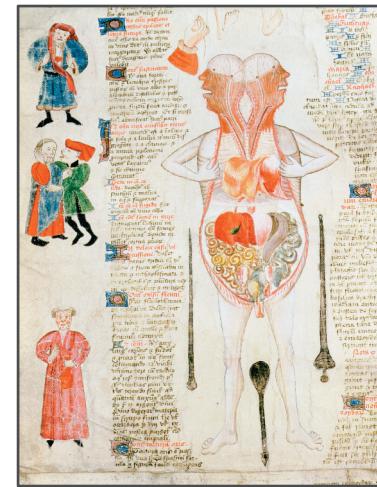


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9

This artwork by John Arderne shows the thirteenth century view of human blood flow.



How Organisms Work

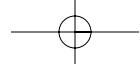
Much of ecology and evolution deals with interactions between many individuals and the properties of whole populations. However, the physiological function of individuals may be affected by the environment. Because proper physiological function also affects the survival and reproductive capacity of individuals, these functions are also subject to natural selection.

Some consequences of adaptation to different environments can be seen in the physiology or morphology of different species. For instance, plants like cacti, which live in very dry environments, have thick, round, photosynthetic structures rather than thin leaves. These types of structures help the cacti

reduce the loss of water, which is a critical stress in a desert environment.

Plants, animals, and microbes can also adapt to their environment in short periods of time. Often this type of microevolution is limited by a species' current morphology or physiology. Thus, in response to an increase in arid conditions, it is unlikely for a rose to evolve thick, waxy leaves in a dozen generations. But this type of short-term evolution is important, because many environments may change over short periods of time. In this chapter we will review how organisms adapt to stresses like desiccation, starvation, and nitrogen waste products.





CHEMICAL TRANSPORT

9.1 Whole organisms must cope with regulating solutes, gases, and water

The problems faced by whole organisms are not necessarily the same as those faced by single cells. But there are certainly areas of overlap. They include managing water and salt balance and transporting wastes and gases.

Water and Solutes The factors affecting the flow of water or solutes across cell membranes are also important for the whole organism. If there is a difference in the concentration of a substance between the inside and the outside of a cell, there will be a tendency for net diffusion in the direction of lower concentration. For whole organisms, the relative magnitude of this problem can be determined by comparing the total concentration of solutes in the organism's cells with the total concentration in the surrounding environment. Figure 9.1A shows the range of animals and environments as a function of the concentration of solutes, with land and freshwater environments having lower concentrations of solutes than do brackish (somewhat salty) water and seawater.

Marine invertebrates and elasmobranchs tend to have body fluids that are very close to seawater in their solute concentrations. Accordingly, we do not expect much flux in water and solute concentrations in these animals. Brine mosquito larvae, by contrast, find themselves in environments with very high solute concentrations relative to their body fluids. Without some type of regulation, we would expect water to be lost from the cells of mosquito larvae in these types of environments. Small organisms like fruit flies that live in the desert have great demands placed on their internal

water reserves (Figure 9.1B). We look more closely at water, gas, heat, and ion exchange in whole organisms in Modules 9.2 and 9.3.

Gas and Water Transport Most cells rely on diffusion for their uptake of oxygen and to rid themselves of carbon dioxide. For whole organisms, this process is much too slow for all but the smallest animals. Most animals rely on some sort of circulatory system to bring oxygen from the external environment to cells, which it can then enter by diffusion. There are a wide variety of circulatory systems in nature. We survey some of these systems in Module 9.6.

Plants also require nutrients and fluids. However, without muscles, plants must depend on nonmotile processes for moving fluids. Yet exceptionally large trees, like redwoods, can transport water over distances of up to 100 meters! We consider water transport in plants in Module 9.5.

Physiological Systems Evolve Different modes of blood transportation have evolved in different animal groups, as we will see in Module 9.6. By studying the different circulatory systems of invertebrates and birds, we get some appreciation for the large-scale changes brought about by evolution. But these types of changes happen slowly across many taxa. Within any population or species the types of changes in physiological systems will be much more modest. Later in this chapter, we look at how physiology may evolve within populations in response to specific environmental stress. 

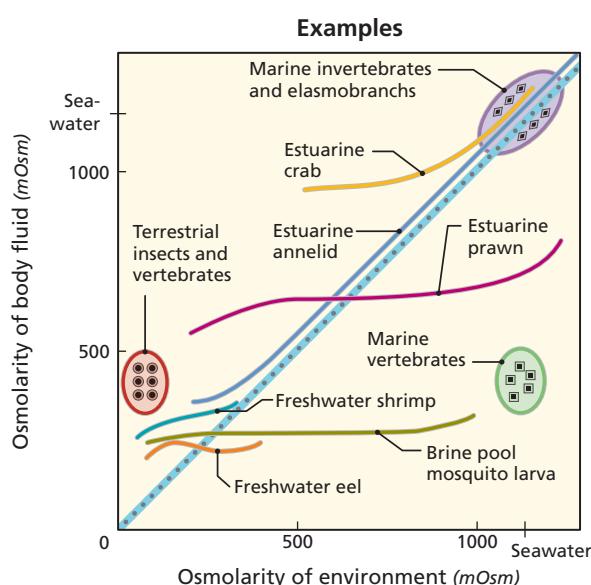
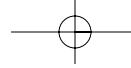


FIGURE 9.1A The relationship between environmental osmolarity and body fluid osmolarity in a variety of animals. Long lines indicate that the animal may live in a range of environmental conditions.



FIGURE 9.1B Small fruit flies live naturally in the rots or wounds in desert cacti.



Mechanisms of osmoregulation vary with environment due to distinct physical properties of air and water 9.2

Animals are mostly made of water. For proper cell function, cells add small amounts of sodium, potassium, calcium, and other ions to their water. The balance of water and ions in animal cells is affected by the outside environment. Many animals live in freshwater, seawater, or brackish (somewhat salty) water. These animals have net flows of water and ions into or out of their cells depending on the concentration of ions in their tissues and in the surrounding water. Terrestrial animals are in direct contact with gaseous air, so they lose water primarily through exposed tissues.

The **osmotic concentration** of a fluid depends on the concentration of all solutes, which include ions and nutrients. Seawater typically has 35 grams of salts per liter of water. Organisms with salt concentrations that are higher than the surrounding environment are called **hyperosmotic**. Their cells experience an influx of water and an outflow of ions. Cells with a lower osmotic concentration than the outside environment are **hypoisomotic**. These cells experience an inflow of ions and an outflow of water.

Aquatic animals have two options. They may keep the osmotic concentration of their cells equal to the environment; that is, they can be **osmoconformers**. Or, they may keep the osmotic concentration of their cells different from the environment; that is, they can **osmoregulate**.

Many marine organisms are osmoconformers, although some fish and marine mammals are hypoisomotic. However, many osmoconformers have specific ions that are either more or less concentrated than in the surrounding water. These ion concentrations are actively regulated by the animal cells. Ocean salinity is relatively constant. Not surprisingly, many marine organisms cannot survive large changes in salinity. Such organisms are called **stenohaline**. Some marine organisms, including small crustaceans, live in high-tide pools that undergo large salinity increases as water evaporates in the summer heat and large salinity decreases when pools fill up with rainwater. Organisms in these environments are usually adapted to withstand large salinity changes and are called **euryhaline**.

Skin and gill surfaces are important for the ion and water regulation of aquatic animals (Figure 9.2A). Hyperosmotic organisms such as fish and invertebrates show active uptake of ions at their gills. In worms and amphibians, the skin is used for osmoregulation. Marine teleost fish are hypoisomotic to their environment. They use their gills to remove ions from their cells. This action occurs at sites in the gills called *chloride cells*, where Na^+ and Cl^- ions are exported. Other animals—like birds and reptiles—that live in marine environments do not have gills but use salt glands to excrete excess ions. Marine mammals can produce urine that is more concentrated than their blood. These animals can rid their bodies of excess ions through their urine.

Because the respiratory structures of land animals are moist, they are important sites of water loss (Figure 9.2B).

Most water intake for terrestrial animals comes from drinking and eating. Some foods produce water as a by-product when metabolized, although this is not a major source of water for most animals. For instance, for every gram of lipid metabolized, about 1.07 grams of water is produced. The water in exhaled air is recovered by some animals by cooling the air prior to exhalation. This recovery is

achieved using the countercurrent circulatory systems that we review in Module 9.3. Cooled air holds less water, so some condensation and water recovery can be achieved by this process.

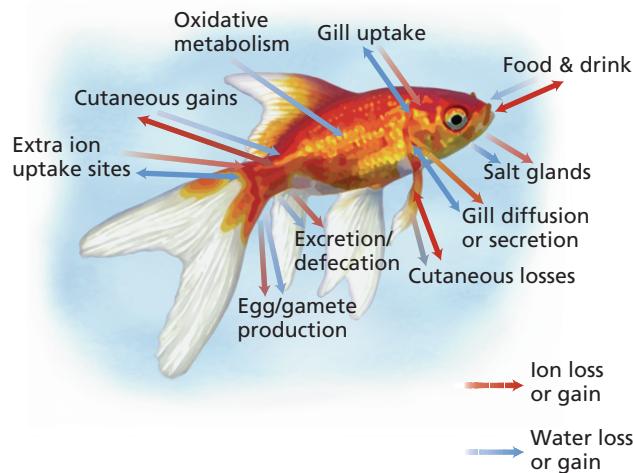


FIGURE 9.2A Water and Ion Loss in Aquatic Animals

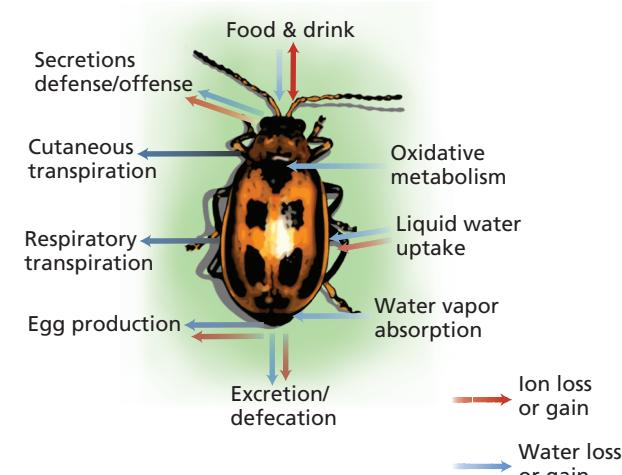
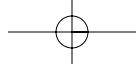


FIGURE 9.2B Water and Ion Loss for Terrestrial Animals



9.3 Countercurrent exchange is used to control gas, heat, and ion flux

Many important physiological processes require the diffusion of ions or molecules in and out of the organism or from one tissue to another. The processes include extracting oxygen from air or water, extracting or eliminating ions between the environment and the organism, and concentrating and eliminating waste products in urine. Many animals employ a common solution to these problems; it is called countercurrent exchange. **Countercurrent exchanges** involve the flow of two liquids, or a liquid and a gas, in opposite directions. Concentration gradients between the two substances cause molecules or heat to move more efficiently between the two flows than would be the case if the flows moved in the same direction.

For instance, in Figure 9.3A we see two flows in opposite directions. The top flow, which moves from right to left, initially has a low concentration of a solute or a low temperature. The bottom flow, moving in the opposite direction, is a source of the solute or heat source and has a very high concentration of the solute or high temperature when it first enters the system, on the left. Because of this difference in concentration or temperature between the two flows, the solute or thermal energy moves from the bottom flow to the top flow. This move-

ment lowers the concentration of the solute in the bottom flow. As this flow moves from left to right, it continues to encounter lower and lower concentrations of the solute in the top flow. This gradient permits the continued movement of the solute from the bottom flow to the top flow. This countercurrent exchange permits the solute in the top flow to reach a much higher concentration than if the two flows had been moving in the same direction.

Fish gills work on the principle of countercurrent exchange (Figure 9.3B). Unoxygenated blood from the heart is pumped into the gills, where a large surface area of capillaries facilitates the diffusion of oxygen from water into the bloodstream. The fish also move water through their gills in a direction that is opposite the flow of blood. The principles of countercurrent exchange are also used in the kidneys of many animals for removing and recovering valuable ions from urine.

Another application of countercurrent flows is heat exchange in tuna. Most extremities of the tuna are at ambient temperatures. However, by using a countercurrent flow of blood to and from their muscles (Figure 9.3C), tuna can keep their muscles at a temperature that is well above ambient. This

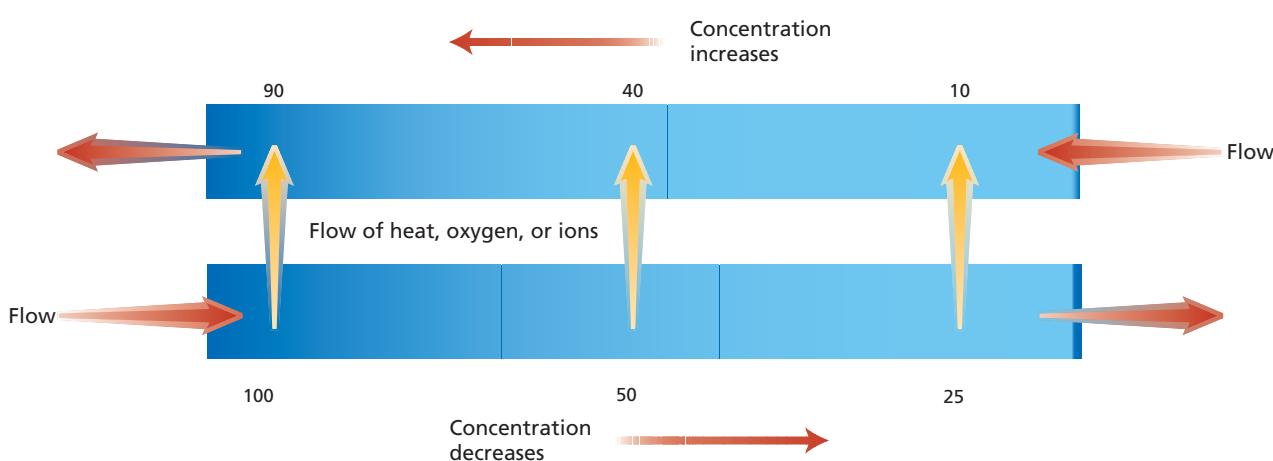


FIGURE 9.3A Countercurrent Exchangers

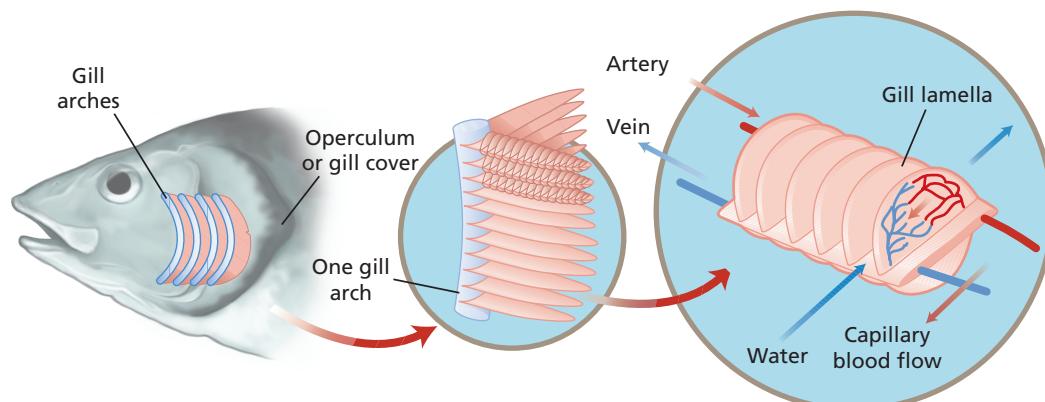
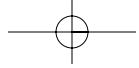


FIGURE 9.3B Oxygen Exchange in the Fish Gill



warmth permits tuna to swim faster and longer than can equivalently sized fish without heat exchangers. The activity of the tuna's swimming muscles produces metabolic heat that warms up the venous blood. As this blood flows away from the muscles, cool arterial blood moving in the opposite direction and in close proximity to the venous blood is warmed prior to reaching the muscles. The heat generated by these muscles can be substantial. Tuna fishermen who have worked especially hard to land a tuna notice that the fish can become overheated and "burnt." The meat of these "burnt tuna" is less valuable as a result.

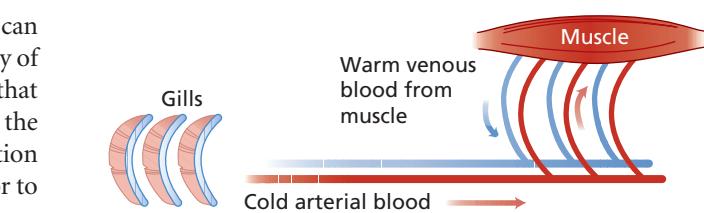
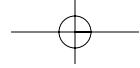


FIGURE 9.3C Heat Exchanger in Tuna





9.4 The uptake of oxygen by animals is accomplished by gills, lungs, and occasionally skin

The most efficient means of extracting energy from glucose is by complete oxidation in the Krebs cycle. This process requires that oxygen be delivered to cells constantly as it is consumed and that the waste product of respiration, carbon dioxide, be removed. Oxygen is abundant in the atmosphere, making up about 21 percent of our air. It is reasonable to ask why animals cannot simply let oxygen diffuse from the air into their cells.

The answer is that diffusion is a slow process. Even with the high levels of oxygen in the Earth's atmosphere, diffusion would not deliver enough oxygen for organisms much larger than 2 millimeters (mm) in diameter. As a result, most organisms have organs for extracting oxygen from the atmosphere and then some kind of circulatory system for delivering this oxygen to cells.

In most aquatic animals the extraction of oxygen is done by the **gills**, which are skin surfaces turned outward (Figure 9.4A). These gills may appear as *tufts* similar to those found in marine tube worms or as modifications of tube feet used by echinoderms. *Filamentous* gills have elaborate circulation. They are found on aquatic arthropods and in some salamanders and tadpoles. *Lamellar* gills are arranged as a series of flat plates that can be oriented toward the flow of water to generate countercurrent flows. These gills are found in fish and some crustaceans.

If water simply stands next to the gill surfaces, the available oxygen will be depleted locally, and the animal will find itself in low-oxygen or **hypoxic** conditions. To avoid this problem,

the water must be continually moved to bring fresh water with high levels of oxygen into contact with the gill surfaces. Many fish accomplish this through movement (Figure 9.4B). The fish opens and closes its mouth and operculum (the covering of the gills) to create water flow past the gills. The fish first opens its mouth, letting in fresh water, while closing its operculum to prevent water from leaking out. The fish then closes its mouth and reduces the volume of the mouth cavity, while simultaneously opening the operculum. Water then flows over the gills in a single direction, creating the countercurrent flow of water and blood. Certain other fish, such as tuna, can create water flow only by swimming with their mouths open. This technique is called **ram ventilation**. As the fish swim faster, their increased need for oxygen is matched by increased water flow over their gills.

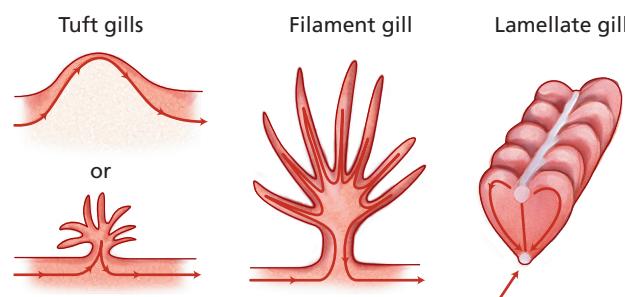


FIGURE 9.4A Different Types of Gills

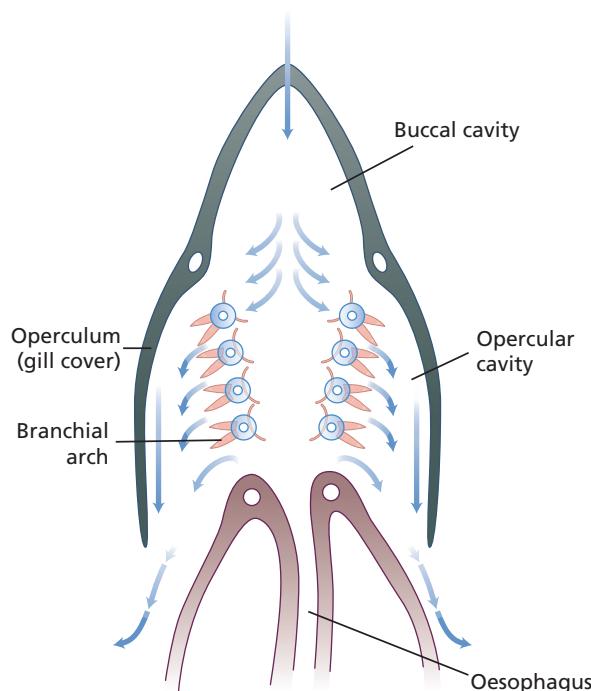
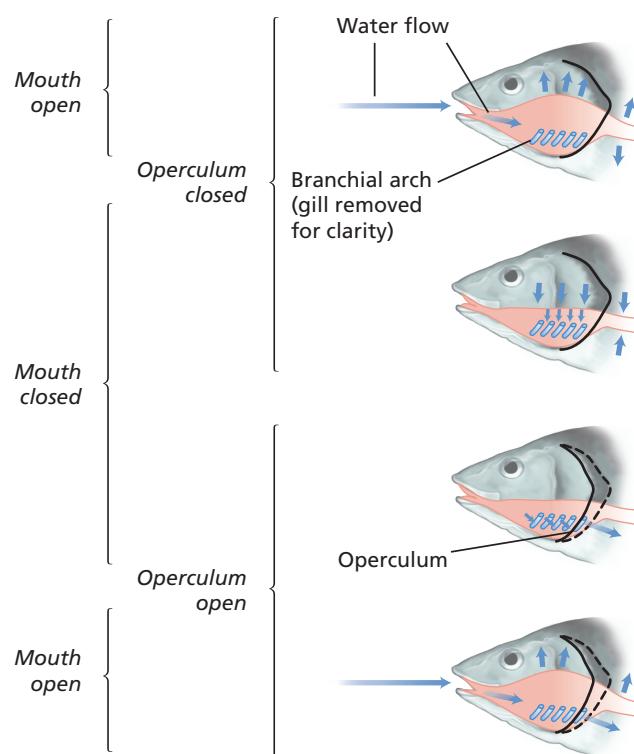


FIGURE 9.4B Ventilation of a Typical Fish Gill



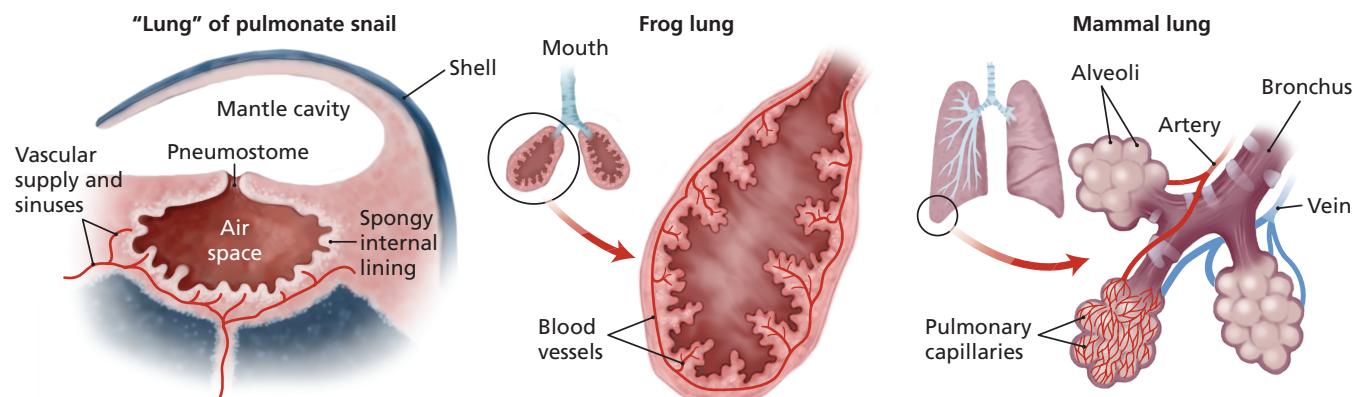


FIGURE 9.4C The Lungs of Several Terrestrial Animals

Terrestrial animals typically use lungs to extract oxygen from the air. A **lung** is an invagination of skin to form a respiratory surface (Figure 9.4C). Lungs are most often found in terrestrial animals, although marine sea cucumbers also have lungs. The morphology of lungs can be simple, like those found in land snails. Snail lungs have a simple invagination with some convoluted skin surface to increase the exposed surface area to air. This basic design is more elaborate in frogs and becomes quite complicated in mammals, where small branched alveoli structures create a large surface area for the exchange of oxygen and carbon dioxide. As mentioned earlier, diffusion occurs only over small spatial scales. In the lung the exchange of gases occurs by diffusion through the moist surfaces of thin membranes. In humans, the total surface area of the lungs is 100 m^2 , about the size of a tennis court.

For lungs to provide a continuous supply of oxygen, fresh air must continuously replace old air. The bird lung is particularly efficient in this regard. The mechanism of air flow in the bird lung is shown in Figure 9.4D. The anterior and posterior sacs act like the bellows of a blacksmith requiring two inhalations and two exhalations. In the first breath, air is pulled down the mesobronchus into the caudal air sacs. In the first exhalation, the air is forced out of these sacs, primarily into the actual lung, through the parabronchi (in one direction). The air in the lung is pulled into the cranial air sacs upon the second inhalation, and at the second exhalation, it is forced from this second set of air sacs out of the body. The directional flow of air out of the lungs permits birds to have capillaries running countercurrent to the flow of air, achieving efficiencies that other vertebrates cannot. This countercurrent configuration permits the bird lung to be somewhat smaller and lighter, which in turn facilitates flight.

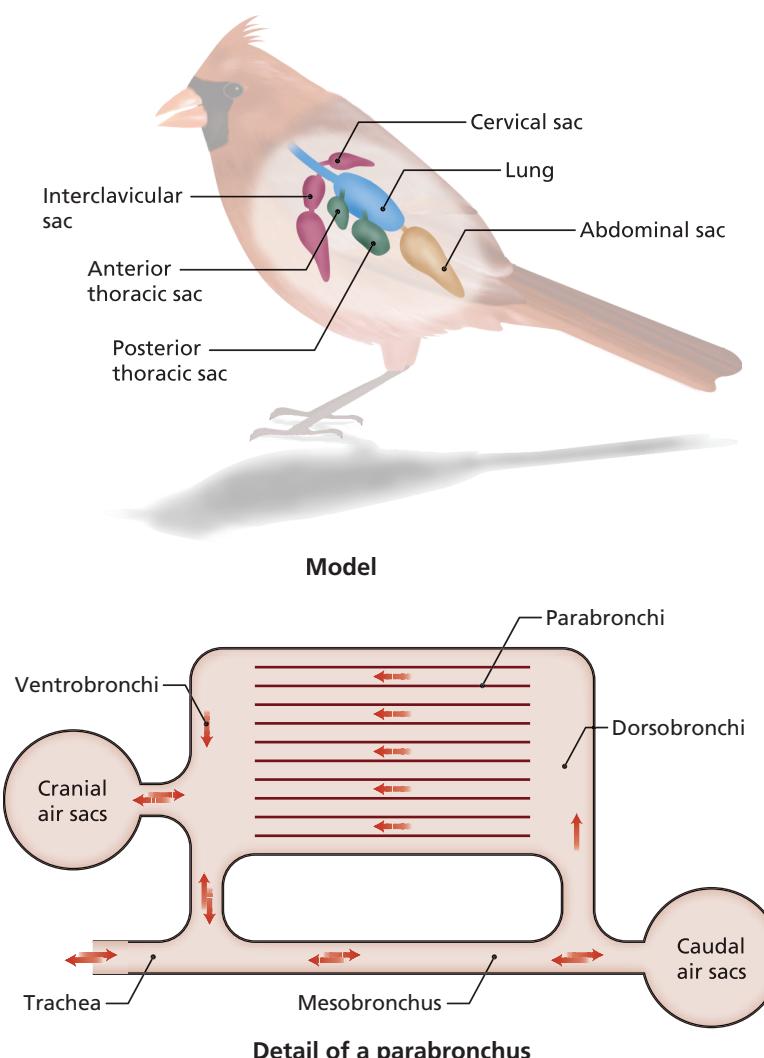
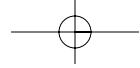


FIGURE 9.4D The Operation of a Bird Lung The cranial air sacs include the anterior thoracic, cervical, and the interclavicular sacs, while the caudal air sacs include the posterior thoracic and abdominal air sacs.



9.5 Transport of water in plants occurs via transpiration and the physical properties of water

One of the biggest problems facing plants is the management of water. This problem includes the reduction of water loss and the transport of water from the roots to the rest of the plant.

About 90 to 95 percent of a plant's water loss occurs through its leaves. As we saw in Module 8.5, leaves must have a large amount of exposed surface area to effectively capture light energy. This surface area is a potential site for water loss. Many plants layer their leaves with hydrophobic waxes that make excellent water barriers. Yet plants must also capture carbon dioxide (CO_2) from the atmosphere to fuel photosynthesis. They do this by allowing air to pass through openings in the leaf called **stomata**. These small pores also permit water vapor to escape. The diffusion of water vapor through the stomatal pores is called **stomatal transpiration**.

Stomates are very effective at gas diffusion (Figure 9.5A). Typically the amount of gas that can diffuse through a circu-

lar opening is proportional to its area. However, for very small openings, the relative diffusion efficiency increases (Figure 9.5A). The reason for this greater efficiency is that the amount of gas passing through an opening is constrained by the size of the opening; but once the gas is through, it can bend around the edges, creating an increased rate of flow. For a circular opening with a radius of r , the area is πr^2 while its circumference (edge) is $2\pi r$. Thus, if the radius is cut in half, the area is reduced by three-fourths; but the edge is reduced by only one-half. This means that several small openings will permit more gas flow than will one large opening of the same area. The efficiency of CO_2 gain also means water vapor is lost quickly.

Although stomates close to conserve water when carbon dioxide intake is not needed, or when the plant is severely stressed, the plant must still have some means of transporting

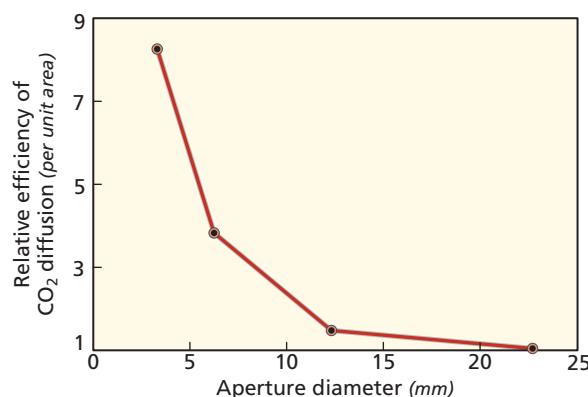
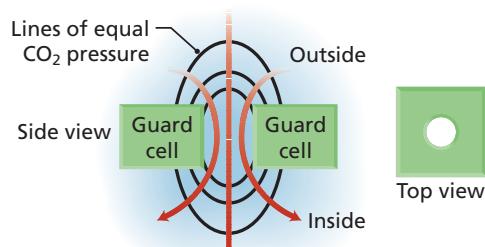


FIGURE 9.5A CO_2 Gain and Water Loss through Stomates

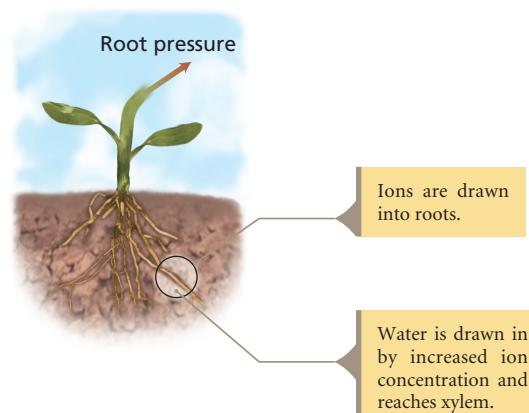
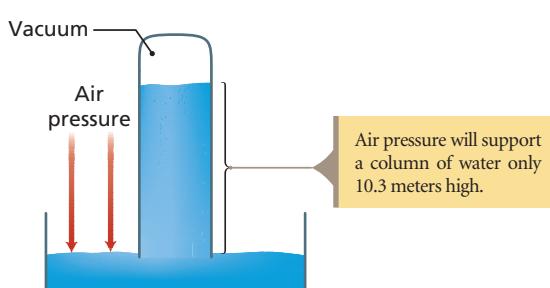


FIGURE 9.5B Air and root pressure cannot account for water movement in the tallest trees.

water to its leaves (Figure 9.5B). For redwoods and Douglas fir trees, water collected at the roots must travel over 100 meters to reach the top of the tree! If a vacuum could be created in the water vascular system of plants, called the **xylem**, then air pressure alone might push the water to a height of about 10.3 m at sea level. Air pressure alone cannot push water higher than this.

There is also a pressure created at the roots of some plants. As plants collect ions in the roots, the concentration difference between the plant cells and the soil can draw water into the cells, creating a positive pressure in the xylem. This pressure can be measured in some plants, but at best could account for about 16 percent of the pressure needed to move water up the tallest trees. In any case, positive root pressures are not always present, so they cannot be a general explanation for water movement in plants.

The best explanation for water movement in plants involves **cohesion**, the tendency of water molecules to stick together. This explanation begins with water being lost from the leaves by transpiration. The loss of water through the stomates creates a negative pressure that begins to pull on the water column in the xylem. Two forces are crucial for transmitting this pull all the way to the roots of the plants. The first is the cohesive forces holding water molecules together. These forces arise from the polar nature of water molecules and the hydrogen bonds that form between neighboring molecules. The second force is an adhesive force between water and the lining of the xylem. This lining is hydrophilic and also forms hydrogen bonds between water and the walls of the xylem cells. The result is an effective transmission of the negative pressure created by transpiration down the entire water column.

How exactly does the loss of water through the stomates create a pull in the first place? Water that is exposed to air loses some molecules that have sufficient energy to leave the liquid phase and become gaseous (Figure 9.5C). Gaseous water may also condense and return to the liquid phase. Dry air in contact with water takes some time to reach an equilibrium in which

the number of molecules leaving the liquid phase equals the number entering it (Figure 9.5C). When this equilibration has occurred, so that condensation equals evaporation, the force exerted by the gaseous water creates **vapor pressure**. In the space inside the leaf just beyond the stomates, there is a great deal of exposed water that is subject to vapor pressure. The rate of transpiration depends on the difference between the vapor pressure in the stomatal spaces and the vapor pressure in the air just outside the stomates (Figure 9.5D).

Under still conditions a thin layer of air called a **boundary layer** can develop, just outside of the stomates, that has a higher vapor pressure than the surrounding air. This boundary layer can reduce the loss of water from the stomates. However, strong winds can increase water loss by removing the boundary layer. Some plants have hairlike structures, called **trichomes** (Figure 9.5D), around the stomates to foster the creation of the boundary layer and thus reduce water loss.

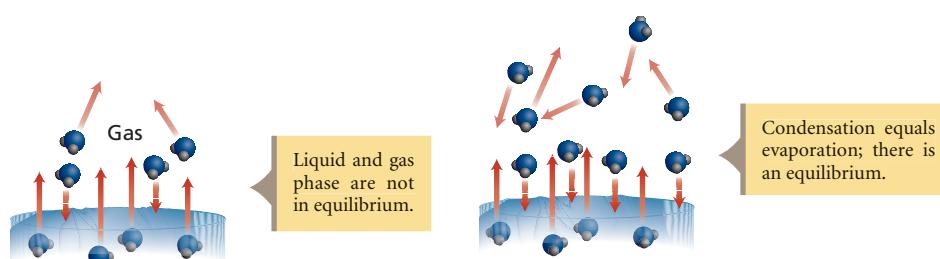


FIGURE 9.5C Vapor pressure is the force exerted by a gas in equilibrium with its liquid phase.

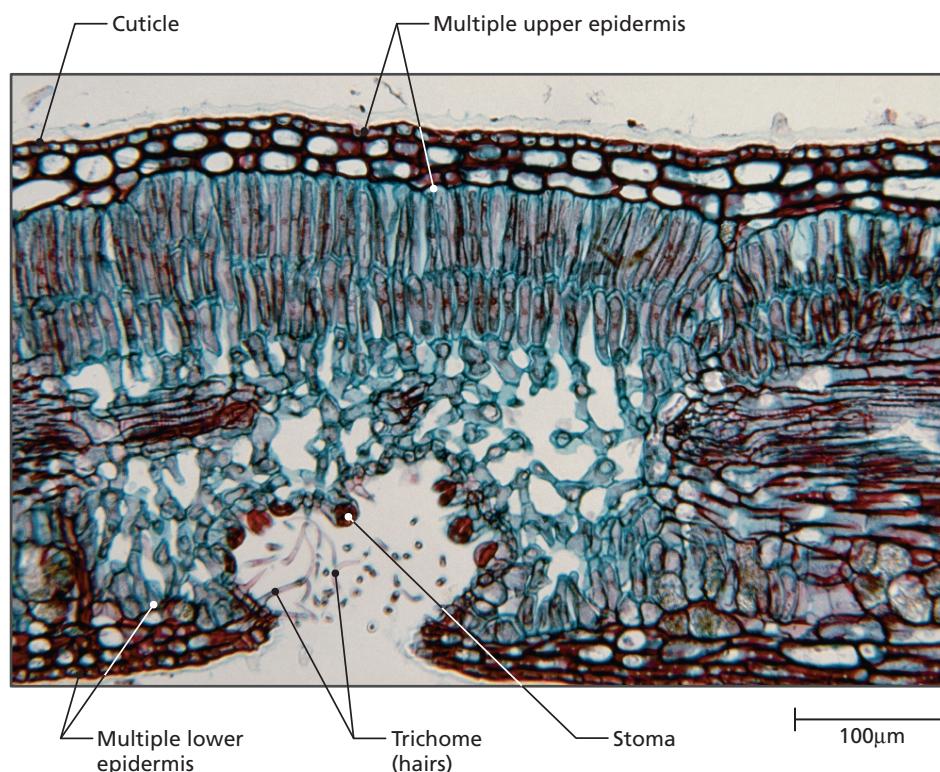
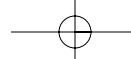


FIGURE 9.5D Leaf Structure



9.6 Animals transport fluids using specialized circulatory systems

Circulating fluids in animals supply metabolites and remove wastes. They carry nutrients and oxygen to tissues, and they remove carbon dioxide and other waste products. This circulation is accomplished by either of two designs: open or closed circulation.

In some **open circulatory systems** there are no specialized vessels for transporting fluids. Transport is accomplished by movement of the body wall. In other open systems, like those found in molluscs and crustaceans (Figure 9.6A), specialized vessels transport fluids through part of the organism; the vessels then open up into a body cavity. These open systems may include hearts and vessels with valves to prevent the backflow of fluid.

Closed circulatory systems do not open directly into body cavities, and the provisioning of nutrients and gases occurs across the thin walls of the smallest circulatory vessels, the **capillaries**. In closed circulatory systems, the fluid is usually called **blood**. Closed circulation permits stable blood composition.

For large, active animals, circulation requires a pump. It may be as simple as a thickened section of one of the principal vessels that conduct fluids. Pumps with nervous system synchronization and internal valves that ensure one-way flow are referred to as **hearts**. Both open and closed circulatory systems may include hearts.

The flow of blood through the major organs differs in invertebrates and vertebrates.

The flow of blood through the major organs differs in invertebrates and vertebrates, as Figure 9.6B shows. Invertebrates have one-way blood flow. After

leaving the body tissues, the blood goes to the gills, then to the heart, and finally back to the tissues. In vertebrates, blood leaving the tissues goes first to the heart. In vertebrates with one-way blood flow, like fish, the blood leaving the heart then goes to the gills, receives oxygen, and finally passes directly to the tissues. Other vertebrates have a dual circuit of blood flow. The **pulmonary circuit** carries deoxygenated blood, under low blood pressure, to the lungs for gas exchange and then returns oxygenated blood to the heart. The **systemic circuit** carries oxygenated blood, under

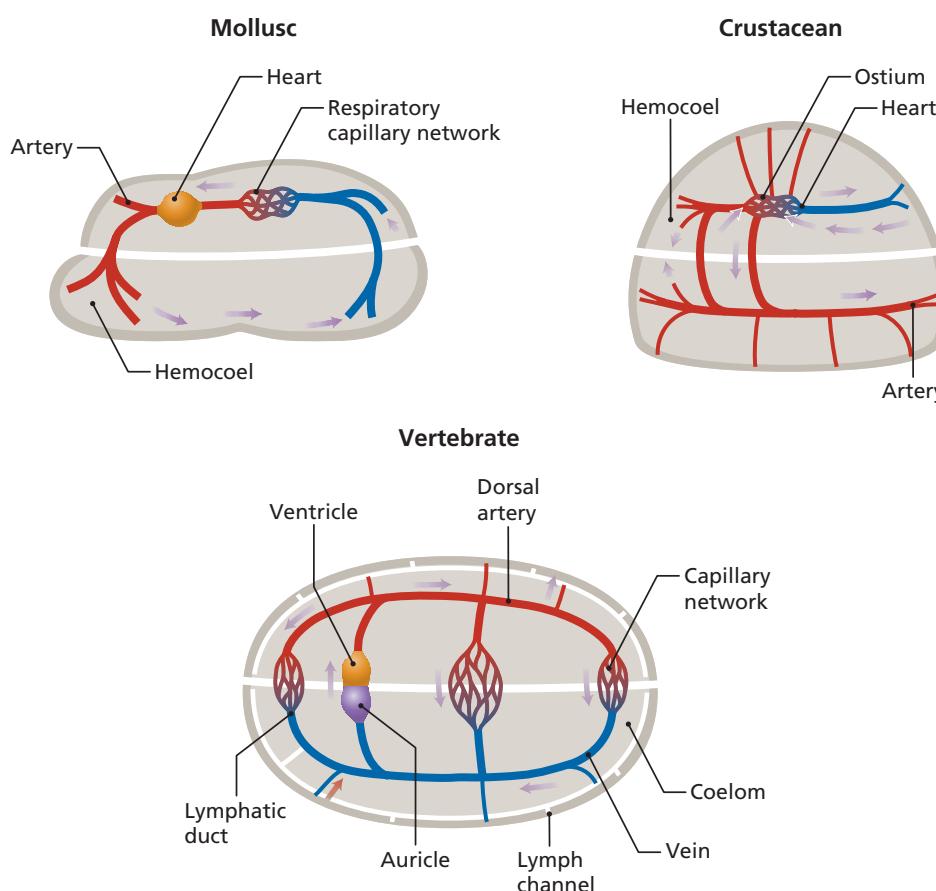
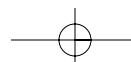
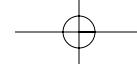


FIGURE 9.6A Open and Closed Circulatory Systems





high blood pressure, to all body tissues for gas exchange and then returns deoxygenated blood to the heart. In mammals about 50% of the blood volume will be found in the veins, 21%–25% in the arteries and capillaries, with the remainder in the heart and pulmonary circulation.

Besides the heart, the blood vessels affect the flow of blood. Figure 9.6C shows how the velocity, pressure, and volume of blood changes as it circulates through the body of a mammal. For instance, the **aorta**, the artery leaving the heart, contains the highest blood pressure. The aorta is connected to numerous arteries. These arteries have thick, muscular walls that prevent them from collapsing as they twist through the body. The narrower arteries are called **arterioles**. They can respond to a variety of stimuli to expand or contract; these processes are called **vasodilation** and **vasoconstriction** respectively. This responsiveness gives arterioles a key role in regulating blood pressure. The capillaries cover a large surface area in the organism (Figure 9.6C). There are more **venules** (small veins) and veins in the body

than arteries, and these veins and venules have the capacity to hold large volumes of blood. The walls of veins are elastic, allowing them to expand as blood volume increases. The veins and venules also have valves to prevent the backward flow of blood, which can occur because the pressure in veins is very low.

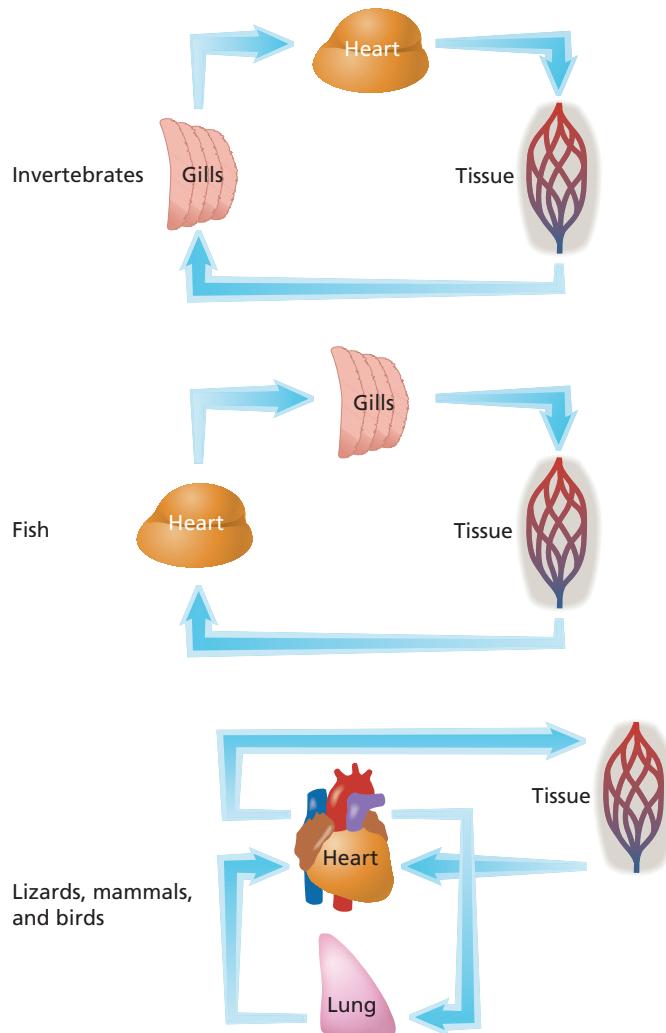


FIGURE 9.6B Comparative Circuitry

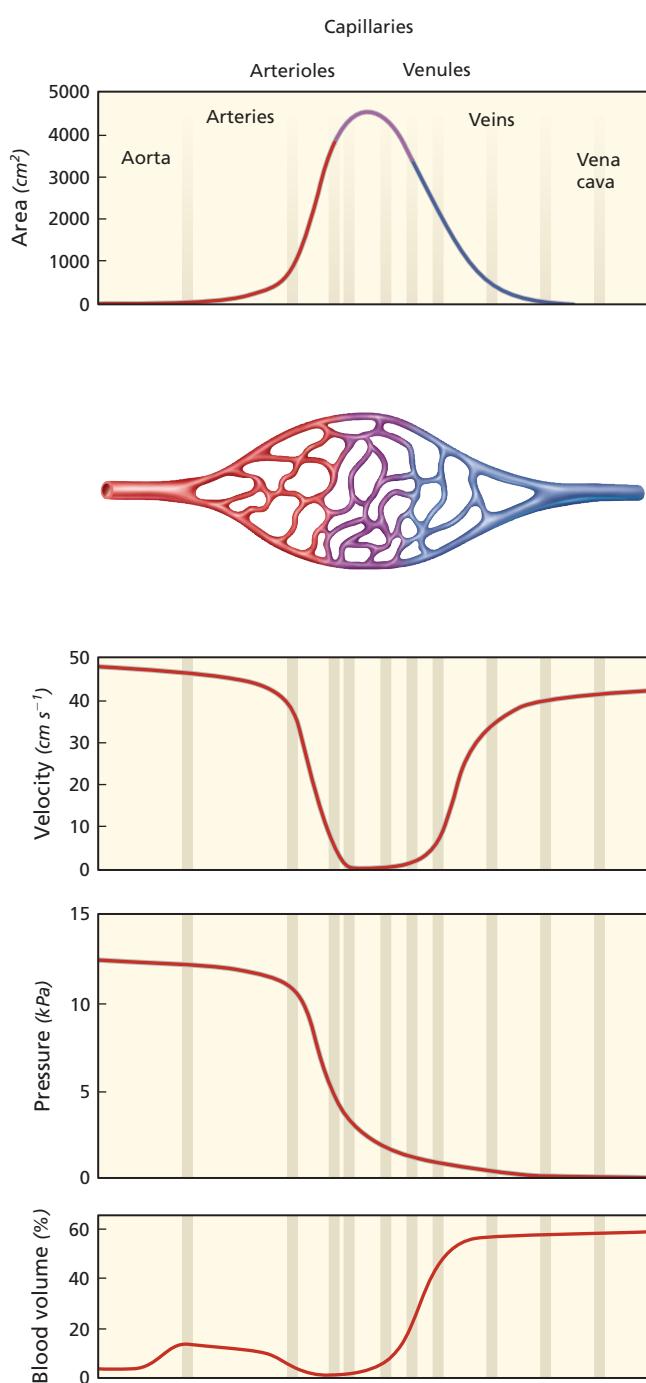
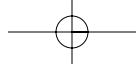


FIGURE 9.6C The panels follow three properties of blood in the body of mammals: blood velocity, blood pressure, and blood volume (as a percent of the total).



EVOLUTION OF PHYSIOLOGICAL SYSTEMS

9.7 Desiccation is a major problem for terrestrial life

The exchange of gases in terrestrial plants and animals typically requires contact between air and moist tissue. This contact inevitably leads to water loss through evaporation. Animals that are covered by moist skin will also lose significant amounts of water through their skin. Many terrestrial climates become hot and dry for at least some periods of time, thereby exposing animals and plants to drying conditions.

There are three basic ways to cope with desiccation at the organismal level:

1. The plant or animal may reduce the rate of water loss.
2. The organism can maintain greater amounts of water in its body. This water can either be bulk water, or it can be stored using special storage compounds like glycogen.
3. The organism can develop the ability to tolerate the loss of water.

each generation, the experimental flies experience a prolonged exposure to a desiccating environment; the controls do not.

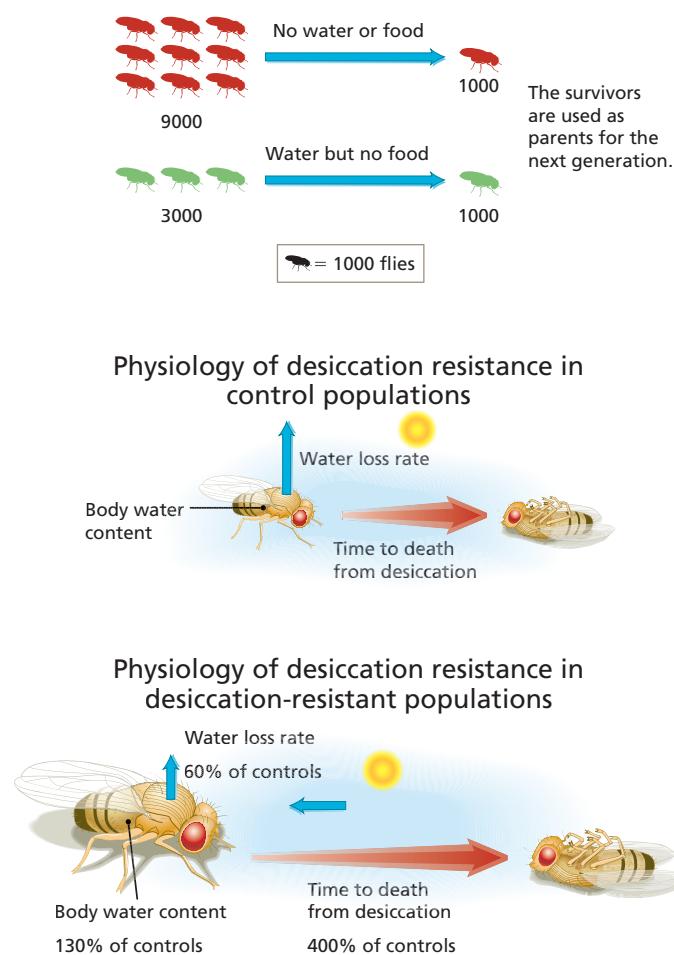
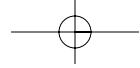


FIGURE 9.7A Laboratory Evolution of Desiccation Resistance

All three of these strategies for coping with water loss are employed by some plants or animals to different degrees. We will examine these in a little more detail by illustrating how evolution alters the physiology of fruit flies that have been selected to survive extended periods of water stress (Figure 9.7A). Biologist Michael Rose and his colleagues developed experimental populations of *Drosophila* by keeping adults in large cages without food or water for a period of about 20–60 hours. A population might start with 9,000 adults, and by the end of the desiccation period there would be only about 1,000 survivors. Control populations were derived from the same starting populations and maintained in the same fashion, except that during the period of desiccation these flies received water but no food. The absence of food would kill about two-thirds of the control population (Figure 9.7A); but these deaths were primarily due to starvation, not desiccation. This selection procedure was repeated for more than 100 generations.

After many generations of selection, the flies selected for desiccation resistance became markedly better at surviving periods of desiccation (Figure 9.7A). These same flies also lose water at about half the rate of the control flies. How did they differ from the control flies? The investigators examined the flies' **cuticle**, or outer covering, which has layers of chitin and protein that are relatively impermeable to water. (Cuticles are more effective water barriers than skin is.) The outer layer of the cuticle is called an **epicuticle**, and it has high levels of lipids that act as effective water barriers. It appears that the exoskeletal cuticle of the desiccation-resistant flies has a greater proportion of long-chain hydrocarbons, although the total amount of hydrocarbon is about the same. These long-chain lipids have higher melting points and are better barriers to water. The changes seen in the chain length of lipids in the *Drosophila* populations are also seen in different insect species. Species that are active in the summer have longer-chain hydrocarbons than do similar species that are active in the winter.

Were other differences found between the desiccation-resistant flies and the control flies? The desiccation-resistant flies also have a greater amount of bulk water per individual than do the control flies. There appears to be no difference in the dehydration tolerance of the two types of flies. When these flies die, they all have roughly the same amount of water as a percentage of their total size. Dehydration tolerance does differ



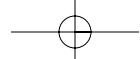
between species. For instance, earthworms, slugs, and snails can tolerate large (40–80 percent) water loss before dying. Most mammals can only tolerate losses of between 5 and 10 percent of their body water. Camels, which can tolerate losing 30 percent of their water, are an interesting exception.

Animals may reduce their water loss in several other ways. Behavior can be important. Many animals are inactive during very hot periods, to avoid water loss. Other an-

imals seek moist conditions under rocks or leaves, where they are surrounded by water-saturated air. Large animals may also reduce water loss by reabsorbing water in their kidneys before they excrete nitrogen wastes. The ability to excrete concentrated urine varies greatly among animal species, although some desert-adapted mammals can excrete urine that is more concentrated than seawater (Figure 9.7B). 



FIGURE 9.7B The Kangaroo Rat Kangaroo rats live in desert habitats and get all their water from their foods, either as bulk water or as a by-product of the metabolism of their food.



9.8 The ability to tolerate nitrogen wastes is molded by natural selection

When animals use proteins and amino acids for energy, they ultimately produce small nitrogen molecules, like ammonia, that are toxic in large concentrations. Consequently, animals have well-developed physiological mechanisms for eliminating nitrogen. Most but not all animals eliminate nitrogen either as ammonia, urea, or uric acid (Table 9.8A). Animals that eliminate ammonia directly are almost always aquatic or live in environments where they are in intimate contact with water. This lifestyle facilitates removal of ammonia, which is very soluble in water. Animals that cannot get rid of ammonia rapidly must convert it to a less-toxic compound, like urea or uric acid, to prevent cell damage. Some animals possess the ability to produce more than one type of nitrogen waste product. Spiders and scorpions excrete guanine. The method of nitrogen excretion also depends on embryonic conditions. In those animals with eggs that are sealed from the environment, a less toxic waste product is required.

The levels of internal or external nitrogen waste products may become high, requiring organisms to develop adaptations to these conditions. For instance, fruit-fly larvae excrete ammonia directly into their larval food environment (Figure 9.8A). In very crowded cultures, the levels of ammonia may become high and contribute to the stress of crowding. Can organisms, like fruit flies, adapt to high levels of nitrogen wastes? To study this problem, Laurence Mueller

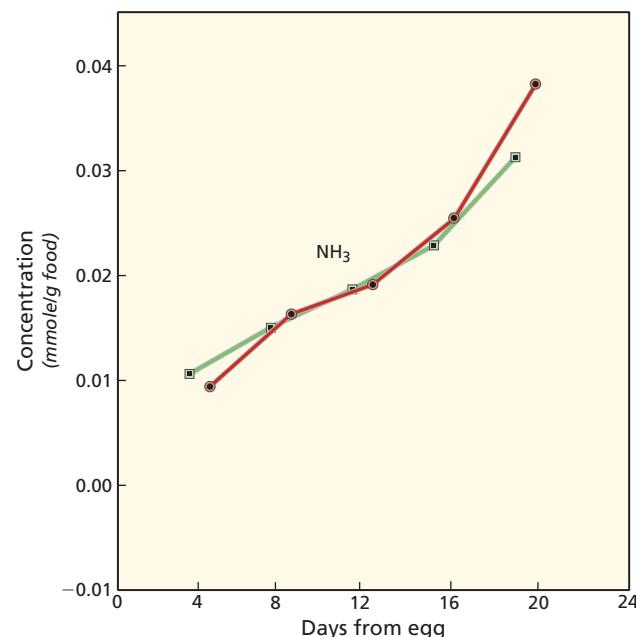
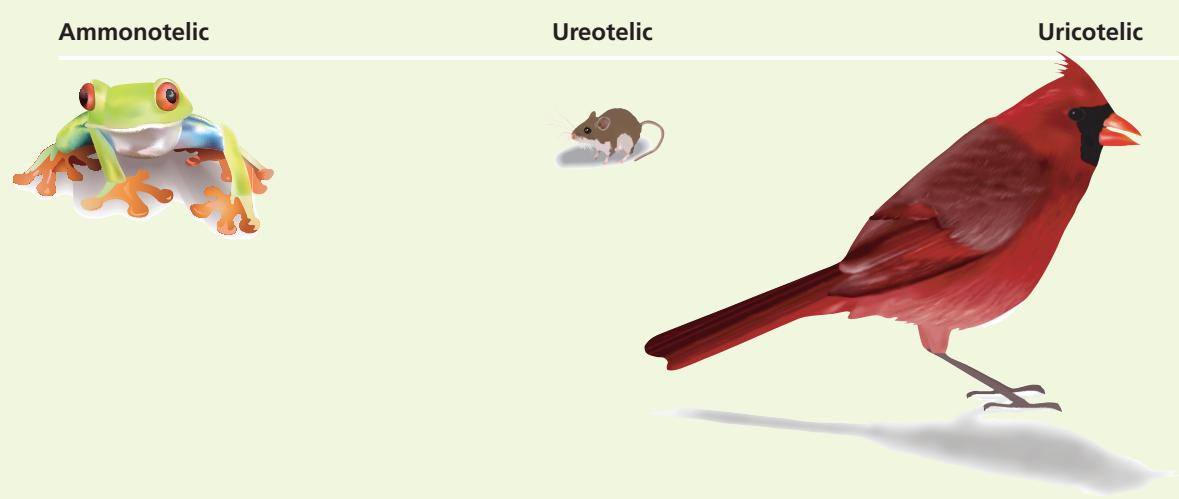


FIGURE 9.8A In crowded cultures of fruit flies, the levels of ammonia increase dramatically due to ammonia excretion by the larvae. The two lines represent two different populations.

TABLE 9.8A Different Routes of Nitrogen Elimination

Mode	Major End Product	Representative Animal Groups
Ammonotelism	NH ₃ , NH ₄ ⁺	Freshwater and marine invertebrates, teleost fish, aquatic amphibians, isopods, <i>Drosophila</i> larvae
Ureotelism	Urea	Adult amphibians, mammals
Uricotelism	Uric acid	Terrestrial gastropods, terrestrial insects, lizards, snakes, birds



and colleagues created multiple populations of fruit flies that either were raised as larvae on high concentrations of ammonia or were raised as controls, in low-ammonia conditions. Over time the populations of fruit flies raised on ammonia were dominated by genotypes that showed elevated resistance to ammonia, relative to controls. This adaptation was easily determined by raising both the ammonia-resistant and control populations on food with high levels of ammonia added directly to the food (Figure 9.8B). The survival from egg to adult in the ammonia-resistant population was about 35 percent greater than that of the control population (Figure 9.8B).

What are the ammonia-resistant populations doing that permits them to withstand such high levels of ammonia? Fruit flies, as well as many other organisms, may convert ammonia to a less-toxic compound, glutamate, by the following reaction: $\text{NH}_4^+ + \text{H}^+ + \text{NADH} + \alpha\text{-ketoglutarate} \leftrightarrow \text{glutamate} + \text{NAD} + \text{H}_2\text{O}$. This reaction is catalyzed by an enzyme called glutamate dehydrogenase. The ammonia-resistant lines make 40 percent more of this enzyme, even when they are raised on normal food. This suggests that ammonia resistance may in part come about by the rapid conversion of ammonia to a less-toxic compound.



Another surprising consequence of ammonia resistance is that resistant larvae feed more slowly and are less vigorous foragers (Figure 9.8C). It is hard to imagine that this behavior could help these larvae survive better. In all likelihood this change in behavior does not directly help develop ammonia resistance, but reflects a trade-off. That is, to marshal sufficient energy to detoxify ammonia, these larvae may have to draw energy from other activities—like their foraging behavior.

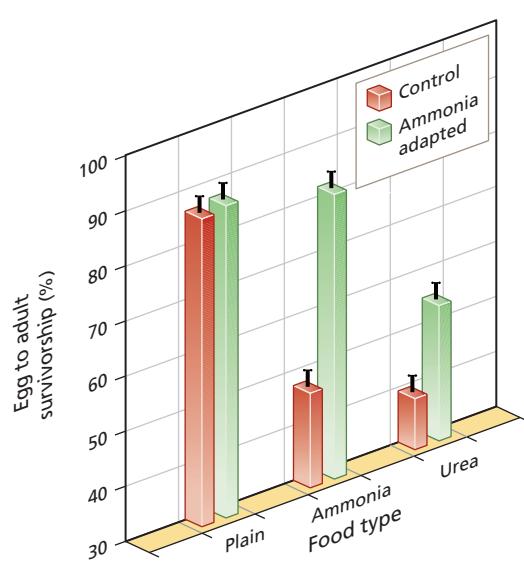


FIGURE 9.8B Populations selected for resistance to ammonia show elevated levels of survival in food laced with ammonia compared with control populations. Interestingly, the ammonia-adapted populations also show increased resistance to the novel compound, urea.

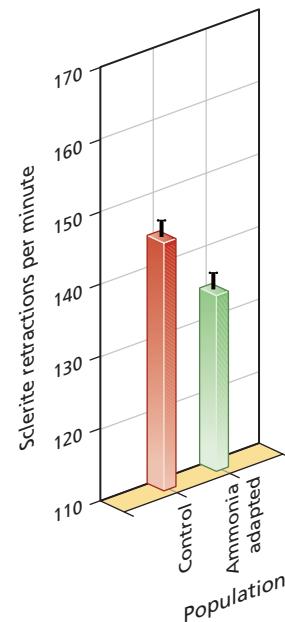
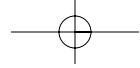


FIGURE 9.8C The ammonia-resistant populations show reduced feeding rates relative to their controls. This may be due to trade-offs in energy requirements for feeding and detoxifying ammonia.



9.9 Fat is beautiful when episodes of starvation are a predictable part of life

There is no more basic requirement for an animal than eating. While reproduction is the ultimate goal of the Darwinian organism, without food an animal may not survive to have an opportunity to reproduce. How animals search for food is an important topic in ecology that will be covered in more detail later in the book. But what happens if an animal is unsuccessful in finding food? We know that if we do not eat, we lose weight as our body metabolizes its fat reserves to produce needed energy. If starvation is severe and regularly encountered, how will animals adapt to these types of conditions?

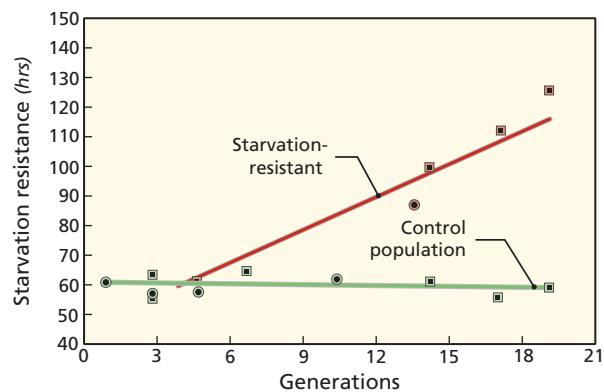


FIGURE 9.9A The average time until death due to starvation for females increases steadily in the starvation-selected populations, but shows no change in the control populations.

To study this problem, evolutionary biologist Michael Rose has created populations of fruit flies that are regularly subjected to several days of starvation conditions early in their adult life. Over time, genotypes that are able to resist

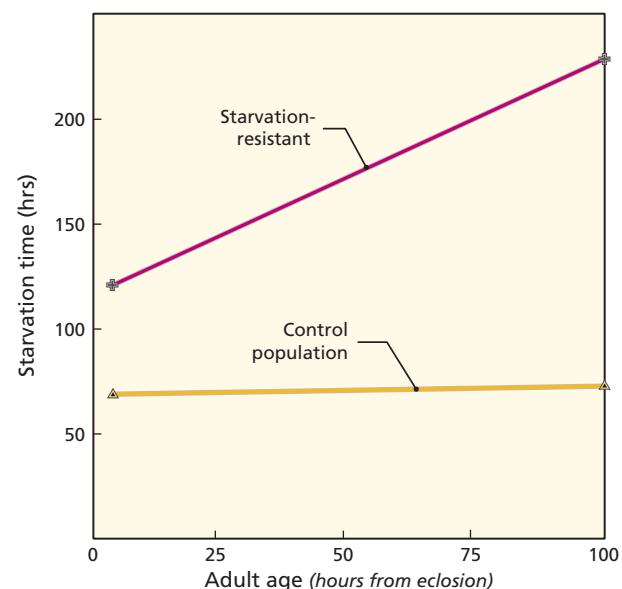
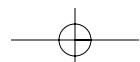


FIGURE 9.9B Very young adult females have poor starvation resistance relative to older adults in the starvation-resistant population.



starvation have become more common in these starvation-resistant populations as compared to controls that never experience starvation (Figure 9.9A). Within 20 generations, the starvation-resistant populations can live almost twice as long (120 hours vs. 60 hours) without food as the controls can. But how are they doing this?

A more careful examination of the starvation-resistant populations shows that the ability of adults to resist starvation is present as soon as the adult has completed metamorphosis (adult age zero hours); this ability increases dramatically over the first 96 hours of adult life (Figure 9.9B). No such change occurs in the control populations. These observations suggest that the flies in the starvation-resistant populations are changing their physiological state during their early adult life.

When the total weight and amount of fats (lipids) are measured in the 96-hour-old adults, we see that the starvation-resistant flies are not only heavier, but have larger reserves of fat (Figure 9.9C). This fat reserve actually increases

substantially during the first 96 hours of adult life in the starvation-resistant populations. Thus, the picture that has developed is that starvation-resistant females feed vigorously during the first four days of adult life and rapidly build up their fat reserves. These reserves, which are in fact being built up during the larval period, slow down the development of the starvation-resistant larvae as well as somewhat decreasing their survival rate. These reserves ultimately permit these flies to withstand the inevitable episode of starvation. In a standard laboratory environment—and in many natural environments—such drastic and predictable episodes of starvation do not occur. Consequently, building up large fat reserves is not useful, and the reduction in larval survival would prevent such evolution. However, in environments with regular bouts of starvation, these reductions in viability are tolerated so adults can survive to reproduce.

The evolution of starvation resistance also affects traits other than those that directly affect the ability to resist starvation. We call such effects pleiotropic effects. In this example,

selection for starvation-resistance has also increased the longevity of the starvation resistant populations (Figure 9.9D). These results are interesting because it is known that populations of fruit flies selected for longevity and late reproduction also show increased starvation resistance. These congruent results suggest a connection between the genes and traits that affect longevity and starvation resistance.

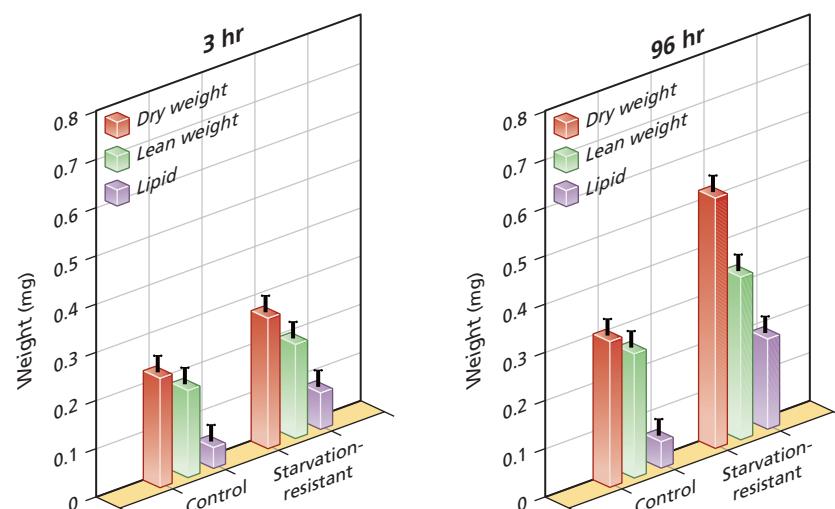


FIGURE 9.9C Starvation-resistant females weigh more than controls, largely due to the storage of lipid.

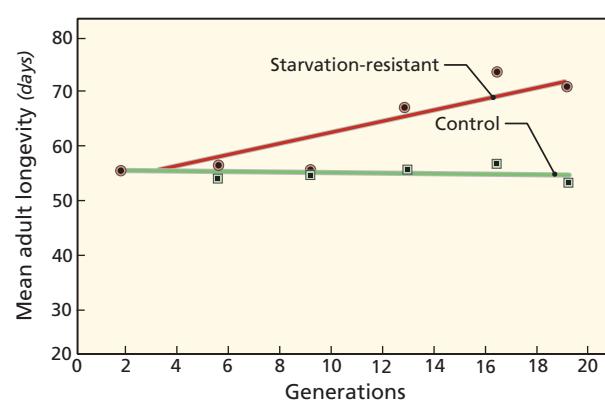
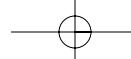


FIGURE 9.9D A correlated response to selection for starvation resistance is increased longevity.



ENERGY PRODUCTION AND UTILIZATION

9.10 Many factors affect energy production and utilization

An animal spends a good portion of its life in searching for and consuming food. Food supplies an animal with water and essential nutrients like vitamins, amino acids, carbohydrates, and lipids. Molecules such as proteins, lipids, and carbohydrates may be broken down or **catabolized** to produce energy. Some of this energy may be used to build large molecules. Collectively these building processes are called **anabolic** processes. Animals typically store energy as adenosine triphosphate (ATP).

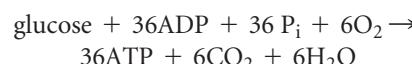
Energy Production Animals can use several catabolic routes in producing ATP. In low-oxygen environments, anaerobic metabolism is used to produce energy. Starting with glucose, here is the simple equation for one of the most common anaerobic pathways:



where ADP is adenosine diphosphate and P_i is a phosphate molecule. This equation shows that glucose is broken down into lactate, and the energy released is used to make ATP from its precursor ADP and phosphate. No oxygen is consumed. Animals may rely on anaerobic metabolism if they live in low-oxygen environments, such as estuarine mud flats, or if they live as parasites in the guts of vertebrates.

Even animals that normally live in well-oxygenated environments may use anaerobic metabolism for brief periods of time. During periods of extreme exercise, animals' muscles utilize anaerobic respiration and produce high levels of lactic acid. Not all animals produce lactic acid, although this compound is the most common end product of anaerobic respiration. Goldfish produce ethanol as the final product, while swimming cephalopods and marine bivalves produce octopine.

Of course, the most efficient catabolic pathway for energy production is aerobic metabolism, which utilizes the Krebs cycle and oxygen. The overall equation is:



The equation shows that glucose is broken down to produce carbon dioxide and water, and the energy released is used to make ATP from ADP and phosphate.

This aerobic pathway releases much more energy from glucose than anaerobic metabolism does. We can see this difference by comparing the numbers in the two equations. Thus, for each molecule of glucose we get 18 times more ATP in aerobic metabolism (36 ATP) than we get in anaerobic metabolism (2 ATP).

We also see from the equation for aerobic metabolism that for every molecule of glucose consumed, six molecules of oxygen are consumed and six molecules of carbon dioxide are produced. Thus, rates of aerobic respiration can be inferred from the amount of oxygen consumed or the amount of carbon dioxide produced. We take a closer look at ways of measuring these rates in Module 9.11.

Net Energy Gain The relative presence or absence of oxygen is not the only environmental factor that affects energy production in organisms. The net gain of energy is the difference between the energy an organism takes in, or consumes, and the amount of energy it loses to the environment. Organisms lose energy in the form of excreted wastes as well as metabolic energy, which generates heat that is dissipated to the atmosphere.

For ectotherms, the temperature of the environment can have a significant impact on energy intake. In the graph at the left in Figure 9.10A, for example, we see that for fish the rate of energy intake increases with temperature until it becomes very hot and approaches the lethal range for this species. Energy loss also increases, mostly due to increases in the background metabolic rate. However, as we see in the graph at the right in Figure 9.10A, there is clearly an optimal temperature

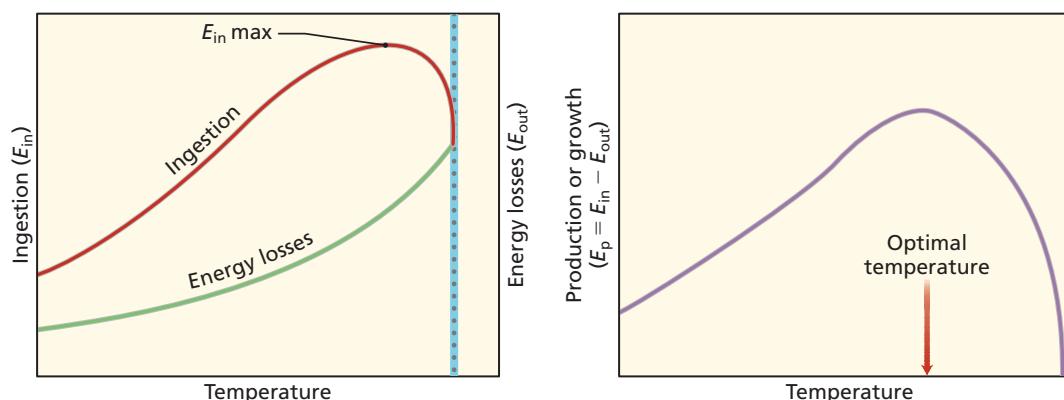


FIGURE 9.10A The effects of temperature on energy ingested (E_{in}) and energy lost (E_{out}) by fish (left graph). The graph on the right shows the effects of temperature on net energy gained (E_p).

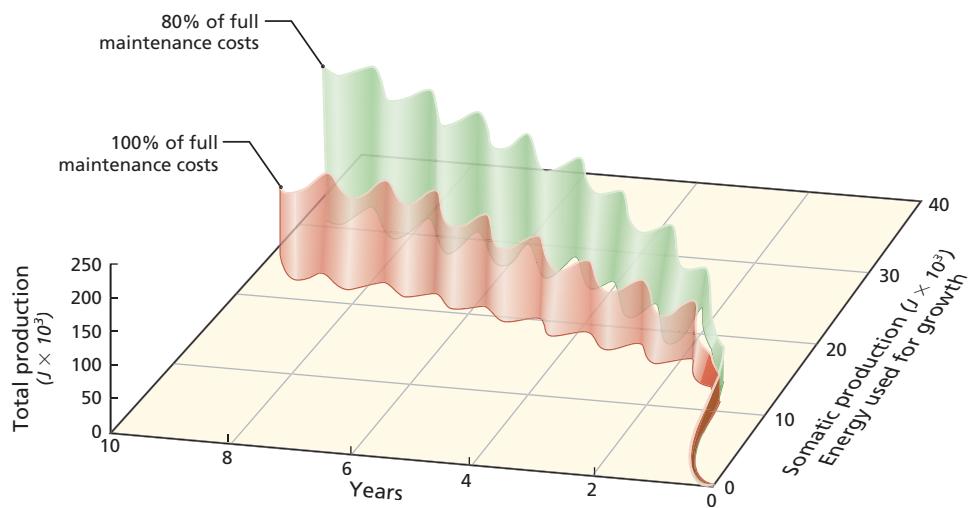


FIGURE 9.10B The effects of reducing maintenance metabolism by 20 percent in the marine mussel *Mytilus edulis*. The amount of energy used for growth is increased by 30 percent, and the total energy available for growth and reproduction is doubled over a 10-year period.

where the net energy gain is greatest. This net energy gain can be used for growth or reproduction.

The allocation of energy is a crucial issue in evolutionary biology. It is often argued that limits are placed on the types of life-history characters that can evolve due to the limited energy any organism has to allocate to different functions. As an example of the possible forces at work, consider Figure 9.10B. Two hypothetical energy budgets were used to model the allocation of energy to growth and all other functions in the marine mussel *Mytilus edulis*. In one budget it was assumed that the normal “housekeeping” metabolic functions could be carried out for 20 percent less energy than the usual amount. Over time this reduction in background energy use permitted the organism to allocate much more energy to growth and reproduction. These types of calculations suggest the important evolutionary role of energy allocation in individual organisms. ♦



9.11 Metabolic rates are determined by a variety of factors

Animals use energy to move, to grow, for general maintenance, and to reproduce. To understand the use of energy, we must first determine the total amount of energy used per unit of time, or the **metabolic rate**. The two principal methods of measuring metabolic rates measure either the amount of oxygen consumed or the amount of carbon dioxide given off. These measurements assume aerobic metabolism of carbohydrates, lipids, and proteins for energy.

The amount of energy used in the consumption of one liter of oxygen or the production of one liter of CO_2 depends on the source of the energy. When carbohydrates are the sole source of energy, there are equal amounts of oxygen consumed and carbon dioxide produced, a one-to-one ratio. For every liter of O_2 consumed, 5.0 kilocalories (kcal) of energy are produced. When lipids are the sole fuel, the ratio of CO_2 formed to O_2 consumed, sometimes called the **respiratory quotient (RQ)**, is 0.7. In this case, 4.7 kcal of energy are produced. In most organisms, the RQ is between 0.7 and 1.0, indicating that a mixture of carbohydrates and lipids is being used to produce energy.

Metabolic rates change when animals become active. The extent to which metabolic rates can change varies greatly among species. When an animal is resting and not under any unusual stress, the metabolic rate is referred to as the **standard metabolic rate**. For ectotherms, this rate depends on the ambient temperature, as we saw in Module 8.3. For endotherms, the metabolic rate is relatively independent of the ambient temperature, and the standard metabolic rate is called the **basal metabolic rate**. As animals become progressively active, the metabolic rate rises until it reaches the **maximum metabolic rate**.

The ratio of the maximum metabolic rate to the basal metabolic rate is called the **factorial aerobic scope**. For vertebrates the factorial aerobic scope is 5–12; for invertebrates it is typically 2–10. Insects that fly may show factorial aerobic scopes of 30–50 due to the very high metabolic rates of insect flight muscles. The aerobic scope indicates the capacity for sudden bursts of high activity.

In Module 8.8, we saw that the *specific metabolic rate*, or metabolic rate per kilogram, decreases with increasing size in mammals. Longevity also tends to increase with increasing size (Figure 9.11A). These two relationships suggest that longevity also

increases with decreasing metabolic rates. Obviously longevity is not determined universally by metabolic rate, although there may be particular taxa for which it is important.

How then could we test the idea that increased life span would be associated with decreased metabolic rates? Experimental fruit-fly populations, called O's, have been successfully selected for postponed senescence and live almost three times as long as their controls, called B's. If the hypothesis that longevity depends on metabolic rates were true, we would expect these O-populations to have demonstrably lower metabolic rates. In fact their metabolic rates are almost the same as the normal B-populations (Figure 9.11B). Longevity cannot be attributed to lower metabolic rates.

All energy that animals absorb is excreted as waste, or used for growth, reproduction, or internal metabolism. Metabolic energy in turn can be partitioned to bodily maintenance functions, processing and digesting food, and locomotion or other physical activities. In growing *Drosophila* larvae, for example, a major portion of their energy budget is spent on feeding and movement. As *Drosophila* larvae feed, they extend their mouth hooks, grab food, and then retract their mouth hooks. This movement also pulls the rear of the body

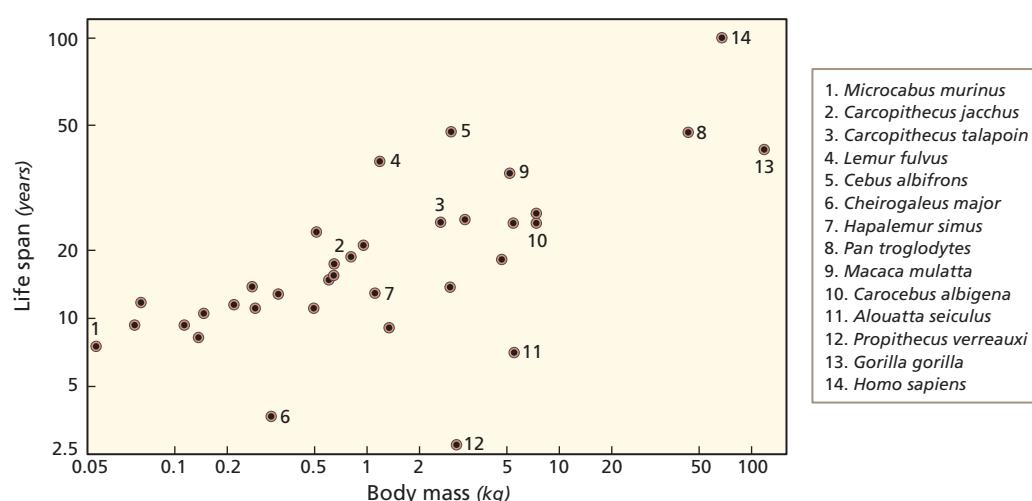


FIGURE 9.11A Is Longevity Related to Metabolic Rates? Larger animals tend to live longer and have lower metabolic rates.

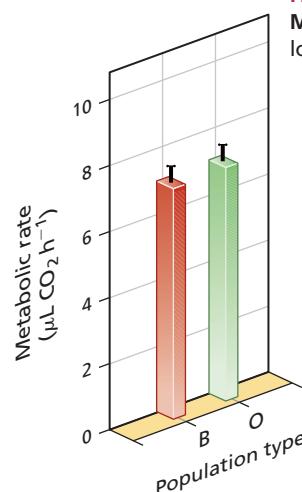


FIGURE 9.11B Is Longevity Related to Metabolic Rates? Populations of *Drosophila melanogaster* selected for increased longevity (O) show no difference in the metabolic rates of active tissue compared to controls (B).

forward, causing the larvae to move as they feed. A good-sized larva performs this feeding extension and retraction movement 120–160 times per minute! These larvae are the epitome of eating machines.

In stressful larval environments, *Drosophila* slow their feeding rates, presumably reducing the amount of energy used in feeding so it may be diverted to cope with the new stress (Figure 9.11C). For *Drosophila*, these stresses include high levels of ammonia or urea in their larval food, larval crowding, and exposure to parasites that attack feeding larvae. Because energy is used for growth and reproduction, it is likely that the energy budgets of organisms have been well tuned by natural selection.

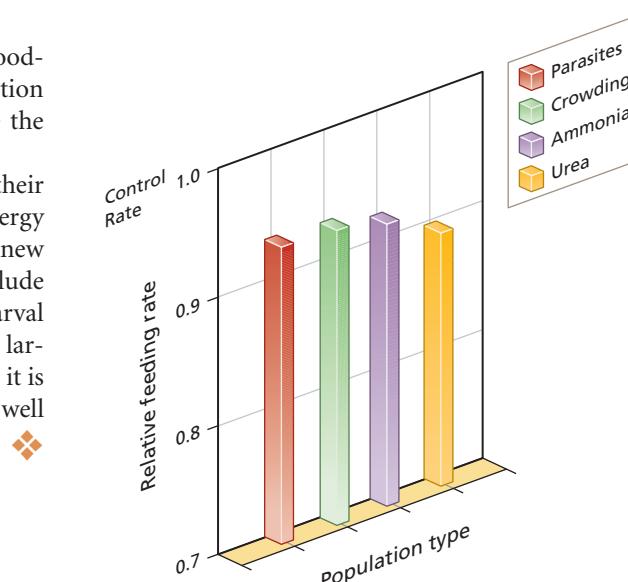
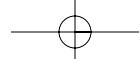


FIGURE 9.11C Activity Decreased in Populations Adapted to Stress The feeding rates of populations of *D. melanogaster* adapted to various stresses are compared to the controls producing a relative feeding rate. The populations adapted to the stress show a reduction in their feeding activity, possibly as a means of conserving energy needed to cope with the stress.





9.12 The “cost of transport” is a key metric of the energetic expense of moving in motile organisms

The importance of movement was highlighted in Module 9.11. There we saw that the feeding rates of *Drosophila* larvae slowed as the populations adapted to stressful environments that placed additional demands on their energy budgets. In general, movement requires more energy than resting does. Most of us can appreciate this from our own experience. For instance, it is fairly easy to sustain a walking pace of 15 minutes per mile. For short periods, healthy people can walk at this pace without breathing hard or getting fatigued. However, if we try to run at the speed of a world-class marathoner—5 minutes per mile—we will quickly become exhausted.

As animals increase their speed, they adjust their movements to reduce their energy ex-

penditure. For instance, horses have three different gaits: walk, trot, and gallop (Figure 9.12A). As horses move faster, they switch from walking to trotting and then to galloping. When horses are made to move at different speeds using just one gait, their energy use per meter traveled has a minimum at intermediate speeds but increases at lower and higher speeds (Figure 9.12A). The minimum energy consumed per meter traveled is actually the same for all three gaits. The histograms in Figure 9.12A show the speeds that horses themselves choose when moving by each of these gaits. Horses select the speed that consumes the least energy for a given gait.

To study different modes of transportation, we need to have some measure of the energetic requirements of movement. If we measure the amount of oxygen consumed by an animal while moving, then we know how much energy is being used. To standardize these energy measurements, we can then calculate how much energy is used per meter traveled per kilogram of animal. For example, in Figure 9.12B the cost of transport is measured in calories per gram-kilometer (cal/g-km). With these units, we can calculate the **cost of transport** to compare the movement of different species.

The cost of transport in different media (air, water, or land) varies because of two factors. First is the energy needed to support the animal. Second is the cost of resistance from moving through the medium.

In water, the energy needed for support is less than that needed in air or on land, due to the buoyancy of animals in water. Land animals need to support their weight, but they receive support from the land while in contact with it. Animals that travel in the air need to supply energy continuously to support themselves.

On the other hand, water offers the greatest resistance to motion due to the higher viscosity of water compared to air. When we compare the costs of locomotion in different

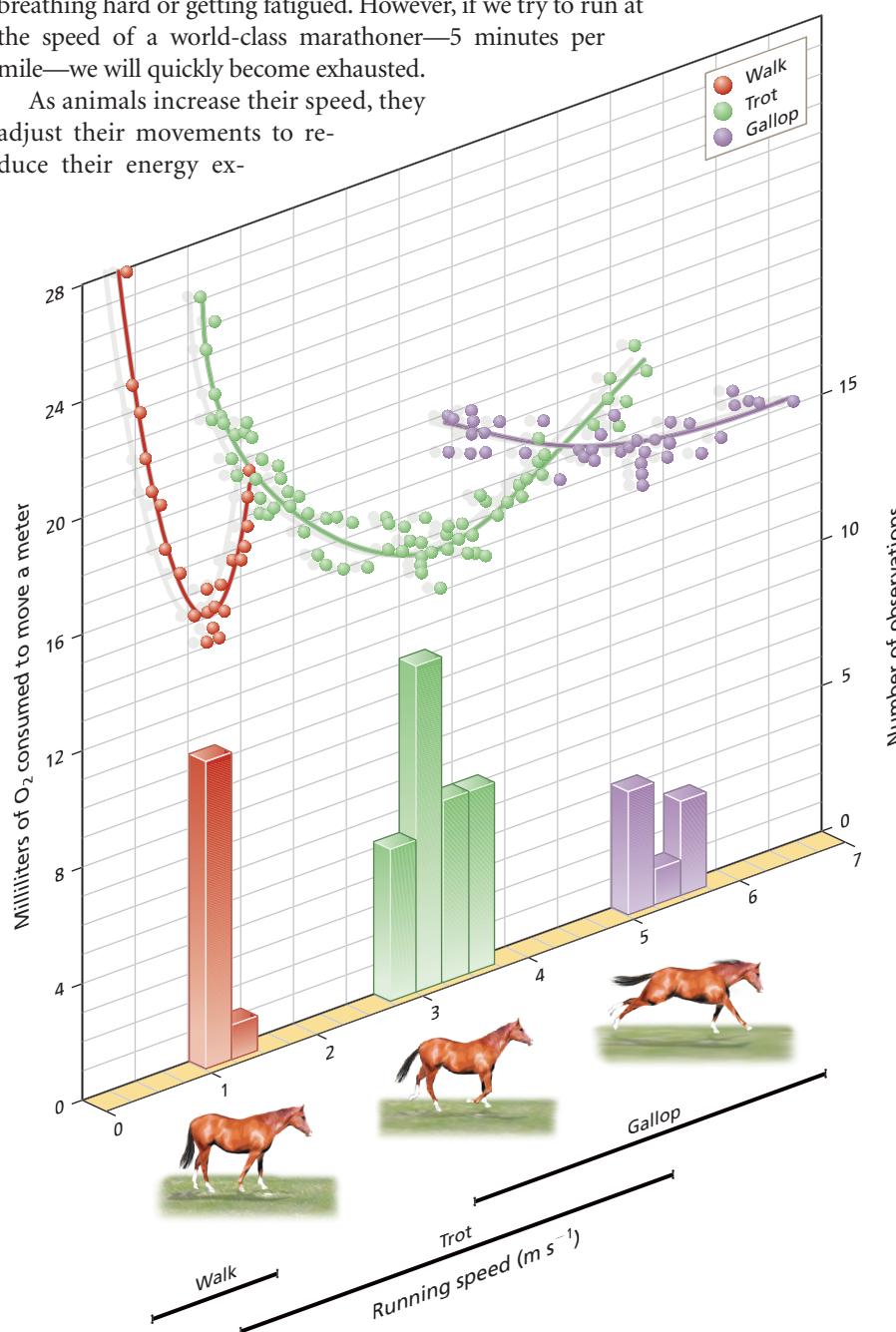
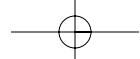


FIGURE 9.12A Metabolic Rate of Horses as a Function of Speed



media, there is a decrease in the energy costs for larger animals. Animals of similar sizes reveal that the cost of transport is greatest on land and least in water, as Figure 9.12B shows. Transport in water can be efficient if the speed of travel is kept low, thus reducing the energy lost to drag, because almost no energy is needed for support. These results also explain why animals that migrate very long distances either fly or swim.

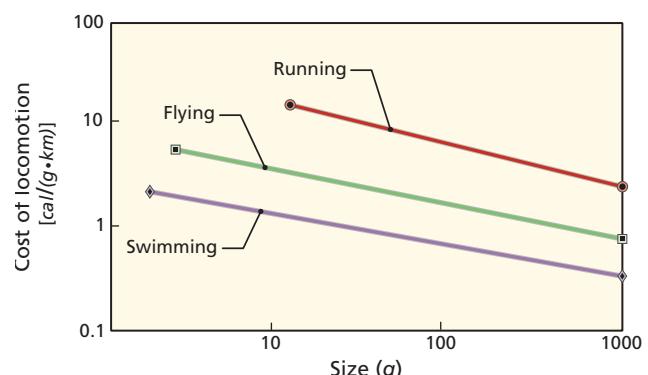
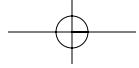


FIGURE 9.12B Costs of Different Modes of Transportation





9.13 Energy is the basis of trade-offs for the evolution of many traits

It seems simple to suppose that natural selection will favor increases in reproductive rates, competitive ability, immune system competence, and many other traits. But we might wonder if there is any limitation to the improvements natural selection can make. A central organizing assumption in evolutionary theory has been that the energy intake of organisms will be limited; and thus adaptations that require energy will often have to get it by diverting energy from some other component of the individual's energy budget.

An early articulation of these ideas was made by Martin Cody in 1966. He was interested in understanding why there was a gradient in the numbers of eggs laid by birds as one goes from high latitudes toward the equator (Figure 9.13A). Specifically, birds of

many different species that live in high latitudes tend to lay many more eggs per clutch than do birds that live near the equator. The generality of this trend certainly suggests there must be some common explanation based on fundamental aspects of biology rather than on the detailed peculiarities of the ecology of any particular bird species. Cody's explanation was based on the assumption that each bird



will have a limited amount of energy to spend on the activities of competition, predator avoidance, and egg production (Figure 9.13A). In the tropics there are relatively more competing species and predators. Thus, Cody reasoned that these tropical species will have less energy available for egg production and ultimately will produce smaller clutches.

These ideas were developed further by Madhav Gadgil and William Bossert in 1970, in a formal model. The focus of their model was to understand the timing and levels of reproduction during an organism's life. They considered time and energy to be limited and required for maintenance, reproduction, and growth. Thus, expending more energy in maintenance might increase the chance of survival but then would take energy away from reproduction. Evolutionary biologists consider that the key to understanding how different life-histories evolve revolves around understanding how organisms can best allocate energy to these different functions and achieve the greatest gains in fitness.

Another example of the effects of energetic trade-offs was developed by Derek Roff and his colleagues. They studied a species of sand cricket (*Gryllus firmus*), that has two different wing morphologies, long winged and short winged. The long-winged morphs are capable of dispersal but have new additional energy requirements due to the flight muscles that have high respiration rates. Roff measured metabolic rates directly and found female long-winged morphs to have significantly higher metabolic rates (Figure 9.13C). However, as postulated by Gadgil and Bossert, if there is an increase in maintenance energy there should also be a corresponding decrease in some other component of the energy budget. In this case Roff documented substantial declines in the biomass of female gonads of the long-winged forms (Figure 9.13C). 

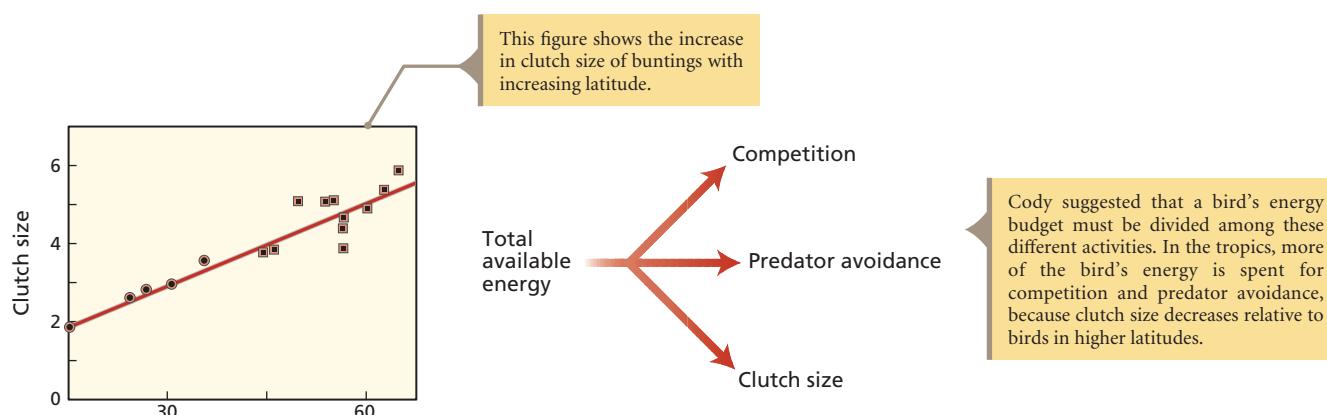


FIGURE 9.13A Cody proposed an energetic explanation for variation in avian clutch size.

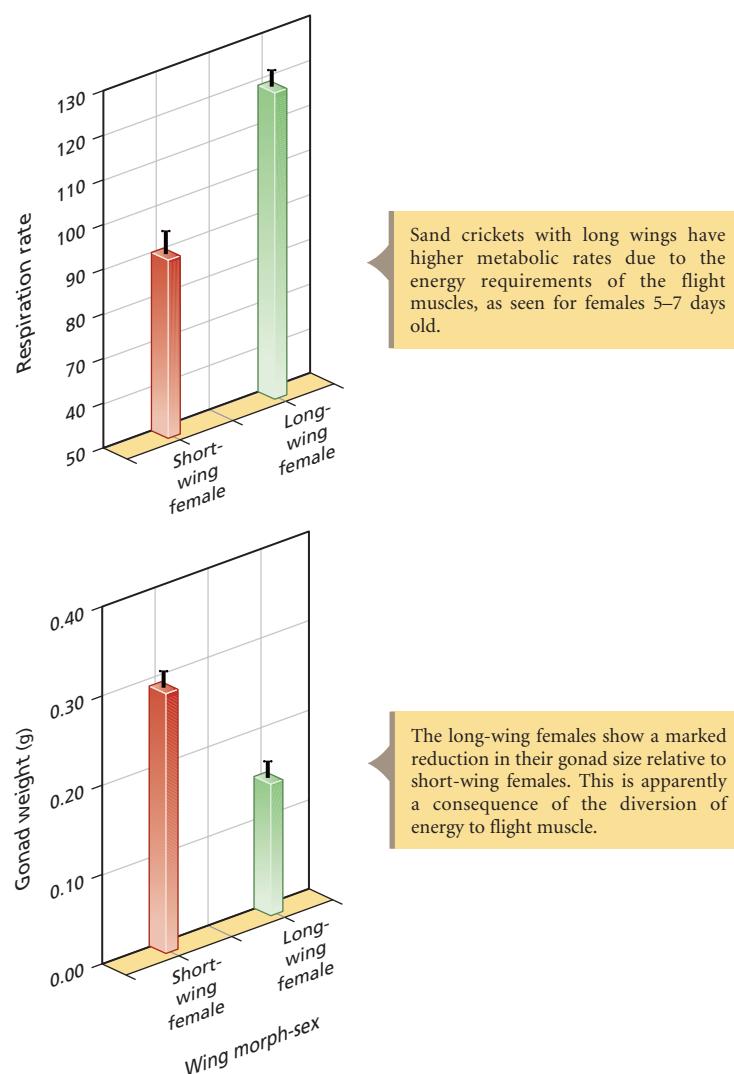
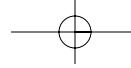


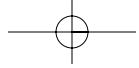
FIGURE 9.13C Reproduction and dispersal capability trade-off in sand crickets.



FIGURE 9.13B The Long-Winged Form of the Sand Cricket, *Gryllus firmus*

SUMMARY

1. Animals in aquatic environments will experience net flows of water and ions in or out of their cells, depending on the osmotic concentration of the surroundings. Some animals are osmoconformers and do not try to regulate the concentration of solutes of their cells. Others animals maintain concentration gradients.
2. Animals must also take up oxygen from the environment to fuel aerobic metabolism. This is most often accomplished with gills and lungs. These organs typically have large surface areas exposed to oxygenated water or air.
3. Many physiological systems for oxygen uptake, heat exchange, and ion reabsorption use countercurrent exchange to improve efficiency.
4. Plants must transport water over large distances. In some trees the distances from roots to treetop can be 100 meters. This transporting of water is accomplished through the joint effects of transpiration and the cohesive forces of water.
5. Many plants and animals live in hot, dry environments and must cope with high rates of water loss. Desiccation, like many physiological systems, is subject to natural selection.
6. Fruit flies adapt to dry environments by storing more water and slowing down their rate of water loss.
7. Fruit flies increase their fat reserves to resist starvation and evolve increased longevity as a correlated response to starvation resistance.
8. Transportation is a major portion of the energy budget of most animals. The standardized cost of transportation is greatest on land and smallest in water.
9. Life-history evolution involves allocating energy between maintenance, growth, and reproduction in a manner that has the greatest effect on fitness.



REVIEW QUESTIONS

1. Review the types of stress placed on the cells of animals that live in hyperosmotic conditions vs. hypoosmotic conditions.
2. Give two examples of countercurrent exchange systems, and explain how they work.
3. Why can't air pressure alone explain the movement of water through plants?
4. What are trichomes, and how do they prevent water loss in plants?
5. Why do veins in blood circulatory systems have valves on them?
6. What physiological changes occur in populations of fruit flies selected for desiccation resistance?
7. What are the major patterns of nitrogen excretion used by animals?
8. Fruit flies selected for starvation resistance change in a number of ways, including the storage of lipids. Why don't all fruit flies employ these adaptations?
9. How can the respiratory quotient be used to infer the type of fuels an organism is using to produce energy?
10. How does energy affect the course of life-history evolution?

KEY TERMS

ammonotelism	countercurrent exchange	maximum metabolic rate	stenohaline
anabolic	cuticle	metabolic rate	stomata
aorta	epicuticle	Mueller, Laurence	stomatal transpiration
arteriole	eutraphaline	open circulatory system	systemic circuit
basal metabolic rate	factorial aerobic scope	osmoconformer	trichome
blood	gait	osmotic concentration	ureotelism
boundary layer	gills	osmoregulate	uricotelism
capillary	heart	pulmonary circuit	vasoconstruction
catabolize	hyperosmotic	ram ventilation	vasodilation
closed circulatory system	hypoosmotic	respiratory quotient	vapor pressure
Cody, Martin	hypoxic	Rose, Michael	venule
cohesion	lung	standard metabolic rate	xylem
cost of transport			

FURTHER READINGS

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