, they must act in concert with one another. For example, when the wolf shown in Figure 32.2 is hunting, it regulates blood flow in its circulatory system to bring adequate nutrients and gases to its leg muscles, which in turn are controlled by the brain in response to cues detected by the nose. What signals are used to coordinate activity? How do the signals move within the body?

An Overview of Coordination and Control

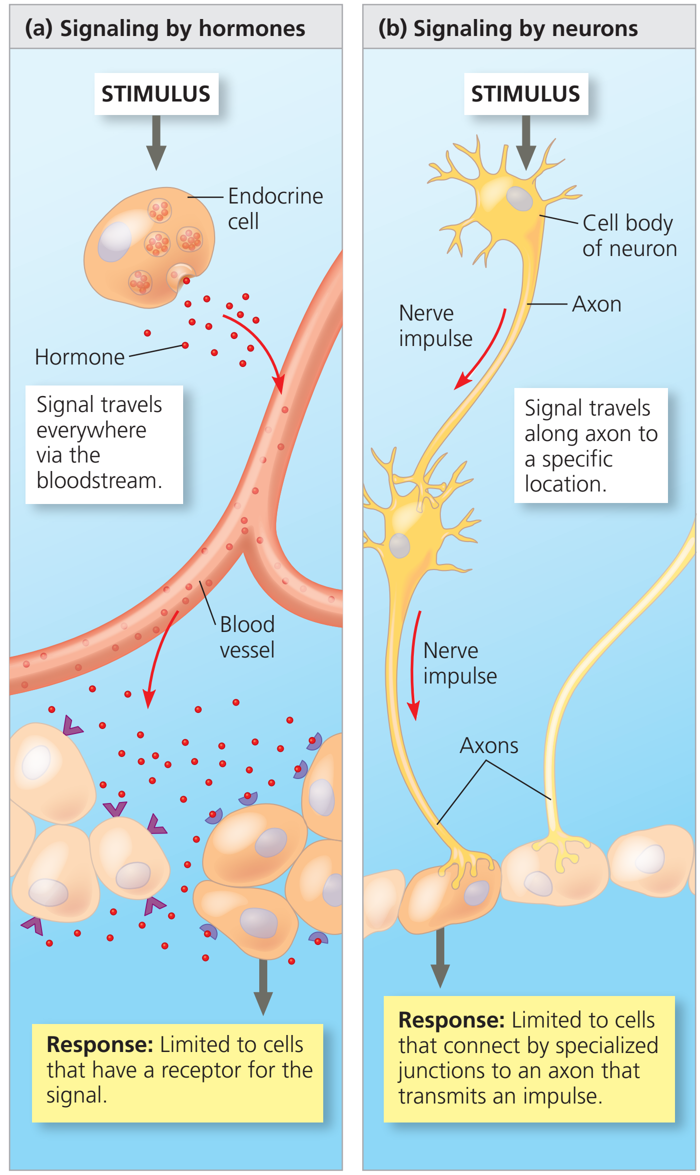
Animals have two major systems for coordinating and controlling responses to stimuli: the endocrine system and the nervous system (**Figure 32.4**). In the **endocrine system**, signaling molecules released into the bloodstream by endocrine cells are carried to all locations in the body. In the **nervous system**, neurons transmit signals along dedicated routes connecting specific locations in the body.

The signaling molecules broadcast throughout the body by the endocrine system are called **hormones** (from the Greek *horman*, to excite). Different hormones cause distinct effects, and only cells that have receptors for a particular hormone respond (see Figure 32.4a). 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. It takes many seconds for hormones to be released into the bloodstream and carried throughout the body. The effects are often long-lasting, however, because hormones can remain in the bloodstream for minutes or even hours.

In the nervous system, signals called nerve impulses travel to specific target cells along communication lines consisting mainly of extensions called axons (see Figure 32.4b). Nerve impulses can act on other neurons, on muscle cells, and on cells and glands that produce secretions. Unlike the endocrine system, the nervous system conveys information by the particular *pathway* the signal takes. For example, a person can distinguish different musical notes because within the ear each note's frequency activates neurons that connect to slightly different regions of 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. In contrast, passing information from one neuron to another often involves very short-range chemical signals. Overall, transmission in the nervous system is extremely fast: Nerve impulses take only a fraction of a second to reach the target and last only a fraction of a second.

▼ **Figure 32.4** **Signaling in the endocrine and nervous systems.**



The two major communication systems of the body differ in signal type, transmission, speed, and duration. All these differences reflect adaptation to different functions. The endocrine system is especially well adapted for coordinating gradual changes that affect the entire body, such as growth, development, reproduction, metabolic processes, and digestion. The nervous system is well suited for directing immediate and rapid responses to the environment, such as reflexes and other rapid movements. Although the general functions of the endocrine and nervous systems are distinct, the two systems often work in close coordination, as we will explore shortly.

We'll investigate nervous system organization and function in detail in Chapters 37 and 38. Here we'll focus on the components of the endocrine system and the organization of pathways for endocrine signaling.

Endocrine Glands and Hormones

Within the body, endocrine cells are often grouped in ductless organs called **endocrine glands**. The major endocrine glands of humans and the hormones that they produce are illustrated in **Figure 32.5**. Some endocrine cells are instead found in organs that are part of other organ systems. For example, the stomach contains isolated endocrine cells that regulate digestion by secreting the hormone gastrin in response to ingested food.

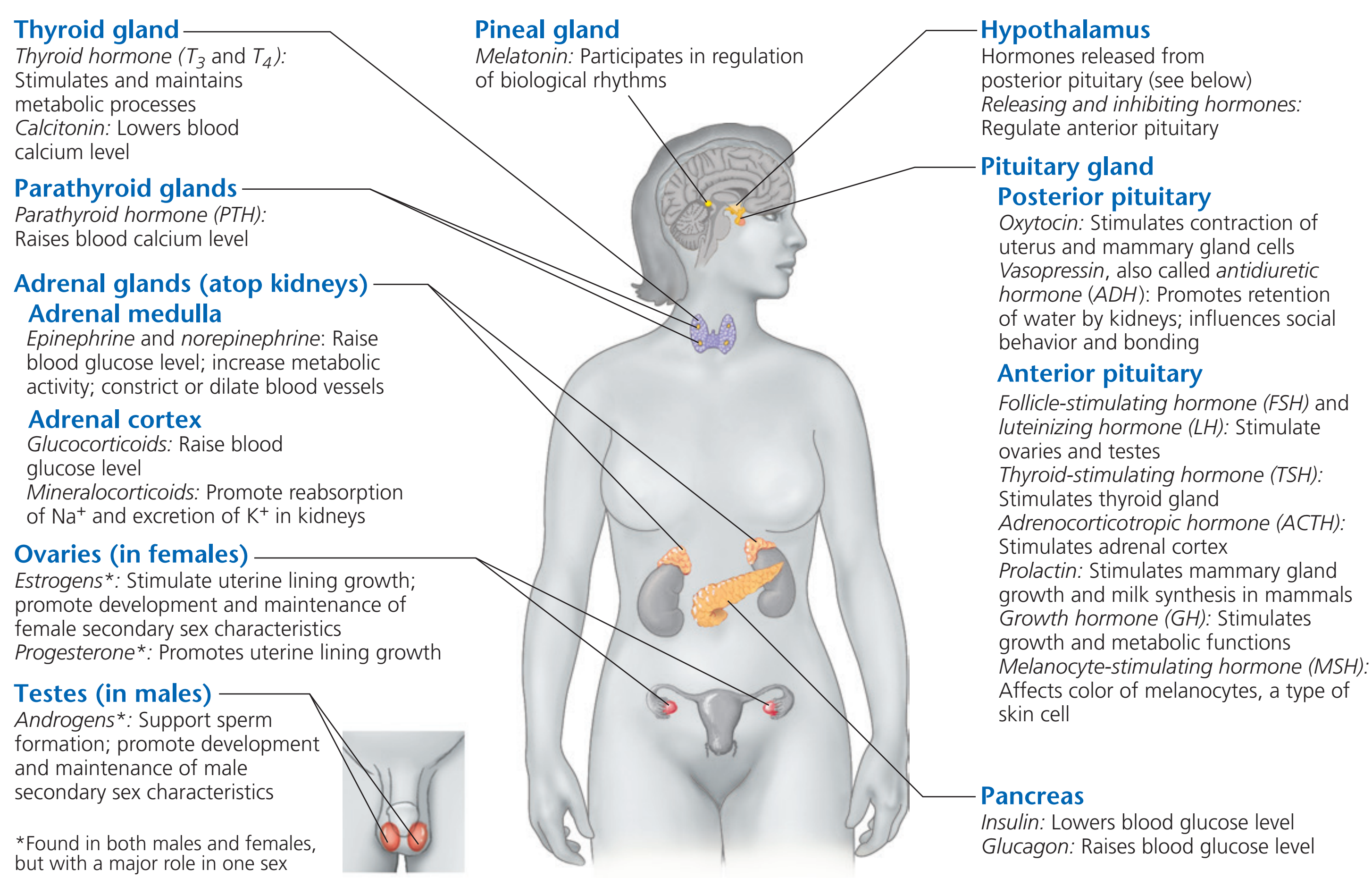
Endocrine cells and glands secrete hormones directly into the surrounding fluid. From there, the hormones enter the circulatory system. In contrast, *exocrine glands*, such as salivary glands, have ducts that carry enzymes or other secreted substances into body cavities or onto body surfaces.

Regulation of Endocrine Signaling

The stimuli that cause endocrine cells and glands to release hormones are varied. In some cases, organic molecules or ions trigger the endocrine response. For example, high levels of glucose stimulate the pancreas to secrete insulin, a hormone that causes a decrease in the level of glucose in the blood. In other cases, the nervous system provides the stimulus for hormone release, a type of control called *neuroendocrine signaling*. The **hypothalamus**, an almond-sized region of the brain (see Figure 32.5), controls most neuroendocrine signaling in mammals. Finally, some hormones are secreted in response to other hormones. Hormones that regulate other hormones have essential roles in growth, metabolism, and reproduction, as you will learn in this and later chapters.

Regulation of a signaling process involves not only its initiation but also its termination. How is an endocrine pathway turned off? Typically, the control process involves **negative feedback**, also called feedback inhibition, a control circuit or loop that reduces, or "damps," the stimulus. In the case of insulin, for example, the secreted hormone triggers a reduction in blood glucose levels, which in turn eliminates the stimulus for further insulin release. Because negative feedback prevents excessive pathway activity, this type of control circuit is common in endocrine pathways that keep physiological systems within normal limits.

A few hormone pathways are controlled by **positive feedback**, a control mechanism in which the response reinforces the stimulus, leading to an even greater response. Whereas a negative feedback loop prevents excessive pathway activity, a positive feedback loop helps drive a process to completion. Positive feedback plays a central role in several processes associated with reproduction, including the uterine contractions of childbirth.



▲ **Figure 32.5 The human endocrine system.**

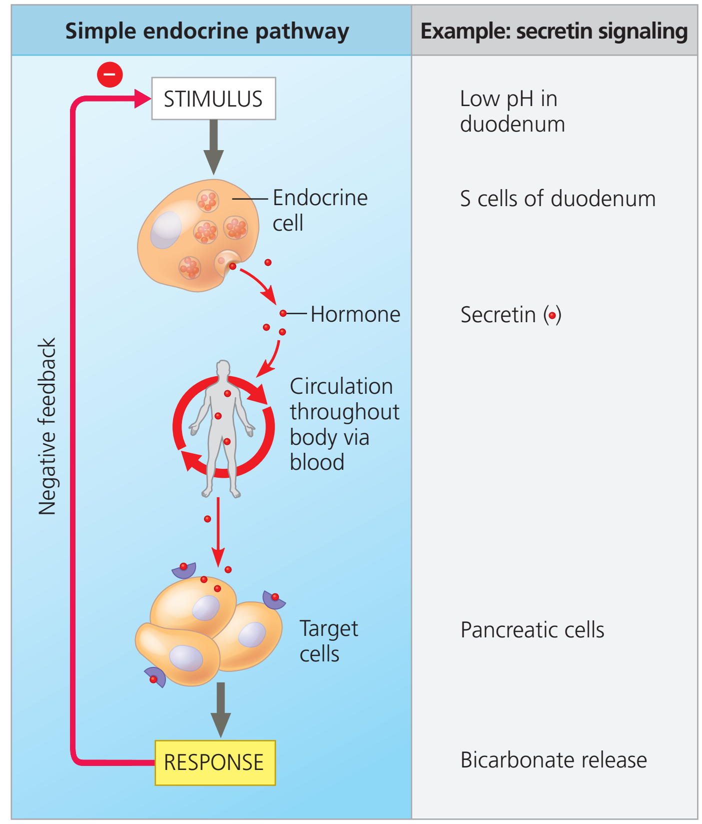
Simple Endocrine Pathways

In the simplest endocrine pathways, endocrine cells respond directly to an internal or environmental stimulus by secreting a particular hormone. The hormone travels in the bloodstream to target cells, where it interacts with its specific receptors. Signal transduction within target cells brings about a response.

As an example of a simple endocrine pathway, we will again turn to the human digestive system. After processing of food in the stomach, partially digested material passes to the *duodenum*, the first part of the small intestine. The digestive juices of the stomach are extremely acidic and must be neutralized before further steps of digestion can occur. To learn how neutral pH is restored, we will consider the pathway outlined in **Figure 32.6**.

Endocrine cells called S cells, found in the lining of the duodenum, recognize the low pH of the partially digested food arriving from the stomach. The S cells respond by secreting the hormone secretin into the bloodstream. Secretin in turn triggers release of bicarbonate from the **pancreas**, a gland located behind the stomach. The bicarbonate travels along ducts leading to the duodenum. There, the bicarbonate neutralizes the acidic contents, raising pH and allowing digestion to proceed.

Note that the pH increase that results from secretin signaling eliminates the stimulus and thus shuts off the endocrine pathway. Secretin signaling is thus an example of a pathway under negative feedback control.



▲ **Figure 32.6 A simple endocrine pathway.** Endocrine cells respond to a change in some internal or external variable—the stimulus—by secreting a particular hormone that triggers a specific response by target cells. In the case of secretin signaling, the simple endocrine pathway is self-limiting because the response to secretin (bicarbonate release) reduces the stimulus (low pH) through negative feedback.

Neuroendocrine Signaling

For many hormones, secretion is triggered when the nervous system detects and processes a stimulus. In vertebrates, such neuroendocrine signaling involves the hypothalamus and the **pituitary gland**, found at its base. The pituitary is actually two glands fused together. One is the **posterior pituitary**, which is an extension of the hypothalamus. The posterior pituitary stores and secretes hormones synthesized in the hypothalamus. In contrast, the **anterior pituitary** is an endocrine gland that both synthesizes and secretes hormones.

Posterior Pituitary Pathways

As an example of a neuroendocrine pathway, we will consider the regulation of milk release during nursing in mammals. When an infant suckles, it stimulates sensory neurons in the nipples, generating nerve impulses that reach the hypothalamus. This input triggers the release of the hormone **oxytocin** from the posterior pituitary (**Figure 32.7**). Oxytocin in turn stimulates the mammary glands, which respond by secreting milk.

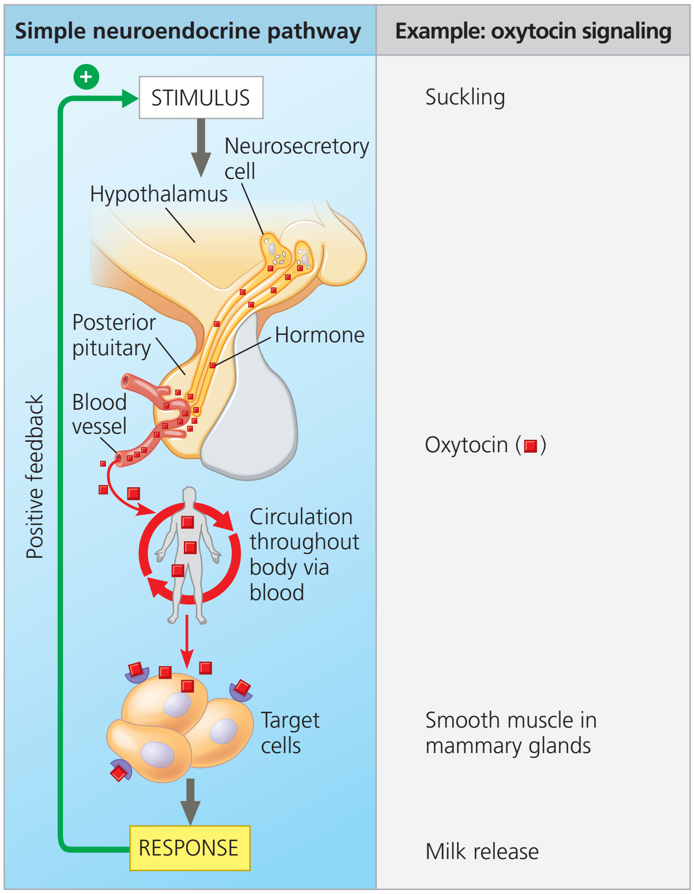
Milk released in response to oxytocin leads to more suckling and therefore more stimulation. Pathway activation continues until the baby stops suckling. Thus, oxytocin regulation of milk release involves positive feedback control. Other functions of oxytocin, such as stimulating contractions of the uterus during birthing, also exhibit positive feedback.

Oxytocin is one of just two posterior pituitary hormones. The other, **antidiuretic hormone (ADH)**, also called **vasopressin**, will be discussed later in this chapter.

Anterior Pituitary Pathways

The anterior pituitary synthesizes and secretes a diverse set of hormones, each regulated by one or more hormones from the hypothalamus. Anterior pituitary hormones range in function from reproduction and growth to metabolism and stress responses (see Figure 32.5). Some, such as growth hormone, regulate cells outside the endocrine system. Others, such as thyroid-stimulating hormone (TSH), regulate endocrine glands.

Anterior pituitary hormones that target endocrine tissues often form part of a *hormone cascade*. Such a cascade is kicked off when the nervous system conveys a stimulus to the hypothalamus. In response, the hypothalamus secretes a factor that regulates release of a specific anterior pituitary hormone. This hormone in turn stimulates an endocrine organ to secrete yet another hormone, which exerts effects on specific target tissues.



▲ **Figure 32.7** **A simple neuroendocrine pathway.** Sensory neurons respond to a stimulus by sending nerve impulses to a neurosecretory cell, triggering hormone secretion. Upon reaching its target cells, the hormone binds to its receptor, causing a specific response. In oxytocin signaling, the response increases the stimulus, forming a positive-feedback loop that amplifies signaling.

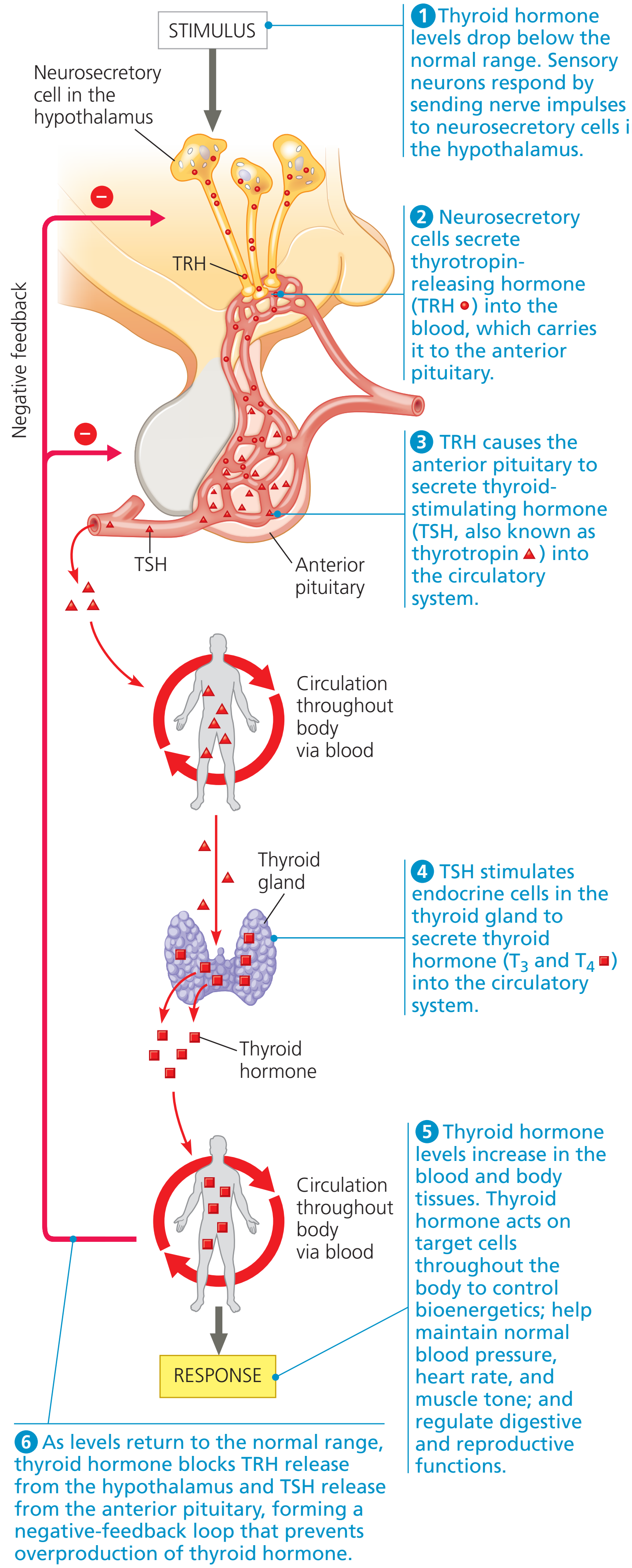
Figure 32.8 outlines such a hormone cascade pathway, using the specific example of thyroid regulation.

Because hormone cascade pathways in a sense redirect signals from the hypothalamus to other endocrine glands, the anterior pituitary hormones in these pathways are sometimes called *tropic* hormones, or tropins, from the Greek word for bending or turning. Thus, for example, TSH is also known as thyrotropin.

Feedback regulation often occurs at multiple levels in hormone cascade pathways. For example, thyroid hormone exerts negative feedback on the hypothalamus and on the anterior pituitary, in each case blocking release of the hormone that promotes its production (see Figure 32.8).

Hormone Solubility

Many hormones, including secretin, ADH, and oxytocin, are soluble in water but not in lipids. For this reason, they are unable to pass through the plasma membranes of target cells. Instead, they bind to cell-surface receptors, triggering events at the plasma membrane that result in a cellular response. The series of changes in cellular proteins that converts the



▲ **Figure 32.8** **A hormone cascade pathway.**

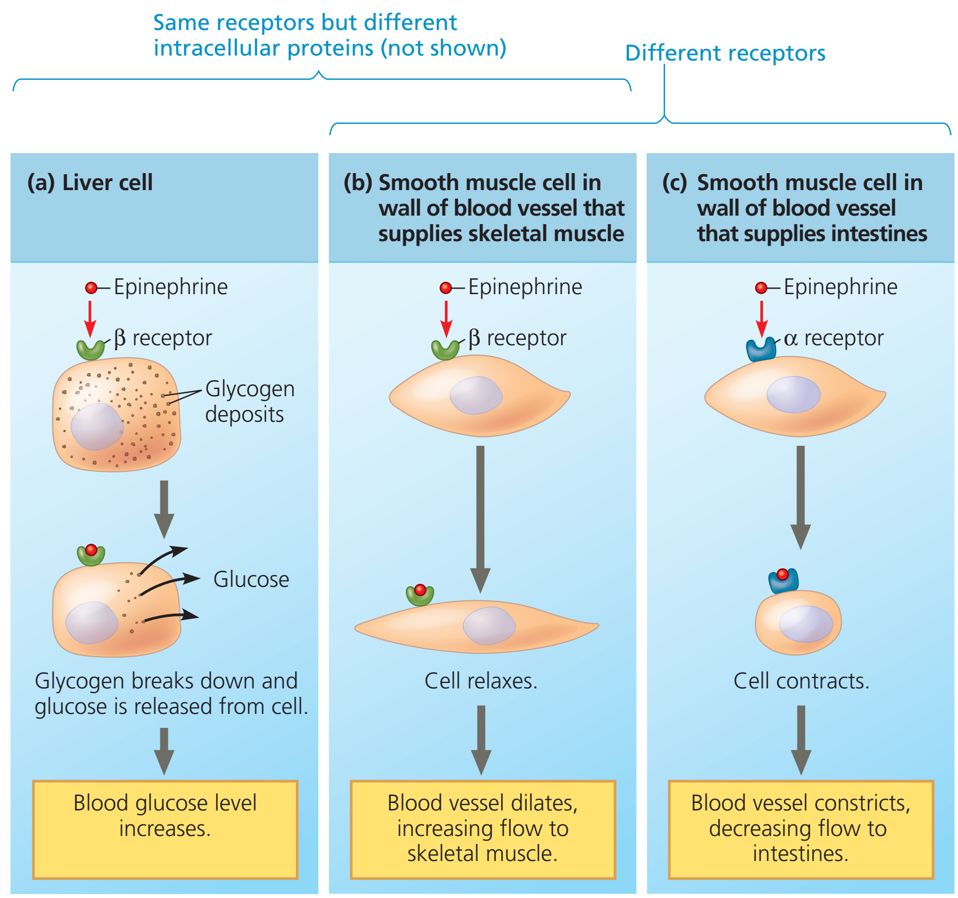
extracellular signal to a specific intracellular response is called *signal transduction*. A signal transduction pathway typically has multiple steps, each involving specific molecular interactions (see Concept 5.6).

There are also hormones that are lipid-soluble, including the sex hormones estradiol and testosterone (as well as thyroid hormone). The major receptors for steroid hormones are located in the cytosol rather than on the cell surface. When a steroid hormone binds to its cytosolic receptor, a hormone-receptor complex forms, which moves into the nucleus (see Figure 5.23). There, the receptor portion of the complex alters transcription of particular genes.

Multiple Effects of Hormones

Many hormones elicit more than one response. Consider, for example, epinephrine. Also called *adrenaline*, **epinephrine** is secreted by the *adrenal glands*, which lie atop the kidneys (see Figure 32.5). When you are in a stressful situation, perhaps running to catch a bus, the release of epinephrine rapidly triggers responses that help you chase the departing bus: raising blood glucose levels, increasing blood flow to muscles, and decreasing blood flow to the digestive system.

How can one hormone have such different effects? Target cells can vary in their response if they differ in their receptor type or in the molecules that produce the response. In the liver, epinephrine binds to a β-type epinephrine receptor in the plasma membrane of target cells. This receptor activates the enzyme protein kinase A, which regulates enzymes of glycogen metabolism, causing release of glucose into the bloodstream **(Figure 32.9a)**. In blood vessels supplying skeletal muscle, the same kinase activated by the same receptor inactivates a muscle-specific enzyme. The result is smooth muscle relaxation, vasodilation, and hence increased blood flow **(Figure 32.9b)**. In contrast, intestinal blood vessels have an α-type epinephrine receptor **(Figure 32.9c)**. Rather than activating protein kinase A, the α receptor triggers a distinct signaling pathway involving different enzymes. The result is smooth muscle contraction, vasoconstriction, and restricted blood flow to the intestines.



▲ **Figure 32.9 One hormone, different effects.** Epinephrine, the primary "fight-or-flight" hormone, produces different responses in different target cells. As shown by the brackets at the top of the figure, two types of differences between cells can alter the response to a hormone. Target cells with the same receptor exhibit different responses if they have different signal transduction pathways and/or effector proteins; compare **(a)** with **(b)**. Target cells with different receptors for the hormone often exhibit different responses; compare **(b)** with **(c)**.

Evolution of Hormone Function

EVOLUTION Over the course of evolution, the functions of a given hormone often diverge between species. An example is thyroid hormone, which across many evolutionary lineages plays a role in regulating metabolism (see Figure 32.8). In frogs, the thyroid hormone thyroxine (T_4) has taken on an apparently unique function: stimulating the resorption of the tadpole's tail during metamorphosis **(Figure 32.10)**.

The hormone prolactin has an especially broad range of activities. Prolactin stimulates mammary gland growth and milk synthesis in mammals, regulates fat metabolism and reproduction in birds, delays metamorphosis in amphibians, and regulates salt and water balance in freshwater fishes. These varied roles indicate that prolactin is an ancient hormone with functions that have diversified during the evolution of vertebrate groups.

▲ Tadpole

▲ Adult frog

▲ **Figure 32.10 Specialized role of a hormone in frog metamorphosis.** The hormone thyroxine is responsible for the resorption of the tadpole's tail as the frog develops into its adult form.

CONCEPT CHECK 32.2

1. Can cells differ in their response to a hormone if they have the same receptor for that hormone? Explain.
2. **WHAT IF?** If a hormone pathway provides a transient response to a stimulus, how would shortening the stimulus duration affect the need for negative feedback?
3. **MAKE CONNECTIONS** What parallels can you identify in the properties and effects of epinephrine and the plant hormone auxin (see Concept 31.1)?

For suggested answers, see Appendix A.

Regulating and Conforming

An animal is a **regulator** for an environmental variable if it uses internal mechanisms to control internal change in the face of external fluctuation. The river otter in **Figure 32.11** is a regulator for temperature, keeping its body at a temperature that is largely independent of that of the water in which it swims. In contrast, an animal is a **conformer** for an environmental variable if it allows its internal condition to change in accordance with external changes. The bass in Figure 32.11 conforms to the temperature of the lake it inhabits. As the water warms or cools, so does the bass's body.

Note that 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, it regulates the solute concentration in its blood and **interstitial fluid**, the fluid that surrounds body cells.

Homeostasis

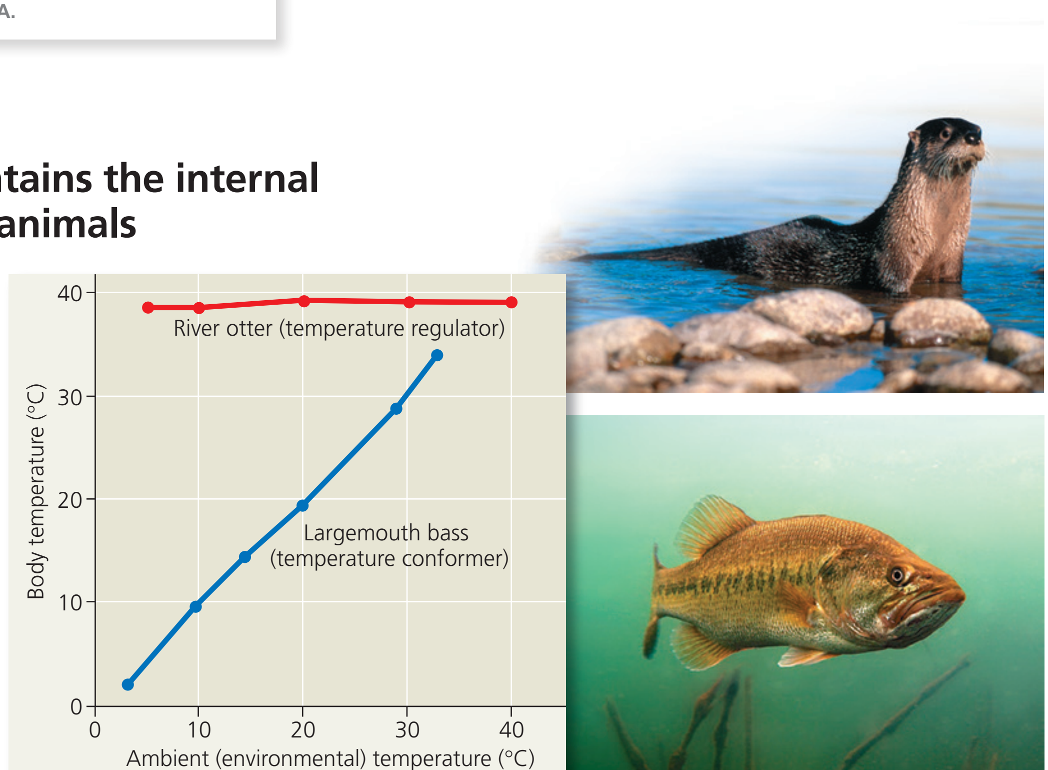
The steady body temperature of a river otter and the stable concentration of solutes in a freshwater bass are examples of **homeostasis**, which means "steady state," referring to the maintenance of internal balance. In achieving homeostasis, animals maintain a relatively constant internal environment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

Many animals exhibit homeostasis for a range of physical and chemical properties. For example, humans maintain a fairly constant body temperature of about 37°C (98.6°F), a blood pH within 0.1 pH unit of 7.4, and a blood glucose concentration that is predominantly in the range of 70–110 mg per 100 mL of blood.

CONCEPT 32.3

Feedback control maintains the internal environment in many animals

Managing an animal's internal environment can present a major challenge. Imagine if your body temperature soared every time you took a hot shower or drank a freshly brewed cup of coffee. Faced with environmental fluctuations, animals manage their internal environment by either regulating or conforming.

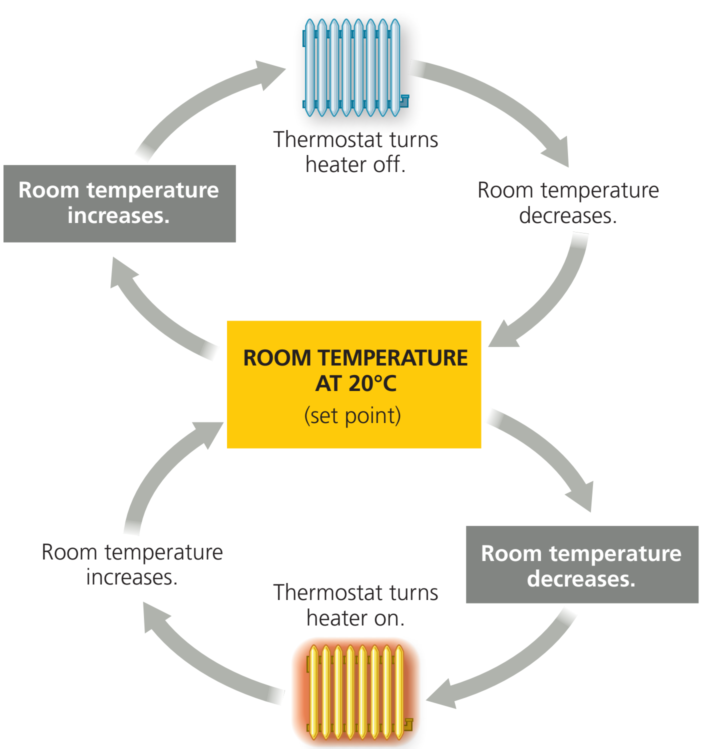


▶ **Figure 32.11 Regulating and conforming.** The river otter regulates its body temperature, keeping it stable across a wide range of environmental temperatures. The largemouth bass allows its internal environment to conform to the water temperature.

Before exploring homeostasis in animals, let's first consider a nonliving example: the regulation of room temperature **(Figure 32.12)**. Let's assume you want to keep a room at 20°C (68°F), a comfortable temperature for normal activity. You set a control device—the thermostat—to 20°C. A thermometer in the thermostat monitors the room temperature. If the temperature falls below 20°C, the thermostat responds by turning on a radiator, furnace, or other heater. Once the room temperature reaches 20°C, the thermostat switches off the heater. If the temperature then 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**. A fluctuation in the variable above or below the set point serves as the **stimulus** detected by a **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.

Like the circuit shown in Figure 32.12, homeostasis in animals relies largely on negative feedback. For example, when you exercise vigorously, you produce heat, which increases your 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.



▲ **Figure 32.12 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? *Label at least one stimulus, response, and sensor/control center in the above figure. How would adding an air conditioner to the system contribute to homeostasis?*

Homeostasis moderates but doesn't eliminate changes in the internal environment. Fluctuation is greater if a variable has a *normal range*—an upper and lower limit—rather than a set point. This is equivalent to a heating system that begins producing heat when the temperature drops to 19°C (66°F) and stops heating when the temperature reaches 21°C (70°F).

Although the set points and normal ranges for homeostasis are usually stable, certain regulated changes in the internal environment are essential. Some of these changes are associated with a particular stage in life, such as the radical shift in hormone balance during puberty. Others are cyclic, such as the monthly variation in hormone levels responsible for a woman's menstrual cycle (see Figure 36.12).

Thermoregulation: *A Closer Look*

As a physiological example of homeostasis, we'll examine **thermoregulation**, the process by which animals maintain their body temperature within a normal range. Body temperatures outside this range can reduce the efficiency of enzymatic reactions, alter the fluidity of cellular membranes, and affect other temperature-sensitive biochemical processes, potentially with fatal results.

Endothermy and Ectothermy

Heat for thermoregulation can come from either internal metabolism or the external environment. Humans and other mammals, as well as birds, are **endothermic**, meaning that they are warmed mostly by heat generated by metabolism. In contrast, amphibians, many fishes and nonavian reptiles, and most invertebrates are **ectothermic**, meaning that they gain most of their heat from external sources. However, endothermy and ectothermy are not mutually exclusive. For example, although a bird is mainly endothermic, it may warm itself by basking in the sun on a cold morning, much as an ectothermic lizard does.

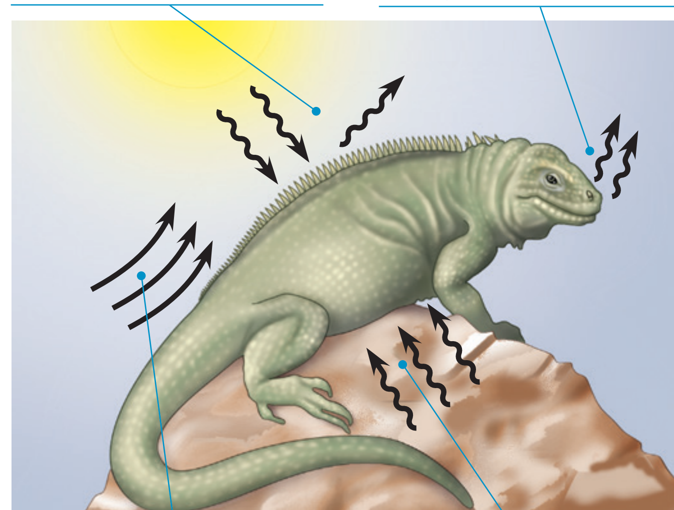
Endotherms can maintain a stable body temperature even in the face of large fluctuations in the environmental temperature. In a cold environment, an endotherm generates enough heat to keep its body substantially warmer than its surroundings **(Figure 32.13a)**. In a hot environment, endothermic vertebrates have mechanisms for cooling their bodies, enabling them to withstand heat loads that are intolerable for most ectotherms.

Many ectotherms can adjust their body temperature by behavioral means, such as seeking out shade or basking in the sun **(Figure 32.13b)**. Because their heat source is largely

(a) A walrus, an endotherm

(b) A lizard, an ectotherm

▲ **Figure 32.13 Endothermy and ectothermy.** Endotherms obtain heat from their internal metabolism, whereas ectotherms rely on heat from their external environment.



▲ **Figure 32.14 Heat exchange between an organism and its environment.**

? *Which type or types of heat exchange occur when you fan yourself on a hot day?*

environmental, ectotherms generally need to consume much less food than endotherms of equivalent size—an advantage if food supplies are limited. Overall, ectothermy is an effective and successful strategy in most environments, as shown by the abundance and diversity of insects and other ectotherms.

Balancing Heat Loss and Gain

Thermoregulation depends on an animal's ability to control the exchange of heat with its environment. An organism, like any object, exchanges heat by radiation, evaporation, convection, and conduction **(Figure 32.14)**. Note that heat is always transferred from an object of higher temperature to one of lower temperature.

Numerous adaptations that enhance thermoregulation have evolved in animals. Mammals and birds, for instance, have insulation that reduces the flow of heat between an animal's body and its environment. Such insulation may include hair or feathers as well as layers of fat formed by adipose tissue, such as a whale's thick blubber.

Circulatory Adaptations for Thermoregulation

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 surface. 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, blood flow in the outer layer of the body increases. In endotherms, vasodilation usually warms the skin and increases the transfer of body heat to the environment. The reverse process, *vasoconstriction*, reduces blood flow and heat transfer by decreasing the diameter of superficial vessels.

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 32.15)**. As warm blood leaves 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.

Acclimatization in Thermoregulation

Acclimatization—a physiological adjustment to environmental changes—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 near 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 5.5). Some ectotherms that experience subzero body temperatures produce antifreeze proteins that prevent ice formation in their cells. These compounds enable certain fishes to survive in Arctic or Antarctic water as cold as –2°C (28°F).

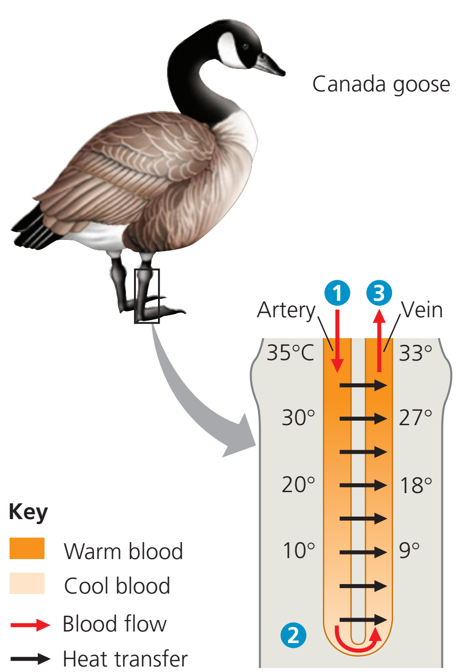
Physiological Thermostats

The regulation of body temperature in humans and other mammals is based on feedback mechanisms. The sensors for thermoregulation are concentrated in the hypothalamus region of the brain. Within the hypothalamus, a group of nerve cells functions as a thermostat, responding to body temperatures outside a normal range by activating mechanisms that promote heat loss or gain **(Figure 32.16)**.

At body temperatures below the normal range, the thermostat inhibits heat loss mechanisms while activating mechanisms that either save heat, including vasoconstriction of vessels in the skin, or generate heat, such as shivering. In response to elevated body temperature, the thermostat shuts down heat retention mechanisms and promotes cooling by vasodilation of vessels in the skin, sweating, or panting.

In the course of certain bacterial and viral infections, mammals and birds develop *fever*, an elevated body temperature. Experiments have shown that fever reflects an increase in the biological thermostat's set point. Indeed, one hypothesis is that fever enhances the body's ability to fight infection, although how fever is beneficial remains a subject of debate.

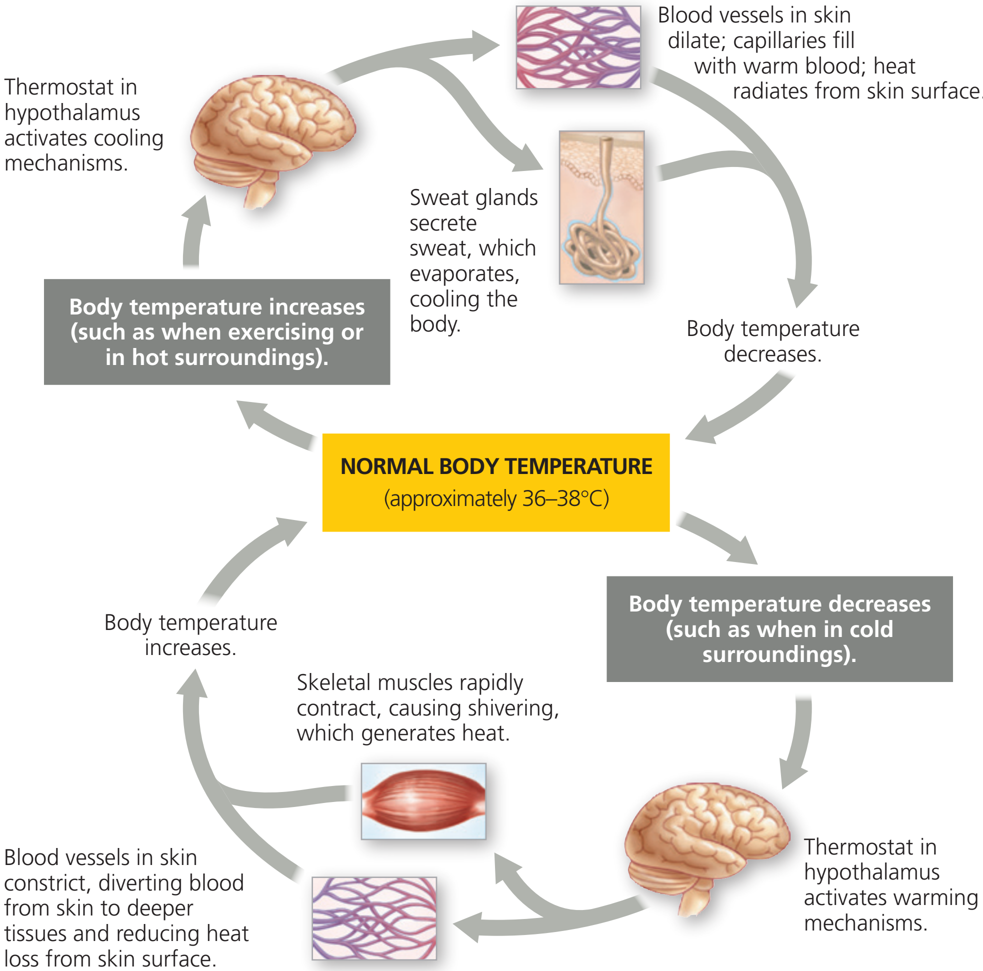
▶ **Figure 32.15 A countercurrent heat exchanger.** A countercurrent heat exchange system traps heat in the body core, thus reducing heat loss from the extremities, particularly when they are immersed in cold water or in contact with ice or snow. In essence, heat in the arterial blood emerging from the body core is transferred directly to the returning venous blood instead of being lost to the environment.



1. Arteries carrying warm blood to the animal's extremities are in close contact with veins conveying cool blood in the opposite direction, back toward the trunk of the body. This arrangement facilitates heat transfer from arteries to veins along the entire length of the blood vessels.

2. Near the end of the leg, where arterial blood has been cooled to far below the animal's core temperature, the artery can still transfer heat to the even colder blood in an adjacent vein. The blood in the veins continues to absorb heat as it passes warmer and warmer blood traveling in the opposite direction in the arteries.

3. As the blood in the veins approaches the center of the body, it is almost as warm as the body core, minimizing the heat loss that results from supplying blood to body parts immersed in cold water.



◀ **Figure 32.16 The thermostatic function of the hypothalamus in human thermoregulation.**

CONCEPT CHECK 32.3

1. Is it accurate to define homeostasis as a constant internal environment? Explain.
2. **MAKE CONNECTIONS** How does negative feedback in thermoregulation differ from feedback inhibition in an enzyme-catalyzed biosynthetic process (see Figure 6.19)?
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 32.4

A shared system mediates osmoregulation and excretion in many animals

Now that we've considered thermoregulation as an example of homeostasis, we'll turn to another example, the maintenance of salt and water balance in body fluids. Maintaining the fluid environment of animal tissues requires that the relative concentrations of water and solutes be kept within fairly narrow limits. In addition, ions such as sodium and calcium must be maintained at concentrations that permit normal activity of muscles, neurons, and other body cells. Homeostasis thus requires **osmoregulation**, the general term for the processes by which animals control solute concentrations in the interstitial fluid and balance water gain and loss.

In safeguarding their internal fluid environment, animals must deal with a hazardous metabolite produced by the dismantling of proteins and nucleic acids. Breakdown of *nitrogenous* (nitrogen-containing) molecules releases ammonia, a very toxic compound. Several different mechanisms have evolved for **excretion**, the process that rids the body of nitrogenous metabolites and other metabolic waste products. Because systems for excretion and osmoregulation are structurally and functionally linked in many animals, we will consider both of these processes here.

Osmosis and Osmolarity

All animals—regardless of their habitat and the type of waste they produce—need to balance water uptake and loss. If animal cells take up too much water, the cells swell and burst; if the cells lose too much water, they shrivel and die (see Figure 5.11). Water enters and leaves cells by osmosis, which occurs whenever two solutions separated by a membrane differ in osmotic pressure, or **osmolarity** (total solute concentration expressed as molarity, that is, moles of solute per liter of solution).

If two solutions separated by a selectively permeable membrane have the same osmolarity, they are said to be *isoosmotic*. When two solutions differ in osmolarity, the one with the greater concentration of solutes is said to be *hyperosmotic*, and the more dilute solution is said to be *hypoosmotic*. Water flows by osmosis from a hypoosmotic solution to a hyperosmotic one.

Osmoregulatory Challenges and Mechanisms

An animal can maintain water balance in two ways. One is to be an **osmoconformer**: to be isoosmotic with its surroundings. All osmoconformers are marine animals. The second way to maintain water balance is to be an **osmoregulator**: to control internal osmolarity independent of the environment. Osmoregulators are found in a wide range of environments, including fresh water and terrestrial habitats that are uninhabitable for osmoconformers.

The opposite osmoregulatory challenges of marine and freshwater environments are illustrated in **Figure 32.17**. For the marine cod (see Figure 32.17a), the ocean is a strongly dehydrating environment. Constantly losing water by osmosis, such fishes balance the water loss by drinking large amounts of seawater. In ridding themselves of salts, they make use of both their gills and kidneys. In the gills, specialized *chloride cells* actively transport chloride ions (Cl^-) out and allow sodium ions (Na^+) to follow passively. In the kidneys, excess calcium, magnesium, and sulfate ions are excreted with the loss of only small amounts of water.

The freshwater perch (see Figure 32.17b), lives in an environment with a very low osmolarity. As a result, it faces the problem of gaining water by osmosis and losing salts by diffusion. Like many freshwater animals, the perch solves this problem by drinking almost no water and excreting large amounts of very dilute urine. At the same time, salts lost by diffusion and in the urine are replenished by eating. Freshwater fishes such as the perch also replenish salts by uptake across the gills.

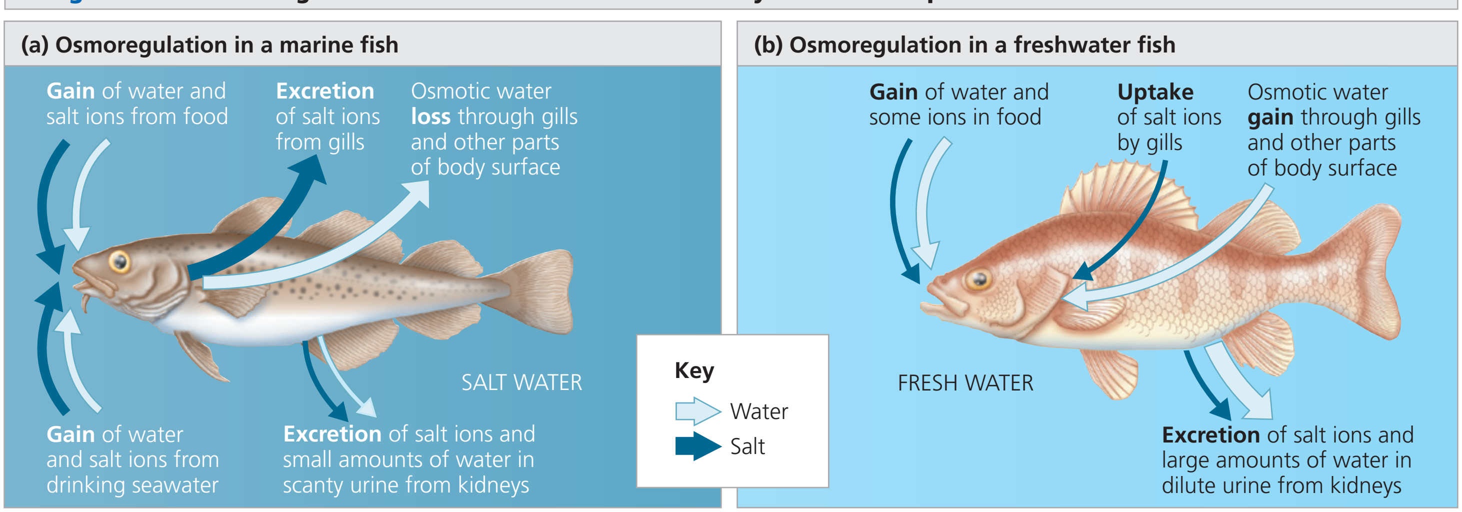
For land animals, the threat of dehydration is a major regulatory problem. Although most terrestrial animals have body coverings that help prevent dehydration, they lose water through many routes: in urine and feces, across their skin, and from the surfaces of gas exchange organs. Land animals maintain water balance by drinking and eating moist foods and by producing water metabolically through cellular respiration. In the **Scientific Skills Exercise**, you can examine water balance in one species of desert-dwelling mammal.

Nitrogenous Wastes

Because most metabolic wastes must be dissolved in water to be excreted from the body, the type and quantity of an animal's waste products may have a large impact on osmoregulation. In this regard, some of the most significant waste products are the nitrogenous breakdown products of proteins and nucleic acids **(Figure 32.18)**. When proteins and nucleic acids are broken apart for energy or converted to carbohydrates or fats, enzymes remove nitrogen in the form of **ammonia** (NH_3). Ammonia is very toxic, in part because its ion, ammonium (NH_4^+), interferes with oxidative phosphorylation. Although some animals excrete ammonia directly, many species expend energy to convert it to a less toxic compound, either urea or uric acid, prior to excretion.

Animals that excrete nitrogenous wastes as ammonia need access to lots of water because ammonia can be tolerated only at very low concentrations. Therefore, ammonia excretion is most common in aquatic species. The highly soluble ammonia molecules, which interconvert between NH_3 and NH_4^+, easily

▼ **Figure 32.17 Osmoregulation in marine and freshwater bony fishes: a comparison.**



Scientific Skills Exercise

Describing and Interpreting Quantitative Data

How Do Desert Mice Maintain Osmotic Homeostasis? The sandy inland mouse, recently reclassified as *Pseudomys hermannsburgensis*, is an Australian desert mammal that can survive indefinitely on a diet of dried seeds without drinking water. To study this species' adaptations to its arid environment, researchers conducted a laboratory experiment in which they controlled access to water. In this exercise, you will analyze some of the data from the experiment.

How the Experiment Was Done Nine captured mice were kept in an environmentally controlled room and given birdseed (10% water by weight) to eat. In Part A of the study, the mice had unlimited access to tap water for drinking; in Part B of the study, the mice were not given any additional water for 35 days, similar to conditions in their natural habitat. At the end of parts A and B, the researchers measured the osmolarity and urea concentration of the urine and blood of each mouse. The mice were also weighed three times a week.

Data from the Experiment

Access to Water	Mean Osmolarity (mOsm/L)		Mean Urea Concentration (m*M*)	
	Urine	Blood	Urine	Blood
Part A: Unlimited	490	350	330	7.6
Part B: None	4,700	320	2,700	11

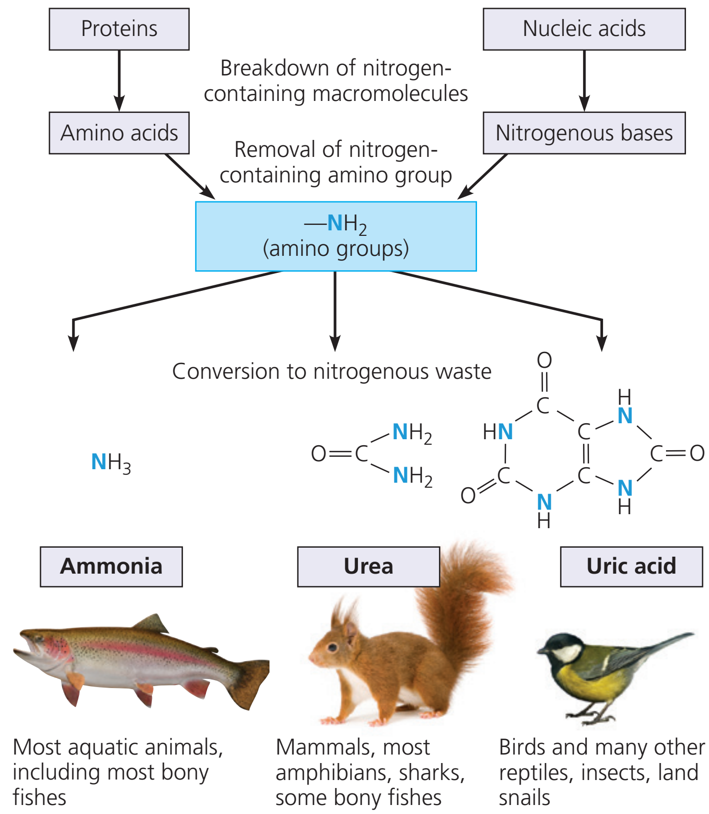
In part A, the mice drank about 33% of their body weight each day. The change in body weight during the study was negligible for all mice.

Data from R. E. MacMillen et al., Water economy and energy metabolism of the sandy inland mouse, *Leggadina hermannsburgensis*, *Journal of Mammalogy* 53:529–539 (1972).

INTERPRET THE DATA

1. (a–d) In words, describe how the data differ between the unlimited-water and no-water conditions with regard to (a) urine osmolarity, (b) blood osmolarity, (c) urea concentration in urine, and (d) urea concentration in blood. (e) Does this data set provide evidence of homeostatic regulation? Explain.
2. (a) Calculate the ratio of urine osmolarity to blood osmolarity for mice with unlimited access to water. (b) Calculate this ratio for mice with no access to water. (c) What conclusion would you draw from these ratios?
3. If the amount of urine produced were different in the two conditions, how would that affect your calculation? Explain.

MB A version of this Scientific Skills Exercise can be assigned in MasteringBiology.



▲ **Figure 32.18 Forms of nitrogenous waste.**

pass through membranes and are readily lost by diffusion to the surrounding water.

Most terrestrial animals and many marine species cannot afford to lose the amount of water necessary to routinely excrete ammonia. Instead, they mainly excrete a different nitrogenous waste, **urea**. In vertebrates, urea is the product of an energy-consuming metabolic cycle that combines ammonia with carbon dioxide in the liver. The main advantage of urea for nitrogenous waste excretion is its very low toxicity.

Insects, land snails, and many reptiles, including birds, excrete **uric acid** as their primary nitrogenous waste. Uric acid is relatively nontoxic and does not readily dissolve in water. It therefore can be excreted as a semisolid paste with very little water loss. However, uric acid is even more energetically expensive to produce than urea.

Excretory Processes

In most animals, both osmoregulation and metabolic waste disposal rely on **transport epithelia**, one or more layers of epithelial cells specialized for moving particular solutes in controlled amounts in specific directions. Transport epithelia are typically arranged in complex tubular networks with extensive surface areas. Some transport epithelia face the outside environment directly, while others line channels connected to the outside by an opening on the body surface.

Animals across a range of species produce a fluid waste by the process outlined in **Figure 32.19**. First, blood, coelomic fluid, or hemolymph is brought in contact with a transport epithelium. In most cases, hydrostatic pressure (blood pressure in many animals) drives **filtration**. Cells, as well as proteins and other large molecules, cannot cross the epithelial membrane and remain in the body fluid. In contrast, water and small solutes, such as salts, sugars, amino acids, and nitrogenous wastes, cross the membrane, forming a solution called the **filtrate**. Selective **reabsorption** returns useful molecules and water from the filtrate to the body fluids. Valuable solutes such as glucose, vitamins, and amino acids are reabsorbed by active transport. Nonessential solutes and wastes are left in the filtrate or undergo selective **secretion** into the filtrate by active transport. Finally, the processed filtrate is released from the body as urine during excretion.

The systems that perform the basic excretory functions vary. We'll examine examples from invertebrates and vertebrates.

Invertebrates

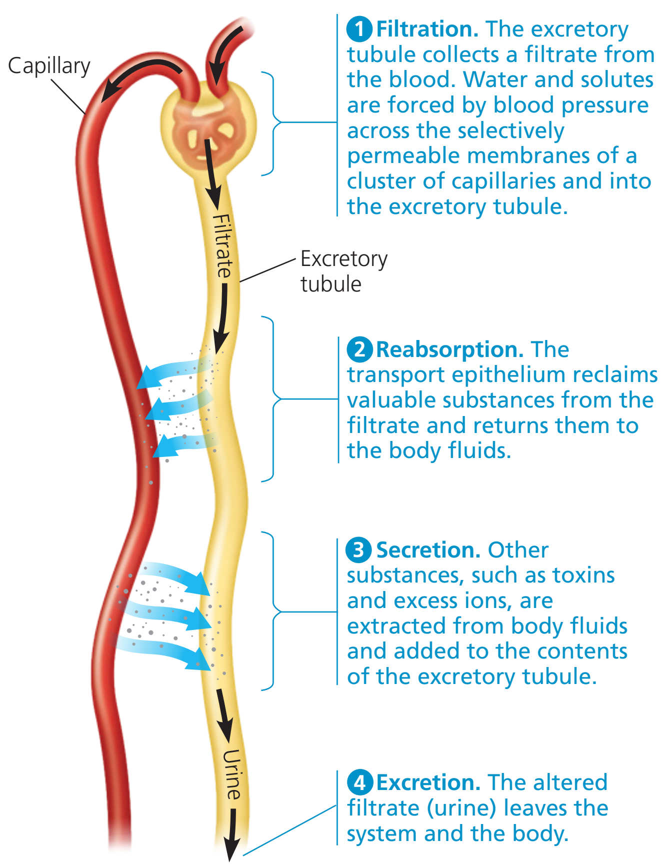
Flatworms (phylum Platyhelminthes), which lack a coelom or body cavity, have excretory systems called *protonephridia* **(Figure 32.20)**. Tubules connected to external openings branch throughout the body. Cellular units called *flame bulbs* cap each branch. Consisting of a tubule cell and a cap cell, each flame bulb has a tuft of cilia projecting into the tubule. During filtration, the beating cilia draw the interstitial fluid through the flame bulb, releasing filtrate into the tubule network. (The moving cilia resemble a flickering flame, hence the name *flame bulb*.) The processed filtrate is then emptied as urine into the external environment. Because the urine excreted by freshwater flatworms has a low solute concentration, its production helps to balance the osmotic uptake of water from the environment.

Natural selection has adapted protonephridia to different tasks in different environments. In the freshwater flatworms, protonephridia serve chiefly in osmoregulation. However, in some parasitic flatworms, which are isoosmotic to the surrounding fluids of their host organisms, the main function of protonephridia is the disposal of nitrogenous wastes.

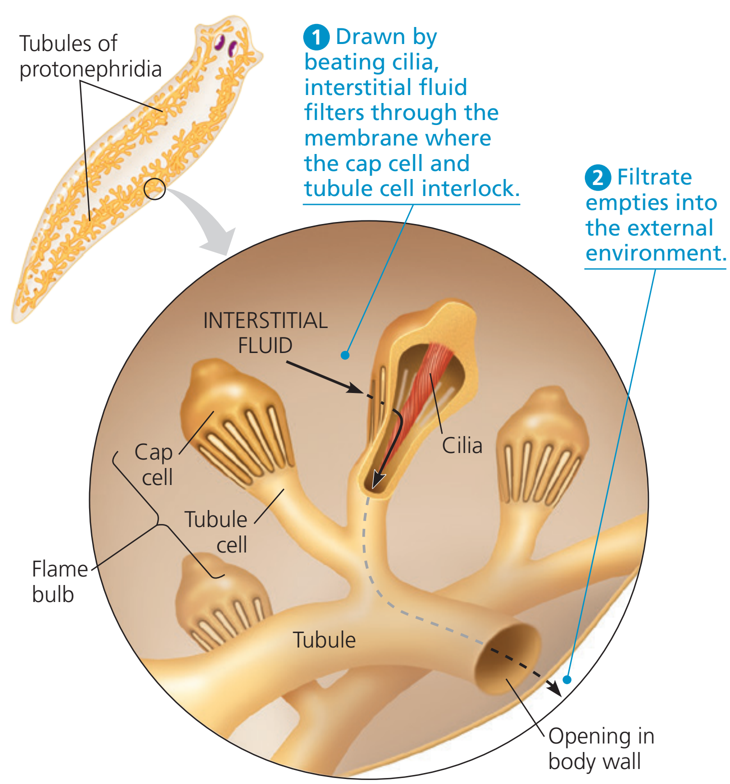
In insects and other terrestrial arthropods, the filtration step is absent. Instead, the transport epithelium of organs called *Malpighian tubules* secretes certain solutes and wastes into the lumen of the tubule. The filtrate passes to the digestive tract, where most solutes are pumped back into the hemolymph, and water is reabsorbed by osmosis. Nitrogenous wastes are eliminated as nearly dry matter along with the feces, conserving water. Indeed, this excretory system was a very important adaptation for arthropod colonization of land.

Vertebrates

In vertebrates and some other chordates, a compact organ called the **kidney (Figure 32.21)** functions in both osmoregulation and excretion. Like the excretory organs of most animal

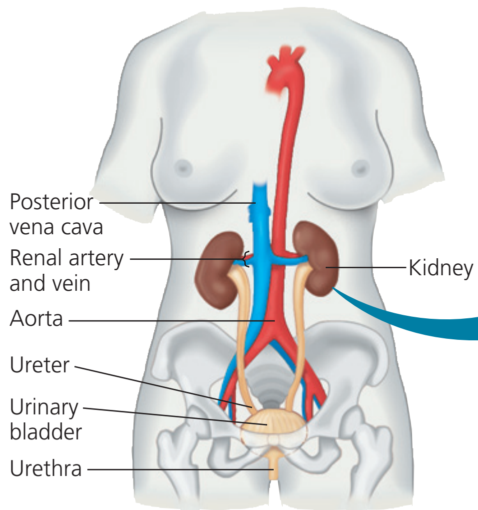


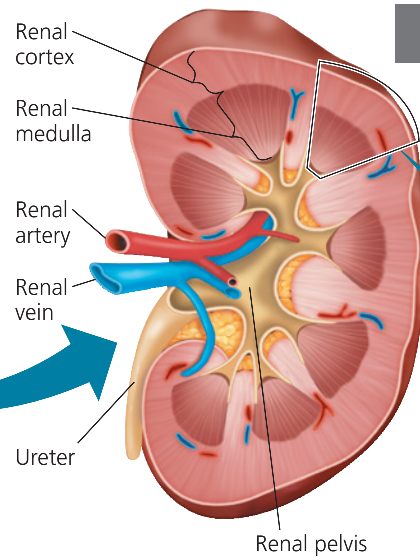
▲ **Figure 32.19 Key steps of excretory system function: an overview.** Most excretory systems produce a filtrate by pressure-filtering body fluids and then modify the filtrate's contents. This diagram is modeled after the vertebrate excretory system.



▲ **Figure 32.20 Protonephridia in a planarian.**

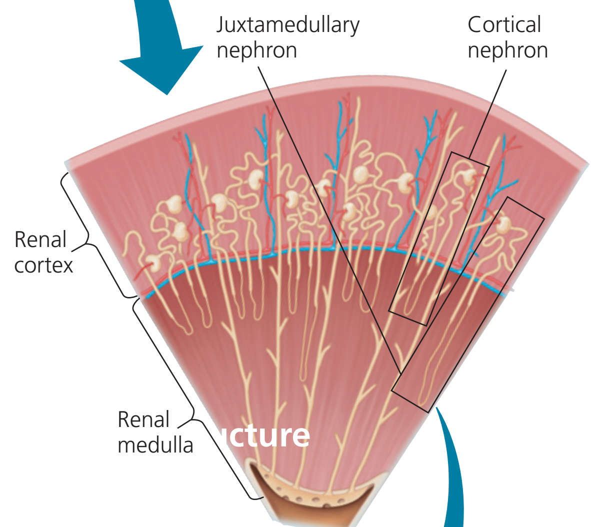
▼ Figure 32.21 **Exploring the Mammalian Excretory System**





Kidney Structure

Each kidney has an outer **renal cortex** and an inner **renal medulla**. Both regions are supplied with blood by a renal artery and drained by a renal vein. Within the cortex and medulla lie tightly packed excretory tubules and associated blood vessels. The inner **renal pelvis** collects urine from the excretory tubules and passes it to the urinary bladder.



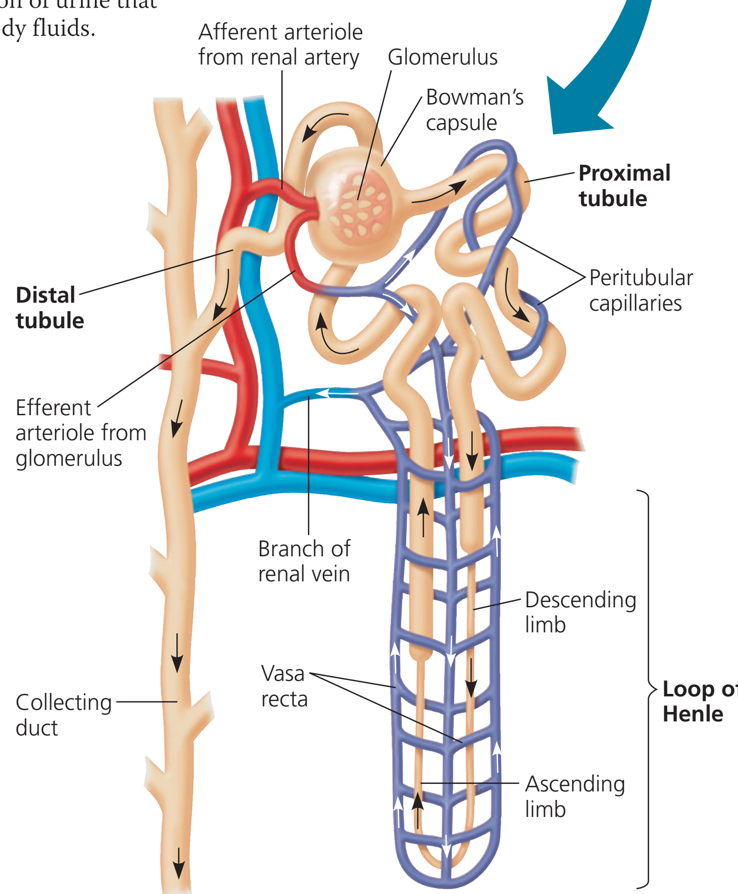
In humans, the excretory system consists of a pair of **kidneys**, bean-shaped organs about 10 cm in length, as well as organs for transporting and storing urine. Urine produced by each kidney exits through a duct called the ureter; the two ureters drain into a common sac called the **urinary bladder**. During urination, urine is expelled from the bladder through a tube called the **urethra**, which empties to the outside near the vagina in females and through the penis in males. Sphincter muscles near the junction of the urethra and bladder regulate urination.

Nephron Types

Weaving back and forth across the renal cortex and medulla are the **nephrons**, the functional units of the vertebrate kidney. Most of these are cortical nephrons, which reach only a short distance into the medulla. The remainder, the **juxtamedullary nephrons**, extend deep into the medulla. Juxtamedullary nephrons are essential for production of urine that is hyperosmotic to body fluids.

Nephron Organization

Each nephron consists of a single long tubule and a ball of capillaries called the **glomerulus**. The blind end of the tubule forms a cup-shaped swelling, called **Bowman's capsule**, which surrounds the glomerulus. Filtrate is formed when blood pressure forces fluid from the blood in the glomerulus into the lumen of Bowman's capsule. Processing occurs as the filtrate passes through three major regions of the nephron: the **proximal tubule**, the **loop of Henle** (a hairpin turn with a descending limb and an ascending limb), and the **distal tubule**. A **collecting duct** receives processed filtrate from many nephrons and transports it to the renal pelvis. Each nephron is supplied with blood by an *afferent arteriole*, an offshoot of the renal artery that branches and forms the capillaries of the glomerulus. The capillaries converge as they leave the glomerulus, forming an *efferent arteriole*. Branches of this vessel form the **peritubular capillaries**, which surround the proximal and distal tubules. Other branches extend downward and form the **vasa recta**, hairpin-shaped capillaries that serve the renal medulla and surround the loop of Henle.



phyla, kidneys consist of tubules. The tubules of these organs are arranged in a highly organized manner and are closely associated with a network of capillaries. The vertebrate excretory system also includes ducts and other structures that carry urine from the tubules out of the kidney and, eventually, the body. Familiarizing yourself with the terms and diagrams in Figure 32.21 will provide you with a solid foundation for learning about filtrate processing in the kidney, the focus of the last section of this chapter.

CONCEPT CHECK 32.4

1. What is the function of the filtration step in excretory systems?
2. What advantage does uric acid offer as a nitrogenous waste in arid environments?
3. **WHAT IF?** A camel standing in the sun requires much more water when its fur is shaved off, although its body temperature remains the same. What can you conclude about the relationship between osmoregulation and the insulation provided by fur?

For suggested answers, see Appendix A.

CONCEPT 32.5

The mammalian kidney's ability to conserve water is a key terrestrial adaptation

As illustrated in Figure 32.21, the basic unit of the mammalian kidney is the nephron. Here, we will consider the role of the nephron in forming the filtrate in the mammalian kidney. We will then focus on how tubules, capillaries, and the surrounding tissue of the nephron function together in processing that filtrate.

In the human kidney, filtrate forms when fluid passes from the bloodstream to the lumen of Bowman's capsule in each nephron. The glomerular capillaries retain blood cells and large molecules such as plasma proteins but are permeable to water and small solutes. Consequently, the filtrate contains salts, glucose, amino acids, vitamins, nitrogenous wastes, and other small molecules. Because such molecules pass freely between glomerular capillaries and Bowman's capsule, the concentrations of these substances in the initial filtrate are the same as those in blood plasma.

Under normal conditions, roughly 1,600 L of blood flows through a pair of human kidneys each day, yielding about 180 L of initial filtrate. Of this, about 99% of the water and nearly all of the sugars, amino acids, vitamins, and other organic nutrients are reabsorbed into the blood, leaving only about 1.5 L of urine to be transported to the bladder.

From Blood Filtrate to Urine: *A Closer Look*

To explore how filtrate is processed into urine, we'll follow the filtrate along its path through a nephron **(Figure 32.22)**. Each circled number refers to the processing in transport epithelia as the filtrate moves through the cortex and medulla of the kidney.

1 **Proximal tubule.** Reabsorption in the proximal tubule is critical for the recapture of ions, water, and valuable nutrients from the huge volume of initial filtrate. Because a large amount of water *and* salt is reabsorbed, the filtrate's volume decreases substantially, but its osmolarity remains about the same.

NaCl (salt) in the filtrate enters the cells of the transport epithelium by facilitated diffusion and cotransport mechanisms and then is transferred to the interstitial fluid by active transport (see Concept 5.4). This transfer of positive charge out of the tubule drives the passive transport of Cl^-.

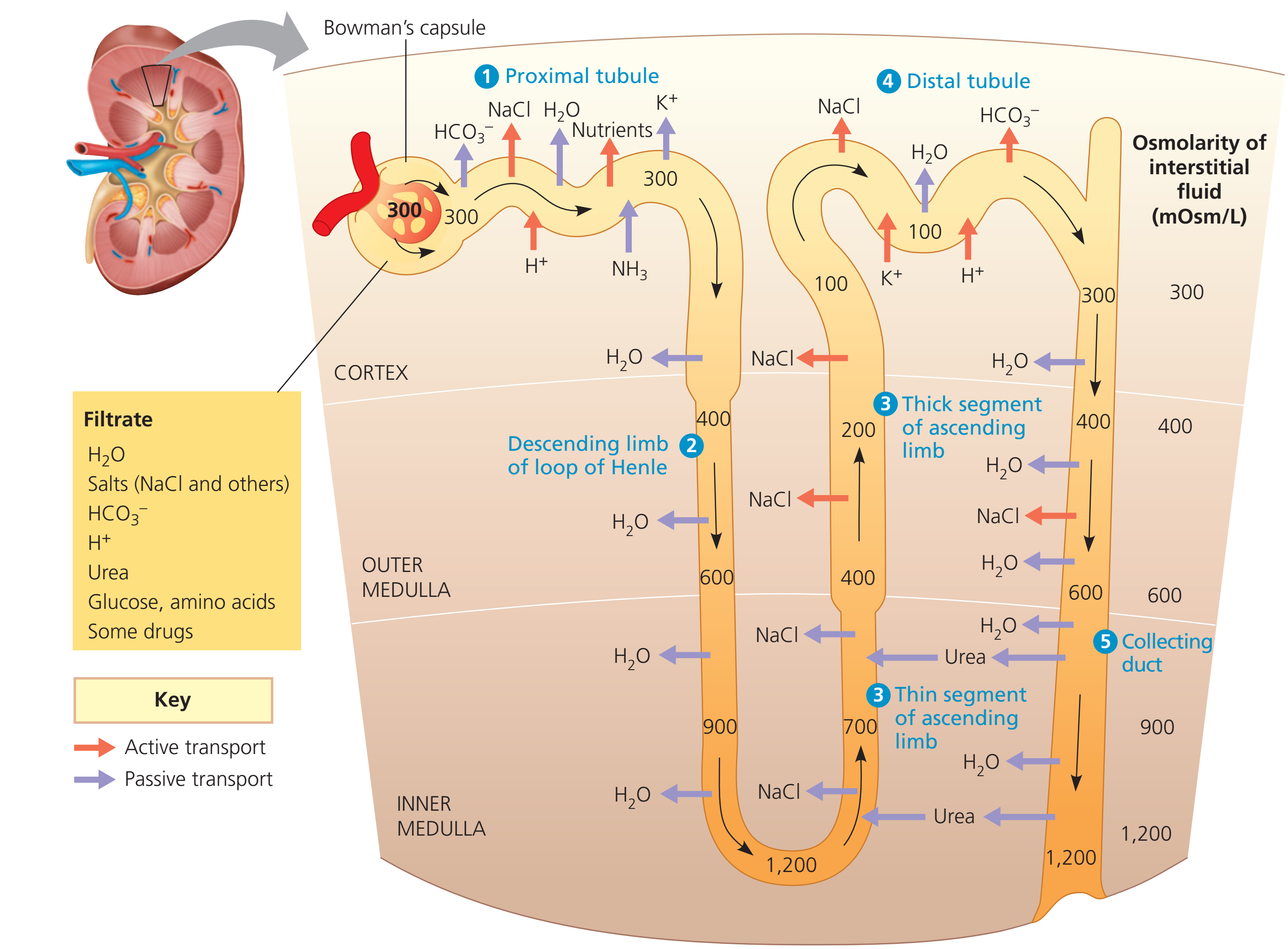
As salt moves from the filtrate to the interstitial fluid, water follows by osmosis. The salt and water then diffuse from the interstitial fluid into the peritubular capillaries (see Figure 32.21). Glucose, amino acids, potassium ions (K^+), and other essential substances are also actively or passively transported from the filtrate to the interstitial fluid and then into the peritubular capillaries. In contrast, some toxic materials, such as drugs and toxins that have been processed in the liver, are actively secreted into filtrate by the transport epithelium.

2 **Descending limb of the loop of Henle.** Upon leaving the proximal tubule, filtrate enters the loop of Henle, which further reduces filtrate volume via distinct stages of water and salt movement. In the first portion of the loop, the descending limb, numerous water channels formed by **aquaporin** proteins make the transport epithelium freely permeable to water. In contrast, there are almost no channels for salt and other small solutes, resulting in very low permeability for these substances.

For water to move out of the tubule by osmosis, the interstitial fluid bathing the tubule must be hyperosmotic to the filtrate. This condition is met along the entire length of the descending limb because the osmolarity of the interstitial fluid increases progressively from the cortex to the inner medulla of the kidney. Consequently, the filtrate loses water and increases in solute concentration all along its journey down the descending limb. The highest osmolarity (about 1,200 mOsm/L) occurs at the elbow of the loop of Henle.

3 **Ascending limb of the loop of Henle.** Once the filtrate reaches the tip of the loop of Henle, it returns to the cortex within the ascending limb. Unlike the descending portion of the loop, the ascending limb has a transport epithelium that lacks water channels. As a result, in this region the epithelial membrane that faces the filtrate is impermeable to water.

The ascending limb has two specialized regions: a thin segment near the loop tip and a thick segment adjacent to the distal tubule. As filtrate ascends in the thin segment, NaCl, which became highly concentrated in the descending limb, diffuses out of the permeable tubule into the interstitial fluid. This movement of NaCl out of the tubule helps maintain the osmolarity of the interstitial fluid in the medulla.



▲ **Figure 32.22 How the human kidney concentrates urine: regional functions of the transport epithelium.** The numbered regions in this diagram are keyed to the circled numbers in the text discussion of kidney function.

WHAT IF? *The drug furosemide blocks the cotransporters for Na^+ and Cl^- in the ascending limb of the loop of Henle. What effect would you expect this drug to have on urine volume?*

In the thick segment of the ascending limb, the movement of NaCl out of the filtrate continues. Here, however, the epithelium actively transports NaCl into the interstitial fluid. As a result of losing salt but not water, the filtrate becomes progressively more dilute as it moves up to the cortex in the ascending limb of the loop.

4 **Distal tubule.** The distal tubule plays a key role in regulating the K^+ and NaCl concentrations of body fluids. This regulation involves variation in the amount of K^+ secreted into the filtrate as well as the amount of NaCl reabsorbed from the filtrate. The distal tubule also contributes to pH regulation by the controlled secretion of H^+ and reabsorption of HCO_3^-.

5 **Collecting duct.** The collecting duct processes the filtrate into urine, which it carries to the renal pelvis (see Figure 32.21). As filtrate passes along the transport epithelium of the collecting duct, regulation of permeability and transport across the epithelium determines the extent to which the urine becomes concentrated.

When the kidneys are conserving water, aquaporin channels in the collecting duct allow water molecules to cross the epithelium. The filtrate becomes increasingly concentrated, losing more and more water by osmosis to the hyperosmotic interstitial fluid. In the inner medulla, the duct becomes permeable to urea. Because of the high urea concentration in the filtrate at this point, some urea diffuses out of the duct and into the interstitial fluid. The net result is urine that is hyperosmotic to the general body fluids.

When maintaining salt and water balance requires the production of dilute rather than concentrated urine, the collecting duct actively transports NaCl out of the filtrate and into the surrounding medulla. At the same time, aquaporin channels are removed from the collecting duct epithelium, with the result that water cannot follow the salts by osmosis.

As we will see, the state of the collecting duct epithelium is controlled by hormones that together maintain homeostasis for osmolarity, blood pressure, and blood volume.

Concentrating Urine in the Mammalian Kidney

The ability of the mammalian kidney to conserve water is a key adaptation for terrestrial habitats. In humans, the osmolarity of blood is about 300 mOsm/L (milliOsmoles per liter), but the kidney can excrete urine up to four times as concentrated.

The loop of Henle and surrounding capillaries act as a type of countercurrent system to generate the steep osmotic gradient between the medulla and cortex. Recall that some endotherms have a countercurrent heat exchanger that reduces heat loss (see Figure 32.15). In that system there is passive movement along a heat gradient. In contrast, the countercurrent system of the loop of Henle involves active transport and thus an expenditure of energy. The active transport of NaCl from the filtrate in the upper part of the ascending limb of the loop maintains a high salt concentration in the interior of the kidney, enabling the kidney to form concentrated urine. Such a system, which expends energy to create a concentration gradient, is called a **countercurrent multiplier system**.

When the human kidney concentrates urine maximally, the urine reaches an osmolarity of 1,200 mOsm/L. Some mammals can do even better: Australian hopping mice, small marsupials that live in dry desert regions, can produce urine with an osmolarity of 9,300 mOsm/L, 25 times as concentrated as the animal's blood.

Adaptations of the Vertebrate Kidney to Diverse Environments

EVOLUTION Vertebrates occupy habitats ranging from rain forests to deserts and from some of the saltiest bodies of water to the nearly pure waters of high mountain lakes. Variations in nephron structure and function equip the kidneys of different vertebrates for osmoregulation in their various habitats. These adaptations are made apparent by comparing species that inhabit a range of environments or by comparing the responses of different vertebrates to similar conditions.

Mammals that excrete the most hyperosmotic urine, such as hopping mice, kangaroo rats, and other desert mammals, have loops of Henle that extend deep into the medulla. Long loops maintain steep osmotic gradients in the kidney, resulting in urine becoming very concentrated as it passes from cortex to medulla in the collecting ducts.

Birds have loops of Henle that extend less far into the medulla than those of mammals. Thus, bird kidneys cannot concentrate urine to the high osmolarities achieved by mammalian kidneys. Although birds can produce hyperosmotic urine, their main water conservation adaptation is excreting their nitrogenous waste in the form of uric acid.

In mammals, both the volume and osmolarity of urine are adjusted according to an animal's water and salt balance. In situations of high salt intake and low water availability, a mammal can excrete small volumes of hyperosmotic urine with minimal water loss. If salt is scarce and fluid intake is high, the kidney can instead produce large volumes of hypoosmotic urine, getting rid of the excess water with little salt loss. At such times, the urine can be as dilute as 70 mOsm/L.

▶ Figure 32.23 A vampire bat (*Desmodus rotundus*), a mammal with unique excretory challenges.

The vampire bat shown in **Figure 32.23** illustrates the versatility of the mammalian kidney. This species feeds at night on the blood of large birds and mammals. The bat uses its sharp teeth to make a small incision in the prey's skin and then laps up blood from the wound (the prey animal is typically not seriously harmed). Anticoagulants in the bat's saliva prevent the blood from clotting. Because a vampire bat may fly long distances to locate a suitable victim, when it does find prey it benefits from consuming as much blood as possible—often more than half its body mass. By itself, this blood intake would make the bat too heavy to fly. As the bat feeds, however, its kidneys enable it to excrete large volumes of dilute urine, up to 24% of body mass per hour. Having lost enough weight to take off, the bat can fly back to its roost in a cave or hollow tree, where it spends the day.

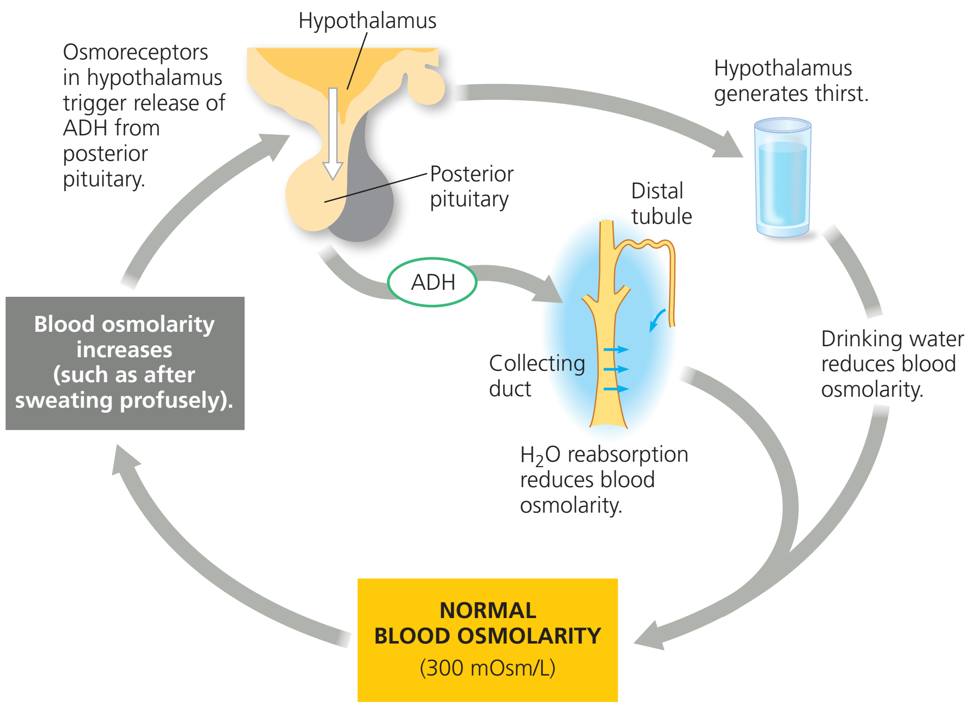
In the roost, the vampire bat faces a different regulatory problem. Most of the nutrition it derives from blood comes in the form of protein. Digesting proteins generates large quantities of urea, but roosting bats lack access to the drinking water necessary to dilute it. Instead, their kidneys shift to producing small quantities of highly concentrated urine (up to 4,600 mOsm/L), an adjustment that disposes of the urea load while conserving as much water as possible. The bat's ability to alternate rapidly between large amounts of dilute urine and small amounts of very hyperosmotic urine is an essential part of its adaptation to an unusual food source.

Homeostatic Regulation of the Kidney

A combination of nervous and hormonal inputs regulates the osmoregulatory function of the mammalian kidney. Through their effect on the amount and osmolarity of urine, these inputs contribute to homeostasis for both blood pressure and blood volume.

Antidiuretic Hormone

One key hormone in the regulatory circuitry of the kidney is antidiuretic hormone (ADH), also called vasopressin **(Figure 32.24)**. Osmoreceptor cells in the hypothalamus monitor



▲ **Figure 32.24 Regulation of fluid retention in the kidney by antidiuretic hormone (ADH).** Osmoreceptors in the hypothalamus monitor blood osmolarity via its effect on the net diffusion of water into or out of the receptor cells. When blood osmolarity increases, signals from the osmoreceptors trigger a release of ADH from the posterior pituitary, as well as thirst. Drinking water and increased water reabsorption reduce blood osmolarity, inhibiting further ADH secretion and thereby completing the feedback circuit.

the osmolarity of blood and regulate release of ADH from the posterior pituitary. ADH binds to receptor molecules on epithelial cells in the collecting duct, leading to a temporary increase in the number of aquaporin proteins in the plasma membrane. Because aquaporin proteins form water channels, the net effect is an increased permeability of the epithelium to water.

To see how the response to ADH in the kidney contributes to osmoregulation, let's consider first what occurs when blood osmolarity rises, such as after eating salty food or losing water through sweating. When osmolarity rises above the set point (300 mOsm/L), ADH release into the bloodstream is increased. The collecting duct's permeability to water rises, resulting in water reabsorption, which concentrates urine, reduces urine volume, and lowers blood osmolarity back toward the set point. (Only the gain of additional water in food or drink can fully restore osmolarity to 300 mOsm/L.) As the osmolarity of the blood falls, a negative-feedback mechanism reduces the activity of osmoreceptor cells in the hypothalamus, and ADH secretion is reduced.

What happens if, instead of ingesting salt or sweating profusely, you drink a large amount of water? The resulting reduction in blood osmolarity below the set point causes a drop in ADH secretion to a very low level. The number of aquaporin channels decreases, lowering permeability of the collecting ducts. Water reabsorption is reduced, resulting in discharge of large volumes of dilute urine. (A high level of urine production is called diuresis; ADH opposes this state and is therefore called antidiuretic hormone.)

Coordination of Kidney Regulation

The release of ADH is a response to an increase in blood osmolarity, as when the body is dehydrated from excessive water loss or inadequate water intake. However, an excessive loss of both salt and body fluids—caused, for example, by a major wound or severe diarrhea—will reduce blood volume *without* increasing osmolarity. Given that this will not affect ADH release, how does the body respond? It turns out that an endocrine circuit called the *renin-angiotensin-aldosterone system* (*RAAS*) also regulates kidney function. The RAAS responds to the drop in blood volume and pressure by increasing water and Na^+ reabsorption. Thus, ADH and the RAAS are partners in homeostasis.

One product of the RAAS is a peptide called *angiotensin II*. Functioning as a hormone, angiotensin II triggers vasoconstriction, increasing blood pressure and decreasing blood flow to capillaries in the kidney (and elsewhere). Angiotensin II also triggers events that cause nephrons to increase Na^+ and water reabsorption, thus increasing blood volume and pressure. Because angiotensin II increases blood pressure, drugs that block angiotensin II production are widely used to treat hypertension (chronic high blood pressure). Many of these drugs are specific inhibitors of angiotensin converting enzyme (ACE), which catalyzes one of the steps in the production of angiotensin II.

In all animals, some of the intricate physiological machines we call organs work continuously in maintaining solute and water balance and excreting nitrogenous wastes. The details that we have reviewed in this chapter only hint at the great complexity of the neural and hormonal mechanisms involved in regulating these homeostatic processes.

CONCEPT CHECK 32.5

1. Why could it be dangerous to drink a very large amount of water in a short period of time?
2. Many medications make the epithelium of the collecting duct less permeable to water. How would taking such a drug affect kidney output?
3. **WHAT IF?** If blood pressure in the afferent arteriole leading to a glomerulus decreased, how would the rate of blood filtration within Bowman's capsule be affected? Explain.

For suggested answers, see Appendix A.

32 Chapter Review

Go to MasteringBiology® for Assignments, the eText, and the Study Area with Animations, Activities, Vocab Self-Quiz, and Practice Tests.

SUMMARY OF KEY CONCEPTS

VOCAB SELF-QUIZ
goo.gl/gbai8v

CONCEPT 32.1

Animal form and function are correlated at all levels of organization (pp. 664–667)

- Animal bodies are based on a hierarchy of cells, **tissues**, **organs**, and **organ systems**. **Epithelial tissue** forms active interfaces on external and internal surfaces; **connective tissue** binds and supports other tissues; **muscle tissue** contracts, moving body parts; and **nervous tissue** transmits nerve impulses throughout the body.
- Animals and plants exhibit both shared and diverse adaptations to common life challenges.

? *Describe how the epithelial tissue that lines the stomach lumen is well suited to its function.*

CONCEPT 32.2

The endocrine and nervous systems act individually and together in regulating animal physiology (pp. 668–673)

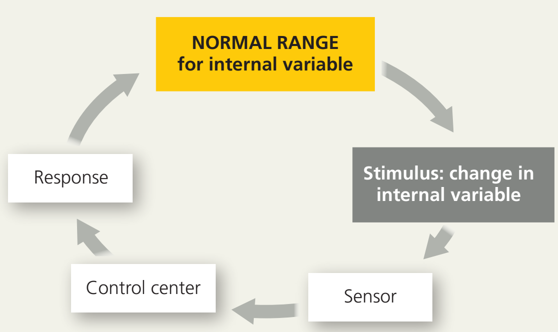
- In communicating between different locations in the body, the **endocrine system** broadcasts signaling molecules called **hormones** everywhere via the bloodstream. Only certain cells are responsive to each hormone. The **nervous system** uses dedicated cellular circuits involving electrical and chemical signals to send information to specific locations. Hormone pathways may be regulated by **negative feedback**, which damps the stimulus, or **positive feedback**, which amplifies the stimulus and drives the response to completion.

? *Why would a water-soluble hormone likely have no effect if injected directly into the cytosol of a target cell?*

CONCEPT 32.3

Feedback control maintains the internal environment in many animals (pp. 673–677)

- Animals *regulate* certain internal variables while allowing other internal variables to *conform* to external changes. **Homeostasis** is the maintenance of a steady state despite internal and external changes.



- 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. The **hypothalamus** acts as the thermostat in mammalian regulation of body temperature.

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

CONCEPT 32.4

A shared system mediates osmoregulation and excretion in many animals (pp. 677–682)

- Cells balance water gain and loss through **osmoregulation**, a process based on the controlled movement of solutes between internal fluids and the external environment and on the movement of water, which follows by osmosis.
- Protein and nucleic acid metabolism generates **ammonia**, which in many animals is converted to **urea** or **uric acid** for **excretion**. Most excretory systems carry out **filtration**, **reabsorption**, **secretion**, and **excretion**. Excretory tubules (consisting of **nephrons** and **collecting ducts**) and blood vessels pack the mammalian **kidney**.

DRAW IT *Construct a table summarizing the three major types of nitrogenous wastes and their relative toxicity, energy content, and associated water loss during excretion.*

CONCEPT 32.5

The mammalian kidney's ability to conserve water is a key terrestrial adaptation (pp. 682–685)

- Within the nephron, selective secretion and reabsorption in the **proximal tubule** alter **filtrate** volume and composition. The *descending limb* of the **loop of Henle** is permeable to water but not salt, whereas the *ascending limb* is permeable to salt but not water. The **distal tubule** and collecting duct regulate K^+ and NaCl levels in body fluids.
- In a mammalian kidney, **a countercurrent multiplier system** involving the loop of Henle maintains the gradient of salt concentration in the kidney interior. In response to hormonal signals, urine can be concentrated in the collecting duct.
- Natural selection has shaped the form and function of nephrons in vertebrates to the challenges of the animals' habitats. For example, desert mammals, which excrete the most hyperosmotic urine, have loops of Henle that extend deep into the **renal medulla**.
- When blood **osmolarity** rises, the posterior pituitary releases **antidiuretic hormone (ADH)**, which increases permeability to water in collecting ducts by increasing the number of water channels. A second endocrine pathway, the renin-angiotensin-aldosterone system (RAAS), regulates blood pressure and volume, functions that partially overlap with those of ADH.

? *How do the nephrons of kangaroo rats and birds differ in structure and in their ability to concentrate urine?*

TEST YOUR UNDERSTANDING

PRACTICE TEST
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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) muscle.
   (D) 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

3. Which process in the nephron is *least* selective?
   (A) filtration
   (B) reabsorption
   (C) active transport
   (D) secretion

Level 2: Application/Analysis

4. Homeostasis typically relies on negative feedback because positive feedback
   (A) requires a response but not a stimulus.
   (B) drives processes to completion rather than to a balance point.
   (C) acts within, but not beyond, a normal range.
   (D) can decrease but not increase a variable.

5. Which of the following is an accurate statement about thermoregulation?
   (A) Endotherms are regulators and ectotherms are conformers.
   (B) Endotherms maintain a constant body temperature and ectotherms do not.
   (C) Endotherms and ectotherms differ in their primary source of heat for thermoregulation.
   (D) Endothermy has a lower energy cost than ectothermy.

6. In which of the following species should natural selection favor the highest proportion of nephrons with loops of Henle that extend deep into the renal medulla?
   (A) a river otter
   (B) a mouse species living in a temperate broadleaf forest
   (C) a mouse species living in a desert
   (D) a beaver

7. African lungfish, which are often found in small, stagnant pools of fresh water, produce urea as a nitrogenous waste. What is the advantage of this adaptation?
   (A) Urea takes less energy to synthesize than ammonia.
   (B) Small, stagnant pools do not provide enough water to dilute the toxic ammonia.
   (C) Urea forms an insoluble precipitate.
   (D) Urea makes lungfish tissue hypoosmotic to the pool.

Level 3: Synthesis/Evaluation

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. Label each feature that represents a sensor, stimulus, or response.

9. **INTERPRET THE DATA** Use the data below to draw four pie charts for water gain and loss in a kangaroo rat and a human.

	Kangaroo Rat	Human
Water Gain (mL)		
Ingested in food	0.2	750
Ingested in liquid	0	1,500
Derived from metabolism	1.8	250
Water Loss (mL)		
Urine	0.45	1,500
Feces	0.09	100
Evaporation	1.46	900

Which routes of water gain and loss make up a much larger share of the total in a kangaroo rat than in a human?

10. **FOCUS ON EVOLUTION**
Merriam's kangaroo rats (*Dipodomys merriami*) live in North American habitats ranging from moist, cool woodlands to hot deserts. Assuming that natural selection has resulted in differences in water conservation between *D. merriami* populations, devise a hypothesis concerning the relative rates of evaporative water loss by populations that live in moist versus dry environments. Describe how you could test your hypothesis using a humidity sensor to detect evaporative water loss by kangaroo rats.

11. **FOCUS ON ORGANIZATION**
In a short essay (100–150 words), compare how membrane structures in the loop of Henle and collecting duct of the mammalian kidney enable water to be recovered from filtrate in the process of osmoregulation.

12. **SYNTHESIZE YOUR KNOWLEDGE**

These macaques (*Macaca fuscata*) are partially immersed in a hot spring in a snowy region of Japan. What are some ways that form, function, and behavior contribute to homeostasis for these animals?

For selected answers, see Appendix A.