

Animals and Environments: Function on the Ecological Stage

Animal physiology is the study of animal function—the study of “how animals work.” Physiologists—the scientists who carry out this study—bring a special perspective to scenes such as birds migrating. They wonder how much energy the birds must expend to fly, where and when the birds obtain the energy, and how the birds stay oriented toward their destination so as to arrive efficiently. More broadly stated, physiologists seek to identify the functional challenges that migrating birds face and learn how those challenges are met.

Billions of animals migrate over the face of the planet every year, making the functional properties of migrating animals a subject of paramount importance. By definition, however, migrating animals are on the move; they do not stay in one place where they might be investigated with ease. Consequently, researchers have had to be inventive to study these animals.

Physiologists now have high-quality methods for measuring the cost of flight. Sandpipers such as those shown in the opening figure are trained to fly in a wind tunnel, where their speed of flight can be controlled. While the birds fly, their rates of energy use are measured by techniques designed not to disturb them. One such technique makes use of unusual, benign isotopes of oxygen and hydrogen. These isotopes are injected into the sandpipers before they start flying, and then the rates of loss of the isotopes from the birds are measured as they fly unencumbered in the wind tunnel. From the isotope data, their rates of energy use can be calculated as they fly at speeds typical of migratory flight. These rates turn out to be very high: about seven or eight times the birds’ resting rates of energy use.¹ Physiologists have then combined this information with field observations on food ingestion and processing to learn how the birds obtain sufficient energy and how they manage their energy supplies to meet their flight needs during migration. One population of the sandpipers is famous for migrating every spring from southern South America to the Arctic—a distance of 15,000 km (9300 mi). In common with other populations of the same species, when these birds migrate, they alternate between extended *stopover periods*, during which they “refuel” by feeding, and *flight periods*, during which they fly nonstop for long distances—sometimes more than 5000 km (3100 mi). Based on the information available, the sandpipers fuel each long, uninterrupted flight by eating lots of clams, snails, and other food during the stopover period—often lasting 3–4 weeks—that immediately precedes the flight. By the time they take off, the birds must have enough stored energy to fuel the entire next leg of their journey because they do not eat as they fly.

During a stopover period, as the birds eat day after day, they store a great amount of energy as fat, and their body weight can increase by 50%. Physiologists have discovered, however, that the birds’ adjustments during a stopover period are far

¹The method of measuring rate of energy consumption discussed here, known as the *doubly-labeled water method*, is explained in greater detail on page 208.

Long-distance migrants Some populations of these sandpipers, which are known as red knots (*Calidris canutus*), breed in the high Arctic every summer but overwinter in southern Argentina. They thus migrate almost halfway around the globe twice a year. They use energy at relatively high rates not only while migrating but also during several other phases of their annual life cycle, such as their period of nesting on the cold, exposed Arctic tundra.



more complex than simply storing fat. For part of the time, the birds' stomach and intestines are large, aiding them in processing food at a high rate. During the week before they take flight, however, several organs that they will not use during flight, including their stomach and intestines, decrease significantly in size. Other organs, such as their heart, grow larger. Overall, during that week, the body of each bird is re-proportioned in ways that poise the bird to fly strongly, while reducing the amount of unnecessary weight to be carried. By investigating these phenomena, physiologists have revealed that the fascinating migrations of these birds are, in truth, far more fascinating than anyone could have imagined prior to the detailed study of function.

As you start your study of physiology, we—your authors—believe you are at the beginning of a great adventure. We feel privileged to have spent our professional lives learning how animals work, and we are eager to be your guides. If we could hop with you into a fantastic machine and tour Earth in the realms we are about to travel in this book, we would point out sperm whales diving an hour or more to depths of a mile or more, electric fish using modified muscles to generate 500-V shocks, newborn reindeer calves standing wet with amniotic fluid in the frigid Arctic wind, reef corals growing prolifically because algae within their tissues permit internal photosynthesis, and moths flying through cool nights with bodies as warm as those of mammals. Each of these scenes draws the interest of physiologists and continues to spark new physiological research.

The Importance of Physiology

Why is the study of animal physiology important to you and to people in general? Not the least of the reasons is the one we have already emphasized—namely, that a full understanding and appreciation of all the marvels and other phenomena of the animal world depends on an analysis of how animals work. The study of physiology draws us beyond surface impressions into the inner workings of animals, and nearly always this venture is not only a voyage of discovery, but also one of revelation.

The study of physiology also has enormous practical applications because physiology is a principal discipline in the understanding of health and disease. The analysis of many human diseases—ranging from aching joints to heart failure—depends on understanding how the “human machine” works. A physician who studies heart disease, for instance, needs to know the forces that make blood flow into the heart chambers between one heartbeat and the next. The physician also needs to know how pressures are developed to eject blood into the arteries, how the cells of the heart muscle coordinate their contractions, and how the nutrient and O₂ needs of all parts of the heart muscle are met. We discuss these and other aspects of mammalian physiology extensively in this book. Even when we turn our attention to other types of animals, our study will often have application to human questions. One reason is that nonhuman animals are often used as “models” for research that advances understanding of human physiology. Research on squids, for instance, has been indispensable for advancing knowledge of human neurophysiology because some of the nerve cells of squids are particularly large and therefore easily studied.

Physiology is as important for understanding the health and disease of nonhuman animals as it is for understanding health and disease in humans. An example is provided by studies of another

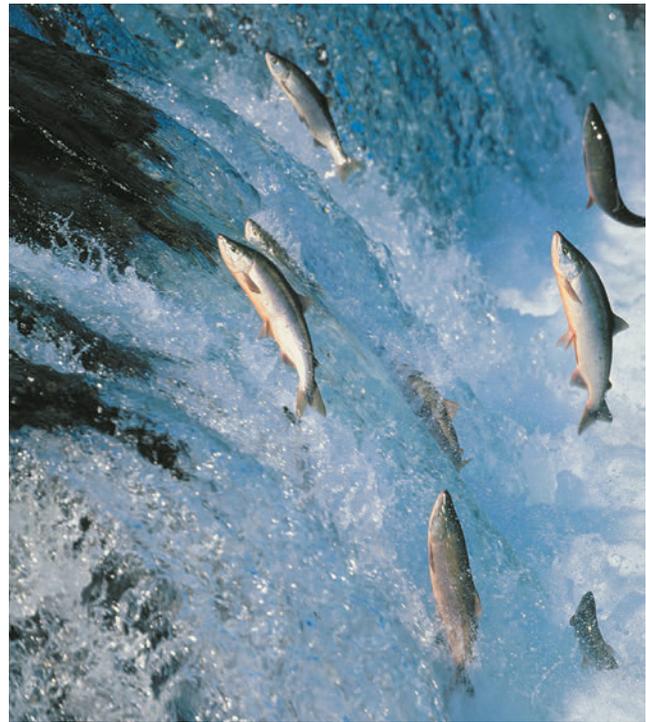


FIGURE 1.1 Pacific salmon migrating upriver to their spawning grounds Having spent several years feeding and growing in the Pacific Ocean, these fish have once again found the river in which they were conceived. Now they must power their way back to their birthplace to spawn, even though they ate their last meal at sea and will starve throughout their upriver journey. Shown are sockeye salmon (*Oncorhynchus nerka*).

group of migrating animals, the Pacific salmon—which swim up rivers to reach their spawning grounds (Figure 1.1). Physiologists have measured the costs these fish incur to swim upstream and leap waterfalls. This research has enabled better understanding of threats to their health. For instance, although each individual dam along a river might be designed to let salmon pass, a series of dams might so increase the overall cost of migration that the fish—which don't eat and live just on their stores of energy when migrating—could run out of energy before reaching spawning grounds. With knowledge of the energetics of swimming and leaping, managers can make rational predictions of the cumulative effects of dams, rather than simply altering rivers and waiting to see what happens. The effects of water pollutants, such as heavy metals and pesticides, are other important topics in salmon physiology. Examples in other animals include studies of stress and nutrition. Conservation biologists gauge the stress experienced by wild vertebrate animals by measuring levels of stress-response hormones in their blood (see page 433). Careful studies of nutrition have solved mysterious cases of population decline by revealing that the animals were unable to find adequate amounts of acceptable foods.

In brief, physiology is one of the key disciplines for understanding

- The fundamental biology of all animals
- Human health and disease
- The health and disease of nonhuman animals of importance in human affairs

Physiology is also important because *it is one of biology's most integrative disciplines*. Physiologists study all the levels of organization of the animal body. In this respect, they are much like detectives

who follow leads wherever the leads take them. To understand how an organ works, for instance, information about the nervous and hormonal controls of the organ might be required, plus information about enzyme function in the organ, which might lead to studies of the activation of genes that code for enzyme synthesis. Physiology not only pursues all these levels of biological organization within individual animals but also relates this knowledge to the ecology and evolutionary biology of the animals. Students often especially enjoy their study of physiology because the discipline is so integrative, bringing together and synthesizing many concepts that otherwise can seem independent.

Consider again, for example, the Pacific salmon. As juveniles, these fish migrate from rivers to the open ocean. Years later, they return to the very rivers of their conception to procreate the next generation. Before a returning salmon enters freshwater, it maintains its blood more dilute than the seawater in which it swims. After it enters freshwater, however, it must maintain its blood more concentrated than the dilute freshwater now surrounding it. Another challenge the salmon faces is meeting the energy costs of its migration. Once in its natal river, a salmon no longer eats. Yet it may swim for many weeks before it reaches its spawning grounds—sometimes traveling against the river current as far as 1100 km (680 mi) and, in mountainous regions, climbing 1.2 km (0.75 mi) in altitude. During this trip, because the fish is starving, it gradually breaks down the substance of its body to supply its energy needs; 50–70% of all tissues that can supply energy are typically used by the time the fish reaches its destination.

As physiologists study salmon, they take a highly integrative approach, illustrated in **Figure 1.2**. As part of their background of knowledge, they recognize that the populations and species of salmon alive today not only are products of evolution but also are still evolving (see **Figure 1.2a**). Physiologists also recognize that the laws of chemistry and physics need to be considered (see **Figure 1.2b**), because animals must obey those laws—and sometimes they *exploit* them. For understanding swimming, multiple levels of organization must be considered (see **Figure 1.2c**). The nervous system generates coordinated nerve impulses that travel to the swimming muscles, which contract using energy drawn from adenosine triphosphate (ATP) that is synthesized from organic food molecules. The contraction of the swimming muscles then exerts biomechanical forces on the water that propel the fish forward. The investigation of swimming illustrates, too, the important general point that the study of *function* typically goes hand in hand with the study of *form*; knowledge of anatomy often sets the stage for understanding physiology, and as function is clarified, it typically helps account for anatomy. Often, the ultimate goal of a physiological study is to understand how an animal functions in its natural environment. Thus, an ecological perspective is vital as well. As seen in **Figure 1.2d**, when an individual salmon's fluid environment changes from saltwater to freshwater, the fish alters the set of ion-transporting proteins expressed in its gills, permitting inward ion pumping in freshwater whereas ions were pumped outward in saltwater. The distance a fish swims is another important ecological consideration. Different populations of salmon travel vastly different distances. Going far upriver can provide advantages of certain kinds, such as providing pristine spawning grounds. However, this ecological factor has other consequences as well. Females that exert great effort to reach their spawning grounds, such as by swimming great

distances, spawn fewer eggs because swimming diverts energy away from use in reproduction (see **Figure 1.2d**).

Mechanism and Origin: Physiology's Two Central Questions

Physiology seeks to answer two central questions about how animals work: (1) What is the mechanism by which a function is accomplished, and (2) how did that mechanism come to be? To understand why there are *two* questions, consider the analogous problem of how a car works. In particular, how is an engine-driven wheel made to turn?

To understand this function, you could disassemble a car and experiment on its parts. You could study how the pistons inside the cylinders of the engine are made to oscillate by forces released from exploding gasoline, how the pistons and connecting rods turn the drive shaft, and so forth. From studies like these, you would learn how the car works.

At the conclusion of such studies, however, you would have only half the answer to the question of how the car works. Presuming that you have investigated a routine design of modern car, your experiments will have revealed how a routine internal combustion engine turns a wheel by way of a routine transmission. Let your mind run free, however, and you may quickly realize that there are alternative designs for a car. The engine could have been a steam engine or a fuel cell–based engine, for example. Accordingly, when you ponder how a wheel turns, you see that you really face two questions: the *immediate* question of how a particular design of car makes a wheel turn, and the *ultimate* question of how that particular design came into being. Physiologists also face these two questions of *mechanism* and *origin*.

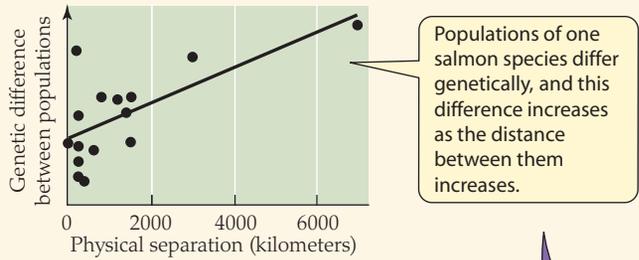
The study of mechanism: How do modern-day animals carry out their functions?

If you examine a particular car and its interacting parts to understand how it works, you are learning about the *mechanisms* of function of the car. Likewise, if you study the interacting parts of a particular animal—from organs to enzymes—to learn how it works, you are studying the animal's *mechanisms*. In physiology, **mechanism** refers to the components of actual, living animals and the interactions among those components that enable the animals to perform as they do.

Curiosity about mechanism is what inspires most physiologists to study animals, and studies of mechanism dominate physiological research. Physiology, in fact, is most clearly distinguished from other biological disciplines with which it is related, such as morphology or ecology, by its central focus on the study of mechanism. A physiologist typically begins an investigation by observing a particular capability that excites curiosity or needs to be understood for practical purposes. The capability of the human visual system to distinguish red and blue is an example. Another example is the ability of certain types of nerve cells to conduct nerve impulses at speeds of over 100 meters per second. Whatever the capability of interest, the typical goal of physiological research is to discover its mechanistic basis. What cells, enzymes, and other parts of the body are employed, and how are they employed, to enable the animal to perform as it does?

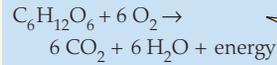
For a detailed example of a mechanism, consider how the light organ of a firefly emits flashes, starting with the biochemistry of light

(a) **Evolution** Today's animals are products of evolution and are still evolving



(b) **Chemistry and physics**

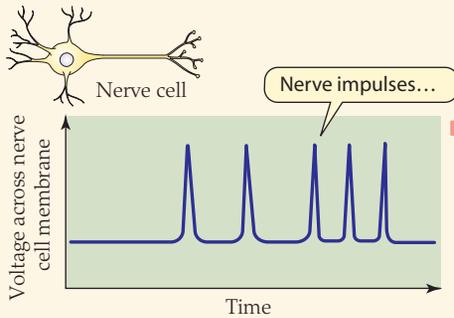
$$\text{Thrust} - \text{Drag} = \text{Mass} \times \text{Acceleration}$$



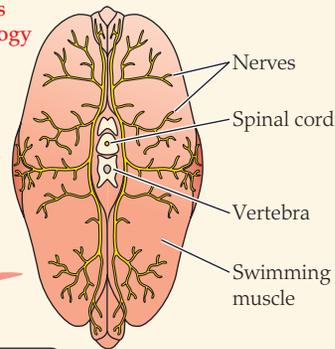
Animals must adhere to the laws of chemistry and physics—and sometimes they take advantage of them.

(c) **Physiology** depends on all levels of organization

Cell physiology



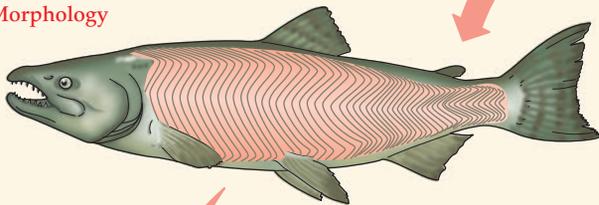
Systems physiology



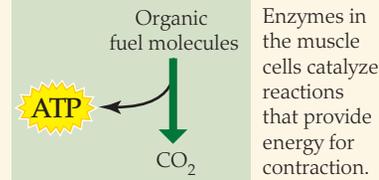
...delivered through the nervous system...

...activate the swimming muscles.

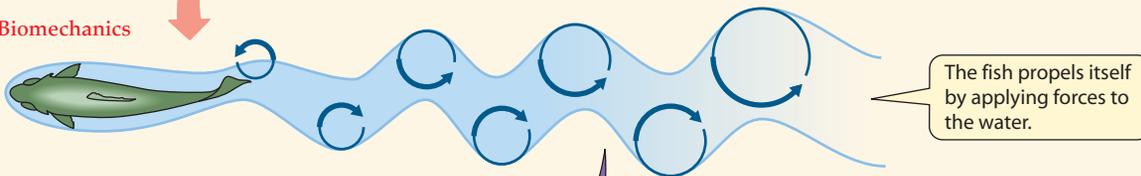
Morphology



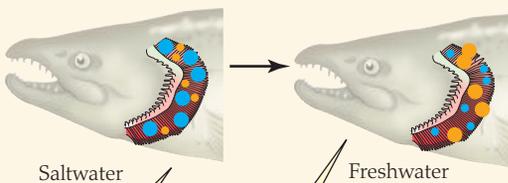
Biochemistry



Biomechanics

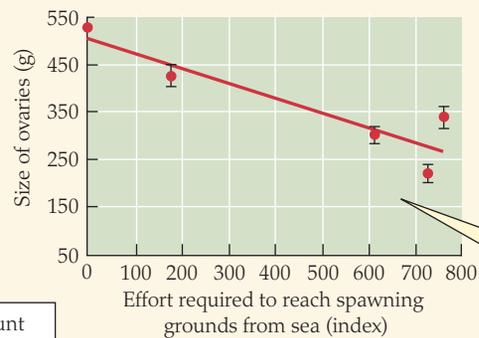


(d) **Ecology** Physiology acts within an ecological context



KEY

- Sizes of circles symbolize amount
- One cell-membrane protein
- Another cell-membrane protein



◀ **FIGURE 1.2 The study of physiology integrates knowledge at all levels of organization** To understand the physiology of fish, physiologists consider (a) evolutionary biology, (b) the laws of chemistry and physics, and (d) ecological relations—as well as (c) body function at all levels of organization. All elements shown are for fish in a single genus, *Oncorhynchus*, the Pacific salmonid fish. In (c) the drawing in “Systems physiology” is a cross section of the body; the salmon in “Morphology” is a chinook salmon. (Graph in a—which pertains to populations of chum salmon—after Hendry et al. 2004; cross section, salmon, and biomechanics illustration in c after Videler 1993; graph in d—which pertains to sockeye salmon—after Crossin et al. 2004.)

production (Figure 1.3a). A chemical compound (a benzothiazol) named *firefly luciferin* first reacts with ATP to form luciferyl-AMP (AMP, adenosine monophosphate). Then, if O_2 —molecular oxygen—can reach the luciferyl-AMP, the two react to form a chemical product in which electrons are boosted to an excited state, and when this electron-excited product returns to its ground state, it emits photons. This sequence of reactions requires a protein catalyst, an enzyme called *firefly luciferase*. A question only recently answered is how cells within the light organ are controlled so that they flash at certain times but remain dark at others. When a firefly is not producing light (Figure 1.3b), any O_2 that reaches the insect’s light cells via its gas-transport tubules is intercepted (and thereby prevented from reacting with luciferyl-AMP) by mitochondria that are positioned between the gas-transport tubules and the sites of the luciferin reactions. The light cells produce light (Figure 1.3c) when, because of stimulation by the nervous system, the mitochondria become bathed with nitric oxide (NO). The NO blocks mitochondrial use of O_2 , allowing O_2 through to react with luciferyl-AMP. Facts like these form a description of the *mechanism* by which fireflies produce light.

The study of a mechanism may become so intricate that decades or centuries are required for a mechanism to be fully understood. By definition, however, the complete mechanism of any given function is present for study in the here and now. A scientist can, in principle, fully describe the mechanism of a process merely by studying existing animals in ever-finer detail.

The study of origin: Why do modern-day animals possess the mechanisms they do?

Suppose a youngster observes a firefly produce a flash of light and asks you to explain what he has seen. One way you could interpret the request is as a question about mechanism. Thus you could answer that the brain of the insect sends nerve impulses that cause the light cells to become bathed with nitric oxide, resulting in the production of excited electrons through the reaction of O_2 with luciferyl-AMP. However, the youngster who asks you to explain the flashing of a firefly is probably interested in something else. The *reason* the firefly makes light is probably what is on your young friend’s mind, rather than the mechanism. That is, the youngster is probably wondering *why* the firefly possesses a mechanism to make light.

For biologists, the answer lies in *evolutionary origins*. The mechanisms of modern-day animals are products of evolution, and thus the reasons for the existence of mechanisms lie in evolutionary processes. The study of evolutionary origins is a central aim of modern physiology because it promises to reveal the *significance* of mechanisms. If we can learn why evolution produced a mechanism, we will better understand what (if anything) animals gain by having the mechanism.

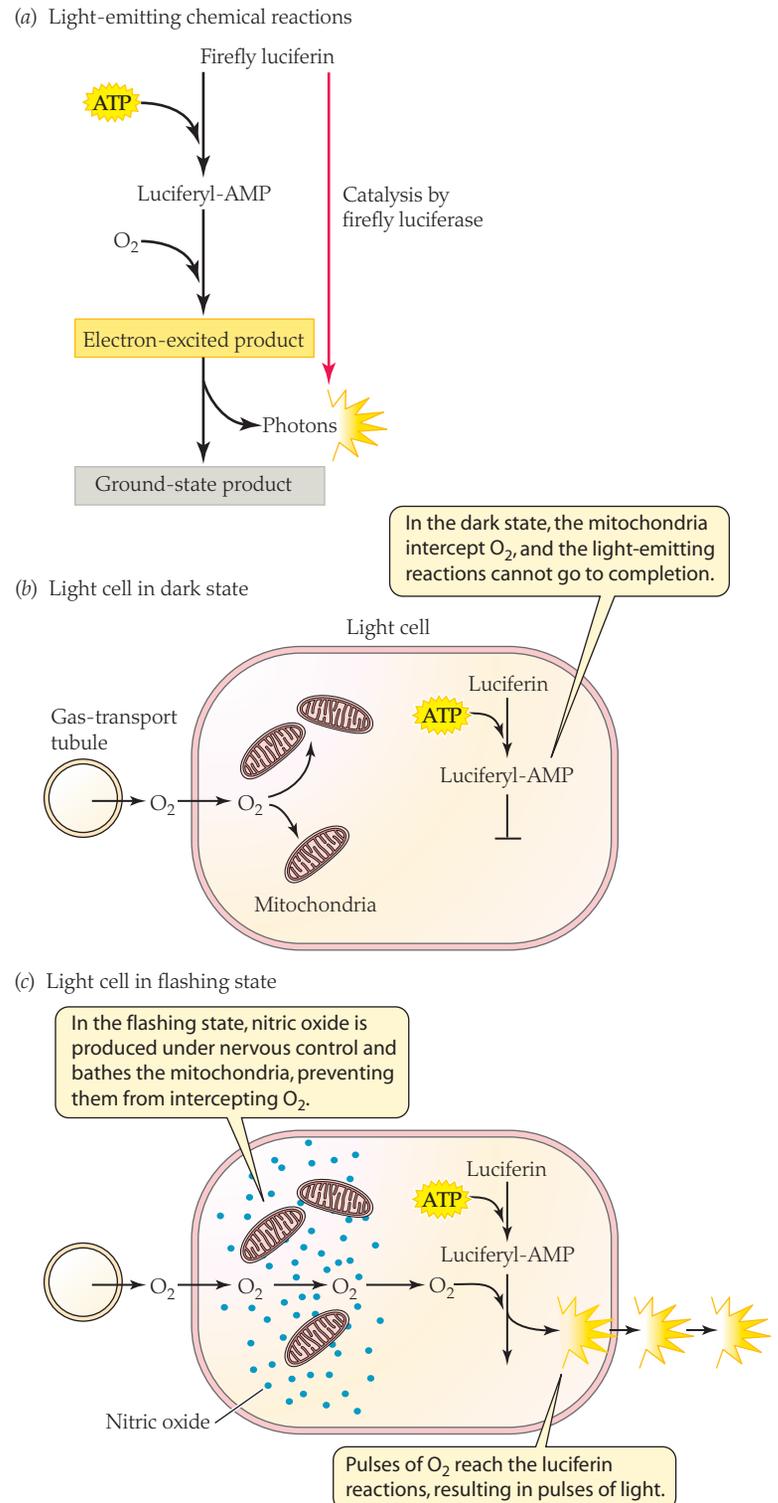


FIGURE 1.3 The mechanism of light production by fireflies (*Photinus*) (a) The chemistry of light production. (b,c) In the light cells—the cells that compose the light organ—the luciferin reactions are spatially separated from mitochondria. When a light cell is not flashing (b), the mitochondria intercept O_2 . However, when a cell is flashing (c), O_2 gets through to the luciferin reactions. Understanding of firefly flashing is a work in progress; thus, parts of this scenario are hypothetical. AMP = adenosine monophosphate; ATP = adenosine triphosphate.

Because modern-day mechanisms evolved in the past, the question of origins is fundamentally historical. The origins of a mechanism, unlike the mechanism itself, cannot usually be observed directly in the here and now. Instead, origins must usually be studied indirectly, by means of inferences about the past derived from observations we can make in the present. The reliance on indirect reasoning means that evolutionary origins are rarely understood with the same certainty as mechanisms.

Natural selection is a key process of evolutionary origin

Natural selection is just one of several processes by which animals acquire traits during evolution, as we discuss later in this chapter. Natural selection, however, holds a place of special importance for biologists because, of all the modes of evolutionary change, natural selection is believed to be the principal process by which animals become fit to live in their environments.

Natural selection is the increase in frequency of genes that produce phenotypes that raise the likelihood that animals will survive and reproduce. During evolution by natural selection, such genes increase in frequency—over the course of generations—because animals with the genes are differentially successful relative to other members of their species. If we find that a physiological mechanism originated by natural selection within the prevailing environment, we can conclude that the mechanism is an asset; that is, it improves an animal's chances of survival and reproduction within the environment the animal occupies.

Adaptation is an important sister concept to natural selection. Because we discuss adaptation at length later, here we simply state that an adaptation is a physiological mechanism or other trait that is a product of evolution by natural selection. Adaptations are assets; because of the way they originated, they aid the survival and reproduction of animals living in the environment where they evolved. When we speak of the **adaptive significance** of a trait evolved by natural selection, we refer to the reason *why* the trait is an asset: that is, the reason *why* natural selection favored the evolution of the trait.

The light flashes of fireflies usually function to attract mates. The males of each species of firefly emit light flashes in a distinctive, species-specific pattern as they fly, thereby signaling their species identity to females (Figure 1.4). Using various sorts of evidence, students of fireflies infer that the firefly light-producing mechanism evolved by natural selection because light flashes can be used to bring the sexes together. Thus the mechanism of light production is an adaptation, and its adaptive significance is mate attraction.

Mechanism and adaptive significance are distinct concepts that do not imply each other

Why have we stressed that physiology faces *two* central questions? We have emphasized both that that physiology studies mechanism and that it studies evolutionary origins to understand adaptive significance. Why *both*? Physiologists must seek answers to both questions because *mechanism and adaptive significance do not imply each other*. If you know the mechanism of a process, you do not necessarily know anything about its adaptive significance. If you know the adaptive significance, you do not necessarily know anything about the mechanism. Thus, to understand both mechanism and adaptive significance, you must study both.

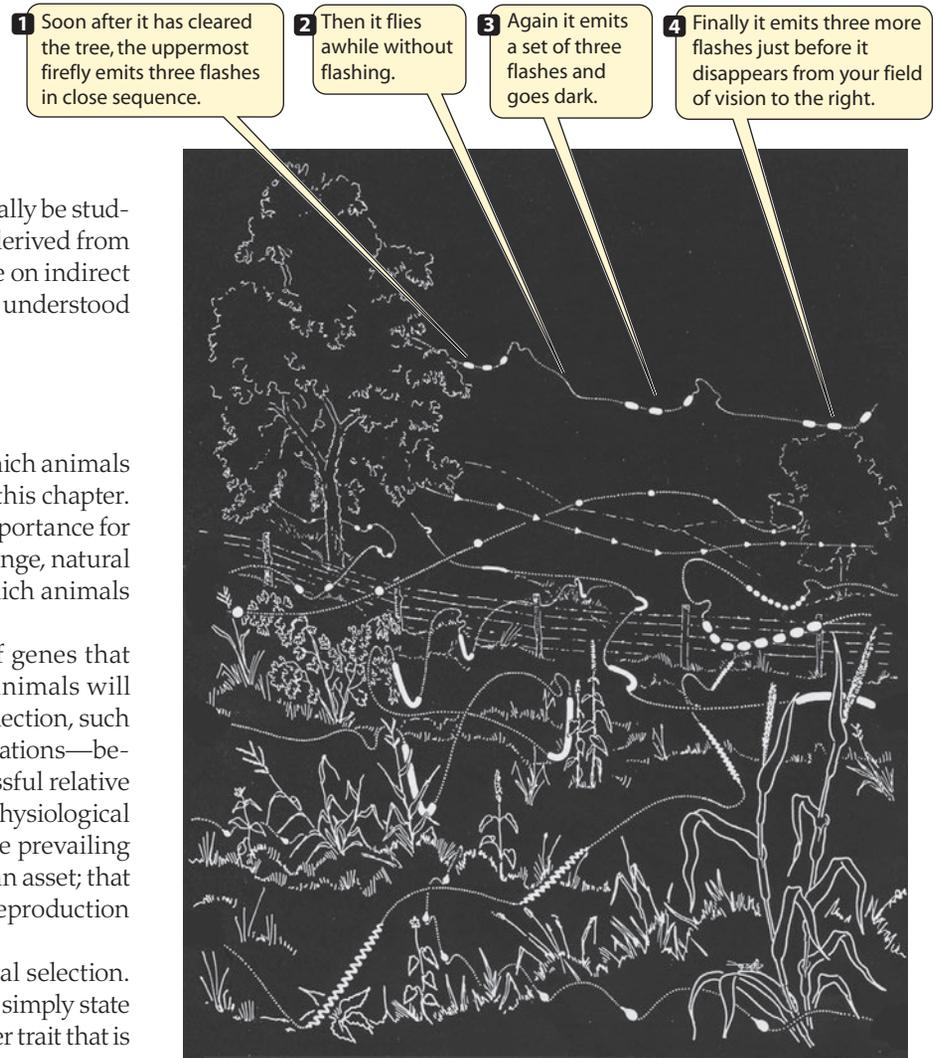


FIGURE 1.4 Male fireflies employ their mechanism of light production for an adaptive function: mate attraction. The drawing shows representative flashing patterns and flight paths of males of nine different species of fireflies of the genus *Photinus* from the eastern and central United States. Each line of flight represents a different species. For instance, the uppermost line represents *Photinus consimilis*, a species that flies high above the ground. To understand the format that you are watching the uppermost firefly as it leaves the tree, imagine that you are watching the uppermost firefly as it follows the numbered sequence. The differences in flashing and flight patterns among species allow males to signal their species to females. (From a drawing by Dan Otte in Lloyd 1966.)

As an example, consider light production by fireflies once again. Physiologists know of many mechanisms by which organisms can produce light.² Thus, even if fireflies were *required* to attract their mates with light, their mechanism of making light would not be limited theoretically to just the mechanism they use. The mechanism of light production by fireflies cannot be deduced from simple knowledge of the purpose for which the mechanism is used. Conversely, light flashes could be used for purposes other than mate attraction, such as luring prey, distracting predators, or

²The number of known mechanisms is partly obscured by the fact that *luciferin* and *luciferase* are generic terms, each used to refer to many distinctly different chemical compounds. For example, more than 30 distinctly different compounds are called *luciferin*. Accordingly, although many bioluminescent organisms are said to use a “luciferin–luciferase system” to make light, all such organisms are not by any means employing the same chemistry.

synchronizing biorhythms. The significance of light production cannot be deduced from the simple fact that light is made or from knowledge of the mechanism by which it is made.

François Jacob (b. 1920), a Nobel laureate, asked in a famous article whether evolution by natural selection more closely resembles engineering or tinkering. An engineer who is designing a machine can start from scratch. That is, an engineer can start by thinking about the very best design and then build that design from raw materials. A tinkerer who is building a new machine starts with parts of preexisting machines.

Evolution is like tinkering, Jacob argued: A population of animals that is evolving a new organ or process rarely starts from scratch; instead, it starts with elements that it already has on hand for other reasons. The lungs of mammals, for example, originated as outpocketings of a food-transport tube, the *esophagus*, in the ancient fish that gave rise to the tetrapods living on land today. Those fish, moreover, were not the only fish to evolve air-breathing organs. Today, as discussed in Chapter 23 (see page 593), there are various different groups of fish that use the *stomach*, *intestines*, *mouth cavity*,

or outpocketings of the *gill chambers* as air-breathing organs. This diversity reminds one of a tinkerer who, in the course of assembling a garden cart, might try to use axles and wheels taken from a discarded bicycle, an outdated trailer, or an old children's wagon.

Throughout evolution, animals in a sense have had to remain capable of living in their old ways even as they have developed new ways. Thus design from first principles—the engineering approach—has not been possible.

The tinkering aspect of evolution is a key reason why mechanism and adaptive significance do not imply each other. The mechanism employed to perform a particular function is not an abstraction but instead bears an imprint of the structures and processes that came before in any particular evolutionary line. Consider, for instance, the eyes of two groups of active aquatic animals: the cephalopod molluscs (squids and octopuses) and the fish. Both groups have evolved sophisticated eyes that permit lifestyles based on excellent vision. However, these eyes are built on very different retinal designs (Figure 1.5). The photoreceptors in the retinas of fish point *away* from the light; those of squids and octopuses point *toward* the light.

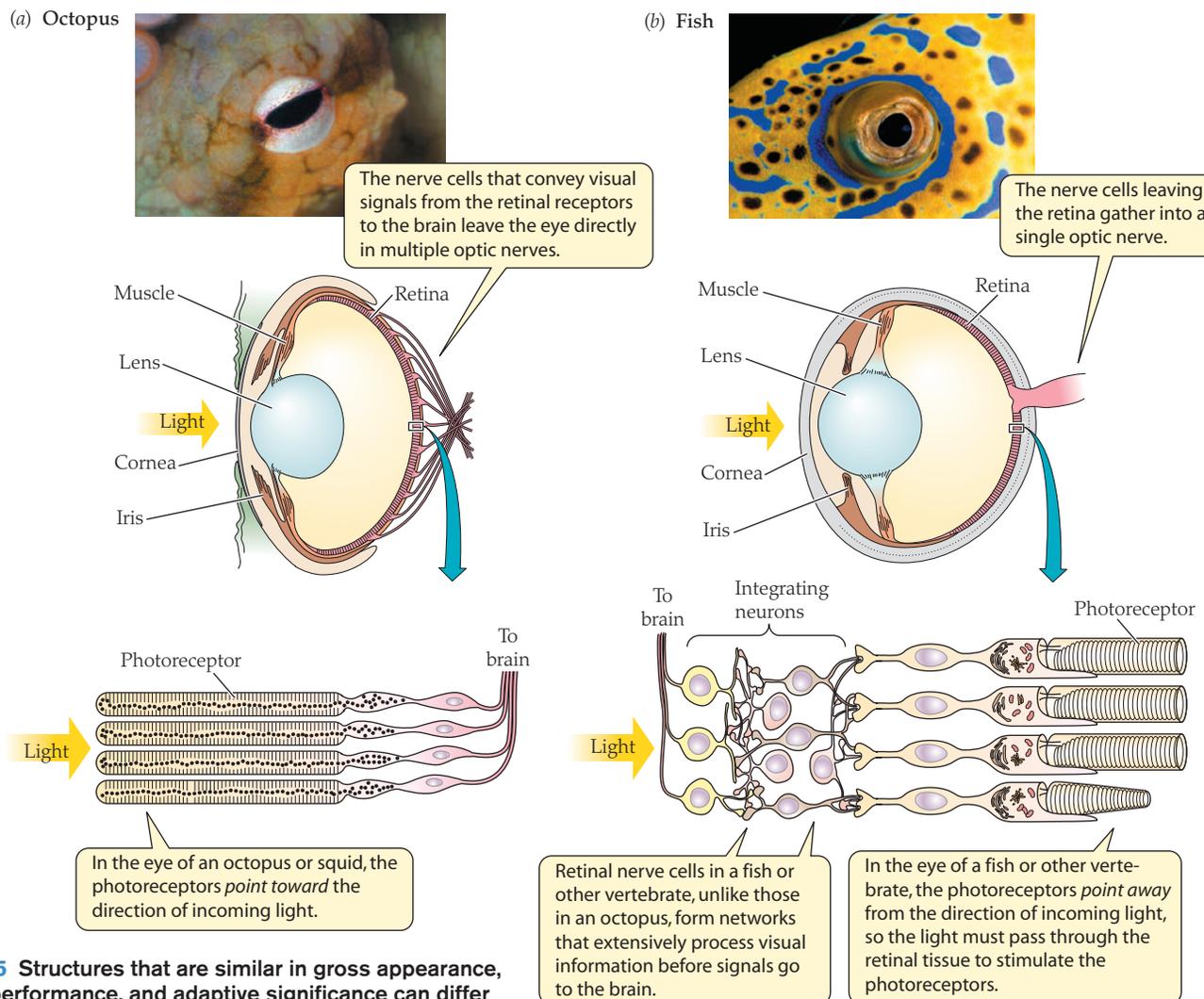


FIGURE 1.5 Structures that are similar in gross appearance, functional performance, and adaptive significance can differ dramatically in details of how they are assembled and work. Both cephalopod molluscs and fish have evolved excellent vision, but they see using different detailed mechanisms. (a after Wells 1966 and Young 1971; b after Walls 1942.)

Moreover, whereas visual signals from the fish photoreceptors are extensively processed by networks of integrating nerve cells *within* the retina before visual information is sent to the brain in a single optic nerve, in squids and octopuses the photoreceptors send their visual signals more directly to the brain in multiple optic nerves. The adaptive significance of excellent vision in the two groups of animals is similar, but the detailed mechanisms are not. A major reason for the differences in mechanisms is undoubtedly that the two groups built their eyes from different preexisting structures.

This Book's Approach to Physiology

Mechanistic physiology, which emphasizes the study of mechanism, and **evolutionary physiology**, which emphasizes the study of evolutionary origins, have become recognized as major approaches to the study of animal physiology in recent years. The two approaches share the same overall subject matter: They both address the understanding of animal function. They differ, however, in the particular aspects of physiology they emphasize. The viewpoint of this book, as stressed already, is that both approaches are essential for physiology to be fully understood.

Comparative physiology and **environmental physiology** are additional approaches to the study of animal physiology. These approaches overlap mechanistic and evolutionary physiology, and they overlap each other. Comparative physiology is the synthetic study of the function of all animals. It contrasts, for example, with *human physiology* or *avian physiology*, each of which addresses only a limited set of animals. Comparative physiology is termed *comparative* because one of its major goals is to compare systematically the ways that various sorts of animals carry out similar functions, such as vision, breathing, or circulation. Environmental physiology (also called *physiological ecology*) is the study of how animals respond physiologically to environmental conditions and challenges, or—more briefly—“ecologically relevant physiology.” **Integrative**

physiology is a relatively new term referring to investigations with a deliberate emphasis on *synthesis across levels of biological organization*, such as research that probes the relations between molecular and anatomical features of organs.

Our viewpoint in this book is mechanistic, evolutionary, comparative, environmental, and integrative. In other words, we stress:

- The mechanisms by which animals perform their life-sustaining functions
- The evolution and adaptive significance of physiological traits
- The ways in which diverse phylogenetic groups of animals both resemble each other and differ
- The ways in which physiology and ecology interact, in the present and during evolutionary time
- The importance of all levels of organization—from genes to proteins, and tissues to organs—for the full understanding of physiological systems

Overlapping with the classifications already discussed, physiology is divided also into various branches or disciplines based on the *types of functions* that are performed by animals. The organization of this book into parts and chapters is based on the types of function. As **Table 1.1** shows, the book consists of six major subdivisions, Parts I through VI, each of which focuses on a particular set of functions. The chapters within each part discuss particular aspects of the part topic. The last chapter in each part (except Part I) is an “At Work” chapter that takes a synthetic approach to a prominent, curiosity-provoking topic in the part. *The principal goal of the “At Work” chapters is to show how the material in each of the parts can be used in an integrated way to understand animal function.*

Now, as they say in theater, “Let the play begin.” As we consider the principal subject of this chapter—function on the ecological stage—the three major players are animals, environments, and evolutionary processes (see Figure 1.2). We now address each.

TABLE 1.1 The organization of this book

The “At Work” chapters, printed in italics, exemplify how the material covered in each part of the book can be used synthetically to understand a problem in animal physiology.

Parts	Topics within parts
Part I: Fundamentals of Physiology	• Animals and Environments (Chapter 1) • Molecules and Cells (Chapter 2) • Genomics and Proteomics (Chapter 3) • Physiological Development and Epigenetics (Chapter 4) • Transport of Solutes and Water (Chapter 5)
Part II: Food, Energy, and Temperature	• Nutrition, Feeding, and Digestion (Chapter 6) • Energy Metabolism (Chapter 7) • Aerobic and Anaerobic Metabolism (Chapter 8) • Exercise (Chapter 9) • Thermal Relations (Chapter 10) • <i>Mammals in Frigid Places (Chapter 11)</i>
Part III: Integrating Systems	• Neurons (Chapter 12) • Synapses (Chapter 13) • Sensory Processes (Chapter 14) • Nervous Systems; Biological Clocks (Chapter 15) • Endocrine and Neuroendocrine Physiology (Chapter 16) • Reproduction (Chapter 17) • <i>Animal Navigation (Chapter 18)</i>
Part IV: Movement and Muscle	• Control of Movement (Chapter 19) • Muscle (Chapter 20) • <i>Muscle Plasticity in Use and Disuse (Chapter 21)</i>
Part V: Oxygen, Carbon Dioxide, and Internal Transport	• Oxygen and Carbon Dioxide Basics (Chapter 22) • Breathing (Chapter 23) • Gas Transport in Blood (Chapter 24) • Circulation (Chapter 25) • <i>Diving by Marine Mammals (Chapter 26)</i>
Part VI: Water, Salts, and Excretion	• Water and Salt Basics (Chapter 27) • Water and Salt Physiology of Animals in Their Environments (Chapter 28) • Kidneys and Excretion (Chapter 29) • <i>Mammals of Deserts and Dry Savannas (Chapter 30)</i>

Animals

The animal properties that deserve mention in an initial overview are the properties that are of overriding importance. These include that (1) animals are *structurally dynamic*, (2) animals are *organized* systems that *require energy* to maintain their organization, and (3) both *time* and *body size* are of fundamental significance in the lives of all animals.

One of the most profoundly important properties of animals is that the atoms of their bodies—their material building blocks—are in dynamic exchange with the atoms in their environments throughout life. This structural dynamism—memorably termed “the dynamic state of body constituents” by Rudolf Schoenheimer, who discovered it³—is a fundamental and crucially important way in which animals differ from inanimate objects such as telephones. After a telephone is manufactured, the particular carbon and iron atoms that are built into its substance remain as long as the telephone exists. One might think by casual observation that the composition of a person, lion, or crab is similarly static. This illusion was abruptly dispelled, however, when Schoenheimer and others began using chemical isotopes as research tools.

Isotopes proved to be revealing because they permit atoms to be labeled and therefore tracked. Consider iron as an example. Because most iron atoms in the natural world are of atomic weight 56 (⁵⁶Fe), an investigator can distinctively label a particular set of iron atoms by substituting the unusual (but *stable*) alternative isotope of iron having an atomic weight of 58 (⁵⁸Fe). Suppose that we make a telephone in which all the iron atoms are of the unusual ⁵⁸Fe isotope, so that we can distinguish those iron atoms from the ones generally available. Years later, all the iron atoms in the telephone will still be of the unusual ⁵⁸Fe type. Suppose, however, that we create a ⁵⁸Fe-labeled person by feeding the person over the course of a year the unusual ⁵⁸Fe isotope, so that isotopically distinctive iron atoms are built into hemoglobin molecules and other iron-containing molecules throughout the person’s body. Suppose we then stop providing the unusual iron isotope in the person’s diet. Thereafter—as time goes by—the isotopically distinctive ⁵⁸Fe atoms in the body will leave and will be replaced with atoms of the ordinary isotope, ⁵⁶Fe, from the environment. Years later, all the unusual iron atoms will be gone. We see, therefore, that although the person may outwardly appear to be structurally constant like a telephone, the iron atoms in the substance of the person’s body at one time differ from those at another time.

The mechanistic reason for the turnover of iron atoms in an animal is that the molecular constituents of an individual’s body break down and are rebuilt. A human red blood cell, for example, typically lives for only 4 months. When a red blood cell is discarded and replaced, some of the iron atoms from the hemoglobin molecules of the old cell are excreted into the environment, and some of the iron atoms built into the new cell are acquired from food. In this way, even though the number of red blood cells remains relatively constant, the iron atoms of the cells are in dynamic exchange with iron atoms in the environment.

Essentially all the atoms in the substance of an animal’s body undergo similar dynamic exchanges. Calcium atoms enter an animal’s skeleton and later are withdrawn; some of the withdrawn atoms are replaced with newly ingested calcium atoms from the environment. Proteins and fats throughout an animal’s body are continually broken down at substantial rates,⁴ and their resynthesis is carried out in part with molecules newly acquired from the environment, such as amino acids and fatty acids from foods. Adult people typically resynthesize 2–3% of their body protein *each day*, and about 10% of the amino acids used to build the new protein molecules are acquired from food.

Have you ever wondered why you need to worry *every week* about whether you are eating enough calcium, iron, magnesium, and protein? The explanation is provided by the principles we are discussing. If you were an inanimate object, enough of each necessary element or compound could be built into your body at the start, and you would then have enough forever. Instead, because you are alive and dynamic—rather than inanimate and static—you lose elements and compounds every day and must replace them.

As this discussion has illustrated, the *material boundaries* between an animal and its environment are blurred, not crisp. Atoms cross the boundaries throughout life, so that an atom that is part of an animal’s tissues on one day may be lying on the forest floor or drifting in the atmosphere the next day, and vice versa. Possibly the most profound implication of these facts is that *an animal is not a discrete material object*.

The structural property of an animal that persists through time is its organization

If the atomic building blocks of an animal are transient, by what structural property is an animal *defined*? The answer comes from imagining that we can see the individual molecules in an adult animal’s body. If we could, we would observe that the molecular structures and the spatial relations of molecules in tissues are relatively constant over time, even though the particular atoms constructing the molecules change from time to time. A rough analogy would be a brick wall that retains a given size and shape but in which the bricks are constantly being replaced, so that the particular bricks present during one month are different from those present a month earlier.

The structural property of an animal that persists through time is the *organization* of its atomic building blocks, not the building blocks themselves. *Thus an animal is defined by its organization*. This characteristic of animals provides the most fundamental reason why animals require inputs of energy throughout life. As we discuss in detail in Chapter 7, the second law of thermodynamics says that for organization to be maintained in a dynamic system, use of energy is essential.

Most cells of an animal are exposed to the internal environment, not the external environment

Shifting our focus now to the cells of an animal’s body, it is important first to stress that the conditions experienced by most of an animal’s cells are the conditions *inside* the body, not those outside. Most cells are bathed by the animal’s tissue fluids or blood. Thus

³As chemists learned about and started to synthesize unusual isotopes in the 1930s, Rudolf Schoenheimer (1898–1941) was one of the first to apply the newfound isotopes to the study of animal metabolism. His classic book on the subject, published posthumously as World War II raged, is titled *The Dynamic State of Body Constituents*.

⁴See Chapter 2 (page 55) for a discussion of the ubiquitin–proteasome system that tags proteins for breakdown and disassembles them.

the *environment* of most cells consists of the set of conditions prevailing in the tissue fluids or blood. Claude Bernard (1813–1878), a Frenchman who was one of the most influential physiologists of the nineteenth century, was the first to codify this concept. He coined the term **internal environment** (*milieu intérieur*) to refer to the set of conditions—temperature, pH, sodium (Na^+) concentration, and so forth—experienced by cells within an animal's body. The conditions outside the body represent the **external environment**.

The internal environment may be permitted to vary when the external environment changes, or it may be kept constant

Animals have evolved various types of relations between their internal environment and the external environment. If we think of the organization of the body as being hierarchically arranged, the relations between the internal and external environments represent one of the potential hierarchical levels at which animals may exhibit organization. At a primary level, *all* animals consistently exhibit structural organization of their atoms and molecules. At this additional, secondary level, animals sometimes—but only sometimes—exhibit further organization by keeping their internal environment distinct from their external environment.

Animals display two principal types of relation between their internal and external environments. On the one hand, when the conditions outside an animal's body change, the animal may permit its internal environment to match the external conditions and thus change along with the outside changes. On the other hand, the animal may maintain constancy in its internal environment. These alternatives are illustrated with temperature in Figure 1.6. If the temperature of an animal's external environment changes, one option is for the animal to let its internal temperature change to match the external temperature (see Figure 1.6a). Another option is for the animal to maintain a constant internal temperature (see Figure 1.6b). If an animal permits internal and external conditions to be equal, it is said to show **conformity**. If the animal maintains internal constancy in the face of external variability, it shows **regulation**. Conformity and regulation are extremes; intermediate responses are common.

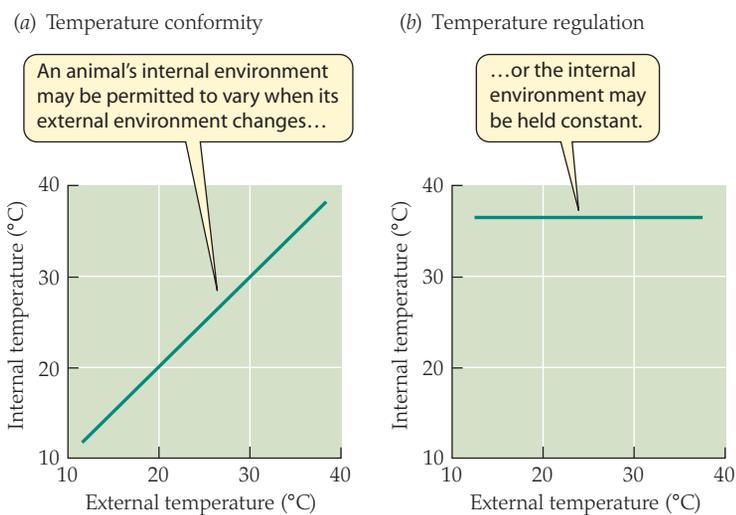


FIGURE 1.6 Conformity and regulation These examples from the study of temperature illustrate the general principles of conformity (a) and regulation (b).

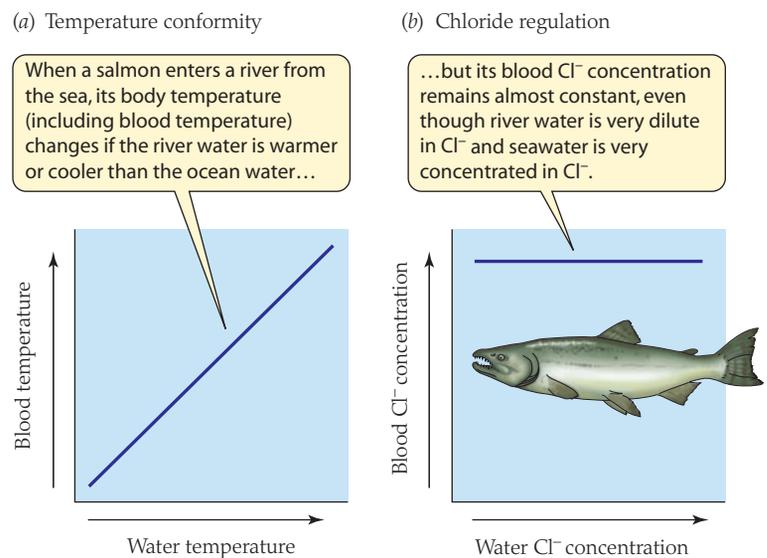


FIGURE 1.7 Mixed conformity and regulation in a single species Salmon are temperature conformers but chloride regulators. The presentation of Cl^- regulation is diagrammatic; the blood Cl^- concentration is not in fact absolutely constant but is a little higher when the fish are in seawater than when they are in freshwater.

Animals frequently show conformity with respect to some characteristics of their internal environment while showing regulation with respect to others. Consider a salmon, for example (Figure 1.7). Like most fish, salmon are *temperature conformers*; they let their internal temperature match the surrounding water temperature (see Figure 1.7a). Simultaneously, salmon are excellent *chloride regulators*; they maintain a nearly constant concentration of Cl^- ions in their blood, regardless of how high or low the outside Cl^- concentration is (see Figure 1.7b).

Regulation demands more energy than conformity because regulation represents a form of organization. During regulation, organization is manifested both by the maintenance of *constancy* inside the body and by the maintenance of a *distinction* between inside and outside conditions. A familiar analogy for the energy costs of regulation in animals is provided by home heating. A great deal of energy is required to keep the inside of a house at 22°C (72°F) during the cold of winter. This energy cost is entirely avoided if the inside temperature is simply allowed to match the outside temperature.

Homeostasis in the lives of animals: Internal constancy is often critical for proper function

Homeostasis is an important concept regarding the *nature* and *significance* of internal constancy. Soon we will define homeostasis using the words of Walter Cannon (1871–1945), who coined the term. To fully appreciate the concept, however, we must first recognize its historical roots in medicine. The two men who contributed the most toward developing the concept of homeostasis, Claude Bernard and Walter Cannon, were physicians and medical researchers, concerned primarily with human physiology. Healthy humans maintain remarkable constancy of conditions in their blood and tissue fluids. The notion of homeostasis was thus conceived during studies of a species that exhibits exceptional internal constancy, and later the notion was extrapolated to other animals.

BOX 1.1 NEGATIVE FEEDBACK

The type of control that Claude Bernard discovered in his studies of blood glucose is what today we call *negative feedback*. In any control system, the **controlled variable** is the property that is being kept constant or relatively constant by the system's activities. The **set point** is the level at which the controlled variable is to be kept. **Feedback** occurs if the system uses information on the controlled variable itself to govern its actions. In **negative feedback**, the system responds to changes in the controlled variable by bringing the variable back toward its set point; that is, the system *opposes deviations* of the controlled variable from the set point. There are many detailed mechanisms by which negative feedback can be brought about in physiological systems. Negative feedback, however, is virtually synonymous with homeostasis and occurs in all homeostatic systems.

In the case of the blood glucose level that so intrigued Claude Bernard, the control system adds glucose to the blood if the blood glucose concentration—the controlled variable—falls below its set-point concentration, thereby opposing the deviation of the blood concentration from the set point. The control system removes glucose from the blood if the glucose concentration rises too high, thereby again opposing the deviation of the concentration from its set point. Biologists and engineers who study control systems have established that no control system can maintain perfect constancy in a controlled variable; putting the case roughly, a controlled variable must be a moving target for a control system to act on it. Thus the blood glucose concentration is not kept perfectly constant by the glucose control system, but during normal health it is kept from varying outside a narrow range.

Box 10.2 will provide greater detail about control systems based on negative feedback.

In **positive feedback**, a control system *reinforces deviations* of a controlled variable from its set point. Positive feedback is much less common in physiological systems than negative feedback. It is more common during normal function than is usually recognized, however. For example, positive feedback occurs when action potentials (nerve impulses) develop in nerve cells (see Figure 12.16), and it also occurs during the birth process in mammals (see Figure 17.16). In the first case, a relatively small change in the voltage across the nerve-cell membrane modulates the properties of the membrane in ways that amplify the voltage change. In the second, muscular contractions acting to expel the fetus from the uterus induce hormonal signals that stimulate ever-more-intense contractions.

Claude Bernard was the first to recognize the impressive stability of conditions that humans maintain in their blood and tissue fluids. One of Bernard's principal areas of study was blood glucose in mammals. He observed that the liver takes up and releases glucose as necessary to maintain a relatively constant glucose concentration in the blood. If blood glucose rises, the liver removes glucose from the blood. If blood glucose falls, the liver releases glucose into the blood. Bernard stressed that, as a consequence, most cells in the body of a mammal experience a relatively constant environment with respect to glucose concentration (Box 1.1). Bernard's research and that of later investigators also revealed that most cells in a mammal's body experience relative constancy of temperature, O₂ level, osmotic pressure, pH, Na⁺ concentration, Cl⁻ concentration, and so on because various organs and tissues regulate these properties at consistent levels in the body fluids bathing the cells.

Claude Bernard devoted much thought to the *significance* of internal constancy in humans and other mammals. He was greatly impressed with how freely mammals are able to conduct their lives regardless of outside conditions. Mammals, for example, can wander about outdoors in the dead of winter, seeking food and mates, whereas fish or insects—in sharp contrast—are often driven into a sort of paralysis by winter's cold. Bernard reasoned that mammals are able to function in a consistent way regardless of varying outside conditions because the cells inside their bodies enjoy constant conditions. He thus stated a hypothesis that remains probably the most famous in the history of animal physiology: "*Constancy of the internal environment is the condition for free life.*" A modern translation might go like this: Animals are able to lead lives of greater freedom and independence to the extent that they maintain a stable internal environment, sheltering their *cells* from the variability of the outside world.

Walter Cannon, a prominent American physiologist who was born in the same decade that Claude Bernard died, introduced the concept of homeostasis to refer to internal constancy in animals. In certain ways, Bernard's and Cannon's views were so similar that

Bernard might have invented the homeostasis concept, but the implications of internal constancy were clearer by Cannon's time. Because animals dynamically interact with their environments, the temperature, pH, ion concentrations, and other properties of their bodies are incessantly being drawn away from stability. Cannon emphasized that for an animal to be internally stable, vigilant physiological mechanisms must be present to correct deviations from stability. Thus, when Cannon introduced and defined the term **homeostasis**, he intended it to mean not just internal constancy, but also the existence of regulatory systems that automatically make adjustments to maintain internal constancy. In his own words, Cannon at one point described homeostasis as "the coordinated physiological processes which maintain most of the [constant] states in the organism."

An essential aspect of Cannon's perspective was his conviction that homeostasis is good. Cannon argued, in fact, that homeostasis is a signature of highly evolved life. He believed that animal species could be ranked according to their degree of homeostasis; in his view, for example, mammals were superior to frogs because of their greater degree of homeostasis. Late in life, Cannon even argued that human societies could be ranked on a scale of homeostasis—self-regulatory and internally constant societies being inherently superior to others.

HOMEOSTASIS IN THE MODERN STUDY OF ANIMAL PHYSIOLOGY

The concept of ranking animals using degrees of homeostasis seems misguided to most biologists today. Bernard and Cannon, having focused on mammals, articulated ideas that are truly indispensable for understanding mammalian biology and medicine. However, the mere fact that mammals exhibit a high degree of homeostasis does not mean that other animals should be held to mammalian standards. Animals that exhibit less-complete homeostasis than mammals coexist in the biosphere with mammals. Indeed, the vast majority of animals thriving today do not achieve "mammalian standards" of homeostasis. Thus most biologists to-

day would argue that a high degree of homeostasis is merely one of several ways to achieve evolutionary and ecological success. In this view, Bernard and Cannon did not articulate universal requirements for success, but instead they clarified the properties and significance of *one particular road* to success.

Recent research has clarified, in fact, that organisms sometimes achieve success in the biosphere precisely by letting their internal environment *vary* with the external environment: the antithesis of homeostasis. Consider, for example, insects that overwinter within plant stems in Alaska. They survive by ceasing to be active, allowing their internal temperatures to fall to below -40°C , and tolerating such low tissue temperatures. Any attempt by such small animals to maintain an internally constant temperature from summer to winter would be so energetically costly that it would surely end in death; thus the tolerance of the insects to the *change* of their internal temperature in winter is a key to their survival. Even some mammals—the hibernators—survive winter by *abandoning constancy* of internal temperature; hibernating mammals allow their body temperatures to decline and sometimes match air temperature. For lizards in deserts, tolerance of profound dehydration is often a key to success.

Both constancy and inconstancy of the internal environment—regulation and conformity—have disadvantages and advantages:

- **Regulation.** The chief disadvantage of regulation is that it costs energy. The great legacy of Bernard and Cannon is that they clarified the advantage that animals enjoy by paying the cost: Regulation permits cells to function in steady conditions, independent of variations in outside conditions.
- **Conformity.** The principal disadvantage of conformity is that cells within the body are subject to changes in their conditions when outside conditions change. The chief advantage of conformity is that it avoids the energy costs of keeping the internal environment different from the external environment. Conformity is energetically cheap.

Neither regulation nor conformity is categorically a defect or an asset. One cannot understand mammals or medical physiology

without understanding homeostasis, but one cannot understand the full sweep of animal life without recognizing that physiological flexibility is sometimes advantageous.

Time in the lives of animals: Physiology changes in five time frames

Time is a critical dimension for understanding the physiology of all animals because the physiology of animals invariably changes from time to time. Even animals that exhibit homeostasis undergo change. Details of their internal environment may change. Moreover, the regulatory processes that *maintain* homeostasis must change from time to time so that homeostasis can prevail, much as day-to-day adjustments in the fuel consumption of a home furnace are required to maintain a constant air temperature inside the home during winter.

An important organizing principle for understanding the role of time in the lives of animals is to recognize *five major time frames* within which the physiology of an animal can change. The time frames fall into two categories: (1) responses of physiology to changes in the external environment and (2) internally programmed changes of physiology. **Table 1.2** lists the five time frames classified in this way. We will recognize these five time frames throughout this book as we discuss various physiological systems.

The concept of the five time frames overlies other ways of organizing knowledge about animal function. For example, the concept of time frames overlies the concepts of regulation, conformity, and homeostasis that we have just discussed. When we speak of regulation, conformity, and homeostasis, we refer to *types* of responses that animals show in relation to variations in their external environments. When we speak of the time frames, we address *when* those responses occur.

PHYSIOLOGY RESPONDS TO CHANGES IN THE EXTERNAL ENVIRONMENT IN THREE TIME FRAMES

Individual animals subjected to a change in their external environment exhibit *acute* and *chronic* responses to the environmental change. **Acute responses**, by

TABLE 1.2 The five time frames in which physiology changes

Type of change	Description
Changes in physiology that are responses to changes in the external environment	
1. Acute changes	Short-term changes in the physiology of individual animals: changes that individuals exhibit soon after their environments have changed. Acute changes are reversible.
2. Chronic changes (termed <i>acclimation</i> and <i>acclimatization</i> ; also termed <i>phenotypic plasticity</i> or <i>phenotypic flexibility</i>)	Long-term changes in the physiology of individual animals: changes that individuals display after they have been in new environments for days, weeks, or months. Chronic changes are reversible.
3. Evolutionary changes	Changes that occur by alteration of gene frequencies over the course of multiple generations in populations exposed to new environments.
Changes in physiology that are internally programmed to occur whether or not the external environment changes	
4. Developmental changes	Changes in the physiology of individual animals that occur in a programmed way as the animals mature from conception to adulthood and then to senescence (see Chapter 4).
5. Changes controlled by periodic biological clocks	Changes in the physiology of individual animals that occur in repeating patterns (e.g., each day) under control of the animals' internal biological clocks (see Chapter 15).

definition, are responses exhibited during the first minutes or hours after an environmental change. **Chronic responses** are expressed following prolonged exposure to new environmental conditions. You might wonder why an individual's immediate responses to an environmental change differ from its long-term responses. The answer is that the passage of time permits biochemical or anatomical restructuring of an animal's body. When an animal suddenly experiences a change in its environment, its immediate responses must be based on the "old," preexisting properties of its body because the animal has no time to restructure. A morphological example is provided by a person who suddenly is required to lift weights after months of totally sedentary existence. The sedentary person is likely to have small arm muscles, and his immediate, *acute* response to his new weight-lifting environment will likely be that he can lift only light weights. However, if the person lifts weights repeatedly as time goes by, restructuring will occur; his muscles will increase in size. Thus his *chronic* response to the weight-lifting environment will likely be that he can lift heavy weights as well as light ones.

A familiar *physiological* example of acute and chronic responses is provided by human reactions to work in hot weather. We all know that when we are first exposed to hot weather after a period of living in cool conditions, we often feel quickly exhausted; we say the heat is "draining." We also know that this is not a permanent state: If we experience heat day after day, we feel more and more able to work in the heat.

Figure 1.8 shows that these impressions are not merely subjective illusions. Twenty-four physically fit young men who lacked recent

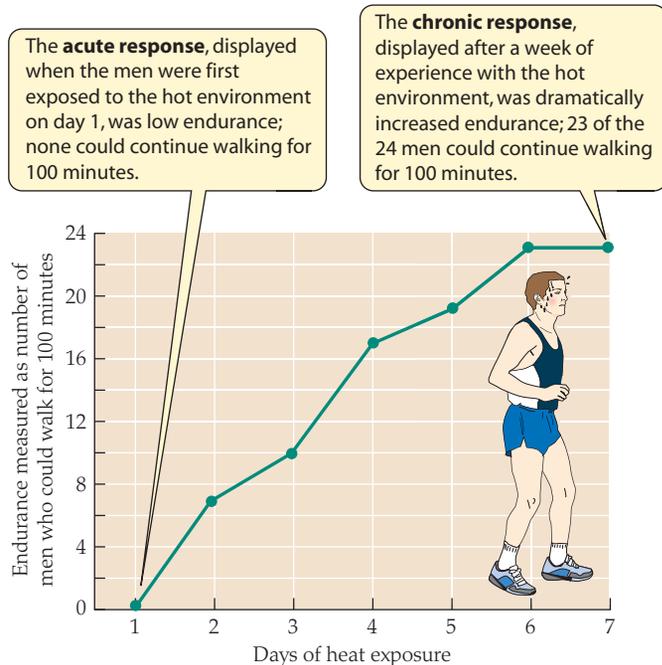


FIGURE 1.8 Heat acclimation in humans as measured by exercise endurance Twenty-four fit young men without recent heat experience were asked to walk at 3.5 miles per hour in hot, dry air (49°C, 20% relative humidity). Their endurance was used as a measure of their physiological capability to engage in moderate work under hot conditions. The acclimation illustrated by the chronic response is reversible; if heat-acclimated men return to a life of no heat exposure, they gradually revert to the level of endurance evident on day 1. (After Pandolf and Young 1992.)

experience with hot weather were asked to walk at a fixed pace in hot, relatively dry air. Their endurance was measured as a way of quantifying their physiological ability to sustain moderate exercise under the hot conditions. None of the men had sufficient endurance to walk for 100 minutes (min) on the first day. However, as the days passed and the men had more and more experience with hot conditions, their endurance increased, as indicated by a steady increase in the number of men who could keep walking for 100 min.

From research on the physiology of human work under hot conditions, physiologists know that endurance under hot conditions changes because as people gain increased experience with heat, their rates of sweat secretion increase, their sweat glands are able to maintain high rates of sweat secretion for dramatically lengthened periods of time, their sweat becomes more dilute (so they lose less salt), the blood flow to their skin becomes more vigorous (improving delivery of internal heat to the body surface), and their heart rates during exercise in the heat become lower. Thus human physiology is restructured in many ways by repeated exposure to heat. For a person who has been living in cool conditions, the *acute* physiological responses to heat exposure are low exercise endurance, a low rate of sweat production, and so forth. Heat training poises a person to express *chronic* physiological responses to heat, such as high exercise endurance and a high capacity to sweat.

The acute and chronic responses are, by definition, phenotypic responses of *individual animals* to environmental change. *Populations* may exhibit a third category of response to environmental change: **evolutionary responses** involving changes of genotypes. Collectively, therefore, animals display responses to environmental change in three time frames:

- Individuals exhibit immediate, *acute* responses.
- Individuals exhibit long-term, *chronic* responses. The length of time that an individual must be exposed to a new environment for chronic responses to be fully expressed is usually a few days to a few weeks.
- Populations exhibit *evolutionary* responses.

Chronic responses by individual animals to environmental change are so common, diverse, and important that their study forms a special discipline with its own terminology. For many physiologists, the concepts of *acclimation* and *acclimatization* provide an important way to classify the chronic responses of individuals to environmental change. A chronic response to a changed environment is called **acclimation** if the new environment differs from the preceding environment in just a few highly defined ways.⁵ Acclimation is thus a laboratory phenomenon. **Acclimatization** is a chronic response of individuals to a changed environment when the new and old environments are different *natural* environments that can differ in numerous ways, such as winter and summer, or low and high altitudes. Thus animals are said to *acclimatize* to winter, but they *acclimate* to different defined temperatures in a laboratory experiment.

Acclimation and acclimatization are types of **phenotypic plasticity**: the ability of an individual animal (a single genotype) to express two or more genetically controlled phenotypes. Phenotypic plasticity is possible because an individual invariably possesses the genetic code

⁵ Some authors restrict use of the word *acclimation* to cases in which just one property differs between environments.

BOX 1.2 THE EVOLUTION OF PHENOTYPIC PLASTICITY

When animals express different genetically controlled phenotypes in different environments—when they acclimate and acclimatize—they require controls that determine which particular phenotypes are expressed in which particular environments. As an illustration, suppose that an individual animal has four possible phenotypes, *P1* through *P4*, and that there are four environments, *E1* through *E4*. One option is that the individual could express phenotype *P1* in environment *E3*, *P2* in *E4*, *P3* in *E1*, and *P4* in *E2*. This set of *correspondences* between phenotypes and environments constitutes the individual's **norm of reaction**; that is, if we think of the phenotypes as one list and the environments as a second list in a matching game, the *norm of reaction* is like the set of lines that we would draw between items on the two lists to indicate which item on one matches which on the other.

Because it is genetically determined, *the norm of reaction itself can evolve and is subject to natural selection*. To see this, suppose that an individual other than the one just discussed expresses phenotype *P1* in environment *E1*, *P2* in *E2*, *P3* in *E3*, and *P4* in *E4*. In this case, the two individuals would differ in their norms of reaction. Suppose, now, that there is a population—living in a variable environment—that is composed half of individuals with the first reaction norm and half of individuals with the second. If individuals of the first sort were to survive and reproduce more successfully as the environment varied, natural selection for the first reaction norm would occur. In this way the reaction norm itself would evolve in ways that would better adapt the animals to the variable environment in which they live.

A simple example is provided by tanning in people with light complexions. Suppose

that there are two possible integumentary phenotypes: *high melanin* and *low melanin*. Suppose also that there are two environments: *high sun* and *low sun*. One possible norm of reaction would be to express high melanin in low sun and low melanin in high sun. Another norm of reaction would be to express high melanin in high sun and low melanin in low sun. If both of these reaction norms once existed, it is easy to understand why individuals with the second reaction norm would have left more progeny than those with the first, leading to the evolution of the sort of reaction norm we see today among people with light complexions.

Phenotypic plasticity *itself* can evolve, and norms of reactions can themselves be adaptations.

to adopt multiple phenotypes (Box 1.2). Growth of the biceps muscle during weight training provides a simple example of a change in phenotype under control of genetically coded mechanisms. Another example is that the particular suite of enzymes active in an adult person may change from one time to another because the genes for one suite of enzymes are expressed under certain environmental conditions, whereas the genes for another suite are expressed under different conditions.⁶ Phenotypic plasticity is discussed in more detail—with several additional examples—in Chapter 4.

PHYSIOLOGY UNDERGOES INTERNALLY PROGRAMMED CHANGES IN TWO TIME FRAMES

The physiological properties of individuals sometimes change even if their external environment stays constant. For instance, the type of hemoglobin in your blood today is different from the type you produced as a newborn. This change in hemoglobin is internally programmed: It occurs even if your external environment stays constant. Sometimes internally programmed changes interact with environmental changes. For instance, an internally programmed change might occur sooner, or to a greater amplitude, in one environment than in another. However, the internally programmed changes do not require any sort of environmental activation. There are two principal types of internally programmed change: developmental changes and changes controlled by periodic biological clocks.

Development is the progression of life stages from conception to senescence in an individual. Different genes are internally programmed to be expressed at different stages of development, giving rise to **developmental changes in an animal's phenotype**. Puberty is a particularly dramatic example of internally programmed developmental change in humans. The environment

may change the timing of puberty—as when the advent of sexual maturity is delayed by malnutrition—but puberty always occurs, no matter what the environment, illustrating that internally programmed changes do not require environmental activation. Physiological development is one of the principal topics addressed in Chapter 4.

Biological clocks are mechanisms that give organisms an internal capability to keep track of the passage of time. Most biological clocks resemble wristwatches in being periodic; that is, after they complete one timing cycle, they start another, just as a wristwatch starts to time a new day after it has completed timing of the previous day. These sorts of biological clocks emit signals that cause cells and organs to undergo internally programmed, repeating cycles in their physiological states, thereby giving rise to **periodic, clock-controlled changes in an animal's phenotype**. An enzyme under control of a biological clock, for instance, might increase in concentration each morning and decrease each evening, not because the animal is responding to changes in its outside environment, but because of the action of the clock. The changes in enzyme concentration might mean that an animal is inherently better able to digest a certain type of food at one time of day than another, or is better able to destroy a certain type of toxin in the morning than in the evening. Biological clocks typically synchronize themselves with the external environment, but they go through their timing cycles inherently, and they can time physiological changes for days on end without environmental input. They are discussed in greater detail in Chapter 15.

Size in the lives of animals: Body size is one of an animal's most important traits

How big is it? is one of the most consequential questions you can ask about any animal. This is true because within sets of related species, many traits vary in regular ways with their body sizes. The

⁶Enzymes that vary in amount as a result of changes in environmental conditions are termed *inducible* enzymes. An excellent illustration is provided by the P450 enzymes discussed at length in Chapter 2 (see page 48).

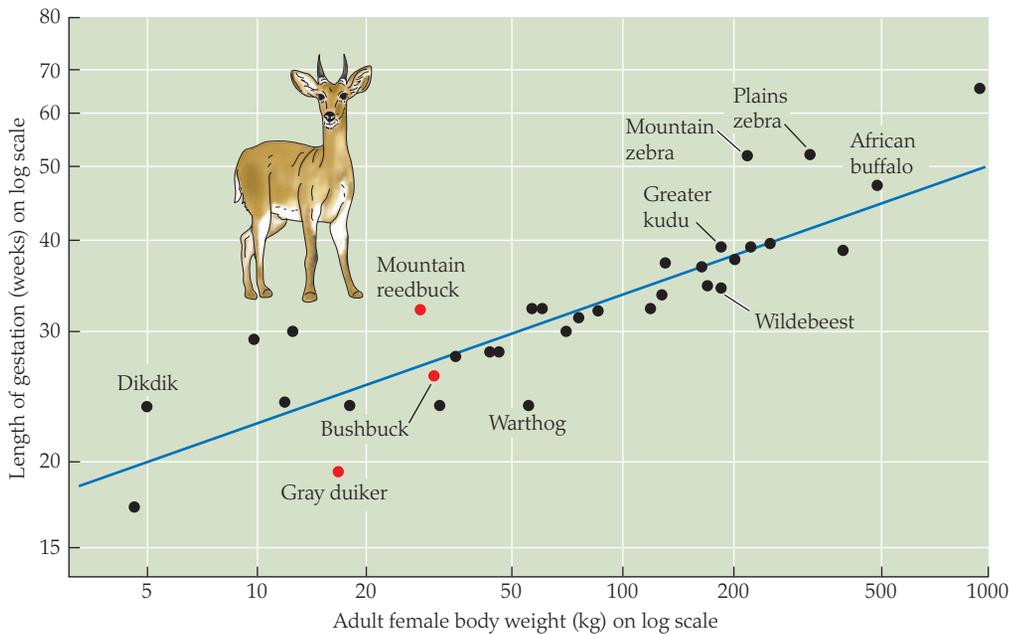


FIGURE 1.9 Length of gestation scales as a regular function of body size in mammals The data points—each representing a different species—are for African herbivorous mammals weighing 5 to 1000 kg as adults. The line (fitted by ordinary least squares regression; see Appendix D) provides a statistical description of the overall trend and thus depicts the gestation length that is statistically expected of an average or ordinary animal at each body size. Both axes use logarithmic scales, explaining why the numbers along the axes are not evenly spaced (see Appendix E). (After Owen-Smith 1988.)

length of gestation, for example, is a regular function of body size in mammals (Figure 1.9). Brain size, heart rate, the rate of energy use, the age of sexual maturity, and hundreds of other physiological and morphological traits are also known to vary in systematic ways with body size in mammals and other phylogenetically related sets of animal species. The study of these relations is known as the study of **scaling** because related species of large and small size can be viewed as *scaled-up* and *scaled-down* versions of their type.

Knowledge of the statistical relationship between a trait and body size is essential for identifying specializations and adaptations of particular species. To illustrate, let's ask if two particular African antelopes, the bushbuck and mountain reedbuck, have specialized or ordinary lengths of gestation. Answering this question is complicated precisely because there is no single norm of mammalian gestation length to use to decide. Instead, because the length of gestation is a regular function of body size, a biologist needs to consider the sizes of the species to know what is average or ordinary.

Statistical methods can be used to derive a line that best fits a set of data. In the study of scaling, the statistical method that has traditionally been considered most appropriate is **ordinary least squares regression** (see Appendix D). The line in Figure 1.9 was calculated by this procedure. This line shows the average trend in the relationship between gestation length and body size. The line is considered to show the length of gestation *expected* of an ordinary species at each body size.

With this information on *expected* gestation lengths, now we can address the question asked earlier: Are the bushbuck and mountain reedbuck specialized or ordinary? Notice that the length of gestation

in the bushbuck is very close to what the line in Figure 1.9 predicts for an animal of its size. The bushbuck, therefore, adheres to what is expected for its size: It has an ordinary gestation length when its size is taken into account. The mountain reedbuck, however, is far off the line. According to the line, as shown in Table 1.3, an animal of the reedbuck's size is expected to have a gestation lasting 26.5 weeks, but actually the reedbuck's gestation lasts 32 weeks. Thus the reedbuck seems to have evolved a specialized, exceptionally long gestation. Similarly, the gray duiker seems to have evolved an exceptionally short length of gestation for *its* size (see Figure 1.9).

In the last 15 years, physiologists have recognized that ordinary least squares regression may not always be the best procedure for fitting lines to scaling data because the ordinary least squares procedure does not take into account the family tree of the species studied; it simply treats each data point as

being fully independent of all the other data points (see Appendix D). Increasingly, therefore, physiologists have fitted lines not only by the ordinary least squares procedure but also by an alternative procedure based on **phylogenetically independent contrasts**, a method that takes the family tree into account (see Appendix G).⁷ Although these two approaches sometimes yield distinctly different results, they most often yield similar results, and in this book, the lines we present for scaling studies will be derived from the method of traditional, ordinary least squares regression.

Body-size relations are important for analyzing almost all sorts of questions in the study of physiology, ecology, and evolutionary biology. If all one knows about an animal species is its body size, one can usually make useful predictions about many of the species' physiological and morphological traits by consulting known statistical relationships between the traits and size. Conversely, there is always the chance that a species is specialized in certain ways, and as soon as one has actual data on the species, one can identify potential specializations by the type of scaling analysis we have discussed.

⁷Appendix G explains the reasons why the family tree should ideally be taken into account, as well as providing a conceptual introduction to phylogenetically independent contrasts.

TABLE 1.3 Predicted and actual gestation lengths for two African antelopes of about the same body size

Species	Predicted gestation length (weeks) ^a	Actual gestation length (weeks)
Bushbuck (<i>Tragelaphus scriptus</i>)	27	26
Mountain reedbuck (<i>Redunca fulvorufula</i>)	26.5	32

^aPredicted lengths are from the statistically fitted line shown in Figure 1.9.

Environments

What is an environment? An important starting point in answering this question is to recognize that an *animal* and its *environment* are interrelated, not independent, entities. They are in fact defined in terms of each other, as noted more than 100 years ago by none other than Claude Bernard. The environment in any particular case cannot be specified until the animal is specified. A dog, for instance, is an animal from our usual perspective, but if the animal of interest is a tapeworm in the dog's gut, then the dog is the environment. All animals, in fact, are parts of the environments of other animals. The birds in the trees around your home are part of your environment, and you are part of theirs. The interdependence of animal and environment is reflected in standard dictionary definitions. A dictionary defines an animal to be a living organism. An **environment** is defined to be all the chemical, physical, and biotic components of *an organism's* surroundings.

Earth's major physical and chemical environments

The physical and chemical environments on our planet are remarkably diverse in their features, providing life with countless challenges and opportunities for environmental specialization. Temperature, oxygen, and water are the “big three” in the set of physical and chemical conditions that set the stage for life. Here we discuss the ranges of variation of temperature, oxygen, and water across the face of the globe. We also discuss highlights of how animals relate to these features. In later chapters, we return to these topics in greater detail.

TEMPERATURE The **temperature** of the air, water, or any other material is a measure of the intensity of the random motions that the atoms and molecules in the material undergo. All atoms and molecules ceaselessly move at random on an atomic-molecular scale. A high temperature signifies that the intensity of this atomic-molecular agitation is high. Although some animals are temperature regulators and (at a cost of energy) keep their tissue temperatures relatively constant whether they experience high or low environmental temperatures, most animals are temperature conformers. As we discuss temperature here, the conformers are our principal interest because the level of atomic-molecular agitation in their tissues matches the level in the environments where they live.

The lowest temperature inhabited by active communities of relatively large, temperature-conforming animals is -1.9°C , in the polar seas. The very lowest temperature at which *any* active communities of temperature-conforming animals live occurs *within* the sea ice near the poles; minute nematodes and crustaceans, as well as algae, live and reproduce within the sea ice at temperatures that, in some places, are a few degrees colder than in the surrounding water. The fish and other animals living in the open waters of the unfrozen polar oceans (Figure 1.10) are far better known than the sea-ice animals, however. The open waters of the polar oceans remain perpetually at about -1.9°C , the lowest temperature at which seawater is liquid. Thus the fish, the shrimplike krill, the sea stars, and the other invertebrates of these oceans have tissue temperatures near -1.9°C from the moment they are conceived until they die. They do not freeze. Whereas some do not freeze because their normal freezing points



FIGURE 1.10 Fish in the sea around Antarctica spend their entire lives at body temperatures near -1.9°C . These rock cod (*Pagotthenia borchgrevinki*) lay their eggs in holes or depressions in ice sheets. They hatch, grow, feed, and mate at body temperatures near -1.9°C . Metabolically synthesized antifreeze compounds keep them from freezing.

are similar to the freezing point of seawater,⁸ others have special protections against freezing. Because the tissues of these animals are very cold, one might imagine that the animals live in a sort of suspended animation. Actually, however, the communities of temperature-conforming animals in the polar seas are active and thriving. In the ocean around Antarctica, for example, a sure sign of the vigor of the populations of fish and krill is that they reproduce and grow prolifically enough to meet the food needs of the famous Antarctic abundance of whales, seals, and penguins.

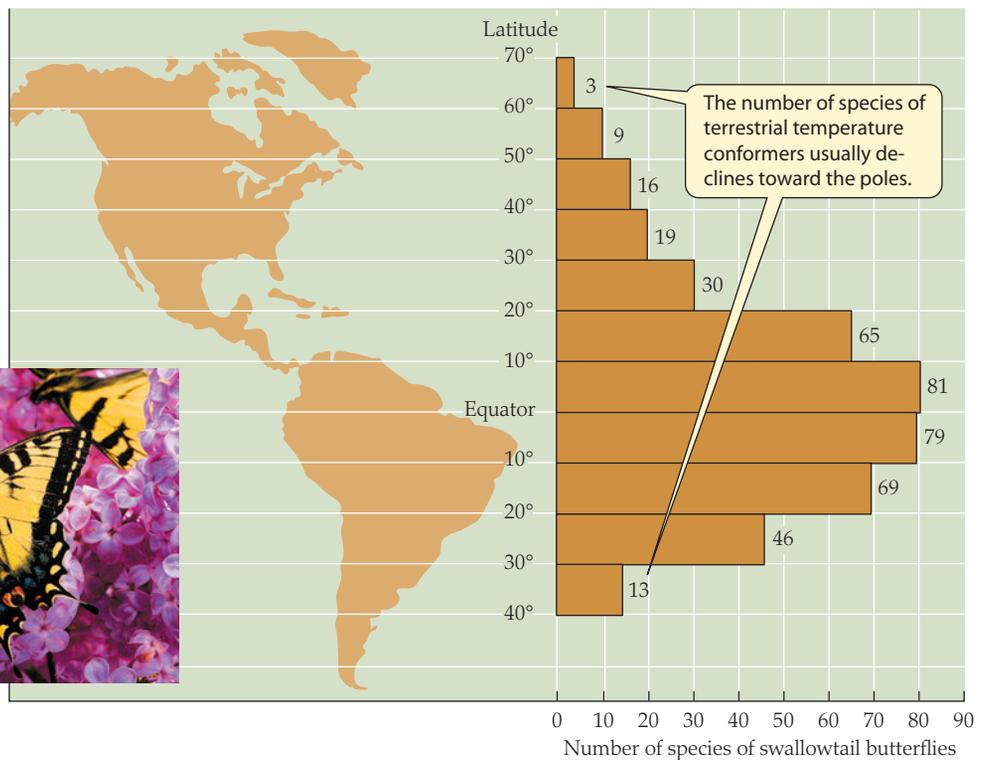
Are the low tissue temperatures of polar fish and invertebrates actually challenging for them, or do they only seem challenging? One way to obtain an answer is to compare polar species with related nonpolar ones. Tropical species of fish clearly find low temperatures to be challenging. Many tropical species, in fact, die if cooled to $+6^{\circ}\text{C}$, even if they are cooled very gradually. Such observations emphasize that success at -1.9°C is not “automatic,” and that the polar species have had to evolve special adaptations to thrive with their tissues perpetually at -1.9°C . The polar species themselves often die if they are warmed to $+6^{\circ}\text{C}$, indicating that the tropical species also have special adaptations—adaptations that poise them to live at tropical temperatures. The evolutionary divergence of these fish is dramatized by the fact that a *single* temperature can be lethally *cold* for tropical species and yet be lethally *warm* for polar species!

Far greater extremes of cold are found on land than in aquatic environments. In Antarctica, the air temperature can drop to -90°C (-130°F); in the Arctic, it can descend to -70°C (-90°F).

⁸Dissolved salts and other dissolved compounds lower the freezing points of solutions. Most marine invertebrates have total concentrations of dissolved matter in their blood similar to the concentration in seawater. Consequently, their blood freezing points are about the same as the freezing point of seawater, and they do not freeze, provided that the seawater remains unfrozen.

FIGURE 1.11 Butterfly biogeography The diagram shows the number of species of swallowtail butterflies (family Papilionidae) at various latitudes. The reason there are relatively few species of animals at high latitudes may not be simply the low temperatures there, but may in part be a relay effect from the effects of cold on plants. Plants decrease in diversity and annual productivity toward the poles, affecting the food supplies of animals. (After Scriber 1973.)

The Canadian tiger swallowtail (*Papilio canadensis*) is one of the species of butterflies that lives farthest from the equator.



The extremes of animal adaptation to low tissue temperature are represented by certain extraordinary species of Arctic insects that spend winters inside exposed plant stems or on the surface of pack ice. The insects are quiescent, not active, at these times. Nonetheless, it is impressive that some endure tissue temperatures of -60°C to -70°C , either in a frozen state (which they have adaptations to tolerate) or in an unfrozen supercooled state. When we look at the diversity of terrestrial temperature-conforming animals, we find that it typically declines as latitude increases from the temperate zone toward the poles, as exemplified by a family of butterflies in **Figure 1.11**. The decline in diversity toward the poles indicates that the very cold terrestrial environments are demanding places for animals to occupy, despite evolutionary adaptability.

The temperature of the air or water on Earth usually does not go higher than $+50^{\circ}\text{C}$ ($+120^{\circ}\text{F}$). Animals on land may experience even higher heat loads, however, by being exposed simultaneously to hot air and the sun's radiation. Some temperature-conforming animals from hot environments—such as certain desert insects and lizards—can function at *tissue* temperatures of 45 – 55°C (**Figure 1.12**).⁹ These are the highest tissue temperatures known for animal life, suggesting that the high levels of molecular agitation at such temperatures pose the greatest challenge that can be met by evolutionary adaptation in animal systems.

The hottest places in the biosphere are the waters of geothermally heated hot springs and underwater hot vents. These waters are often far above the boiling point when they exit Earth's crust. Although aquatic animals typically stay where the waters have cooled to 35 – 45°C or lower, many prokaryotic microbes—bacteria and archaea—thrive at much higher temperatures than animals can. Some prokaryotes even reproduce at temperatures above 100°C .

OXYGEN The need of most animals for oxygen (O_2) is a consequence of their need for metabolic energy. The chemical reactions that animals use to release energy from organic compounds remove some of the hydrogen atoms from the compounds. Each adult person, for example, liberates about one-fifth of a pound of hydrogen every day in the process of breaking down food mol-



FIGURE 1.12 A thermophilic (“heat-loving”) lizard common in North American deserts The desert iguana (*Dipsosaurus dorsalis*) can often be seen abroad as the sun beats down on hot days. Although it does not usually expose itself to body temperatures higher than 42°C , it can survive 48.5°C , one of the highest body temperatures tolerated by any vertebrate animal.

⁹Normal human body temperature is 37°C .

ecules to obtain energy. Hydrogen liberated in this way cannot be allowed to accumulate in an animal's cells. Thus an animal must possess biochemical mechanisms for combining the hydrogen with something, and O_2 is the usual recipient. O_2 obtained from the environment is delivered to each cell, where it reacts with the free hydrogen produced in the cell, yielding water (see Figure 8.2).

The suitability of an environment for animals often depends on the availability of O_2 . In terrestrial environments at low and moderate altitudes, the open air is a rich source of O_2 . Air consists of 21% O_2 , and at low or moderate altitudes it is relatively dense because it is at relatively high pressure. Thus animals living in the open air have a plentiful O_2 resource. Even within burrows or other secluded places on land, O_2 is often freely available because—as counterintuitive as it may sound— O_2 diffuses fairly readily from the open atmosphere through soil to reach burrow cavities, provided the soil structure includes gas-filled spaces surrounding the soil particles.

High altitudes are among Earth's most challenging places, where the numbers of animal species are sharply reduced. Although high altitudes present animals with several stresses, their single greatest challenge is the decline in O_2 concentration with increasing elevation. Air at the top of Mount Everest—8848 m above sea level—is 21% O_2 , like that at sea level; but the total air pressure is much lower than at sea level, and gas molecules within the air are therefore so widely spaced that each liter of air contains only about one-third as much O_2 as at sea level.

At high altitudes, the maximum rate at which animals can acquire O_2 is often much lower than at sea level, and functions are consequently limited. At elevations above 6500 m (21,000 ft), for example, people breathing from the atmosphere find that simply walking uphill is a major challenge because of the limitations on their level of exertion imposed by the low availability of O_2 (Figure 1.13). Some animal species have evolved adaptations to succeed in the dilute O_2 of rarefied air in ways that humans cannot. One of the most remarkable species is the bar-headed goose (*Anser indicus*), which—in ways that physiologists still do not fully comprehend—is able to fly (without an oxygen mask!) over the crests of the Himalayas at 9000 m.

Water-breathing animals typically face a substantially greater challenge to obtain O_2 than air-breathing animals do because the supply of O_2 for water breathers is the O_2 dissolved in water, and the solubility of O_2 in water is not high. Because of the low solubility of O_2 , water contains much less O_2 per liter than air does, even when the water is fully aerated. For example, aerated stream or river water at sea level contains only 3–5% as much O_2 per liter as air at sea level does.

A common problem for animals living in slow-moving bodies of water such as lakes, ponds, or marshes is that the O_2 concentration may be even lower than in aerated water because dissolved O_2 may become locally depleted by the metabolic activities of animals or microbes. *Density layering* of water—which prevents the water from circulating freely—is a common contributing factor to O_2 depletion in the deep waters of lakes and ponds. Density layering occurs when low-density water floats on top of high-density water, causing distinct water layers to form. When this happens, there is often almost no mixing of oxygenated water from the low-density surface layer (where photosynthesis and aeration occur) into the high-density bottom layer. Thus O_2 in the bottom layer is not readily replaced when it is used, and as



FIGURE 1.13 Performance in an O_2 -poor environment Because of the difficulty of acquiring O_2 from rarefied air, the rate at which energy can be released from food molecules for use in work by humans is reduced at high altitudes, and the simple act of walking uphill becomes extremely arduous. Well-conditioned mountaineers are slowed to a walking rate of 100–200 meters per hour near the tops of the world's highest mountains if they are breathing from the air rather than from oxygen tanks. Shown here is Chantal Mauduit (1964–1998) during an unsuccessful attempt to reach the summit of Mt. Everest while breathing only atmospheric air. On an earlier expedition she had been the fourth woman to climb to the peak of K2 (8611 m), second highest mountain on Earth, without supplemental oxygen.

microbes and animals in the bottom layer consume O_2 , the O_2 concentration may fall to very low levels.

In lakes during summer, density layering occurs because of temperature effects: Sun-heated warm water tends to float on top of colder and denser bottom water.¹⁰ The lake studied by a group of university students in Figure 1.14 provides an example of this sort of density layering. The bottom waters of this lake contained essentially *no* dissolved O_2 on the July day when the data were collected. Deep-water O_2 depletion has become more common in recent decades in lakes, ponds, and estuaries as human populations have enriched waters with organic matter. The organic matter supports the growth of microbes that deplete dissolved O_2 . For animals in deep waters to survive, they must be able to tolerate low O_2 levels, or they must temporarily move to other places where O_2 is more available.

In certain sorts of water bodies, animals have faced the challenge of low O_2 concentrations for millennia. Unlike animals confronted

¹⁰In estuarine bodies of water along seacoasts—where freshwater and seawater mix—layering can occur because of salinity effects as well as temperature effects. Low-salinity water is less dense than—and tends to float on top of—high-salinity water.

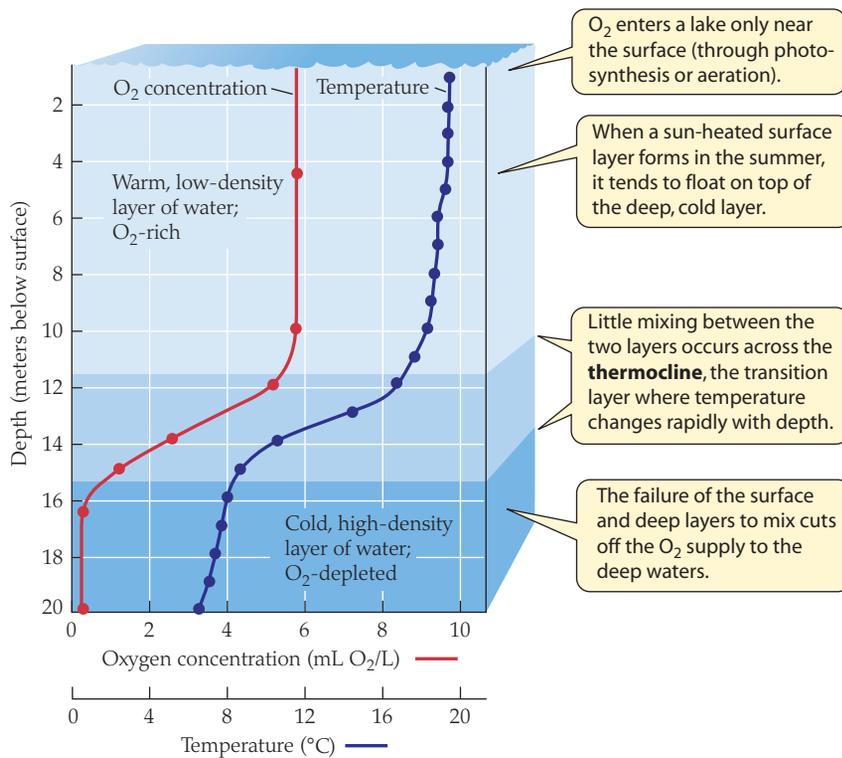


FIGURE 1.14 Density layering can cut off the O_2 supply to the deep waters of a lake. Different densities of water do not mix readily. The O_2 concentration in the deep waters of a lake may fall to near zero because the animals and microbes living there consume O_2 that is not replaced. (From data gathered by a group of animal physiology students on a lake in northern Michigan in July.)

with new, human-induced O_2 depletion, the animals living in primordially O_2 -poor waters have been able to undergo long-term evolutionary adaptation to low- O_2 conditions. Examples of such bodies of water include tropical rivers that are naturally very rich in organic matter, as in the Amazon basin. The warmth of these rivers not only lowers the solubility of O_2 in the water but also promotes rapid multiplication of microbes that use O_2 . In addition, thick forest canopies may create deep shade over the rivers, impeding algal photosynthesis that otherwise could replenish O_2 . Tropical rivers of this sort and their associated wetlands have experienced low levels of dissolved O_2 over eons of geological time.

Among the animals living in such waters, the evolution of air breathing is one of the most remarkable features. Hundreds of species of fish in these waters are air breathers, for example. Some take up inhaled O_2 across well-vascularized mouth linings or lunglike structures. Others swallow air and absorb O_2 in their stomachs or intestines, as mentioned previously. In one of nature's twists of fate, physiologists have discovered that it can be important for these fish to limit gas exchange across their gills because the O_2 they get from breathing air can escape across their gills into the O_2 -depleted waters they inhabit.

For animals confronted with short-term or long-term O_2 deficiency, whether in O_2 -depleted freshwater environments or elsewhere, a potential solution over evolutionary time is to adopt a biochemistry that can attach hydrogen to molecules other than O_2 . Many species—both air breathers and water breathers—have temporary options of this sort. Certain tissues in our own bodies,

for example, can live without O_2 for 10 minutes at a time by attaching hydrogen to pyruvic acid (making lactic acid). Suppose, however, that an animal's entire body must live without O_2 for many hours, days, weeks, or months. Doing so is possible for some animals, but as the period without O_2 lengthens, ever-fewer species have evolved biochemical specializations that enable them to survive. Some exceptional animals are able to meet the most extreme challenge of living indefinitely in O_2 -free environments. Most that are currently known to science are parasites (e.g., nematodes and tapeworms) that live in the O_2 -free environment of the vertebrate gut cavity.

WATER Water is the universal solvent in biological systems—and therefore is required for blood and all other body fluids to have their proper compositions. Water is also important for animals because H_2O bound to proteins and other macromolecules as *water of hydration* is often required for the macromolecules to maintain their proper chemical and functional properties.

Animal life began in Earth's greatest watery environment, the oceans. Most invertebrates that live in the open oceans today—sea stars, corals, clams, lobsters, and so forth—are thought to trace a continuously marine ancestry. That is, their ancestors never left the seas from the time that animal life began, and thus the salinity of the oceans has been a perennial feature of their environment. The blood of these invertebrates (Figure 1.15), although differing a bit from seawater in composition, is similar to seawater in its total salt concentration. These animals therefore do not tend to gain much H_2O from their environment by osmosis, nor do they tend to lose H_2O from their blood to the seawater. Because this situation is almost universal among these animals, we believe it is the

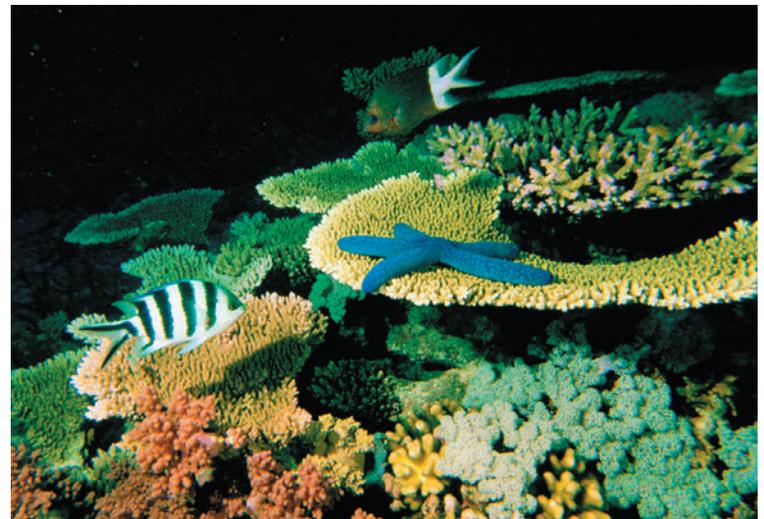


FIGURE 1.15 The sea star and the corals in this ocean scene have body fluids similar to seawater in their total concentration of salts, although the body fluids of the fish are more dilute than seawater. Most scientists believe that the difference between marine invertebrates and marine bony fish is based on their evolutionary histories. The invertebrates' ancestors always lived in the sea, but the fish's ancestors once lived in freshwater.

primordial condition of animal life. Thus we believe that for much of its evolutionary history, animal life lived in a setting where (1) H₂O was abundant in the environment and (2) little danger existed for an animal to be either dehydrated or overhydrated.

This benign situation was left behind by the animals that migrated from the oceans into rivers during their evolution. Freshwater has a very low salinity compared with seawater. When animals from the oceans, with their salty blood, started to colonize freshwater, they experienced a severe challenge: H₂O tended to seep osmotically into their bodies and flood their tissues because osmosis transports H₂O relentlessly from a dilute solution into a more-concentrated one. Today, lakes and rivers are populated by fish, clams, crayfish, sponges, hydras, and so forth, all descended from ocean ancestors. The process of invading freshwater from the sea is probably still continuing, in fact; some freshwater crabs, for example, are thought to be geologically recent immigrants to freshwater because they must return to the sea to breed. Over evolutionary time, freshwater animals reduced their tendency to gain H₂O osmotically from their environment, but they have not eliminated it. A 100-g goldfish, for example, osmotically gains enough water to equal 30% or more of its body weight every day.

Vertebrates and several groups of invertebrates invaded the land from freshwater. In so doing they came face to face with the most severe of all the water challenges on Earth: On land, evaporation of water into the atmosphere tends to dehydrate animals rapidly; moreover, some terrestrial habitats are so dry that replacing lost water borders on impossible. When animals first invaded terrestrial habitats, they probably possessed integuments (body coverings), inherited from aquatic ancestors, that provided little or no barrier to evaporative water loss. This problem ultimately had to be solved for animals to be able to live entirely freely in the open air.

Some of today's land animals have integuments that resemble the primordial types. Leopard frogs, earthworms, and wood lice, for example, have integuments that lack significant evaporation barriers and permit virtually free evaporation. In some cases, water evaporates across these sorts of integuments as fast as it evaporates from an open dish of water of the same surface area! Animals with such integuments dehydrate so rapidly that they cannot possibly live steadily in the open air. Instead, they must stay in protected places where the humidity of the air is high, or if they venture into the open air, they must return often to places where they can rehydrate. The danger of dehydration severely constrains their freedom of action.

For a terrestrial animal to be liberated from these constraints and lead a fully exposed existence in the open air, it must have evolved highly effective barriers to water loss across its integument. Only a few major groups of animals possess such novel water barriers: mammals, birds, other reptiles (see Figure 1.12), insects, and spiders. In each of these groups, excessive evaporation is prevented by integumentary lipids: thin layers of hydrocarbons deposited in the integument. The evolution of these hydrocarbons liberated animals to occupy the open air and was a prerequisite for animals to invade the driest places on Earth, the deserts. In hyperarid deserts, a year or two can pass without rain, yet there are populations of insects, lizards, birds, and mammals that succeed there.

Some terrestrial animals have adapted to land in part by evolving exceptional tolerance of dehydration. Although most terrestrial animals die if they lose half or more of their body water without replacing it, the exceptional types can dehydrate more. The most

extreme cases are certain invertebrates that can lose essentially all their body water and survive in a dormant, crystalline state until water returns. Certain tardigrades (“moss animals” or “water bears”), for example, dry completely when deprived of water and then can blow about like dust, ready to spring back to active life if water becomes available.

Contrary to what intuition might suggest, even some aquatic animals are threatened with dehydration. The bony fish of the oceans, such as the reef fish seen in Figure 1.15, are the most important example. These fish have blood that is only one-third to one-half as salty as seawater, probably because they are descended from freshwater ancestors rather than from ancestors that always lived in the sea. The ocean is a desiccating environment for animals with dilute blood because osmosis transports H₂O steadily from the blood to the more-concentrated seawater. These desiccating fish have an advantage over terrestrial animals desiccating in a desert—namely, that H₂O to replace their losses is abundant in their watery environment. To incorporate H₂O from seawater into their dilute bodies, however, they must in essence possess mechanisms to “distill” the seawater: They must be able to separate H₂O from the salty seawater solution.

The environment an animal occupies is often a microenvironment or microclimate

In a forest, lake, or any other large system, small places inevitably exist where physical or chemical conditions are significantly different from the average in the system. For instance, when the average temperature of the open air in a woodland is 30°C, the temperature under a pile of brush on the forest floor might be 24°C. Although large-bodied animals are often, by necessity, exposed to the statistically average conditions where they live, small-bodied animals may enter the small places—the nooks and crannies—where they may find conditions that are far from average. Places within an environment that potentially differ from the environment at large in their physical or chemical conditions are called **microenvironments**. A related concept is that of **microclimates**. A microclimate is the set of climatic conditions (temperature, humidity, wind speed, and so forth) prevailing in a subpart of a system.

Because we humans are large organisms, our perception of the prevailing conditions in a place may bear little relation to the microclimates that smaller creatures can find by entering distinctive subparts of the place. George Bartholomew (1919–2006), one of the founders of environmental physiology, expressed this important point well:

Most vertebrates are much less than a hundredth of the size of man . . . , and the universe of these small creatures is one of cracks and crevices, holes in logs, dense underbrush, tunnels and nests—a world where distances are measured in yards rather than miles and where the difference between sunshine and shadow may be the difference between life and death. Climate in the usual sense of the word is, therefore, little more than a crude index to the physical conditions in which most terrestrial animals live.¹¹

Desert environments nicely illustrate the point that Bartholomew makes (Figure 1.16). At head level (about 2 m aboveground), a human

¹¹From G. A. Bartholomew. 1964. The roles of physiology and behavior in the maintenance of homeostasis in the desert environment. *Symp. Soc. Exp. Biol.* 18: 7–29.

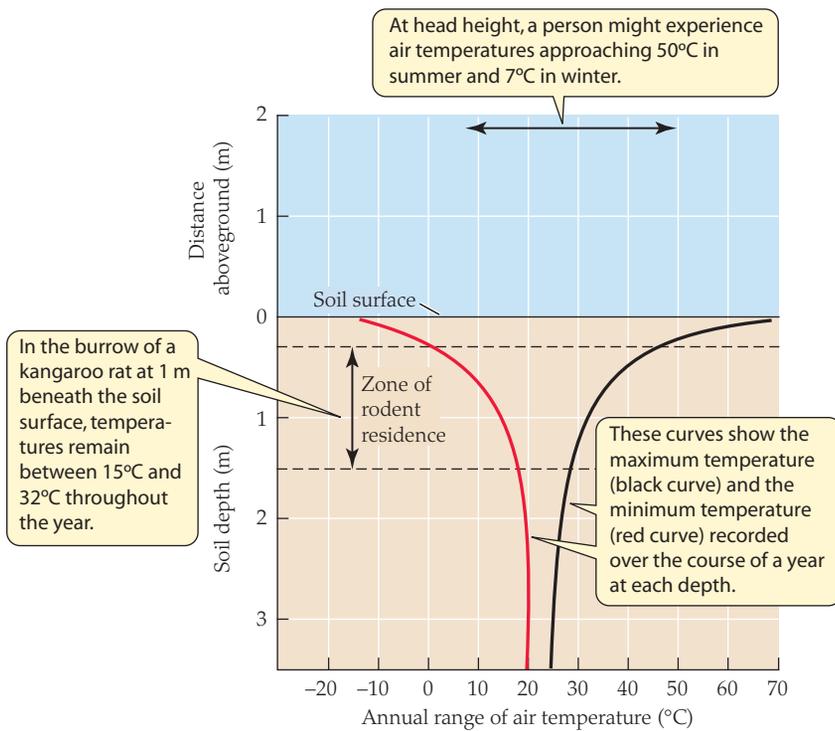


FIGURE 1.16 Microenvironments in the Arizona desert near Tucson The plot shows the *annual range of temperatures* in the soil and air and at the soil surface. (After Misonne 1959.)

or a horse standing in the Arizona desert may experience daytime air temperatures that reach almost 50°C during the summer, combined with intense solar radiation. Humans and horses typically have no choice but to cope physiologically with these conditions because they are too large to escape by going underground or squeezing into patches of shade cast by cacti or desert bushes. Small desert rodents such as kangaroo rats and pocket mice are in a very different situation, however, because they can burrow deep into the soil, where thermal conditions are far different from those that humans associate with deserts. On the surface of the desert soil, the annual temperature range is actually greater than that in the air above (see Figure 1.16); the soil surface becomes hotter than the air during the day as it absorbs solar radiation, and it becomes cooler than the air at night because it radiates infrared energy to the cold nighttime sky (see pages 232–233). Beneath the soil surface, however, the annual range of temperature decreases dramatically as depth increases. At a depth of 1 m, the temperature remains well below the maximum aboveground air temperature during summer and well above the minimum air temperature during winter. In fact, in certain desert regions, such as that shown in Figure 1.16, the rodents never face significant heat or cold stress throughout the year when they are in their burrows!¹²

Microenvironments must be considered in the study of virtually all the physical and chemical features of the places where animals live. In tall grass, for example, the wind speed is likely to be lower than in adjacent open areas, and because the weak wind permits moisture evaporating from the soil and grass to accumulate in the

¹²There are hotter desert regions where even the burrow environment presents thermal challenges in some seasons, but the burrow environment is still far more moderate than the environment aboveground (see Chapter 28).

air rather than being blown away, the humidity also tends to be higher than in adjacent open air. Animals that enter tall grass are thus likely to find a less-desiccating microenvironment than in open fields nearby. Along a river, any side pool cut off from free mixing with the flowing water is likely to form a distinctive microenvironment; the concentration of dissolved O₂ in such a pool might be lower than that in the river at large if there is a lot of microbial decay occurring in the pool, for example. On land in winter, spaces under deep snow in the far north form distinctive microenvironments, often warmer by 20°C (or more) than the open air above (Figure 1.17). Thus a lemming burrowing under the snow experiences a very different environment from a reindeer standing above.

Animals often modify their own environments

An important way in which *animal* and *environment* are interdependent is that animals modify their own environments. In the simplest case, animals behaviorally select the actual environments that they experience from the many that they *could* experience. A frog stressed by desiccation on open terrain, for example, can raise the humidity and lower the wind speed of its environment by hopping into tall grass. The environment of an animal is the animal's surroundings, and the surroundings depend on where the animal places itself.

A more subtle but equally important point is that the very presence of an animal in a place often alters the physical and chemical features of the place. The environmental alteration caused by the animal may then change that selfsame animal's behavior or physiology. Consider, for instance, a squirrel in a small cavity in a tree. In winter, the squirrel will warm the cavity to a higher tem-

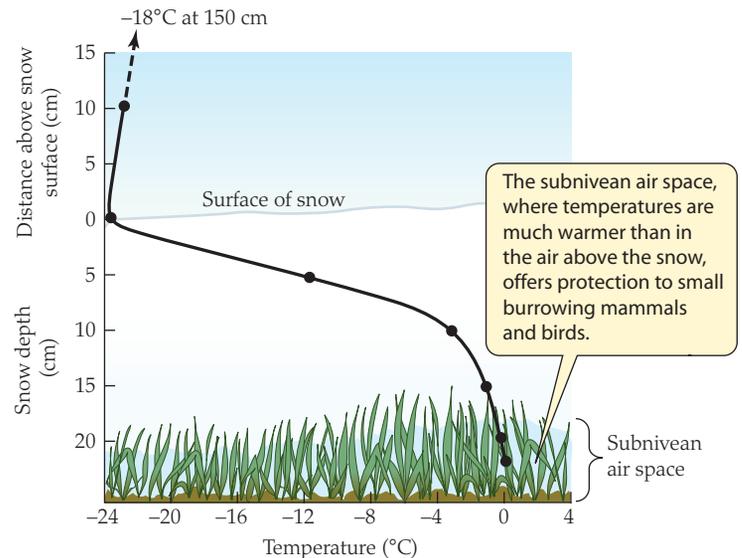


FIGURE 1.17 Microenvironments in deep snow in the far north An air space—termed the subnivean air space—is often trapped beneath deep snow. When lemmings, ptarmigans, or other small mammals or birds burrow under the snow into the subnivean air space, they enter a windless environment where the temperature may be 20°C warmer than in the air above the snow, and where they are protected by the overlying snow from losing heat radiatively to the frigid nighttime sky. The temperatures shown were measured on a March night in Sweden. (After Coulianos and Johnels 1963.)

perature than would prevail in the squirrel's absence. The squirrel will then respond physiologically to the elevated temperature in the cavity, by cutting back its rate of metabolic heat production. In a like manner, a school of fish can deplete water of dissolved O₂ and then must cope with low "environmental" O₂ levels.

Because of phenomena like these, the analysis of an animal–environment interaction often requires dynamic calculations that take into account that the interaction is of a two-way, back-and-forth sort. After an animal has initially altered an environment, the animal may function differently because it is in a changed environment, and thus the animal's future effect on the environment may be different from its original effect.

Global warming represents a planet-sized example of this phenomenon. Most scientists believe that the use of fossil fuels by the global human population is changing Earth's atmosphere toward a composition that increases planetary heat retention. Human activities are therefore raising the global temperature. The warming environment then will alter the ways in which human societies function in the future.

Evolutionary Processes

The evolutionary origins of physiological traits—and the continuing evolution of physiological traits in today's world—form the subject matter of *evolutionary physiology*, one of the two most important branches of the modern study of physiology, as stressed earlier. Physiologists have long recognized that the traits of species are often well matched to the environments they occupy. For example, polar bears are well suited to deal with cold, and dromedary camels with heat. Evolution by natural selection is believed by modern biologists to be the primary process that produces this match between species and the environments they inhabit.

Carefully defined, **evolution** is a *change of gene frequencies over time* in a population of organisms. Suppose a population of animals contains a gene that codes for the oxygen affinity of hemoglobin (the ease with which hemoglobin combines with O₂). The gene has two alleles (alternative forms), one coding for high oxygen affinity (H allele) and one for low oxygen affinity (L allele). At one time in the history of the population, 30% of all copies of this gene were of the H allele and 70% were of the L allele. After 1000 generations have passed, however, 60% of all copies are of the H allele and 40% are of the L allele. In this case, gene frequencies have changed. Therefore, evolution has occurred.

A more-complex question by far is whether *adaptation* has occurred. There are several known processes by which gene frequencies can change. Only one, natural selection, leads to adaptation.

Some processes of evolution are adaptive, others are not

Returning to the hypothetical example just discussed, suppose that in a population of animals occupying a particular environment, individuals with hemoglobin of high oxygen affinity are more likely to survive and reproduce than those with hemoglobin of low affinity. By this very fact, an allele that codes for high affinity will tend to increase in frequency in the population from one generation to the next (and an allele that codes for low affinity will tend to decrease). After many generations, the H allele might become so common that essentially all individuals born into the

population have it. You will recognize this as the process of *natural selection*. Natural selection creates a better match between animals and their environments.

The concept of *adaptation*, which is intimately related to that of natural selection, has a specific meaning in the study of evolutionary biology. By definition, a trait is an **adaptation** if it has come to be present at high frequency in a population because it confers a greater probability of survival and successful reproduction in the prevailing environment than available alternative traits. Thus adaptations are products of the process of natural selection. An adaptation is not necessarily an *optimum* or *ideal* state, because constraints on the freedom of natural selection may have precluded the optimum state from being an option (the optimum state, for instance, might never have arisen through mutation). As the definition stresses, an adaptation is the trait favored by natural selection from among the *available* alternative traits.

Now let's repeat our thought exercise but substitute different assumptions. Consider a population, in the same environment as analyzed before, in which the H and L alleles are both common. Suppose that the population experiences a drop in size, so that it contains fewer than 100 individuals. Suppose also that during this low point, a catastrophe strikes, killing individuals *at random*, regardless of whether they possess the H or L allele. In a small population of 100 or fewer animals, deaths at random could *by sheer chance* eliminate all individuals possessing one of the alleles. All copies of the H allele might, in fact, be eliminated. In a population subjected to this process, when the population later regrows in size, it will have only the L allele, the *less-adaptive* allele. In this case, the process of gene frequency change we have described is a process of **nonadaptive evolution**. Because of chance, an allele that provides a *lower* probability of survival and reproduction than an available alternative comes to be the predominant allele in the population.

Processes in which chance assumes a preeminent role in altering gene frequencies are termed **genetic drift**. We have described, in the last paragraph, one scenario for genetic drift: Gene frequencies may shift in chance directions because of random deaths (or other random blocks to individual reproduction) in populations transiently reduced to small size. Another scenario for genetic drift is that when a species enters a new area and founds a new population there, the new population may exhibit changed gene frequencies, relative to the parent population, simply because of chance—because the founding individuals may by chance be genetically nonrepresentative of the population from which they came (a so-called *founder effect*).

Students of allele frequencies in natural populations believe that they often observe evidence of genetic drift. For example, two populations of mice living 10 km (6 mi) apart in seemingly identical woodlots usually exhibit many differences in allele frequencies thought to be produced by drift of one sort or another. Often the genes affected by drift seem to be ones that have little or no fitness effect; drift, in other words, seems to have its greatest influence on genes not subject to strong natural selection. That is not always the case, however.

Additional processes are known by which evolution may lead to nonadaptive outcomes. These include:

- A trait may be common in a population simply because it is closely correlated with *another* trait that is favored by

natural selection. For instance, a trait that itself diminishes the fitness of animals (their ability to survive and reproduce) may occur because it is coded by a gene that is subject to positive selection because of other, fitness-enhancing effects. The control by an allele of a single gene of two or more distinct and seemingly unrelated traits is called **pleiotropy**. An example is provided by a recently discovered allele of an enzyme-coding gene in the mosquito *Culex pipiens* that simultaneously has two effects. The allele both (1) increases the resistance of the mosquitoes to organophosphate insecticides and (2) decreases the physiological tolerance of the mosquitoes to the cold of winter. When a population of mosquitoes is sprayed with insecticides, the population *may evolve toward a diminished physiological ability to survive winter* because of pleiotropy. Selection will favor alleles that confer insecticide resistance, but the particular allele we have described will also diminish the odds of winter survival.¹³

- A trait may have evolved as an adaptation to an ancient environment, yet persist even though the environment has changed. In the new environment, the trait may no longer be beneficial and thus may not be an adaptation. Traits of this sort are thought by some evolutionary biologists to be quite common, because animals often move to new places, and even if animals stay in one place, climates often change radically over relatively short periods of geological time.¹⁴ The need of many desert amphibians for pools of water to breed, and the possession of eyes by numerous species of arthropods that live obligatorily in caves, are two examples of traits that seem to exist today because they are carryovers from the past, not because they are adaptations to the animals' present environments. Similarly, the dilute blood of the bony fish of the oceans is probably a legacy of life in a different environment, not an adaptation to life in seawater.

A trait is not an adaptation merely because it exists

Prior to about 1980, many physiologists referred to *all* traits of organisms as adaptations. Traits were called *adaptations* merely because they existed, and stories (now sometimes recalled as “just-so” stories) were concocted to explain how the traits were beneficial. This habit ignored the possibility of genetic drift and other forms of nonadaptive evolution. The habit, in fact, reduced adaptation to a nonscientific concept because no empirical evidence was required for a trait to be considered an adaptation.

A major shift in the use of the concept of adaptation was precipitated by Stephen J. Gould and Richard C. Lewontin with the publication of a critique in 1979. They stressed that natural selection in the present environment is just one of several processes by which a species may come to exhibit a trait. A trait, therefore, is not an adaptation merely because it exists. Instead, when physiologists

call a trait an *adaptation*, they are really making a *hypothesis* that natural selection has occurred.

Just as is true of any other hypothesis, data must be gathered to assess whether a hypothesis of adaptation is true or false. Because scientists usually cannot actually witness the evolution of a trait, the data they can gather are often indirect. Nonetheless, Gould and Lewontin emphasized, scientists must attempt to gather the soundest evidence possible. With this objective in mind, the study of adaptation has been maturing gradually into an empirical (i.e., data-based) science.

Adaptation is studied as an empirical science

Biologists today are giving a great deal of attention to the question of how to obtain *data* that will guide a decision on whether or not a trait is an adaptation. Sometimes the biosphere presents a “natural experiment” that permits scientists to *observe* evolution taking place over multiple generations in a natural setting. Scientists cannot depend entirely on such natural experiments to study adaptation, because the natural experiments are uncommon and may not speak to questions of greatest interest. Nonetheless, a natural experiment may provide particularly useful insights into adaptation because it may allow the adaptiveness of a trait to be judged from all the angles that matter.

Industrial melanism is a famous phenomenon—with which you are likely familiar from your study of general biology—that exemplifies a natural experiment for adaptation. *Melanism* refers to a genetically coded dark body coloration. *Industrial melanism* is an evolutionary increase in the frequency of melanism in a population of animals living in an environment modified by human industries. A species of moth in the industrial regions of England has two genetically determined color states: light and dark. The moths were predominantly light-colored prior to the industrial era, when light-colored lichens covered the tree trunks on which they rested during the day. With increasing industrialization, the lichens on the trees were killed by pollutants, and soot from factories darkened the tree trunks. Within 50 years the moth populations in the industrial areas became predominantly dark-colored because, from generation to generation, genes for dark coloration increased in frequency. Studies demonstrated that on dark tree trunks, the dark-colored moths were less likely than light-colored ones to be seen by avian predators.

From the *direct observation* of this natural experiment, we can say the following: In an environment impacted by industrial pollution, dark coloration became common in the moth populations by way of natural selection because it increased an individual's likelihood of survival in comparison with the available alternative coloration. Dark coloration thus met all the standards of our formal definition of adaptation and could be judged, based on evidence, to be an adaptation to the sooty environment.

Usually biologists are not able to observe evolution in action in this way. Thus, to study adaptation empirically, they must adopt other approaches. Several techniques have been developed—or are being developed—to study the question of adaptation when nature fails to provide an ideal natural experiment:

- *The comparative method.* The **comparative method** seeks to identify adaptive traits by comparing how a particular function is carried out by related and unrelated species in

¹³In addition to causation by pleiotropy, traits may also evolve in tandem because of *linkage disequilibrium*, in which alleles of two or more genes on the same chromosome—because of being on a single chromosome—tend to be inherited together to a nonrandomly great extent.

¹⁴Just 18,000 years ago, the arid, warm deserts of Arizona and New Mexico were far more moist than today, and they were on average about 6°C cooler, because of the last ice age. About 10,000 years ago, large expanses of the Sahara Desert experienced far more rain than they do today and were savannas (prairielike landscapes) rather than desert.

similar and dissimilar environments. *This method is based on the premise that although we cannot see evolution occurring in the past, the many kinds of animals alive today provide us with many examples of outcomes of evolution, and patterns we identify in these outcomes may provide insights into processes that occurred long ago.* Figure 1.18 presents a simple example of the use of the comparative method. Terrestrial vertebrates have lungs for breathing. If we were to look *only* at terrestrial vertebrates, we would have just that single isolated bit of knowledge about breathing mechanisms. However, if we also examine other unrelated terrestrial organisms, we discover a pattern: In insects, in land snails, *and* in terrestrial vertebrates, the breathing surfaces are parts of *invaginated* structures that hold the air rather than projecting into the air. This pattern is striking because *evaginated* breathing surfaces, which project into the water, are nearly universal among aquatic animals (note the gills of fish or crayfish). The occurrence of invaginated structures in multiple independent lines of modern terrestrial animals suggests that if we could see into the distant evolutionary past, we would witness individuals with invaginated breathing organs outcompete ones with alternative breathing structures on land. The pattern suggests that natural selection was at work, and that the invaginated breathing organs are adaptations to life on land.

- Studies of laboratory populations over many generations.** Changes in gene frequencies can be observed over multiple generations in laboratory populations of fast-breeding animals such as fruit flies. By exposing such populations to specific, controlled conditions (e.g., high or low desiccation stress), physiologists may observe which alleles are favored by selection when a particular condition prevails. An illustration is provided by studies of fruit fly populations exposed for many generations to high desiccation stress; in such populations, the genetically coded blood volume of flies increases dramatically, and the flies become able to tolerate desiccation for greatly enhanced lengths of time (see Box 28.6). The selection that occurs in cases like this is usually considered to be *laboratory selection* or *artificial selection* because humans are manipulating the circumstances. A concern, therefore, is to assess whether outcomes of *natural selection* in the wild would be likely to be similar.
- Single-generation studies of individual variation.** Individuals in a natural population of a single species typically vary in their physiological properties. For example, various adult individuals in a single wild population of deer mice vary widely in the maximal rate at which they can take in and use O_2 —a rate that is a key determinant of how long and vigorously the various individuals can sustain metabolic effort (Figure 1.19). Such natural variation among individuals of a species can be exploited to carry out single-generation experiments to determine which traits are most advantageous. To illustrate, suppose we trap several hundred mice in a wild population and measure

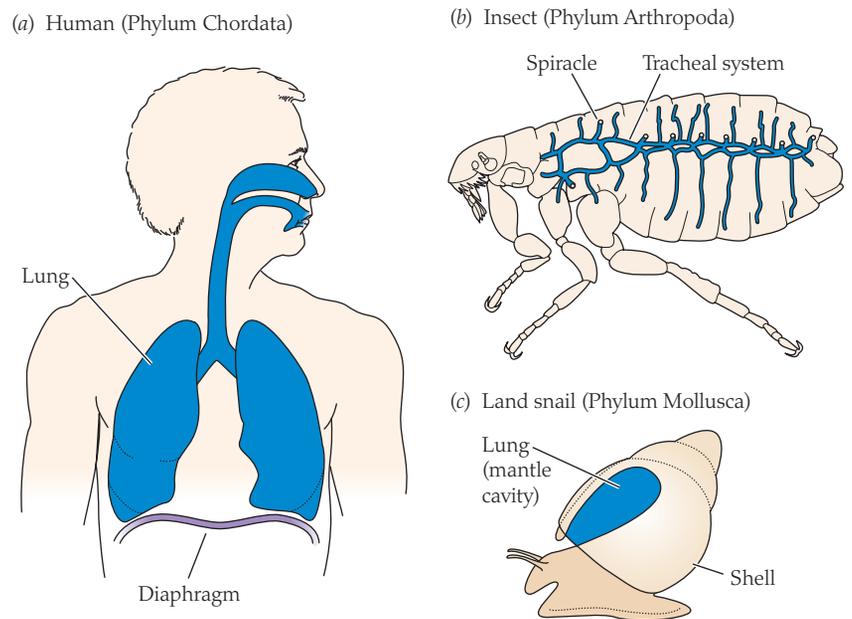


FIGURE 1.18 The comparative method Terrestrial vertebrates (a), insects (b), and land snails (c)—representing three phyla that separately colonized the land—have independently evolved breathing organs that are invaginated into the body. This convergence in the type of breathing organ suggests that invaginated breathing organs are adaptive for living on land.

the maximal rate of O_2 consumption of each, and then we release all the mice back into their natural population, where we monitor them until they die. If we find that individuals with particular O_2 -consumption capabilities produce more young before dying than individuals with

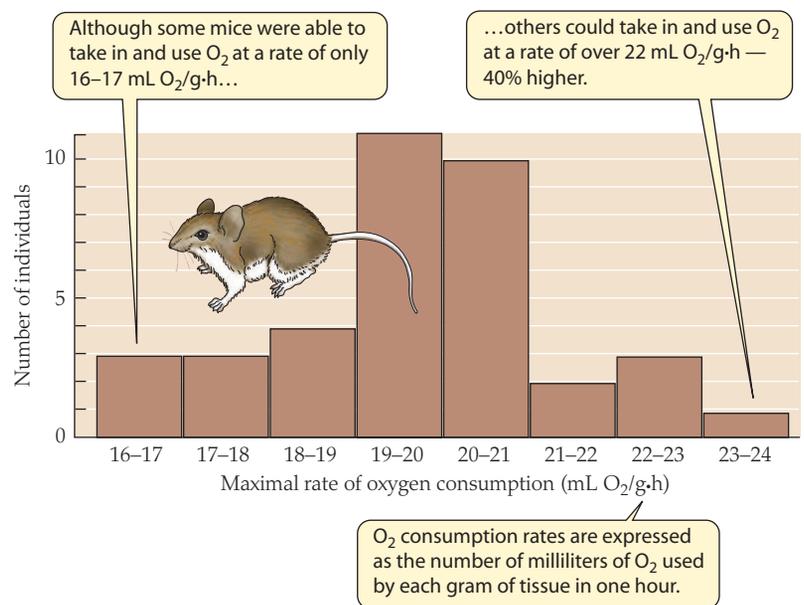


FIGURE 1.19 Physiological variation among individuals of a species This histogram summarizes the measured maximal rates of O_2 consumption of 35 deer mice (*Peromyscus maniculatus*) from a single natural population.

other O₂-consumption capabilities, we will have insight into which capabilities are adaptive.

- *Creation of variation for study.* Biologists may be able to create variation in a trait that shows little or no natural variation among individuals of a species. Then competitive outcomes in natural or laboratory settings may be observed. Years ago, the principal application of this approach was morphological; for instance, the size of the ear cavities of desert rats was morphologically altered to assess which ear-cavity dimensions allowed the surest detection of predators. One newer approach is to employ genetic manipulations. Suppose that the vast majority of individuals of a species have a certain allele for a digestive enzyme but that an unusual mutant allele is found that produces a different molecular form of the enzyme. By controlled breeding, one could create a population rich in both alleles and then observe the relative advantages of the two enzyme forms. Another genetic approach is to employ genetic engineering methods to silence genes. As we discuss in Chapter 3 (see page 79), **knockout animals** that lack functional copies of a gene of interest can be produced, or **RNA interference (RNAi)** can be employed to block transcription of a gene. Individuals manipulated in these ways are unable to synthesize the protein coded by the affected gene and thus can be used to evaluate the functional significance of the protein. Other forms of “engineering” are available for creating individual diversity that can be tested for effects. These include “allometric engineering,” in which the body sizes of individuals are artificially manipulated during development to create variation, and “hormonal engineering,” in which hormone injections are used.
- *Studies of the genetic structures of natural populations.* Natural populations are sometimes genetically structured in revealing ways. Genetic **clines** provide excellent examples. A genetic cline is a progressive change in allele frequencies or gene-controlled phenotype frequencies along an environmental gradient. Investigators find, for instance, that within certain species of fish of the East Coast of the United States, alleles that are common in warm-water Georgia individuals become progressively less common toward the north and are almost absent in cold-water New England individuals (see Figure 2.22). Genetic patterns of this sort often point to ways in which natural selection differs in its effects from place to place.
- *Phylogenetic reconstruction.* The goal of phylogenetic reconstruction is to determine the structure of the *family tree* (the ancestry) of groups of related species, often using molecular genetic data. The family tree is useful in two major ways. First, a family tree often facilitates the estimation of exactly *when* in evolutionary history each trait evolved; thus, for example, we might learn from a family tree whether the evolution of one trait preceded or followed the evolution of another—knowledge that can help us understand the context of the evolution of each trait. Second, a family tree clarifies whether a trait evolved independently more than once; several independent origins in one environment suggest that a trait is adaptive to the

environment. In this book we discuss several analyses of adaptation based on family trees. Chapter 3, for example, starts with a family-tree analysis of the icefish of Antarctic seas, fish that lack red blood cells and sometimes lack myoglobin, a key O₂-transport compound, in their heart muscle (see Figures 3.3 and 3.4).

Evolutionary potential can be high or low, depending on available genetic variation

A key determinant of the course of evolution of a trait in an animal population is the amount of genetic diversity for the trait in the population. If there is no genetic diversity for a trait—that is, if all the individuals in a population are homozygous for a single allele—then evolutionary change in the trait is essentially impossible. As an example, imagine a population of mammals in which all individuals are homozygous for an eye-color allele that codes for brown eyes. In this population as a whole, there would be no genetic diversity for eye color. Thus natural selection of alleles could not possibly alter eye color. By contrast, if the individuals in a population collectively have several different alleles of the gene for eye color—some alleles coding for brown, others for blue or olive—then the frequencies of the various alleles can be modified by natural selection, and eye color can evolve.

Physiologists are just beginning to take into full account the importance of genetic diversity in understanding evolutionary potential. **Figure 1.20** provides a model example of the sorts of insight that can be obtained from considering genetic diversity. House mice were collected from five locations in eastern North America, locations chosen to represent a progression in winter severity, from mild winters in the south to severe winters in the north. The mice collected were from wild populations that had presumably reproduced at the five locations for many generations and were subjected to natural selection. Mice from the five locations had litters in the laboratory, and their offspring were studied. The reason for studying the offspring rather than the wild-caught animals was to gain as clear insight as possible into *genetic* differences among the populations; because all the offspring were born and reared in one environment, their differences were likely to be mostly or entirely caused by differences in genetics, rather than differences in early upbringing.

Four traits of the offspring were measured: their body temperatures, the sizes of the nests they constructed, their body weights, and the fractions of their bodies occupied by *brown fat*, a tissue capable of intense heat production (see p. 257). The offspring of the mice from the five locations differed significantly in body size and nest size; both the body size and the nest size were higher in the colder, northern populations than in the southern ones, as one might expect (see Figure 1.20). However, the offspring from all five sets of mice had the same average body temperature and the same average amount of brown fat. In the abstract, one might expect animals in a cold climate to evolve a lower body temperature and a larger quantity of heat-producing tissue than ones in a warm climate, but neither of these expectations is fulfilled in reality. Why has adaptation occurred in only two of the four traits studied?

Genetic diversity provides an important part of the answer. House mouse populations exhibit relatively high genetic diversity in the genes that control body size and nest size; these two traits have responded to natural selection. However, house mouse populations

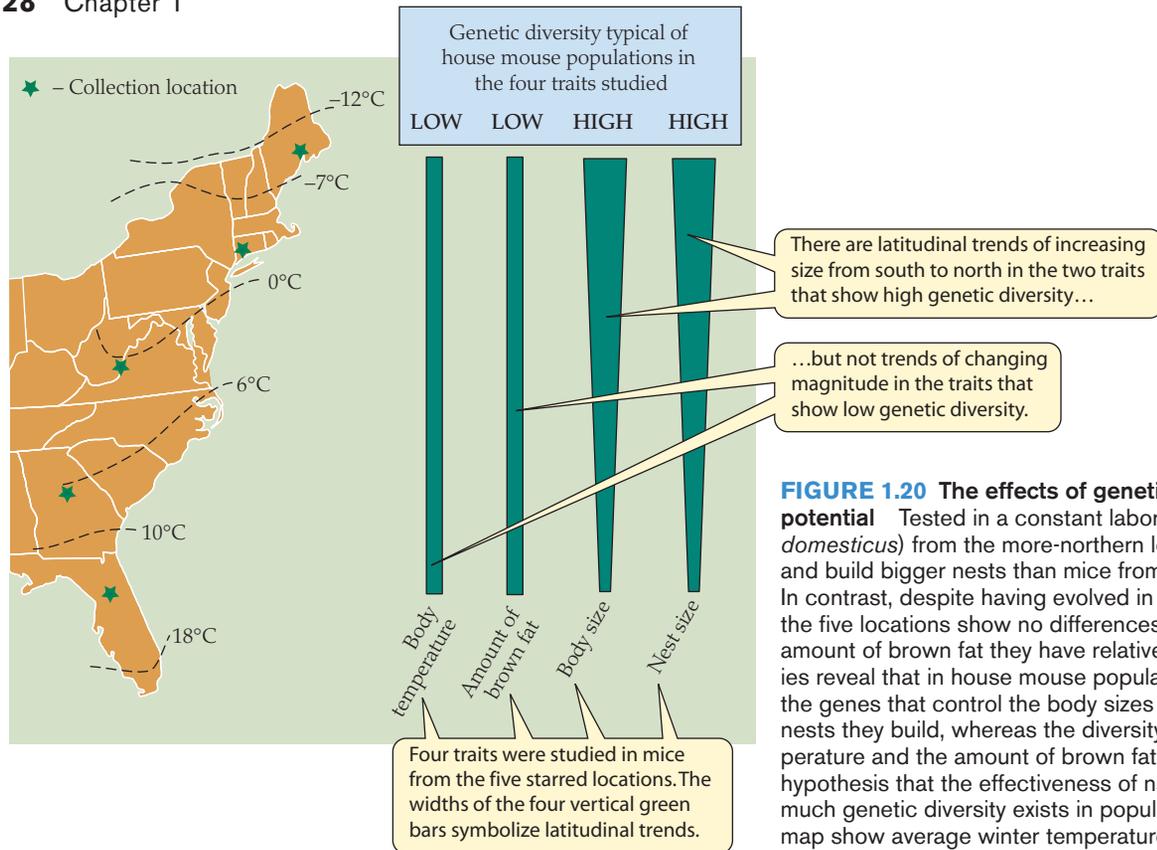


FIGURE 1.20 The effects of genetic diversity on evolutionary potential Tested in a constant laboratory setting, house mice (*Mus domesticus*) from the more-northern locations attain larger body sizes and build bigger nests than mice from the more-southern populations. In contrast, despite having evolved in different climates, mice from the five locations show no differences in body temperature or in the amount of brown fat they have relative to body size. Independent studies reveal that in house mouse populations, there is high diversity in the genes that control the body sizes of the mice and the sizes of the nests they build, whereas the diversity of genes controlling body temperature and the amount of brown fat is low. The results support the hypothesis that the effectiveness of natural selection depends on how much genetic diversity exists in populations. The dashed lines on the map show average winter temperatures. (After Lynch 1992.)

exhibit little diversity in the genes that control body temperature and the amount of brown fat; these two traits have failed to respond to natural selection in the very same mice. We do not know why genetic diversity is high for some traits and low for others. Examples such as this show, however, that evolution by natural selection depends on the underlying genetic structure of populations. It can be only as effective as genetic diversity permits it to be.

Study Questions

- There is a chance that a calcium atom or carbon atom that was once part of Caesar's or Cleopatra's body is now part of your body. Part of the reason is that most calcium and carbon atoms that were parts of these rulers' bodies did not go to their graves with them. Explain both statements. (If you enjoy quantifying processes, also see question 11.)
- Animals do not keep all their detoxification enzymes in a constant state of readiness. Thus they depend on phenotypic plasticity to adapt to changing hazards. An example is provided by the enzyme *alcohol dehydrogenase*, which breaks down ethyl alcohol. People who do not drink alcoholic beverages have little alcohol dehydrogenase. Expression of the enzyme increases when people drink alcohol, but full expression requires many days, meaning that people are incompletely defended against alcohol's effects when they first start drinking after a period of not drinking. Consider, also, that muscles atrophy when not used, rather than being maintained always in a fully developed state. Propose reasons why animals depend on phenotypic plasticity, instead of maintaining all their systems in a maximum state of readiness at all times.
- Whereas the larvae of a particular species of marine crab are bright orange, the adults of the species are white. An expert on the crabs was asked, "Why are the two different life stages different in color?" She replied, "The larvae accumulate orange-colored carotenoid pigments, but the adults do not." Did she recognize all the significant meanings in the question asked? Explain.
- Referring to Figure 1.9, do zebras, warthogs, and greater kudu have normal or exceptional gestation lengths? Justify your position in each case.
- At least three hemoglobin alleles in human populations alter hemoglobin structure in such a way as to impair the transport of O_2 by the blood but enhance resistance of red blood cells to parasitization by malaria parasites. Explain how such alleles exemplify pleiotropy, and discuss whether such alleles could lead to nonadaptive evolution of blood O_2 transport in certain situations.
- What are some of the microclimates that a mouse might find in your professor's home?
- Figure 1.14 seems at first to be simply a description of the physical and chemical properties of a lake. Outline how living organisms participate in determining the physical and chemical (i.e., temperature and O_2) patterns. Consider organisms living both in the lake and on the land surrounding the lake. Consider also a recent research report that shows that dense populations of algae sometimes change the temperature structure of lakes by raising the thermocline and thereby increasing the thickness of the deep, cold layer; how could algal populations do this, and what could be the consequences for deep-water animals?
- Do you agree with François Jacob that evolution is more like tinkering than engineering? Explain.
- Explain how the comparative method, knockout animals, and geographical patterns of gene frequencies might be used to assess whether a trait is adaptive. As much as possible, mention pros and cons of each approach.

10. Certain species of animals tolerate body temperatures of 50°C, but the vast majority do not. Some species can go through their life cycles at very high altitudes, but most cannot. What are the potential reasons that certain exceptional species have evolved to live in environments that are so physically or chemically extreme as to be lethal for most animals? How could you test some of the ideas you propose?
11. Using the set of data that follows, calculate how many of the molecules of O₂ that were used in aerobic catabolism by Julius Caesar are in each liter of atmospheric air today. All values given are expressed at Standard Conditions of Temperature and Pressure (see Appendix C) and therefore can be legitimately compared. Average rate of O₂ consumption of a human male during ordinary daily activities: 25 L/h. Number of years after his birth when Caesar was mortally stabbed near the Roman Forum: 56 years. Number of liters of O₂ per mole: 22.4 L/mol. Number of moles of O₂ in Earth's atmosphere: 3.7 × 10¹⁹ mol. Number of molecules per mole: 6 × 10²³ molecules/mol. Amount of O₂ per liter of air at sea level (20°C): 195 mL/L. Be prepared to be surprised! Of course, criticize the calculations if you feel they deserve criticism.

Go to sites.sinauer.com/animalphys3e for box extensions, quizzes, flashcards, and other resources.

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