



TEMPERATURE AND BODY FLUID REGULATION

Outline

- Homeostasis and Temperature Regulation
 - The Impact of Temperature on Animal Life
 - Heat Gains and Losses
 - Some Solutions to Temperature Fluctuations
 - Temperature Regulation in Invertebrates
 - Temperature Regulation in Fishes
 - Temperature Regulation in Amphibians and Reptiles
 - Temperature Regulation in Birds and Mammals
 - Heat Production in Birds and Mammals
- Control of Water and Solutes (Osmoregulation and Excretion)
 - Invertebrate Excretory Systems
 - Contractile Vacuoles
 - Protonephridia
 - Metanephridia
 - Antennal (Green) and Maxillary Glands
 - Malpighian Tubules
 - Coxal Glands
 - Vertebrate Excretory Systems
 - How Vertebrates Achieve Osmoregulation
 - Vertebrate Kidney Variations
 - How the Metanephric Kidney Functions

Concepts

1. Thermoregulation is a complex and important physiological process that maintains, to varying degrees, an animal's body temperature, despite variations in environmental temperature. Based on this regulation, animals can be categorized as endotherms or ectotherms, and homeotherms or heterotherms.
2. For osmoregulation, some invertebrates have contractile vacuoles, flame-cell systems, antennal (green) glands, maxillary glands, coxal glands, nephridia, or Malpighian tubules.
3. A vertebrate's urinary system functions in osmoregulation and excretion, both of which are necessary for internal homeostasis. Osmoregulation governs water and salt balance, and excretion eliminates metabolic wastes. In fishes, reptiles, birds, and mammals, the kidneys are the primary osmoregulatory structures.

The earth's environments vary dramatically in temperature and amount of water present. In the polar regions, high mountain ranges, and deep oceans, the temperature remains near or below 0° C (32° F) throughout the year. Temperatures exceeding 40° C (103° F) are common in equatorial deserts. Between these two extremes, in the earth's temperate regions, temperatures fluctuate widely. The temperate regions have varying amounts of water, as well as varied habitats—freshwater, saltwater, wetlands, mountains, and grasslands.

Animals have successfully colonized these varied places on earth by possessing homeostatic mechanisms for maintaining a relatively constant internal environment, despite fluctuations in the external environment. This chapter covers three separate but related homeostatic systems that enable animals to survive the variations in temperature, water availability, and salinity (salt concentration) on the earth. The thermoregulatory system maintains an animal's body temperature and/or its responses to shifts in environmental temperature. The osmoregulatory system maintains the level and concentration of water and salts in the body. And the urinary system eliminates metabolic wastes from the body and functions in osmoregulation.

HOMEOSTASIS AND TEMPERATURE REGULATION

The temperature of a living cell affects the rate of its metabolic processes. An animal can grow faster and respond to the environment more rapidly if its cells are kept warm. **In fact, zoologists believe that the ability of some higher animals to maintain a**

This chapter contains evolutionary concepts, which are set off in this font.

456 PART THREE Form and Function: A Comparative Perspective

constant (homeostatic), relatively high body temperature is a major reason for their evolutionary success. This ability to control the temperature of the body is called **thermoregulation** (“heat control”) and involves the nervous, endocrine, respiratory, and circulatory systems in higher animals.

THE IMPACT OF TEMPERATURE ON ANIMAL LIFE

Every animal’s physiological functions are inexorably linked to temperature, because metabolism is sensitive to changes in internal temperature. Thus, temperature has been a strong source of selective pressure on all animals. The rate of cellular respiration increases with temperature up to a point. When the temperature rises above the temperature optima at which enzymes most efficiently catalyze their chemical reactions, the rates decline as the enzymes begin to denature. The chemical interactions holding the enzymes in their three-dimensional shape are also disrupted. **Thus, the results of enzyme evolution have frequently been enzymes with temperature optima that reflect an animal’s habitat.** For example, a digestive enzyme in a trout might function optimally at 10° C, whereas another enzyme in the human body that catalyzes the same reaction functions best at 37° C. Higher temperatures cause the proteins in nucleic acids to denature, and lower temperatures may cause membranes to change from a fluid to a solid state, which can interfere with many cellular processes, such as active-transport pumps.

Animals can guard against these damaging effects of temperature fluctuations by balancing heat gains and heat losses with their environment.

HEAT GAINS AND LOSSES

Animals produce heat as a by-product of metabolism and either gain heat from, or lose it to, the environment. The total body temperature is a result of an interaction of these factors and can be expressed as:

$$\begin{aligned} \text{Body temperature} &= \text{heat produced metabolically} \\ &+ \text{heat gained from the environment} \\ &- \text{heat lost to the environment} \end{aligned}$$

Animals use four physical processes to exchange heat with the environment: conduction, convection, evaporation, and radiation (figure 28.1). **Conduction** is the direct transfer of thermal motion (heat) between molecules of the environment and those on the body surface of an animal. This transfer is always from an area of higher temperature to one of lower temperature because heat moves down thermal gradients. For example, when you sit on the cold ground, you lose heat, and when you sit on warm sand, you gain heat.

Convection is the movement of air (or a liquid) over the surface of a body; it contributes to heat loss if the air is cooler than the body or heat gain if the air is warmer than the body. On a cool day, your body loses heat by convection because your skin temperature is higher than the surrounding air temperature.

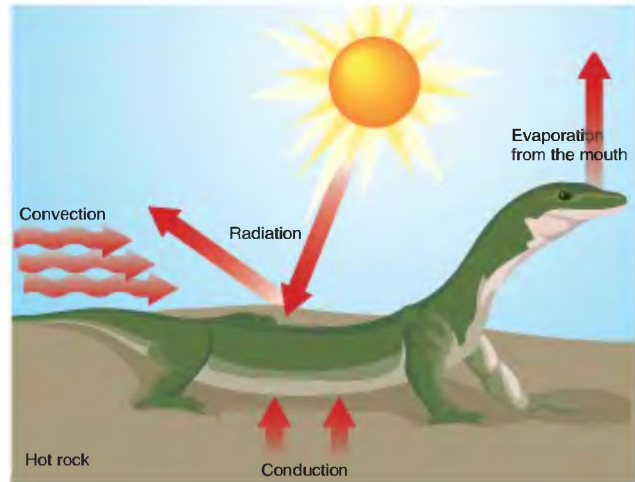


FIGURE 28.1

Heat Gain and Loss for a Terrestrial Reptile in a Typical Terrestrial Environment. Heat is either gained or lost by objects in direct contact with the animal (conduction), by air currents (convection), by exhaled air (evaporation), or by electromagnetic waves (radiation).

Evaporation is loss of heat from a surface as water molecules escape in the form of a gas. It is useful only to terrestrial animals. For example, humans and some other mammals (chimpanzees and horses) have sweat glands that actively move watery solutions through pores to the skin surface. When skin temperature is high, water at the surface absorbs enough thermal energy to break the hydrogen bonds holding the individual water molecules together, and they depart from the surface, carrying heat with them. As long as the environmental humidity is low enough to permit complete evaporation, sweating can rid the mammalian body of excess heat; however, the water must evaporate. Sweat dripping from a mammal has no cooling effect at all.

Radiation is the emission of electromagnetic waves that objects, such as another animal’s body or the sun, produce. Radiation can transfer heat between objects that are not in direct contact with each other, as happens when an animal suns itself (figure 28.2).

SOME SOLUTIONS TO TEMPERATURE FLUCTUATIONS

Animals cope with temperature fluctuations in one of three basic ways. (1) They can occupy a place in the environment where the temperature remains constant and compatible with their physiological processes; (2) their physiological processes may have adapted to the range of temperatures in which the animals are capable of living; or (3) they can generate and trap heat internally to maintain a constant body temperature, despite fluctuations in the temperature of the external environment.

**FIGURE 28.2**

Radiation Warms an Animal. After a cold night in its den on the Kalahari Desert, a meerkat (*Suricata suricatta*) stands at attention, allowing the large surface area of its body to absorb radiation from the sun.

Animals can be categorized as ectotherms or endotherms, based on whether their source of body heat is from internal processes or derived from the environment. **Ectotherms** (Gr. *ectos*, outside) derive most of their body heat from the environment rather than from their own metabolism (figure 28.3). They have low rates of metabolism and are poorly insulated. In general, reptiles, amphibians, fishes, and invertebrates are ectotherms, although a few reptiles, insects, and fishes can raise their internal temperature. Ectotherms tend to move about the environment and find places that minimize heat or cold stress to their bodies.

Birds and mammals are called **endotherms** (Gr. *endos*, within) because they obtain their body heat from cellular processes. A constant source of internal heat allows them to maintain a nearly constant core temperature, despite the fluctuating environmental temperature. (“Core” refers to the body’s internal temperature as opposed to the temperature near its surface.)

Most endotherms have bodies insulated by fur or feathers and a relatively large amount of fat. This insulation enables them to retain heat more efficiently and to maintain a high core temperature. Endothermy allows animals to stabilize their core temperature so that biochemical processes and nervous system functions can proceed at steady, high levels. **Endothermy allows some animals to colonize habitats denied to ectotherms.**

Another way of categorizing animals is based on whether they maintain a constant or variable body temperature. Although most endotherms are **homeotherms** (maintain a relatively constant body temperature), and most ectotherms are **heterotherms**

(have a variable body temperature), there are many exceptions. Some endotherms vary their body temperatures seasonally (e.g., hibernation); others vary it on a daily basis.

For example, some birds (e.g., hummingbirds) and mammals (e.g., shrews) can only maintain a high body temperature for a short period because they usually weigh less than 10 g and have a body mass so small that they cannot generate enough heat to compensate for the heat lost across their relatively large surface area. Hummingbirds must devote much of the day to locating and sipping nectar (a very high-calorie food source) as a constant energy source for metabolism. When not feeding, hummingbirds rapidly run out of energy unless their metabolic rates decrease considerably. At night, hummingbirds enter a sleep-like state, called **daily torpor**, and their body temperature approaches that of the cooler surroundings. Some bats also undergo daily torpor to conserve energy.

Some ectotherms can maintain fairly constant body temperatures. Among these are a number of reptiles that can maintain fairly constant body temperatures by changing position and location during the day to equalize heat gain and loss.

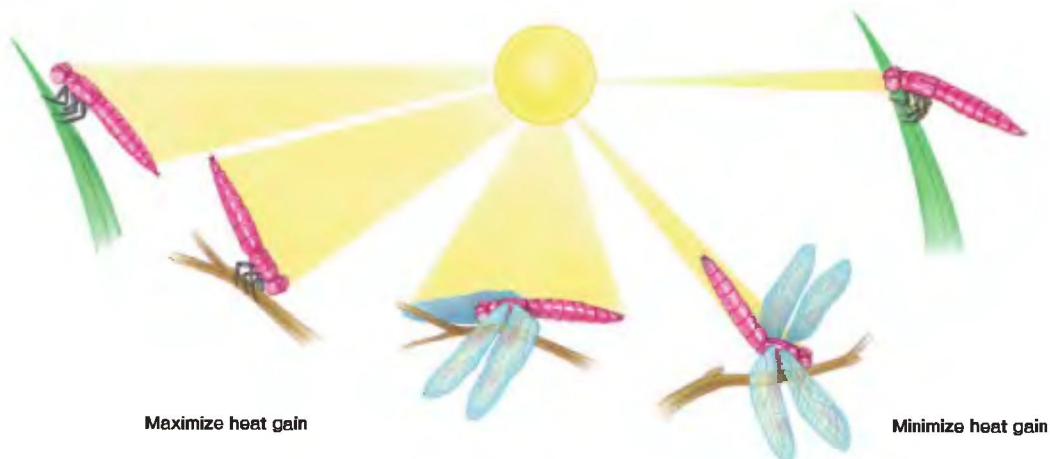
In general, ectotherms are more common in the tropics because they do not have to expend as much energy to maintain body temperature there, and they can devote more energy to food gathering and reproduction. Indeed, in the tropics, amphibians are far more abundant than mammals. Conversely, in moderate to cool environments, endotherms have a selective advantage and are more abundant. Their high metabolic rates and insulation allow them to occupy even the polar regions (e.g., polar bears). In fact, the efficient circulatory systems of birds and mammals can be thought of as adaptations to endothermy and a high metabolic rate.

TEMPERATURE REGULATION IN INVERTEBRATES

As previously noted, environmental temperature is critical in limiting the distribution of all animals and in controlling metabolic reactions. Many invertebrates have relatively low metabolic rates and have no thermoregulatory mechanisms; thus, they passively conform to the temperature of their external environment. These invertebrates are termed **thermoconformers**.

Evidence indicates that some higher invertebrates can directly sense differences in environmental temperatures; however, specific receptors are either absent or unidentified. What zoologists do know is that many arthropods, such as insects, crustaceans, and the horseshoe crab (*Limulus*), can sense thermal variation. For example, ticks of warm-blooded vertebrates can sense the “warmth of a nearby meal” and drop on the vertebrate host.

Many arthropods have unique mechanisms for surviving temperature extremes. For example, temperate-zone insects avoid freezing by reducing the water content in their tissues as winter approaches. Other insects can produce glycerol or other glycoproteins that act as an antifreeze. Some moths and bumblebees warm up prior to flight by shivering contractions of their thoracic flight

**FIGURE 28.3**

Heat Gain in an Insect. Postures a dragonfly adopts to either maximize or minimize heat gain.

muscles. **M**ost large, flying insects have evolved a mechanism to prevent overheating during flight; blood circulating through the flight muscles carries heat from the thorax to the abdomen, which gets rid of the heat—much as coolant circulating through an automobile engine passes through the radiator. Certain cicadas (*Diceroprocta apache*) that live in the Sonoran Desert have independently evolved the complete repertoire of evaporative cooling mechanisms that vertebrates use. When threatened with overheating, these cicadas extract water from their blood and transport it through large ducts to the surface of their body, where it passes through sweat pores and evaporates. In other words, these insects can sweat.

Body posture and orientation of the wings to the sun can markedly affect the body temperature of basking insects. For example, perching dragonflies and butterflies can regulate their radiation heat gain by postural adjustments (figure 28.3).

To prevent overheating, many ground-dwelling arthropods (*Tenebrio* beetles, locusts, scorpions) raise their bodies as high off the ground as possible to minimize heat gain from the ground. Some caterpillars and locusts orient with reference to both the sun and wind to vary both radiation heat gain and convective heat loss. Some desert-dwelling beetles can exude waxes from thousands of tiny pores on their cuticle. These “wax blooms” prevent dehydration and also are an extra barrier against the desert sun.

Color has a significant effect on thermoregulation since 50% of the radiant energy from the sun is in the visible spectrum. A black surface reflects less radiant energy than a white surface. Thus, many black beetles may be more active earlier in the day because they absorb more radiation and heat faster. Conversely, white beetles are more active in the hotter parts of the day because they absorb less heat.

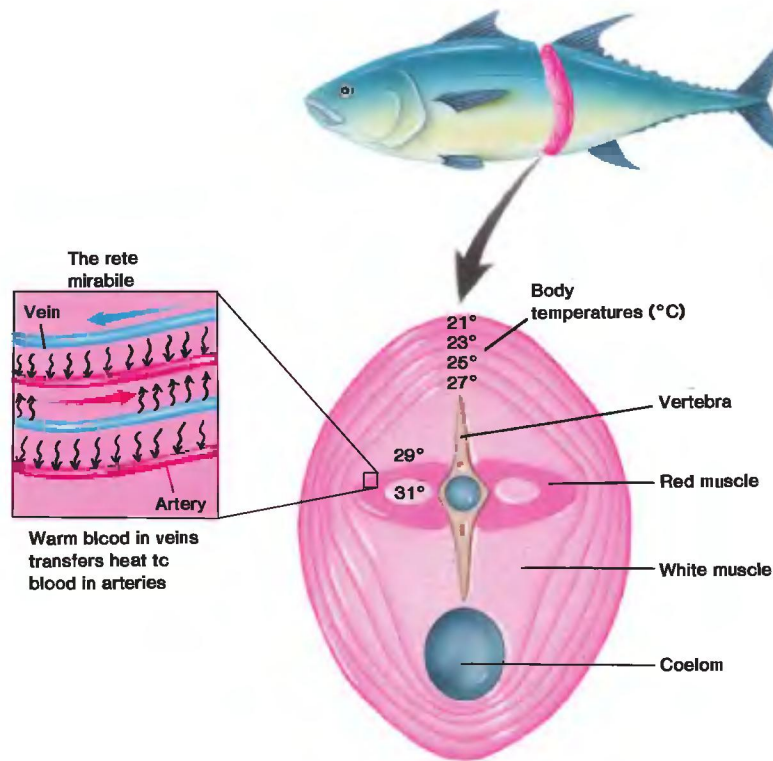
The previous examples of invertebrate temperature regulation give clues to how thermoregulation may have evolved in vertebrates. The endothermic temperature regulation of active insects apparently evolved because locomotion pro-

duced sufficient metabolic heat that thermoregulatory strategies could evolve. An increased locomotor metabolism could well have preceded the evolution of thermoregulation in vertebrates.

TEMPERATURE REGULATION IN FISHES

The temperature of the surrounding water determines the body temperature of most fishes. Fishes that live in extremely cold water have “antifreeze” materials in their blood. Polyalcohols (e.g., sorbitol, glycerol) or water-soluble peptides and glycopeptides lower the freezing point of blood plasma and other body fluids. These fishes also have proteins or protein-sugar compounds that stunt the growth of ice crystals that begin to form. These adaptations enable these fishes to stay flexible and swim freely in a supercooled state (i.e., at a temperature below the normal freezing temperature of a solution).

Some active fishes maintain a core temperature significantly above the temperature of the water. Bluefin tuna and the great white shark have major blood vessels just under the skin. Branches deliver blood to the deeper, powerful, red swimming muscles, where smaller vessels are arranged in a countercurrent heat exchanger called the *rete mirabile* (“miraculous net”) (figure 28.4). The heat that these red muscles generate is not lost because it is transferred in the *rete mirabile* from venous blood passing outward to cold arterial blood passing inward from the body surface. This arrangement of blood vessels enhances vigorous activity by keeping the swimming muscles several degrees warmer than the tissue near the surface of the fish. This system has been adaptive for these fishes. **Their muscular contractions can have four times as much power as those of similar muscles in fishes with cooler bodies. Thus, they can swim faster and range more widely through various depths in search of prey than can other predatory fishes more limited to given water depths and temperatures.**

**FIGURE 28.4**

Thermoregulation in Large, Active Fishes. In the bluefin tuna, the rete mirabile of arteries and veins acts as a countercurrent exchange system that helps reduce the loss of body heat. The cross section through the body shows that the temperature is highest around the red swimming muscles.

TEMPERATURE REGULATION IN AMPHIBIANS AND REPTILES

Animals, such as amphibians and reptiles, that have air rather than water as a surrounding medium face marked daily and seasonal temperature changes. Most of these animals are ectotherms. They derive heat from their environment, and their body temperatures vary with external temperatures.

Most amphibians have difficulty in controlling body heat because they produce little of it metabolically and rapidly lose most of it from their body surfaces. However, as previously noted, behavioral adaptations enable them to maintain their body temperature within a homeostatic range most of the time. Amphibians have an additional thermoregulatory problem because they must exchange oxygen and carbon dioxide across their skin surface, and this moisture layer acts as a natural evaporative cooling system. This problem of heat loss through evaporation limits the habitats and activities of amphibians to warm, moist areas. Some amphibians, such as bullfrogs, can vary the amount of mucus they secrete from their body surface—a physiological response that helps regulate evaporative cooling.

Reptiles have dry rather than moist skin, which reduces the loss of body heat through evaporative cooling of the skin. They

also have an expandable rib cage, which allows for more powerful and efficient ventilation. Reptiles are almost completely ectothermic. They have a low metabolic rate and warm themselves by behavioral adaptations. In addition, some of the more sophisticated regulatory mechanisms found in mammals are first found in reptiles. For example, diving reptiles (e.g., sea turtles, sea snakes) conserve body heat by routing blood through circulatory shunts into the center of the body. These animals can also increase heat production in response to the hormones thyroxine and epinephrine. In addition, tortoises and land turtles can cool themselves through salivating and frothing at the mouth, urinating on the back legs, moistening the eyes, and panting.

TEMPERATURE REGULATION IN BIRDS AND MAMMALS

Birds and mammals are the most active and behaviorally complex vertebrates. They can live in habitats all over the earth because they are homeothermic endotherms; they can maintain body temperatures between 35 and 42° C with metabolic heat.

Various cooling mechanisms prevent excessive warming in birds. Because they have no sweat glands, birds pant to lose heat

460 PART THREE Form and Function: A Comparative Perspective

through evaporative cooling. Some species have a highly vascularized pouch (gular pouch) in their throat that they can flutter (a process called **gular flutter**) to increase evaporation from the respiratory system.

Some birds possess mechanisms for preventing heat loss. Feathers are excellent insulators for the body, especially downy-type feathers that trap a layer of air next to the body to reduce heat loss from the skin (figure 28.5a). (This mechanism explains why goose down is such an excellent insulator and is used in outdoor vests and coats for protection from extreme cold.) Aquatic species, who lose heat from their legs and feet, have peripheral countercurrent heat exchange vessels called a *rete mirabile* in their legs to reduce heat loss (figure 28.5b). Mammals that live in cold regions, such as the arctic fox and barren-ground caribou, also have these exchange vessels in their extremities (e.g., legs, tails, ears, nose). Animals in hot climates, such as jackrabbits, have mechanisms (e.g., large ears) to rid the body of excess heat (figure 28.6).

Thick pelts and a thick layer of insulating fat called **blubber** just under the skin help marine animals, such as seals and whales, to maintain a body temperature of around 36 to 38° C. In the tail and flippers, which have no blubber, a countercurrent system of arteries and veins helps minimize heat loss.

Birds and mammals also use behavioral mechanisms to cope with external temperature changes. Like ectotherms, they sun themselves or seek shade as the temperature fluctuates. Many animals huddle to keep warm; others share burrows for protection from temperature extremes. Migration to warm climates and hibernation enable many different birds and mammals to survive the harsh winter months. Others, such as the desert camel, have a multitude of evolutionary adaptations for surviving in some of the hottest and driest climates on earth.

HEAT PRODUCTION IN BIRDS AND MAMMALS

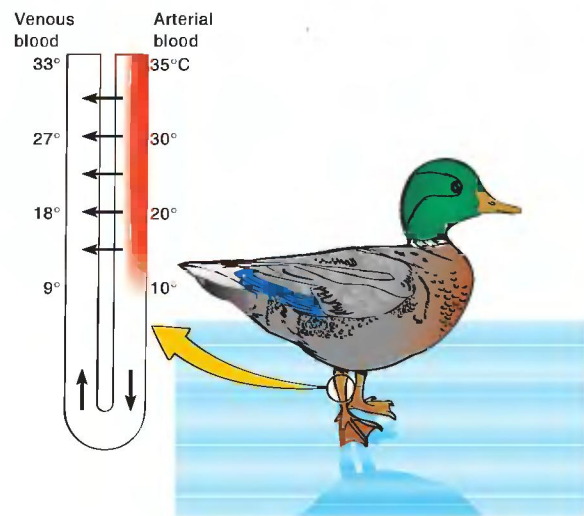
In endotherms, heat generation can warm the body as it dissipates throughout tissues and organs. Birds and mammals can generate heat (**thermogenesis**) by muscle contraction, ATPase pump enzymes, oxidation of fatty acids in brown fat, and other metabolic processes.

Every time a muscle cell contracts, the actin and myosin filaments sliding over each other and the hydrolysis of ATP molecules generate heat. Both voluntary muscular work (e.g., running, flying, jumping) and involuntary muscular work (e.g., shivering) generate heat. Heat generation by shivering is called **shivering thermogenesis**.

Birds and mammals have a unique capacity to generate heat by using specific enzymes of ancient evolutionary origin—the ATPase pump enzymes in the plasma membranes of most cells. When the body cools, the thyroid gland releases the hormone thyroxine. Thyroxine increases the permeability of many cells to sodium (Na^+) ions, which leak into the cells. The ATPase pump quickly pumps these ions out. In the process, ATP is hydrolyzed,



(a)



(b)

FIGURE 28.5

Insulation and Countercurrent Heat Exchange. (a) A thick layer of down feathers keeps these Chinstrap penguins (*Pygoscelis antarctica*) warm. Their covering of short, stiff feathers interlocks to trap air, forming the ornithological equivalent of a diver's suit. (b) The countercurrent heat exchanger in a bird foot. Some aquatic birds, such as this duck, possess countercurrent systems of arteries and veins (*rete mirabile*) in their legs that reduce heat loss. The arteries carry warm blood down the legs to warm the cooler blood in the veins, so that the heat is carried back to the body rather than lost through the feet that are in contact with a cold surface.

releasing heat energy. The hormonal triggering of heat production is called **nonshivering thermogenesis**.

Brown fat is a specialized type of fat found in newborn mammals, in mammals that live in cold climates, and in mammals that hibernate (figure 28.7). The brown color of this fat comes from the large number of mitochondria with their iron-containing cytochromes. Deposits of brown fat are beneath the ribs and in the shoulders. A large amount of heat is produced when brown fat

**FIGURE 28.6**

Temperature Regulation. This antelope jackrabbit (*Lepus alleni*) must get rid of excess body heat. Its huge, thin, highly vascularized ears have a large surface area for heat exchange.

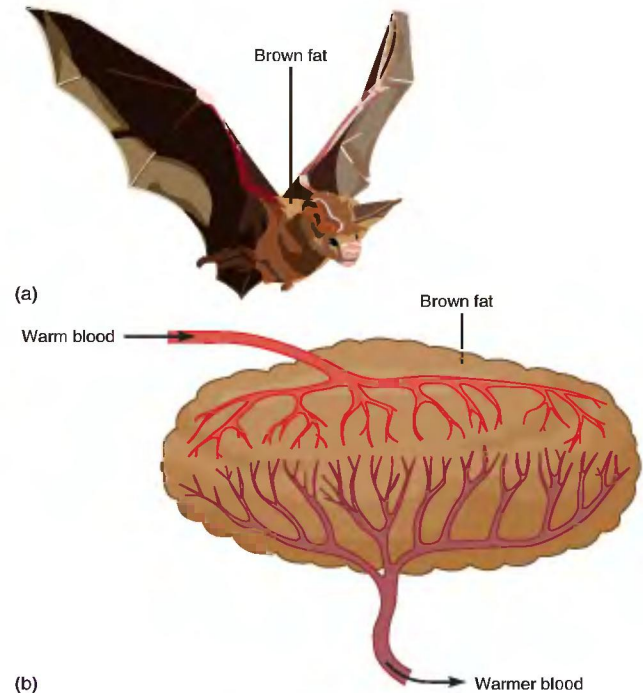
cells oxidize fatty acids, because little ATP is made. Blood flowing past brown fat is heated and contributes to warming the body.

The basal metabolic rate of birds and mammals is high and also produces heat as an inadvertent but useful by-product.

In amphibians, reptiles, birds, and mammals, specialized cells in the hypothalamus of the brain control thermoregulation. The two hypothalamic thermoregulatory areas are the heating center and the cooling center. The heating center controls vasoconstriction of superficial blood vessels, erection of hair and fur, and shivering or nonshivering thermogenesis. The cooling center controls vasodilation of blood vessels, sweating, and panting. Overall, feedback mechanisms (with the hypothalamus acting as a thermostat) trigger either the heating or cooling of the body and thereby control body temperature (figure 28.8). Specialized neuronal receptors in the skin and other parts of the body sense temperature changes. Warm neuronal receptors excite the cooling center and inhibit the heating center. Cold neuronal receptors have the opposite effects.

During the winter, various endotherms (e.g., bats, woodchucks, chipmunks, ground squirrels) go into **hibernation** (*L. hiberna*, winter). During hibernation, the metabolic rate slows, as do the heart and breathing rates. Mammals prepare for hibernation by building up fat reserves and growing long winter pelts. All hibernating animals have brown fat. Decreasing day length stimulates both increased fat deposition and fur growth. Another physiological state characterized by slow metabolism and inactivity is **aestivation** (*L. aestivus*, summer), which allows certain mammals to survive long periods of elevated temperature and diminished water supplies.

Some animals, such as badgers, bears, opossums, raccoons, and skunks, enter a state of prolonged sleep in the winter. Since their body temperature remains near normal, this is not true hibernation.

**FIGURE 28.7**

Brown Fat. (a) Many mammals, such as this bat, have adipose tissue called brown fat between the shoulder blades. (b) The area of brown fat is much warmer than the rest of the body. Blood flowing through the brown fat is warmed.

CONTROL OF WATER AND SOLUTES (OSMOREGULATION AND EXCRETION)

Excretion (*L. excretio*, to eliminate) can be defined broadly as the elimination of metabolic waste products from an animal's body. These products include carbon dioxide and water (which cellular respiration primarily produces), excess nitrogen (which is produced as ammonia from deamination of amino acids), and solutes (various ions). Chapter 26 covers the excretion of respiratory carbon dioxide.

Excretion of nitrogenous wastes is usually associated with the regulation of water and solute (ionic) balance by a physiological process called **osmoregulation**. Osmoregulation is necessary for animals in all habitats. If the osmotic concentration of the body fluids of an animal equals that of the medium (the animal's environment), the animal is an **osmoconformer**. When the osmotic concentration of the environment changes, so does that of the animal's body fluids. Obviously, this type of osmoregulation is not efficient and has limited the distribution of those animals using it. In contrast, an animal that maintains its body fluids at a different osmotic concentration from that of its surrounding environment is an **osmoregulator**.

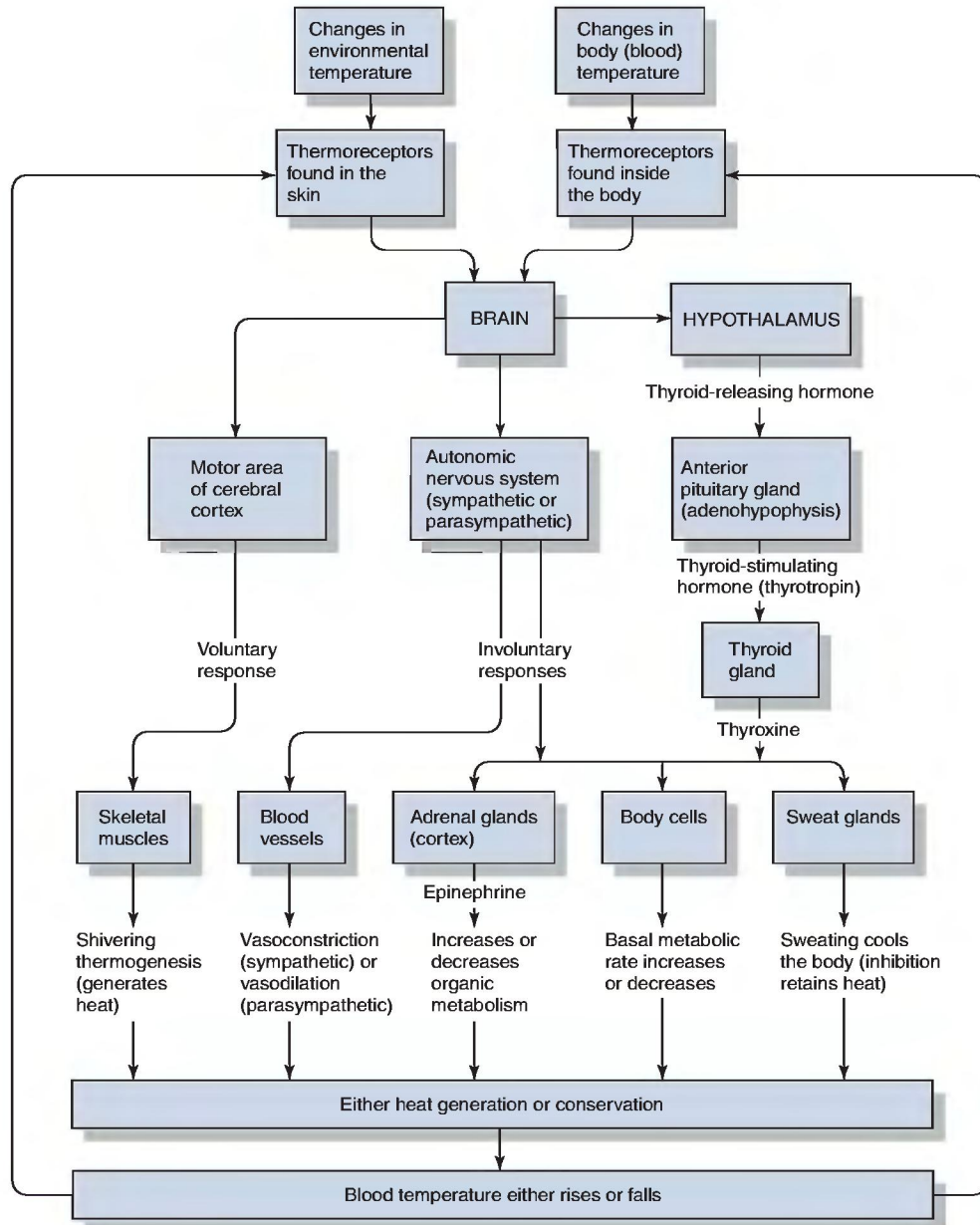
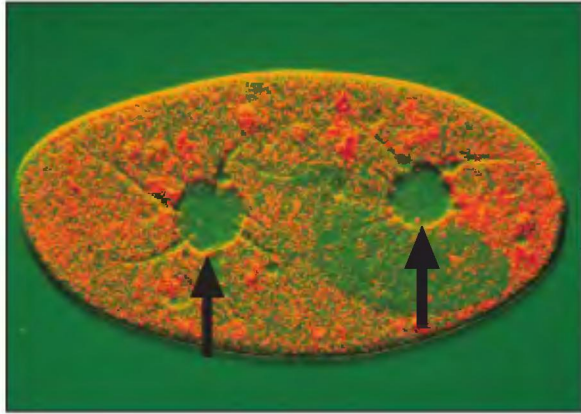


FIGURE 28.8 Thermoregulation. Overview of the feedback pathways that control the core body temperature of a mammal. Arrows show the major control pathways.

Animals living in seawater have body fluids with an osmotic concentration that is about a third less (hypoosmotic) than the surrounding seawater, and water tends to leave their bodies continually. **To compensate for this problem, mechanisms evolved in these animals to conserve water and prevent dehydration.** Fresh-water animals have body fluids that are hyperosmotic with respect to their environment, and water tends to continually enter their bodies. Mechanisms evolved in these animals that excrete

water and prevent fluid accumulation. Land animals have a higher concentration of water in their fluids than in the surrounding air. They tend to lose water to the air through evaporation and may use considerable amounts of water to dispose of wastes.

The form and function of organs or systems associated with excretion and osmoregulation are related both to environmental conditions (saltwater, freshwater, terrestrial) and to body size (especially the surface-to-volume ratio).

**FIGURE 28.9**

Contractile Vacuoles. A photomicrograph ($\times 100$) showing the location of two contractile vacuoles (black arrows) in a stained *Paramecium*. Notice the small tubules surrounding each vacuole. These tubes collect water and deliver it to the contractile vacuole, which expels the fluid through a pore.

INVERTEBRATE EXCRETORY SYSTEMS

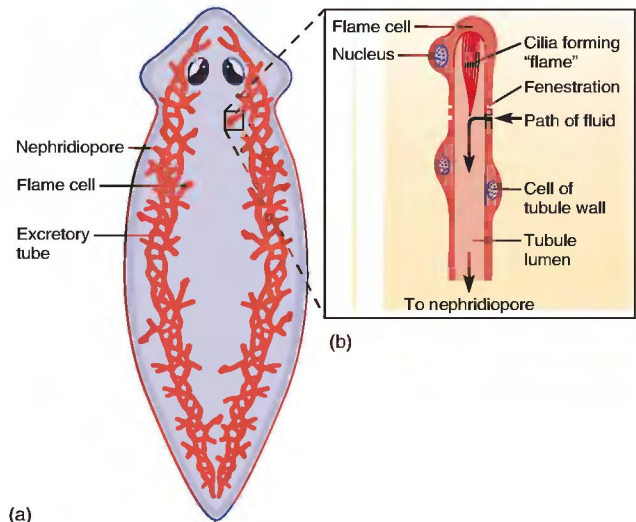
Aquatic invertebrates occur in a wide range of media, from freshwater to markedly hypersaline water (e.g., salt lakes). Generally, marine invertebrates have about the same osmotic concentration as seawater (i.e., they are osmoconformers). This avoids any need to osmoregulate. Most water and ions are gained across the integument, via gills, by drinking, and in food. Ions and wastes are mostly lost by diffusion via the integument, gills, or urine.

Freshwater invertebrates are strong osmoregulators because it is impossible to be isosmotic with dilute media. Any water gain is usually eliminated as urine.

A number of invertebrate taxa have more or less successfully invaded terrestrial habitats. The most successful terrestrial invertebrates are the arthropods, particularly the insects, spiders, scorpions, ticks, mites, centipedes, and millipedes. Overall, the water and ion balance of terrestrial invertebrates is quite different from that of aquatic animals because terrestrial invertebrates face limited water supplies and water loss by evaporation from their integument. Some of the invertebrate excretory mechanisms and systems are now discussed.

CONTRACTILE VACUOLES

Some protists and marine invertebrates (e.g., protozoa, cnidarians, echinoderms, sponges) do not have specialized excretory structures because wastes simply diffuse into the surrounding isosmotic water. In some freshwater species, cells on the body surface actively pump ions into the animal. Many freshwater species (protozoa, sponges), however, have contractile vacuoles that pump out excess water. **Contractile vacuoles** are energy-requiring devices that expel excess water from individual cells exposed to hypoosmotic environments (figure 28.9).

**FIGURE 28.10**

Protonephridial (Excretory) System in a Turbellarian. (a) The system lies in the mesenchyme and consists of a network of fine tubules that run the length of the animal on each side and open to the surface by minute excretory pores called nephridiopores. (b) Numerous fine side branches from the tubules originate in the mesenchyme in enlargements called flame cells.

PROTONEPHRIDIA

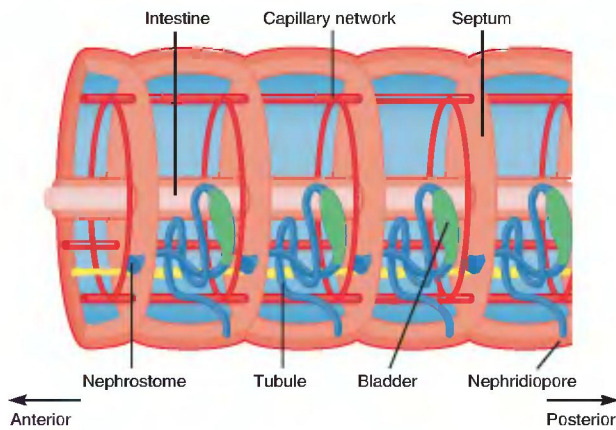
Although a few groups of metazoan invertebrates possess no known excretory structures, most have **nephridia** (Gr. *nephros*, kidney) (sing., nephridium) that serve for excretion, osmoregulation, or both. **Probably the earliest type of nephridium to appear in the evolution of animals was the protonephridium** (Gr. *protos*, first + *nephridium*).

Among the simplest of the protonephridia are flame-cell systems, such as those in rotifers, some annelids, larval molluscs, and some flatworms (figure 28.10). The protonephridial excretory system is composed of a network of excretory canals that open to the outside of the body through excretory pores. Bulblike **flame cells** are located along the excretory canals. Fluid filters into the flame cells from the surrounding interstitial fluid, and beating cilia propel the fluid through the excretory canals and out of the body through the excretory pores. Flame-cell systems function primarily in eliminating excess water. Nitrogenous waste simply diffuses across the body surface into the surrounding water.

METANEPHRIDIA

A more advanced type of excretory structure among invertebrates is the **metanephridium** (Gr. *meta*, beyond + *nephridium*;), (pl., metanephridia). Protonephridia and metanephridia have critical structural differences. Both open to the outside, but metanephridia (1) also open internally to the body fluids and (2) are multicellular.

464 PART THREE Form and Function: A Comparative Perspective

**FIGURE 28.11**

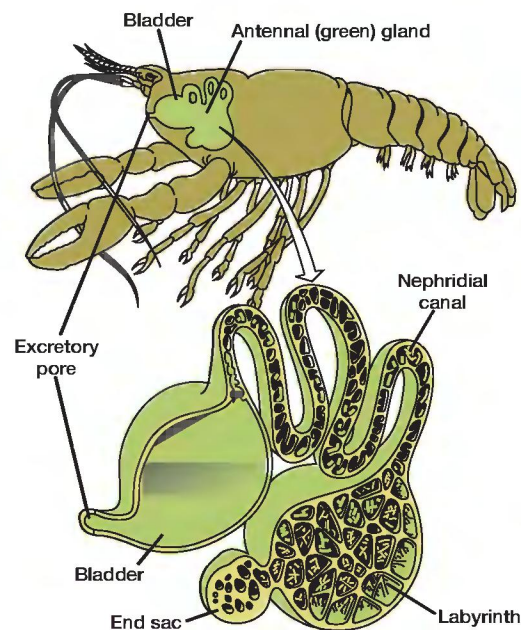
Earthworm Metanephridium. The metanephridium opens by a ciliated nephrostome into the cavity of one segment, and the next segment contains the nephridiopore. The main tubular portion of the metanephridium is coiled and is surrounded by a capillary network. Waste can be stored in a bladder before being expelled to the outside. Most segments contain two metanephridia.

Most annelids (such as the common earthworm) and a variety of other invertebrates have a metanephridial excretory system. Recall that the earthworm's body is divided into segments and that each segment has a pair of metanephridia. Each metanephridium begins with a ciliated funnel, the nephrostome, that opens from the body cavity of a segment into a coiled tubule (figure 28.11). As beating cilia move the fluid through the tubule, a network of capillaries surrounding the tubule reabsorbs and carries away ions. Each tubule leads to an enlarged bladder that empties to the outside of the body through an opening called the nephridiopore.

The excretory system of molluscs includes protonephridia in larval stages and metanephridia in adults.

ANTENNAL (GREEN) AND MAXILLARY GLANDS

In those crustaceans that have gills, nitrogenous wastes are removed by simple diffusion across the gills. Most crustaceans release ammonia, although they also produce some urea and uric acid as waste products. Thus, the excretory organs of freshwater species may be more involved with the reabsorption of ions and elimination of water than with the discharge of nitrogenous wastes. The excretory organs in some crustaceans (crayfish, crabs) are **antennal glands** or **green glands** because of their location near the antenna and their green color (figure 28.12). Fluid filters into the antennal gland from the hemocoel. Hemolymph pressure from the heart is the main driving force for filtration. Marine crustaceans have a short nephridial canal and produce urine that is isosmotic to their hemolymph. The nephridial canal is longer in freshwater crustaceans, which allows more surface area for ion transport.

**FIGURE 28.12**

Antennal (Green) Gland of the Crayfish. The antennal gland, which lies in front of and to both sides of the esophagus, is divided into an end sac, where fluid collects by filtration, and a labyrinth. The labyrinth walls are greatly folded and glandular and appear to be an important site for reabsorption. The labyrinth leads via a nephridial canal into a bladder. From the bladder, a short duct leads to an excretory pore.

In other crustaceans (some malacostracans [crabs, shrimp, pillbugs]), the excretory organs are near the maxillary segments and are termed **maxillary glands**. In maxillary glands, fluid collects within the tubules from the surrounding blood of the hemocoel, and this primary urine is modified substantially by selective reabsorption and secretion as it moves through the excretory system and rectum.

MALPIGHIAN TUBULES

Insects have an excretory system made up of the gut and **Malpighian tubules** attached to the gut (figure 28.13). Excretion involves the active transport of potassium ions into the tubules from the surrounding hemolymph and the osmotic movement of water that follows. Nitrogenous waste (uric acid) also enters the tubules. As fluid moves through the Malpighian tubules, some of the water and certain ions are recovered. All of the uric acid passes into the gut and out of the body.

COXAL GLANDS

Coxal (*L. coxa*, hip) glands are common among arachnids (spiders, scorpions, ticks, mites). These spherical sacs resemble annelid nephridia (figure 28.14). Wastes are collected from the surrounding hemolymph of the hemocoel and discharged through

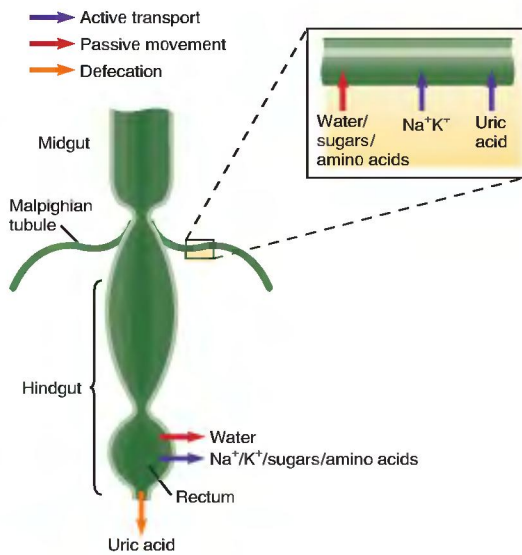


FIGURE 28.13

Malpighian Tubules. Malpighian tubules remove nitrogenous wastes (uric acid) from the hemocoel. Various ions are actively transported across the outer membrane of the tubule. Water follows these ions into the tubule and carries amino acids, sugars, and some nitrogenous wastes along passively. Some water, ions, and organic compounds are reabsorbed in the basal portion of the Malpighian tubules and the hindgut; the rest are reabsorbed in the rectum. Uric acid moves into the hindgut and is excreted.

pores on from one to several pairs of appendages near the proximal joint (coxa) of the leg. Recent evidence suggests that the coxal glands may also function in the release of pheromones.

Other arachnid species have Malpighian tubules instead of, or in addition to, the coxal glands. In some of these species, however, Malpighian tubules seem to function in silk production rather than in excretion.

VERTEBRATE EXCRETORY SYSTEMS

Vertebrates face the same problems as invertebrates in controlling water and ion balance. Generally, water losses are balanced precisely by water gains (table 28.1). Vertebrates gain water by absorption from liquids and solid foods in the small and large intestines, and by metabolic reactions that yield water as an end product. They lose water by evaporation from respiratory surfaces, evaporation from the integument, sweating or panting, elimination in feces, and excretion by the urinary system.

Solute losses also must be balanced by solute gains. Vertebrates take in solutes by absorption of minerals from the small and large intestines, through the integument or gills, from secretions of various glands or gills, and by metabolism (e.g., the waste products of degradative reactions). They lose solutes in sweat, feces, urine, and gill secretions, and as metabolic wastes. The major metabolic wastes that must be eliminated are ammonia, urea, or uric acid.

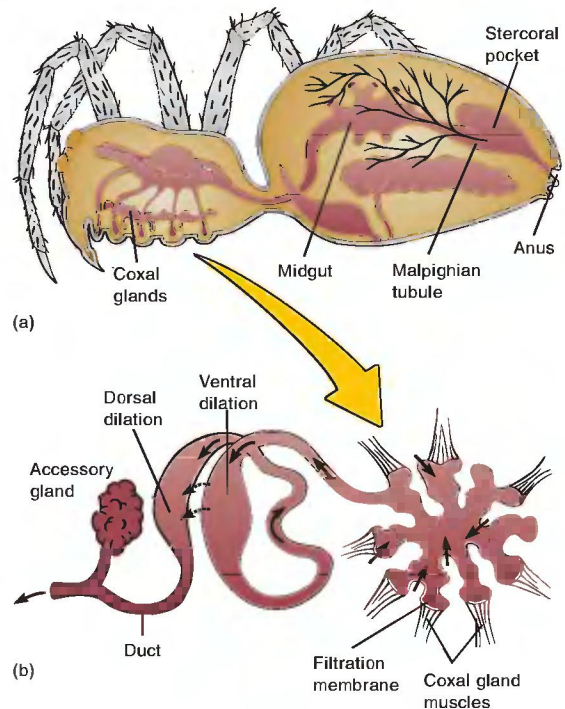


FIGURE 28.14

Coxal Glands in Arachnids. (a) The gut and excretory systems of a spider. (b) Coxal gland muscles attach to the thin saccular filtration membrane. These muscles promote filtration and fluid flow (black arrows) by contracting and relaxing along the tubular duct. Water and solutes are reabsorbed along the tubular duct.

Vertebrates live in saltwater, freshwater, and on land; each of these environments presents different water and solute problems that vertebrates have solved in different ways. The next section discusses how vertebrates avoid losing or gaining too much water and, in turn, how they maintain a homeostatic solute concentration in their body fluids. The disposal (excretion) of certain metabolic waste products is also coupled with osmotic balance and is discussed with the urinary system.

HOW VERTEBRATES ACHIEVE OSMOREGULATION

A variety of mechanisms have evolved in vertebrates to cope with their osmoregulatory problems, and most of them are adaptations of the urinary system. As presented in chapter 26, vertebrates have a closed circulatory system containing blood that is under pressure. This pressure forces blood through a membrane filter in a kidney, where the following three key functions take place:

1. Filtration, in which blood passes through a filter that retains blood cells, proteins, and other large solutes but lets small molecules, ions, and urea pass through
2. Reabsorption, in which selective ions and molecules are taken back into the bloodstream from the filtrate

TABLE 28.1
AVERAGE WATER GAIN AND LOSS IN A HUMAN AND KANGAROO RAT

| VERTEBRATE | WATER GAIN (ML) | | WATER LOSS (ML) | |
|-----------------------------|------------------------|--------------|-----------------|--------------|
| Human (daily) | Ingested in solid food | 1,200 | Feces | 100 |
| | Ingested as liquids | 1,000 | Urine | 1,500 |
| | Metabolically produced | <u>350</u> | Skin and lungs | <u>950</u> |
| | Total | 2,550 | | 2,550 |
| Kangaroo rat (over 4 weeks) | Ingested in solid food | 6 | Feces | 3 |
| | Ingested in liquids | 0 | Urine | 13 |
| | Metabolically produced | <u>54</u> | Skin and lungs | <u>44</u> |
| | Total | 60 | | 60 |

3. Secretion, whereby select ions and end products of metabolism (e.g., K^+ , H^+ , NH_3) that are in the blood are added to the filtrate for removal from the body

VERTEBRATE KIDNEY VARIATIONS

Vertebrates have two kidneys that are in the back of the abdominal cavity, on either side of the aorta. Each kidney has a coat of connective tissue called the renal capsule (*L. renes*, kidney). The inner portion of the kidney is called the medulla; the region between the capsule and the medulla is the cortex.

The structure and function of vertebrate kidneys differ, depending on the vertebrate groups and the developmental stage. Overall, there are three kinds of vertebrate kidneys: the pronephros, mesonephros, and metanephros. The pronephros appears only briefly in many vertebrate embryos, and not at all in mammalian embryos (figure 28.15a). In some vertebrates, the pronephros is the first osmoregulatory and excretory organ of the embryo (tadpoles and other amphibian larvae); in others (hagfishes), it remains as the functioning kidney. During embryonic development of amniotes, or during metamorphosis in amphibians, the mesonephros replaces the pronephros (figure 28.15b). The mesonephros is the functioning embryonic kidney of many vertebrates and also adult fishes and amphibians. The mesonephros gives way during embryonic development to the metanephros in adult reptiles, birds, and mammals (figure 28.15c).

The physiological differences between these kidney types are primarily related to the number of blood-filtering units they contain. The pronephric kidney forms in the anterior portion of the body cavity and contains fewer blood-filtering units than either the mesonephric or metanephric kidneys. The larger number of filtering units in the latter has allowed vertebrates to face the rigorous osmoregulatory and excretory demands of freshwater and terrestrial environments.

What follows is a presentation of how a few vertebrates maintain their water and solute concentrations in different habitats—in the seas, in freshwater, and on land (table 28.2).

Sharks

Sharks and their relatives (skates and rays) have mesonephric kidneys and have solved their osmotic problem in ways different from the bony fishes (figure 28.15b). Instead of actively pumping ions out of their bodies through the kidneys, they have a rectal gland that secretes a highly concentrated salt ($NaCl$) solution. To reduce water loss, they use two organic molecules—urea and trimethylamine oxide (TMO)—in their body fluids to raise the osmotic pressure to a level equal to or higher than that of the seawater.

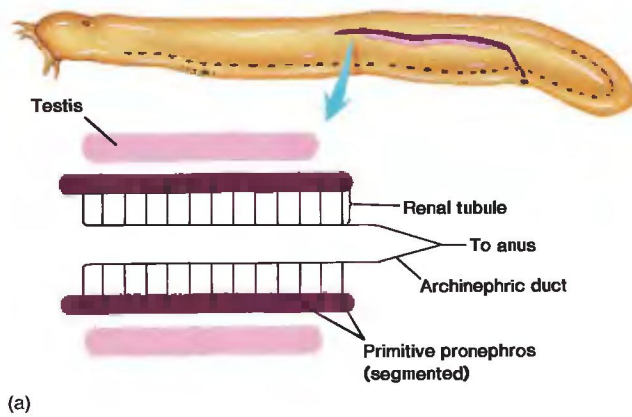
Urea denatures proteins and inhibits enzymes, whereas TMO stabilizes proteins and activates enzymes. Together in the proper ratio, they counteract each other, raise the osmotic pressure, and do not interfere with enzymes or proteins. This reciprocity is termed the counteracting osmolyte strategy.

A number of other fishes and invertebrates have evolved the same mechanism and employ pairs of counteracting osmolytes to raise the osmotic pressure of their body fluids.

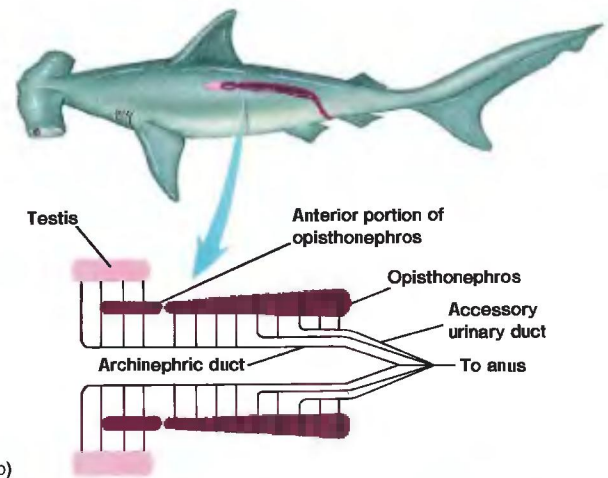
Teleost Fishes

Most teleost fishes have mesonephric kidneys. Because the body fluids of freshwater fishes are hyperosmotic relative to freshwater (see table 28.2), water tends to enter the fishes, causing excessive hydration or bloating (figure 28.16a). At the same time, body ions tend to move outward into the water. To solve this problem, freshwater fishes usually do not drink much water. Their bodies are coated with mucus, which helps stem inward water movement. They absorb salts and ions by active transport across their gills. They also excrete a large volume of water as dilute urine.

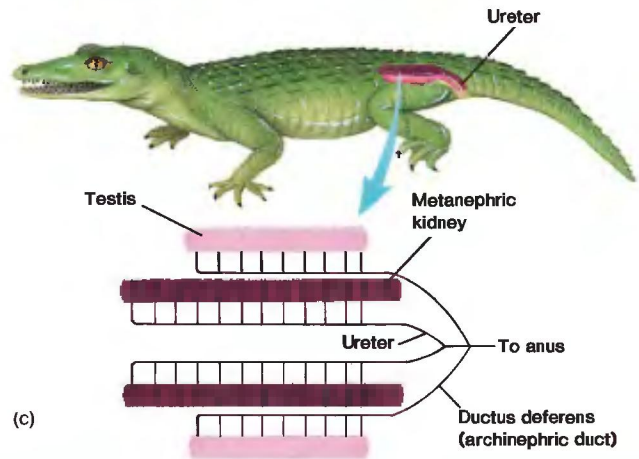
Although most groups of animals probably evolved in the sea, many marine bony fishes probably had freshwater ancestors, as presented in chapter 18. Marine fishes face a different problem of water balance—their body fluids are hypoosmotic with respect to seawater (see table 28.2), and water tends to leave their bodies, resulting in dehydration (figure 28.16b). To compensate, marine fishes drink large quantities of water, and they secrete Na^+ , Cl^- , and K^+ ions through secretory cells in their



(a)



(b)



(c)

FIGURE 28.15

Types of Kidneys in Vertebrates and Their Association with the Male Reproductive System. The brown portions of the drawings represent the mesoderm that forms both the kidneys and gonads. Notice that it extends much of the length of the body during development. (a) The primitive pronephric kidney is found in adult hagfishes and embryonic fishes and amphibians. It is anterior in the body and contains segmental renal tubules that lead from the body of the pronephros to the archinephric duct. Notice that the testes are separated from the kidneys. (b) The mesonephros is the functional kidney in the amniote embryo, adult fishes, and amphibians. It is structurally similar to the nonsegmented opisthonephric (advanced mesonephric) kidney of most nonamniote vertebrates, such as sharks. The anterior portion of the opisthonephros functions in blood cell formation and secretion of sex hormones. Notice that the testes occupy the position of the anterior opisthonephros, and the archinephric duct carries both sperm and urine. (c) The metanephric kidney of adult amniotes (reptiles, birds, and mammals) is the most advanced kidney. Notice the separate ureters (new ducts) for carrying urine. The archinephric duct becomes the ductus deferens for carrying sperm. The kidney is more compact and located more caudally in the body.

TABLE 28.2

HOW VARIOUS VERTEBRATES MAINTAIN WATER AND SALT BALANCE

| ORGANISM | ENVIRONMENTAL CONCENTRATION RELATIVE TO BODY FLUIDS | URINE CONCENTRATION RELATIVE TO BLOOD | MAJOR NITROGENOUS WASTE | KEY ADAPTATION |
|-------------------|---|---------------------------------------|-------------------------|------------------------------------|
| Freshwater fishes | Hypoosmotic | Hypoosmotic | Ammonia | Absorb ions through gills |
| Saltwater fishes | Hyperosmotic | Isoosmotic | Ammonia | Secrete ions through gills |
| Sharks | Isoosmotic | Isoosmotic | Ammonia | Secrete ions through rectal gland |
| Amphibians | Hypoosmotic | Very hypoosmotic | Ammonia and urea | Absorb ions through skin |
| Marine reptiles | Hyperosmotic | Isoosmotic | Ammonia and urea | Secrete ions through salt gland |
| Marine mammals | Hyperosmotic | Very hyperosmotic | Urea | Drink some water |
| Desert mammals | No comparison | Very hyperosmotic | Urea | Produce metabolic water |
| Marine birds | No comparison | Weakly hyperosmotic | Uric acid | Drink seawater and use salt glands |
| Terrestrial birds | No comparison | Weakly hyperosmotic | Uric acid | Drink freshwater |

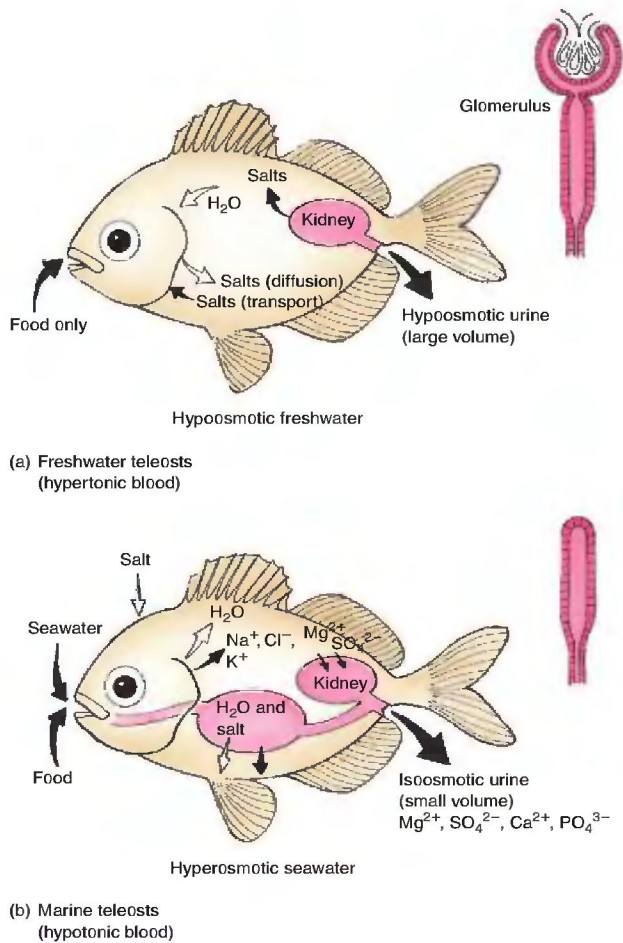


FIGURE 28.16

Osmoregulation. Osmoregulation by (a) freshwater and (b) marine fishes. Large black arrows indicate passive uptake or loss of water or ions. Small black and white arrows indicate active transport processes at gill membranes and kidney tubules. Insets of kidney nephrons depict adaptations within the kidney. Water, ions, and small organic molecules are filtered from the blood at the glomerulus of the nephron. Essential components of the filtrate can be reabsorbed within the tubule system of the nephron. Marine fishes conserve water by reducing the size of the glomerulus of the nephron, and thus reducing the quantity of water and ions filtered from the blood. Ions can be secreted from the blood into the kidney tubules. Marine fishes can produce urine that is isoosmotic with the blood. Freshwater fishes have enlarged glomeruli and short tubule systems. They filter large quantities of water from the blood, and tubules reabsorb some ions from the filtrate. Freshwater fishes produce a hypoosmotic urine.

gills. Channels in plasma membranes of their kidneys actively transport the multivalent ions that are abundant in seawater (e.g., Ca^{2+} , Mg^{2+} , SO_4^{2-} , and PO_4^{3-}) out of the extracellular fluid and into the nephron tubes. The ions are then excreted in a concentrated urine.

Some fishes encounter both fresh- and saltwater during their lives. Newborn Atlantic salmon swim downstream from the

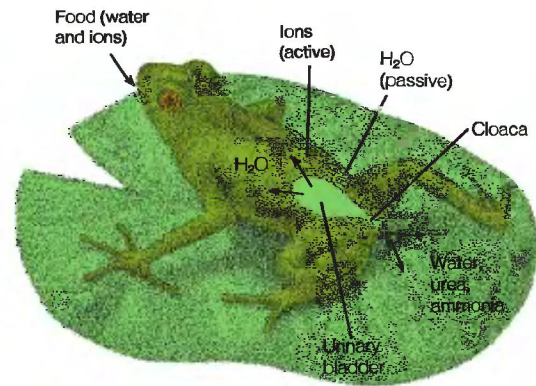


FIGURE 28.17

Water and Ion Uptake in an Amphibian. Water can enter this frog via food, through its highly permeable skin, or from the urinary bladder. The skin also actively transports ions such as Na^+ and Cl^- from the environment. The kidney forms a dilute urine by reabsorbing Na^+ and Cl^- ions. Urine then flows into the urinary bladder, where most of the remaining ions are reabsorbed.

freshwater stream of their birth and enter the sea. Instead of continuing to pump ions in, as they have done in freshwater, the salmon must now rid their bodies of salt. Years later, these same salmon migrate from the sea to their freshwater home to spawn. As they do, the pumping mechanisms reverse themselves.

Amphibians

The amphibian kidney is identical to that of freshwater fishes (figure 28.16a), which is not surprising, because amphibians spend a large portion of their time in freshwater, and when on land, they tend to seek out moist places. Amphibians take up water and ions in their food and drink, through the skin that is in contact with moist substrates, and through the urinary bladder (figure 28.17). This uptake counteracts what is lost through evaporation and prevents osmotic imbalance (see table 28.2).

The urinary bladder of a frog, toad, or salamander is an important water and ion reservoir. For example, when the environment becomes dry, the bladder enlarges for storing more urine. If an amphibian becomes dehydrated, a brain hormone causes water to leave the bladder and enter the body fluid.

Reptiles, Birds, and Mammals

Reptiles, birds, and mammals all possess metanephric kidneys (see figure 28.15c). Their kidneys are by far the most complex animal kidneys, well suited for these animals' high rates of metabolism.

In most reptiles, birds, and mammals, the kidneys can remove far more water than can those in amphibians, and the kidneys are the primary regulatory organs for controlling the osmotic balance of the body fluids. Some desert and marine reptiles and birds build up high salt (NaCl) concentrations in their bodies because they consume salty foods or seawater, and they lose water through evaporation and in their urine and feces. To

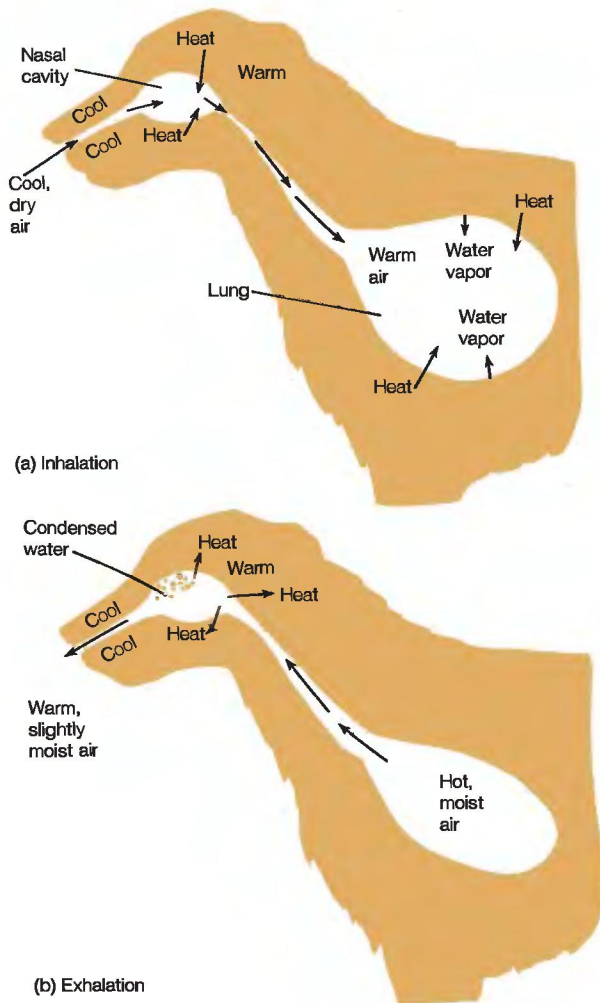


FIGURE 28.18

Water Retention by Countercurrent Heating and Cooling in a Mammal. (a) When this animal inhales, the cool, dry air passing through its nose is heated and humidified. At the same time, its nasal tissues are cooled. (b) When the animal exhales, it gives up heat to the previously cooled nasal tissue. The air carries less water vapor, and condensation occurs in the animal's nose.

rid themselves of excess salt, these animals also have salt glands near the eye or in the tongue that remove excess salt from the blood and secrete it as tearlike droplets.

A major site of water loss in mammals is the lungs. To reduce this evaporative loss, many mammals have nasal cavities that act as countercurrent exchange systems (figure 28.18). When the animal inhales, air passes through the nasal cavities and is warmed by the surrounding tissues. In the process, the temperature of this tissue drops. When the air gets deep into the lungs, it is further warmed and humidified. During exhalation, as the warm moist air passes up the respiratory tree, it gives up its heat to the nasal cavity. As the air cools, much of the water condenses on the

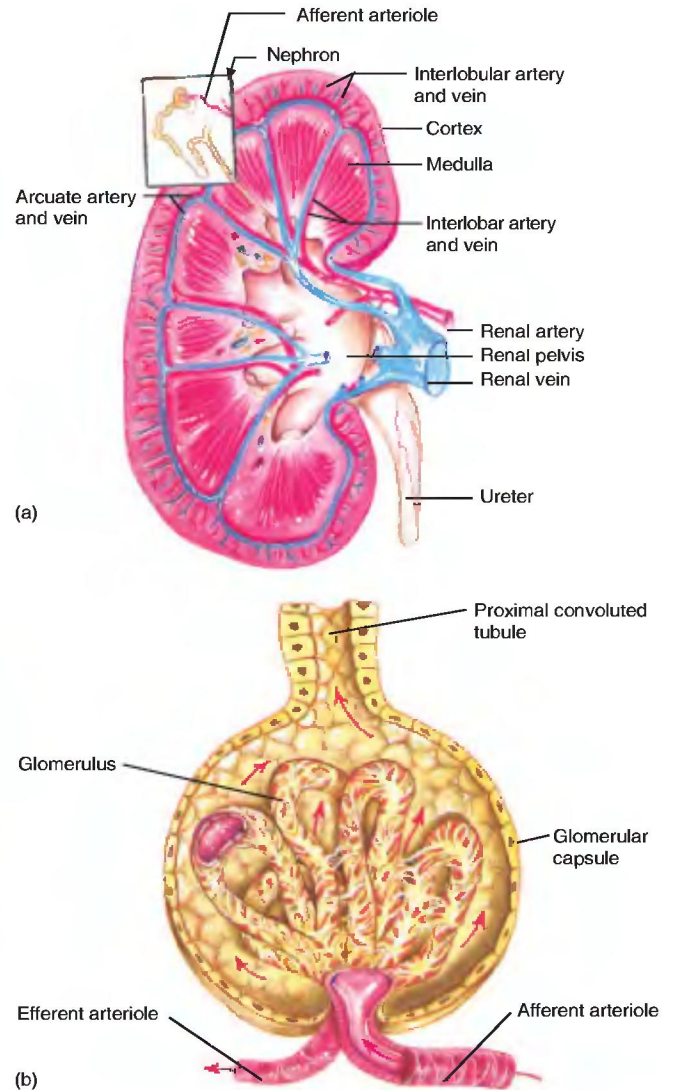


FIGURE 28.19

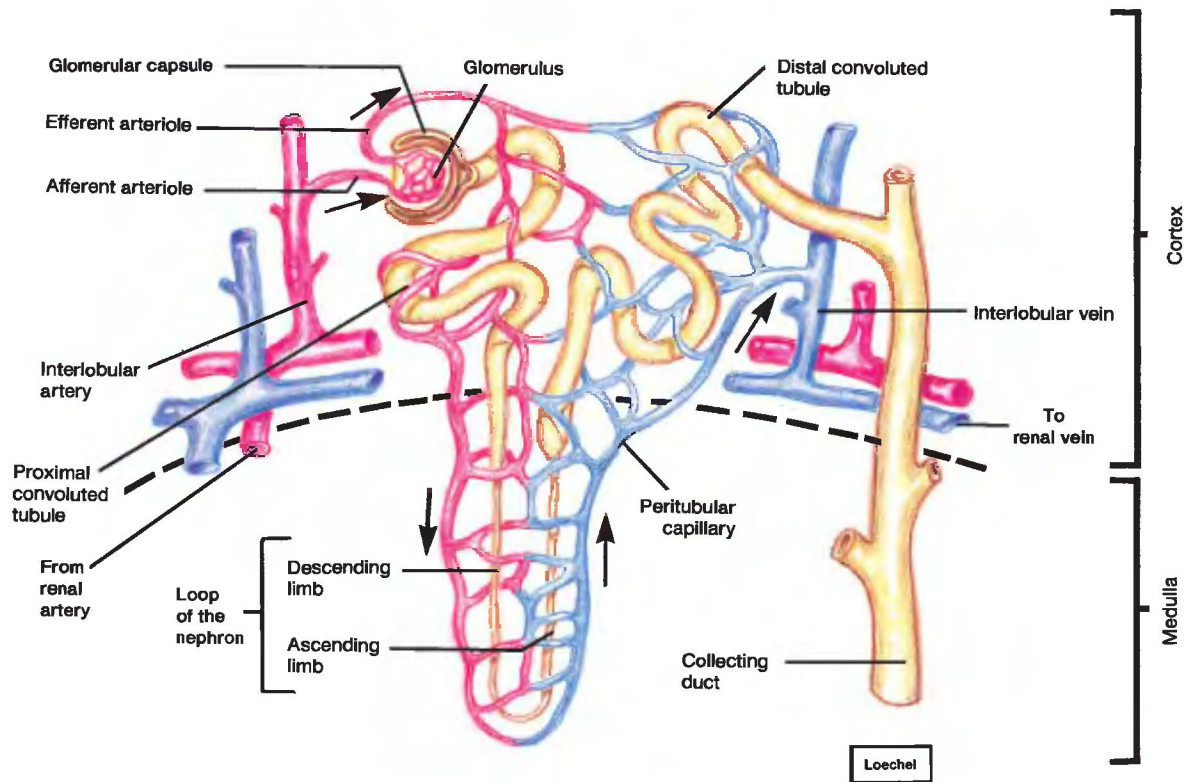
Filtration Device of the Metanephric Kidney. (a) Interior of a kidney, showing the positioning of the nephron and the blood supply to and from the kidney. (b) Glomerular capsule. Red arrows show that high blood pressure forces water and ions through small perforations in the walls of the glomerular capillaries to form the glomerular filtrate.

nasal surfaces and does not leave the body. This mechanism explains why a dog's nose is usually cold and moist.

HOW THE METANEPHRIC KIDNEY FUNCTIONS

The filtration device of the metanephric kidney consists of over one million individual filtration, secretion, and absorption structures called **nephrons** (Gr. *nephros*, kidney + *on*, neuter) (figure 28.19a). At the beginning of the nephron is the filtration apparatus

470 PART THREE Form and Function: A Comparative Perspective

**FIGURE 28.20**

Metanephric Nephron. The proximal convoluted tubule reabsorbs glucose and some ions. The distal convoluted tubule reabsorbs other ions and water. Final water reabsorption takes place in the collecting duct. Black arrows indicate the direction of movement of materials in the nephron.

called the glomerular capsule (formerly Bowman's capsule), which looks rather like a tennis ball that has been punched in on one side (figure 28.19b). The capsules are in the cortical (outermost) region of the kidney. In each capsule, an afferent ("going to") arteriole enters and branches into a fine network of capillaries called the **glomerulus**. The walls of these glomerular capillaries contain small perforations called filtration slits that act as filters. Blood pressure forces fluid through these filters. The fluid is now known as glomerular filtrate and contains small molecules, such as glucose, ions (Ca^{2+} , PO_4^{3-}), and the primary nitrogenous waste product of metabolism—urea or uric acid. Because the filtration slits are so small, large proteins and blood cells remain in the blood and leave the glomerulus via the efferent ("outgoing") arteriole. The efferent arteriole then divides into a set of capillaries called the peritubular capillaries that wind profusely around the tubular portions of the nephron (figure 28.20). Eventually, they merge to form veins that carry blood out of the kidney.

Beyond the glomerular capsule are the proximal convoluted tubule, the loop of the nephron (formerly the loop of Henle), and the distal convoluted tubule. At various places along these structures, the glomerular filtrate is selectively reabsorbed, returning certain ions (e.g., Na^+ , K^+ , Cl^-) to the bloodstream. Both active

(ATP-requiring) and passive procedures are involved in the recovery of these substances. Potentially harmful compounds, such as hydrogen (H^+) and ammonium (NH_4^+) ions, drugs, and various other foreign materials are secreted into the nephron lumen. In the last portion of the nephron, called the collecting duct, final water reabsorption takes place so that the urine contains an ion concentration well above that of the blood. Thus, the filtration, secretion, and reabsorption activities of the nephron do not simply remove wastes. They also maintain water and ion balance, and therein lies the importance of the homeostatic function of the kidney.

Mammalian, and to a lesser extent avian and reptilian, kidneys can remove far more water from the glomerular filtrate than can the kidneys of amphibians. For example, human urine is four times as concentrated as blood plasma, a camel's urine is eight times as concentrated, a gerbil's is 14 times as concentrated, and some desert rats and mice have urine more than 20 times as concentrated as their plasma. This concentrated waste enables them to live in dry or desert environments, where little water is available for them to drink. Most of their water is metabolically produced from the oxidation of carbohydrates, fats, and proteins in the seeds that they eat (see table 28.1). **Mammals and, to a lesser**

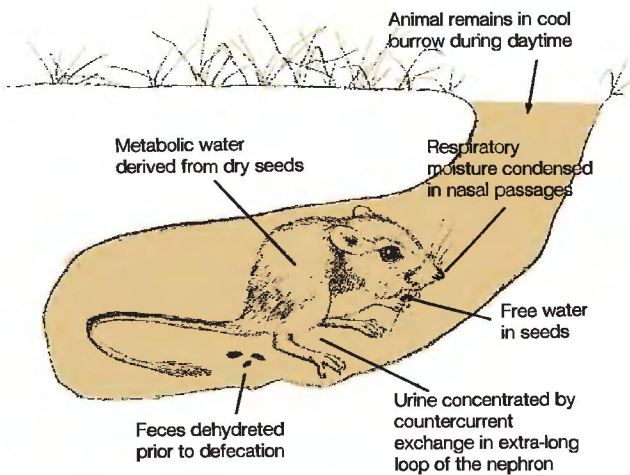


FIGURE 28.21
Kangaroo Rat (*Dipodomys ordii*), a Master of Water Conservation. Its efficient kidneys can concentrate urine 20 times that of its blood plasma. As a result, these kidneys, as well as other adaptations, prevent unnecessary water loss to the environment.

extent, birds achieve this remarkable degree of water conservation by a unique, yet simple, evolutionary adaptation: the bending of the nephron tube into a loop. By bending, the nephron can greatly increase the salt concentration in the tissue through which the loop passes and use this gradient to draw large amounts of water out of the tube.

Countercurrent Exchange

The loop of the nephron increases the efficiency of reabsorption by a countercurrent flow similar to that in the gills of fishes or in the legs of birds, but with water and ions being reabsorbed instead of oxygen or heat. Generally, the longer the loop of the nephron, the more water and ions that can be reabsorbed. It follows that desert rodents (e.g., the kangaroo rat) that form highly concentrated urine have very long nephron loops (figure 28.21). Similarly, amphibians that are closely associated with aquatic habitats have nephrons that lack a loop.

Figure 28.22 shows the countercurrent flow mechanism for concentrating urine. The process of reabsorption in the proximal convoluted tubule removes some salt (NaCl) and water from the glomerular filtrate and reduces its volume by approximately 25%.

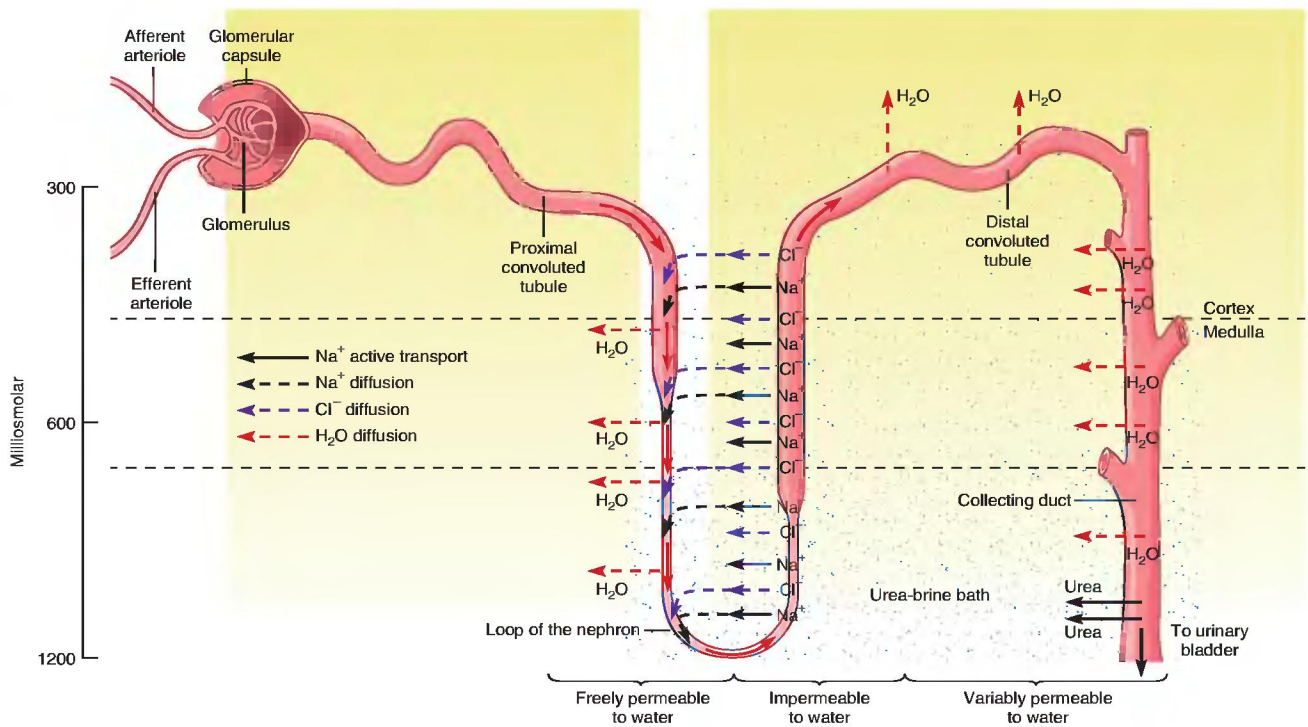


FIGURE 28.22
Countercurrent Exchange. Movement of materials in the nephron and collecting duct. Solid arrows indicate active transport; dashed arrows indicate passive transport. The shading at intervals along the tubules illustrates the relative concentration of the filtrate in milliosmoles.

472 PART THREE Form and Function: A Comparative Perspective

However, the concentrations of salt and urea are still isosmotic with the extracellular fluid.

As the filtrate moves to the descending limb of the loop of the nephron, it becomes further reduced in volume and more concentrated. Water moves out of the tubule by osmosis due to the high salt concentration (the “brine-bath”) in the extracellular fluid.

Notice in figure 28.22 that the highest urea-brine bath concentration is around the lower portion of the loop of the nephron. As the filtrate passes into the ascending limb, sodium (Na^+) ions are actively transported out of the filtrate into the extracellular fluid, with chloride (Cl^-) ions following passively. Water cannot flow out of the ascending limb because the cells of the ascending limb are impermeable to water. Thus, the salt concentration of the extracellular fluid becomes very high. The salt flows passively into the descending loop, only to move out again in the ascending loop, creating a recycling of salt through the loop and the extracellular fluid. Because the flows in the descending and ascending limbs are in opposite directions, a countercurrent gradient in salt is set up. The osmotic pressure of the extracellular brine bath is made even higher because of the abundance of urea that moves out of the collecting ducts.

Finally, the distal convoluted tubule empties into the collecting duct, which is permeable to urea, and the concentrated urea in the filtrate diffuses out into the surrounding extracellular fluid. The high urea concentration in the extracellular fluid, coupled with the high concentration of salt, forms the urea-brine bath that causes water to move out of the filtrate by osmosis as it moves down the descending limb. Finally, the many peritubular capillaries surrounding each nephron collect the water and return it to the systemic circulation.

The renal pelvis of the mammalian kidney is continuous with a tube called the **ureter** that carries urine to a storage organ called the **urinary bladder** (figure 28.23). Urine from two ureters (one from each kidney) accumulates in the urinary bladder. The urine leaves the body through a single tube, the **urethra**, which

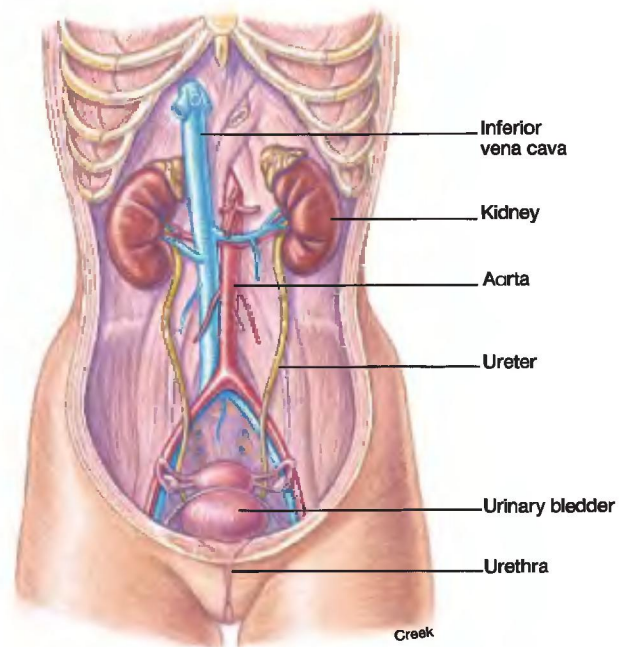


FIGURE 28.23

Component Parts of the Human Urinary System. The positions of the kidneys, ureters, urinary bladder, and urethra.

opens at the body surface at the end of the penis (in human males) or just in front of the vaginal entrance (in human females). As the urinary bladder fills with urine, tension increases in its smooth muscle walls. In response to this tension, a reflex response relaxes sphincter muscles at the entrance to the urethra. This response is called urination. The two kidneys, two ureters, urinary bladder, and urethra constitute the urinary system of mammals.

SUMMARY

1. Thermoregulation is a complex and important physiological process for maintaining heat homeostasis despite environmental changes.
2. Ectotherms generally obtain heat from the environment, whereas endotherms generate their own body heat from metabolic processes.
3. Homeotherms generally have a relatively constant core body temperature, while heterotherms have a variable body temperature.
4. The high, constant body temperature of birds and mammals also depends on insulation, panting, sweating, specific behaviors, vasoconstriction or vasodilation of peripheral blood vessels, and in some species, a rete mirabile system.
5. Thermogenesis involves mainly shivering, enzymatic activity, brown fat, and high cellular metabolism.
6. The hypothalamus is the temperature regulating center that functions as a thermostat with a fixed set point. This set point can either rise or fall during hibernation or torpor.
7. Some invertebrates have contractile vacuoles, flame-cell systems, antennal (green) glands, maxillary glands, coxal glands, nephridia, or Malpighian tubules for osmoregulation.
8. The osmoregulatory system of vertebrates governs the concentration of water and ions; the excretory system eliminates metabolic wastes, water, and ions from the body.
9. Freshwater animals tend to lose ions and take in water. To avoid hydration, freshwater fishes rarely drink much water, have impermeable body surfaces covered with mucus, excrete a dilute urine, and take up ions through their gills.
10. Marine animals tend to take in ions from the seawater and to lose water. To avoid dehydration, they frequently drink water, have