Introductory Biology 2

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1. Chapter 1: Nature of Science

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Introduction

Science is a very specific way of learning, or knowing, about the world. Humans have used the process of science to learn a huge amount about the way the natural world works. Science is responsible for amazing innovations in medicine, hygiene, and technology. There are however, areas of knowledge and human experience that the methods of science cannot be applied to. These include such things as answering purely moral questions, aesthetic questions, or what can be generally categorized as spiritual questions. Science cannot investigate these areas because they are outside the realm of material phenomena, the phenomena of matter and energy, and cannot be observed and measured.

Here are some examples of questions that **can** be answered using science:

- What is the optimum humidity for the growth and proliferation of the giant puffball fungus (Calvatia gigantea)? If you want to learn more about this cool fungus, visit the following link: https://www.nps.gov/articles/species-spotlight-puffballs.htm
- Are birds attracted to other birds of a specific coloration?
- What virus causes a certain disease in a population of sheep?
- What dose of the antibiotic amoxicillin is optimal for treating pneumonia in an 80 year old?

On the other hand, here are some examples of questions that **CANNOT** be answered using science:

- How mean is the Grinch compared to Santa Claus?
- Where do ghosts live?
- How ethical is it to genetically engineer human embryos? To learn more about designer babies, visit the following link: https://www.nature.com/articles/d41586-019-00673-1
- What is the effect of fairies on Texan woodland ecosystems?

Take some time to reflect on each of these questions in order to understand why they can or cannot be answered through the use of science.

Reading Question #1:

Which of the following questions COULD be answered using science?

A. What is Santa Claus' favorite treat?

B. Which sushi roll is better: avocado maki or crunchy california roll?

C. Should abortion be legal or illegal?

D. What is the effect of Purina cat food on cats' fur quality?

Because this is a biology class, we will be focusing on questions that can be answered scientifically. A scientific question is one that can be answered by using the process of science (testing hypotheses, making observations about the natural world, designing experiments).

Sometimes you will directly make observations yourself about the natural world that lead you to ask scientific questions, other times you might hear or read something that leads you to ask a question. Regardless of how you make your initial observation, you will want to do research about your topic before you start setting up an experiment. When you're learning about a topic, it's important to use credible sources of information.

Observations vs. Inferences

The scientific process typically starts with an **observation** (often a problem to be solved) that leads to a question. Remember that science is very good at answering questions having to do with observations about the natural world, but is very bad at answering questions having to do with morals, ethics, or personal opinions. Think back to the questions in Reading Question #1. If you see a question that had to do with an opinion or an ethically-complex matter, it is likely not answerable using science. However, a question that involves observation and data collection, as well as the use of quantitative measures, is likely answerable using science.

Let's think about a simple problem that starts with an observation and apply the **scientific method** to solve the problem. One Monday morning, a student arrives at class and quickly discovers that the classroom is too warm. That is an observation that also describes a problem: the classroom is too warm. The student then asks a question: "Why is the classroom so warm?"

Now, let's get back to contrasting observations and **inferences**. Students will frequently get confused between these two. An observation is obtained usually from a primary source – this is a source that directly witnessed or experienced a certain event. In other words, an observation is easily seen. For instance, if you are a polar bear researcher who is observing the behavior and dietary tendencies of a polar bear from an observatory in Greenland, you are likely to notice that a polar bear consumes meat exclusively. Then, you may infer that the polar bear has a jaw morphology optimized for chewing on meat and a digestive tract optimized for digesting it. However, you cannot scrutinize the jaw morphology or the digestive tract well enough (unlike the polar bear's dietary tendency, which is more evident to you), so this is still an inference rather than an observation. An inference is a conclusion that is drawn based on logical reasoning as well as evidence that is observed. Thus, observations are required to make an inference but they are still distinct.

Existing knowledge is critical to providing oneself with evidence to make an inference. For example, a biology student's prior knowledge may tell them that mammals are viviparous (i.e., they give birth to their offspring). However, as often occurs in science, there are noteworthy exceptions to most rules. This is why science is fun! For example, the duck-billed platypus, echidna, and five monotreme species lay eggs, instead of giving birth to their offspring.

READING QUESTION #2

Which of the following describes the relationship between an observation and inference?

A. An inference constitutes a type of evidence needed to reach an observation.

B. An observation constitutes a type of evidence needed to reach an inference.

C. An observation and inference are interchangeable terms.

D. There is truly no relationship between an observation and inference.

Methods of Scientific Investigation and Scientific Inquiry

One thing is common to all forms of science: an ultimate goal “to know.” Curiosity and inquiry are the driving forces for the development of science. Scientists seek to understand the world and the way it operates. Two methods of logical thinking are used: inductive reasoning and deductive reasoning.

Inductive reasoning is a form of logical thinking that uses related observations to arrive at a general conclusion. This type of reasoning is common in descriptive science. A life scientist such as a biologist makes observations and records them. These data can be qualitative (descriptive) or quantitative (consisting of numbers), and the raw data can be supplemented with drawings, pictures, photos, or videos. From many observations, the scientist can infer conclusions (inductions) based on evidence. Inductive reasoning involves formulating generalizations inferred from careful observation and the analysis of a large amount of data. Brain studies often work this way. Many brains are observed while people are doing a task. The part of the brain that lights up, indicating activity, is then demonstrated to be the part controlling the response to that task.

Deductive reasoning or deduction is the type of logic used in hypothesis-based science. Recall what a **hypothesis**is. In deductive reasoning, the pattern of thinking moves in the opposite direction as compared to inductive reasoning. Deductive reasoning is a form of logical thinking that uses a general principle or law to forecast specific results. From those general principles, a scientist can extrapolate and predict the specific results that would be valid as long as the general principles are valid. For example, a prediction would be that if the climate is becoming warmer in a region, the distribution of plants and animals should change. Comparisons have been made between distributions in the past and the present, and the many changes that have been found are consistent with a warming climate. Finding the change in distribution is evidence that the climate change conclusion is a valid one.

Deductive and inductive reasoning are related to the two main pathways of scientific study, that is, **descriptive science** and **hypothesis-based science**. Descriptive (or discovery) science aims to observe, explore, and discover, while hypothesis-based science begins with a specific question or problem and a potential answer or solution that can be tested. The boundary between these two forms of study is often blurred, because most scientific endeavors combine both approaches. Observations lead to questions, questions lead to forming a hypothesis as a possible answer to those questions, and then the hypothesis is tested. Thus, descriptive science and hypothesis-based science are in continuous dialogue.

Testing hypotheses

Biologists study the living world by posing questions about it and seeking science-based responses. This approach is common to other sciences as well and is often referred to as the scientific method. The scientific method was used even in ancient times, but it was first documented by England's Sir Francis Bacon (Figure 1.1) (1561–1626), who set up inductive methods for scientific inquiry. The scientific method is not exclusively used by biologists but can be applied to almost anything as a logical problem-solving method.

Figure 1.1 Presumably, Sir Francis Bacon is the first philosopher documented to utilize the scientific method.

The scientific process typically starts with an observation (often a problem to be solved) that leads to a question. Let's think about a simple problem that starts with an observation and apply the scientific method to solve the problem. One Monday morning, a student arrives at class and quickly discovers that the classroom is too warm. That is an observation that also describes a problem: the classroom is too warm. The student then asks a question: "Why is the classroom so warm?"

Recall that a hypothesis is a suggested explanation that can be tested. To solve a problem, several hypotheses may be proposed. For example, one hypothesis might be, "The classroom is warm because no one turned on the air conditioning." But there could be other responses to the question, and therefore other hypotheses may be proposed. A second hypothesis might be, "The classroom is warm because there is a power failure, and so the air conditioning doesn't work."

Once a hypothesis has been selected, a prediction may be made. A prediction is similar to a hypothesis but it typically has the format "If . . . then . . . ." For example, the prediction for the first hypothesis might be, "*If* the student turns on the air conditioning, *then* the classroom will no longer be too warm."

A hypothesis must be testable to ensure that it is valid. For example, a hypothesis that depends on what a bear thinks is not testable, because it can never be known what a bear thinks. It should also be falsifiable, meaning that it can be disproven by experimental results. An example of an unfalsifiable hypothesis is "Botticelli's *Birth of Venus* is beautiful." There is no experiment that might show this statement to be false. To test a hypothesis, a researcher will conduct one or more experiments designed to eliminate one or more of the hypotheses. This is important. A hypothesis can be disproven, or eliminated, but it can never be proven. Science does not deal in proofs like mathematics. If an experiment fails to disprove a hypothesis, then we find support for that explanation, but this is not to say that down the road a better explanation will not be found, or a more carefully designed experiment will be found to falsify the hypothesis.

Each experiment will have one or more variables and one or more controls. A variable is any part of the experiment that can vary or change during the experiment. A control is a part of the experiment that does not change. Look for the variables and controls in the example that follows. As a simple example, an experiment might be conducted to test the hypothesis that phosphate limits the growth of algae in freshwater ponds. A series of artificial ponds are filled with water and half of them are treated by adding phosphate each week, while the other half are treated by adding a salt that is known not to be used by algae. The variable here is the phosphate (or lack of phosphate), the experimental or treatment cases are the ponds with added phosphate and the control ponds are those with something inert added, such as the salt. Just adding something is also a control against the possibility that adding extra matter to the pond has an effect. If the treated ponds show lesser growth of algae, then we have found support for our hypothesis. If they do not, then we reject our hypothesis. Be aware that rejecting one hypothesis does not determine whether or not the other hypotheses can be accepted; it simply eliminates one hypothesis that is not valid . Using the scientific method (Figure 1.2), the hypotheses that are inconsistent with experimental data are rejected.

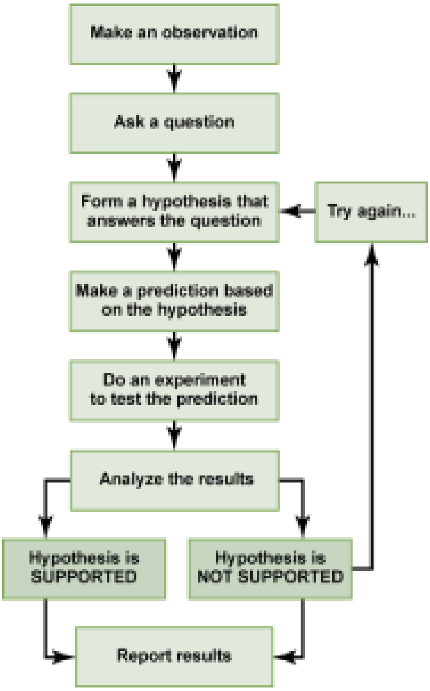

Figure 1.2 The scientific method is a sequential series of steps, ranging from an observation and typically concluding in the reporting of results. If the acquired data does NOT support a given hypothesis, alternative hypotheses should be considered and tested again. Thus, this is often an iterative process. Persistence is key! The limitations of the scientific method as depicted above will be discussed in further detail below. Do not be fooled – this linear method does not accurately reflect how scientists and researchers conduct their work.

In the example below, the scientific method is used to solve an everyday problem. Which part in the example below is the hypothesis? Which is the prediction? Based on the results of the experiment, is the hypothesis supported? If it is not supported, propose some alternative hypotheses.

1. My toaster doesn't toast my bread.
2. Why doesn't my toaster work?
3. There is something wrong with the electrical outlet.
4. If something is wrong with the outlet, my coffeemaker also won't work when plugged into it.
5. I plug my coffeemaker into the outlet.
6. My coffeemaker works.

In practice, the scientific method is not as rigid and structured as it might at first appear. Sometimes an experiment leads to conclusions that favour a change in approach; often, an experiment brings entirely new scientific questions to the puzzle. Many times, science does not operate in a linear fashion; instead, scientists continually draw inferences and make generalizations, finding patterns as their research proceeds. Scientific reasoning is more complex than the scientific method alone suggests.

Please refer to this link to gain an appreciation for why the scientific method is not truly the basic and in some senses, boring process as it is communicated to be in many scientific textbooks. Pay particular attention to the illustrated flowcharts.

Reading Question #3

Biology students are trying to describe the coloration of male cardinals in the Canadian province of Ontario. They find that across three regions, male cardinals are red. Of the following, which best exemplifies INDUCTIVE reasoning?

A. They conclude that all male cardinals in Ontario are red.

B. They predict that in the next regions they will survey, male cardinals will be red.

C. They predict that in the next regions they will survey, female cardinals will also be red.

D. Both A and B.

The importance of peer-review in science

Whether scientific research is basic science or applied science, scientists must share their findings in order for other researchers to expand and build upon their discoveries. Collaboration with other scientists—when planning, conducting, and analyzing results—is important for scientific research. For this reason, important aspects of a scientist's work are communicating with peers and disseminating results to peers. Scientists can share results by presenting them at a scientific meeting or conference, but this approach can reach only the select few who are present. Instead, most scientists present their results in peer-reviewed manuscripts that are published in scientific journals. Peer-reviewed manuscripts are scientific papers that a scientist's colleagues or peers review. Scholarly work is checked by a group of experts in the same field to make sure it meets the journal standards before it is accepted or published. These colleagues are qualified individuals, often experts in the same research area, who judge whether or not the scientist's work is suitable for publication. The process of **peer review** helps to ensure that the research in a scientific paper or grant proposal is original, significant, logical, and thorough. Grant proposals, which are requests for research funding, are also subject to peer review. Scientists publish their work so other scientists can reproduce their experiments under similar or different conditions to expand on the findings.

You've probably done a writing assignment or other project during which you have participated in a peer review process. During this process, your project was critiqued and evaluated by people of similar competence to yourself (your peers). This gave you feedback on which to improve your work. Scientific articles typically go through a peer review process before they are published in an academic journal, including conference journals. In this case, the peers who are reviewing the article are other experts in the specific field about which the paper is written. This allows other scientists to critique experimental design, data, and conclusions before that information is published in an academic journal. Often, the scientists who did the experiment and who are trying to publish it are required to do additional work or edit their paper before it is published. The goal of the scientific peer review process is to ensure that published primary articles contain the best possible science.

There are many journals and the popular press that do not use a peer-review system. A large number of online open-access journals, journals with articles available without cost, are now available many of which use rigorous peer-review systems, but some of which do not. Results of any studies published in these forums without peer review are not reliable and should not form the basis for other scientific work. In one exception, journals may allow a researcher to cite a personal communication from another researcher about unpublished results with the cited author's permission.

The peer-review process for oral communications and poster presentations at scientific conferences is a little less gruelling than for journals, although, a peer-review process is still applied before the work is accepted by conference organisers. Although many scientists will grimace at the mention of 'peer-review', it is through this process that we increase the likelihood that valid science (and not pseudoscience) is shared with the world. Peer review is an essential part of the scientific process, to make important economic and health-related decisions that affect the future prosperity of humanity.

As with all forms of communication, scientific research articles, oral communications and poster presentations need to be prepared and delivered according to specific guidelines and using particular language. It is important that student scientists begin to understand these guidelines and are given opportunities to practise these forms of communication. This chapter provides a roadmap for preparing and delivering these important modes of scientific communication.

Reading Question #4

Imagine you are publishing a paper investigating the immune system's involvement in multiple sclerosis (MS), a condition where the immune system attacks the myelin covering of neurons. Who is MOST qualified to conduct the peer-reviewing in a peer review process and is most likely to provide the highest-quality and most helpful peer review?

A. A family member who knows someone with MS

B. A graduate student studying MS

C. An immunologist who specializes in researching MS

D. A professor with several publications about genetic disorders

Reading Question #5

When are peer reviews warranted?

A. Grant proposals

B. Publication of journal articles

C. Publication of conference articles

D. All of the above

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2. Chapter 2: Natural Selection

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Introduction

All living organisms, from bacteria to baboons to blueberries, evolved at some point from a different species. Although it may seem that living things today stay much the same, that is not the case—evolution is an ongoing process.

The theory of evolution is the unifying theory of biology, meaning it is the framework within which biologists ask questions about the living world. Its power is that it provides direction for predictions about living things that are borne out in ongoing experiments. The Ukrainian-born American geneticist Theodosius Dobzhansky famously wrote that "nothing makes sense in biology except in the light of evolution" (Dobzhansky, 1964). He meant that the tenet that all life has evolved and diversified from a common ancestor is the foundation from which we approach all questions in biology.

Charles Darwin and Natural Selection

In the mid-nineteenth century, two naturalists, Charles Darwin and Alfred Russel Wallace, independently conceived and described **natural selection** – the primary mechanism of evolution. Importantly, each naturalist spent time exploring the natural world on expeditions to the tropics. From 1831 to 1836, Darwin traveled around the world on H.M.S. Beagle, including stops in South America, Australia, and the southern tip of Africa. Wallace traveled to Brazil to collect insects in the Amazon rainforest from 1848 to 1852 and to the Malay Archipelago from 1854 to 1862. Darwin's journey, like Wallace's later journeys to the Malay Archipelago, included stops at several island chains, the last being the Galápagos Islands west of Ecuador. On these islands, Darwin observed species of organisms on different islands that were clearly similar, yet had distinct differences. For example, the ground finches inhabiting the Galápagos Islands comprised several species with unique beak shapes (Figure 2.1). The species on the islands had a graded series of beak sizes and shapes with very small differences between the most similar ones. He observed that these finches closely resembled another finch species on the South American mainland. Darwin imagined that the island species might be species modified from one of the original mainland species. Upon further study, he realized that each finch's varied beaks helped the birds acquire a specific type of food. For example, seed-eating finches had stronger, thicker beaks for breaking seeds, and insect-eating finches had spear-like beaks for stabbing their prey.

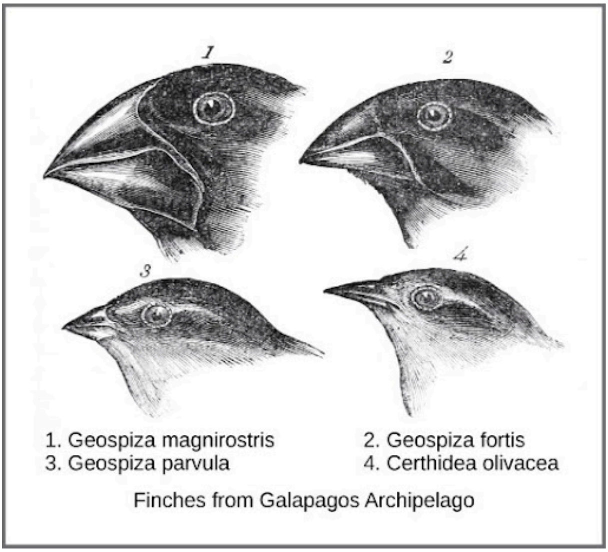

Figure 2.1 Darwin observed that beak shape varies among finch species. He postulated that ancestral species' beaks had adapted over time to equip the finches to acquire different food sources.

Wallace and Darwin both observed similar patterns in other organisms and they independently developed the same explanation for how and why such changes could take place. Darwin called this mechanism natural selection. Natural selection postulates that individuals with traits that are most beneficial in their environment reproduce more prolifically, and this leads to that trait becoming more common in the **population** in the next generation. This increase in frequency of a trait is evolutionary change.

For example, Darwin observed a population of giant tortoises in the Galápagos Archipelago to have longer necks than those that lived on other islands with dry lowlands. These tortoises were "selected" because they could reach more leaves and access more food than those with short necks. In times of drought when fewer leaves would be available, those that could reach more leaves had a better chance to eat and survive than those that couldn't reach the food source. Consequently, long-necked tortoises would be more likely to be reproductively successful and pass the long-necked trait to their offspring. Over time, only long-necked tortoises would become more abundant in the population.

Darwin argued that natural selection was an inevitable outcome of three principles that operated in nature. First, most characteristics of organisms are inherited, or passed from parent to offspring. Although no one, including Darwin and Wallace, knew how this happened at the time. Second, more offspring are produced than are able to survive and reproduce, so resources for survival and reproduction are limited. Thus, there is **competition** for those resources in each generation. Both Darwin and Wallace's understanding of this principle came from reading economist Thomas Malthus' essay that explained this principle in relation to human populations. Third, offspring vary among each other in regard to their characteristics and those variations are inherited. Darwin and Wallace reasoned that offspring with inherited characteristics which allow them to best compete for limited resources will survive and have more offspring than those individuals with variations that are less able to compete. Because characteristics are inherited, these traits will be better represented in the next generation. This will lead to change in populations over generations in a process that Darwin called descent with modification. Ultimately, natural selection leads to greater **adaptation** of the population to its local environment. It is the only mechanism known for adaptive evolution.

In 1858, Darwin and Wallace presented papers at the Linnean Society in London that discussed the idea of natural selection. The following year Darwin's book, On the Origin of Species, was published. His book outlined in considerable detail his arguments for evolution by natural selection.

Question #1

Which of the following correctly describes natural selection?

A. Individuals with beneficial traits reproduce more and thus the beneficial trait becomes more common in the next generation.
B. Individuals acquire more beneficial traits during their lifetime and thus the beneficial trait becomes more common in the next generation.
C. Populations mutate to create new, beneficial traits which help them survive better.
D. Individuals with different variations of traits reproduce randomly and thus there is no change in frequency in traits over time.

Three Requirements of Selection

Natural selection occurs whenever three conditions are met: variation, heritability, and differential reproduction.

Variation

We call the diversity of alleles and genotypes within a population **genetic variance**. Selection can only take place if there is variation, or differences, among individuals in a population. For example, if all of the strawberry plants in a population produce the same amount of fruits of the same size, then there is no basis upon which to select. More desirable traits only exist when there is variation in the trait. A population's individuals often display different phenotypes, or express different alleles of a particular gene, which scientists refer to as **polymorphisms**. We call populations with two or more variations of particular characteristics **polymorphic**. A number of factors, including the population's genetic structure and the environment influence population variation, the distribution of phenotypes among individuals. Understanding phenotypic variation sources in a population is important for determining how a population will evolve in response to different evolutionary pressures. Genetic diversity in a population comes from two main mechanisms: **mutation** and sexual reproduction. Mutation, a change in DNA, is the ultimate source of new alleles, or new genetic variation in any population.

Heritability

Natural selection can only act on heritable traits, namely those that are genetically encoded. This is critical because non-genetic factors can cause variation among individuals, such as an individual's height because of better nutrition rather than different genes. Acquired traits, for the most part, are not heritable. For example, if an athlete works out in the gym every day, building up muscle strength, the athlete's offspring will not necessarily grow up to be a body builder. If there is a genetic basis for the ability to run fast, on the other hand, a parent may pass this to a child. Heritability is the fraction of phenotype variation that we can attribute to genetic differences, or genetic variance, among individuals in a population. The greater the heritability of a population's phenotypic variation, the more susceptible it is to the evolutionary forces that act on heritable variation.

Not all variation observed within a species in heritable, some variation is caused by environmental factors. Someone who spends a lot of time outdoors without sun protection will have darker skin than someone with the same alleles who has minimal exposure to UV rays because humans increase melanin production in response to UV exposure. This is not to be confused with variations in melanization due to different alleles, which also exists. Sun tans will not be passed on to the next generation, but alleles influencing melanin production will. For some species, the environment determines some major characteristics, such as sex. For example, some turtles and other reptiles have temperature-dependent sex determination (TSD). TSD means that individuals develop into males if their eggs are incubated within a certain temperature range, or females at a different temperature range.

Differential Reproduction

When competition is severe enough that only some individuals reproduce, the next generation consists of offspring who inherit the desirable trait from their parents.

Reading Question #2

What are the 3 conditions under which natural selection will occur?

A. Heritability of traits, differential survival, and ongoing evolution
B. Differential survival, differential reproduction, and differential heritability
C. Uniformity of traits, uniform survival, and uniform heritability
D. Heritability of traits, differential reproduction, and variability of traits

Advancing the Theory of Evolution: The Modern Synthesis

Figure 2.2 The pea plant (Pisum sativum) was the focus of Mendel's experiments. photo credit: Stefan.lefnaer

People did not understand the mechanisms of inheritance, or genetics, at the time Charles Darwin and Alfred Russel Wallace were developing their idea of natural selection. This lack of knowledge was a stumbling block to understanding many aspects of evolution. The predominant (and incorrect) genetic theory of the time, **blending inheritance**, made it difficult to understand how natural selection might operate. Darwin and Wallace were unaware of Gregor Mendel's experiments with pea plants that uncovered the principles of genetics. Scholars rediscovered Mendel's work in the early twentieth century at which time geneticists were rapidly coming to an understanding of the basics of inheritance. Initially, the newly discovered particulate nature of genes made it difficult for biologists to understand how gradual evolution could occur. However, over the next few decades scientists integrated genetics and evolution in what became known as the **modern synthesis** – the coherent understanding of the relationship between natural selection and genetics that took shape by the 1940s. Generally, this concept is accepted today. In short, the modern synthesis describes how evolutionary processes, such as natural selection, can affect a population's genetic makeup, and, in turn, how this can result in the gradual evolution of populations and species. The theory also connects population change over time (microevolution), with the processes that gave rise to new species and higher taxonomic groups with widely divergent characters, called macroevolution.

The allele frequency within a given population can change depending on environmental factors; therefore, certain alleles become more widespread than others during the natural selection process. Natural selection alters the population's genetic makeup. An example is if a given allele confers a phenotype that allows an individual to better survive or have more offspring. Because many of those offspring will also carry the beneficial allele, and often the corresponding phenotype, they will have more offspring of their own that also carry the allele, thus, perpetuating the cycle. Over time, the allele will spread throughout the population. Some alleles will quickly become fixed in this way, meaning that every individual of the population will carry the allele, while detrimental mutations may be swiftly eliminated if derived from a dominant allele from the gene pool. The gene pool is the sum of all the alleles in a population.

Career Connection: Field Biologist

Many people hike, explore caves, scuba dive, or climb mountains for recreation. What if your job entailed working in the wilderness? Field biologists by definition work outdoors in the "field." The term field in this case refers to any location outdoors, even under water. A field biologist typically focuses research on a certain species, group of organisms, or a single habitat.

One objective of many field biologists includes discovering new, unrecorded species. Not only do such findings expand our understanding of the natural world, but they also lead to important innovations in fields such as medicine and agriculture. Plant and microbial species, in particular, can reveal new medicinal and nutritive knowledge. Other organisms can play key roles in ecosystems or, if rare, require protection. When discovered, researchers can use these important species as evidence for environmental regulations and laws.

Fitness and Adaptation

Charles Darwin coined the famous term "survival of the fittest." We often think of "**fitness**" as being related to physical strength and endurance, but Darwin was referring to how well an individual "fits" with its environment. Of course sometimes physical strength improves evolutionary fitness, but it is not necessarily the case. Although Darwin focused on survival, it is important to remember that natural selection is really driven by differential reproduction. Survival is necessary for reproduction, so survival is important, but only if it leads to increased reproduction.

We call a heritable trait that improves an organism's survival and reproduction in its present environment an **adaptation**. Scientists describe groups of organisms adapting to their environment when a genetic variation occurs over time that increases or maintains the population's "fit" to its environment. A platypus's webbed feet are an adaptation for swimming. A snow leopard's thick fur is an adaptation for living in the cold. A cheetah's fast speed is an adaptation for catching prey.

New adaptations can only arise via mutations. However, not all mutations are adaptations. Mutations can have one of three outcomes on the phenotype. A mutation could be harmful and reduce and organism's fitness (meaning they will produce fewer offspring), in which case it is called a deleterious mutation. A mutation could produce a phenotype with a beneficial effect on fitness, in which case it is an adaptation. Finally, a mutation could have no effect on the phenotype's fitness, in which cased it would be called a neutral mutation.

Whether a trait is favorable, harmful, or neutral depends on the environment in which it exists. Environmental conditions can change over time, and a trait that was adaptive in one situation could be neutral or harmful in another. Consider the example of the Galápagos finches that first inspired Darwin. Peter and Rosemary Grant and their colleagues have studied Galápagos finch populations every year since 1976. The Grants found changes from one generation to the next in beak shape distribution with the medium ground finch on the Galápagos island of Daphne Major. The birds inherit variation in their bill shape with some having wide deep bills and others having thinner bills. During a period in which rainfall was higher than normal because of an El Niño, there was a lack of large hard seeds of which the large-billed birds ate; however, there was an abundance of the small soft seeds which the small-billed birds ate. Therefore, the small-billed birds were able to survive and reproduce. In the years following this El Niño, the Grants measured beak sizes in the population and found that the average bill size was smaller. Since bill size is an inherited trait, parents with smaller bills had more offspring and the bill evolved into a much smaller size. As conditions improved in 1987 and larger seeds became more available, the trend toward smaller average bill size ceased.

Reading Question #3

In an evolutionary context, what does fitness refer to?

A. The strength of an organism.
B. The maximum speed at which an organism can move.
C. The amount of muscle mass in an organism.
D. How well an organism fits with its environment.

Reading Question #4

What is the relationship between fitness and adaptation?

A. Adaptation refers to an organism's degree of fitness.
B. An adaptation is a trait that improves an organism's fitness.
C. Fitness refers to an organism's ability to adapt.
D. Adaptation is interchangeable with the term fitness.

The Result of Selection is Changes in Allele Frequency in a Population

With the Modern Synthesis, we know that organisms' traits are determined by the alleles they have for a given gene. A gene for a particular trait may have several variants (called alleles) that code for different traits associated with that character. Traits are passed on as alleles as they are inherited from parent to offspring. In the early twentieth century, biologists in the area of population genetics began to study how selective forces change a population through changes in allele and genotypic frequencies.

The **allele frequency** is the rate at which a specific allele appears within a population. Until now we have discussed evolution as a change in the characteristics of a population of organisms, but behind that phenotypic change is genetic change. In population genetics, scientists define the term **evolution** as a change in the allele's frequency in a population.

To summarize, variation in a trait is caused by the existence of alleles for a given gene existing in a population. When a particular allele results in an adaptation (a trait that increases an organism's fitness), that individual can reproduce more successfully than others who lack that allele. Thus, individuals carrying the beneficial allele pass it onto the next generation more successfully than individuals with the less beneficial allele; and the beneficial allele becomes more frequent in the next generation. The next generation then has a higher frequency of the beneficial trait due to this underlying change in allele frequency.

Misconceptions of Evolution

Although the theory of evolution generated some controversy when

Darwin first proposed it, biologists almost universally accepted it within 20 years after publication of On the Origin of Species. Nevertheless, evolution is a nuanced theory and misconceptions about how it works abound.

Evolution Is “Just” a Theory

Some people attempt to diminish the importance of the theory of evolution by purposefully confounding the everyday usage of the word “theory” with the way scientists use the word. In science, we understand a “theory” to be a body of thoroughly tested and verified explanations for a set of observations of the natural world. Scientists have a theory of the atom, a theory of gravity, and the theory of relativity, each which describes understood facts about the world. In the same way, the theory of evolution describes facts about the living world. As such, a theory in science has survived significant efforts to discredit it by scientists. In contrast, a “theory” in common vernacular is a word meaning a guess or suggested explanation. This meaning is more akin to the scientific concept of “hypothesis.” When critics of evolution say it is “just a theory,” they are implying that there is little evidence supporting it and that it is still in the process of rigorous testing. This is a mischaracterization.

Individuals Evolve

Evolution is the change in a population’s genetic composition over time, specifically over generations, resulting from differential reproduction of individuals with certain alleles. Individuals do change over their lifetime, obviously, but this is development and involves changes programmed by the set of genes the individual acquired at birth in coordination with the individual’s environment.

When thinking about the evolution of a characteristic, it is most accurate to think about the change of the average value of the characteristic in the population over time. For example, when natural selection leads to bill-size change in medium ground finches in the Galápagos, this does not mean that individual bills on the finches are changing. If one measures the average bill size among all individuals in the population at one time and then measures them in the population several years later, this average value will be different as a result of evolution. Although some individuals may survive from the first time to the second, they will still have the same bill size; however, there will be many new individuals who contribute to the shift in average bill size.

Organisms Evolve on Purpose

Statements such as "organisms evolve in response to a change in an environment" are quite common, but such statements can lead to two types of misunderstandings. First, do not interpret the statement to mean that individual organisms evolve. The statement is shorthand for "a population evolves in response to a changing environment." However, a second misunderstanding may arise by interpreting the statement to mean that the evolution is somehow intentional. A changed environment results in some individuals in the population, those with particular phenotypes, benefiting and therefore producing proportionately more offspring than other phenotypes. This results in change in the population if the characteristics are genetically determined.

It is also important to understand that the variation that natural selection works on is already in a population and does not arise in response to an environmental change. For example, applying antibiotics to a population of bacteria will, over time, select a population of bacteria that are resistant to antibiotics). The resistance, which a gene causes, did not arise because of applying the antibiotic. The gene for resistance was already present in the bacteria's gene pool, likely at a low frequency. The antibiotic, which kills the bacterial cells without the resistance gene, strongly selects individuals that are resistant, since these would be the only ones that survived and divided. Experiments have demonstrated that mutations for antibiotic resistance do not arise as a result of antibiotic.

Summary

Natural selection describes a process in which individuals who are better at obtaining resources and escaping predation are more likely to survive and reproduce, passing on their heritable traits to future generations. Through this process individuals become more adapted to their environment and if this continues for several generations, there will eventually be a measurable change in the genetic composition of a population. This is what scientists define as evolutionary change.

Question #5

What is the result of natural selection?

A. Evolution
B. Change in allele frequency
C. New mutations
D. A and B
E. A, B, and C

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3. Chapter 3: Sexual Selection

MASON TEDESCHI; LISA LIMERI; AND ANASTASIA CHOUVALOVA

Sexual Selection

When discussing **natural selection** and adaptations, we often focus on traits that help an organism survive – surviving cold winters, avoiding predators, obtaining food, etc. But what about traits that do not directly aid in survival? Or better yet, what about traits that actually hinder survival? Picture the elaborate tail feathers of a peacock. These feathers, while visually stunning, make it nearly impossible for an individual to fly. Not only that, but these feathers also make it easier for a predator to spot a peacock from a distance and they can also be used by a predator to apprehend a peacock so it cannot escape. Rather than helping a peacock survive, their tail feathers actually make it more difficult to escape predation. So does such a trait evolve?

This question can be answered by viewing this trait not as aiding in survival, but as a trait that aids in reproduction. Exaggerated traits, like the tail feathers of a peacock, are used to attract females for mating, ensuring that a male passes his genes on to the next generation.

Elaborate peacock trains (Fig 3.1) represent an example of **sexual selection.** Sexual selection is a "special case" of natural selection in which individuals compete for mates in order to pass on their genes to future generations. The peacock's train is used to attract females for mating, ensuring that a male passes his genes on to the next generation. In essence, sexual selection acts on an individual's ability to successfully reproduce- even if that ability comes at a cost to survival.

Figure 3.1 Rather than aiding in survival, the peacock's tail aids in his reproduction. Males adorn these elaborate traits to attract the attention of females. Wikimedia CC-BY-SA-3.0.

Darwin identified a special case of natural selection that he called sexual selection. Sexual selection acts on traits that affect an individual's ability to attract mates and thus produce offspring. Sexual selection often leads to the evolution of dramatic traits that often appear maladaptive in terms of survival but persist because they give their owners greater reproductive success. Sexual selection can be so strong that it selects traits that are actually detrimental to the individual's survival.

Sexual selection occurs through two mechanisms: **intrasexual selection** of mates, also known as mate competition and $null$ and **intersexual selection**, also known as mate selection/choice.

Mechanisms of Sexual Selection

Sexual selection, the process through which individuals compete for mates, primarily takes two forms: intersexual selection and intrasexual selection. Intersexual selection, often referred to as mate choice, involves individuals of one sex choosing among members of the opposite sex based on the attractiveness of certain traits that those individuals possess. Intrasexual selection, also called mate competition, involves one sex competing with members of the same sex for access to mates.

Sexual selection results from competition over mates. Which sex competes for mates and which sex is choosy? In general, the sex that invests more resources in offspring is the one that will be more choosy, because they have more to lose by making a bad choice about a mate. This investment difference begins with gametes. Females produce eggs, which are much larger in size (and thus more costly to produce) and males produce sperm, which are small and energetically cheap (Fig 3.2). This difference in gamete investment is known as **anisogamy**.

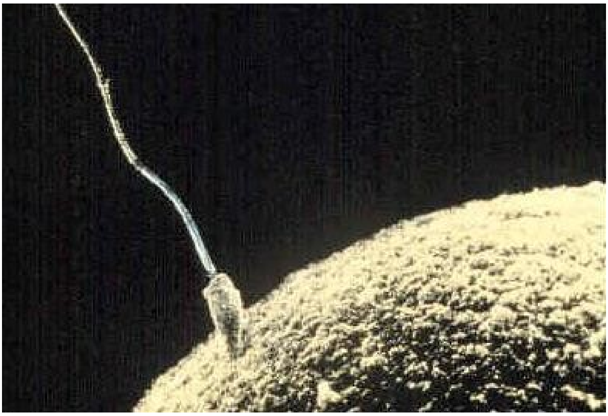

Figure 3.2 Notice the difference between the size of the human egg versus the human sperm. This size difference is called anisogamy.

This early investment difference resulting from anisogamy causes the general trend that in most species, females are the choosy sex and males are the sex competing for female to mate with. Another reason why females are typically the choosy sex has to do with the level of investment in offspring care, known as parental care. For example, following sexual reproduction and **fertilization**, most mammals develop within the body of their mothers. The developing offspring of most mammals then get their food and oxygen from the blood of their mothers through a spongy organ called the placenta. Even marsupial offspring, though not fully developed when born, are usually carried by their mothers in a pouch until they are able to walk on their own.

However, it is important to note that not all species follow this trend. In some animals, males provide a great deal of parental care to their offspring. For example, in emperor penguins each female produces a single egg. She then transfers the egg to her male mate and leaves to spend the winter in the open ocean in search of food and other resources. During the Antarctic winter, which lasts about four months, male emperor penguins huddle in groups, guarding their eggs and keeping them warm. Another example is seahorses, where males **incubate** eggs and care for young in a pouch. When they mate, a female deposits eggs into the male's pouch and leaves, providing no further parental care. Thus, male seahorses invest far more resources into offspring than females do, and it's the males who are the choosy sex and females compete for male mates.

Question #1

Which sex is typically the choosy sex? The sex that…

A. invests more resources into offspring
B. produces a larger number of gametes
C. is larger in size
D. has more elaborate coloration and ornamentation

Intrasexual Selection: Competition

Intrasexual (within sex) competition takes the form of conflicts between members of a sex competing for mates. These intrasexual competitions are often ritualized, but may also pose significant threats to the competitors' survival. Intrasexual selection involves mating displays and aggressive mating rituals such as rams butting heads—the winner of these battles is the one that is able to mate. Many of these rituals use up considerable energy but result in the selection of the healthiest, strongest, and/or most dominant individuals for mating. Sometimes the competition is for territory, with prospective mates more likely to mate with individuals with higher quality territories.

Intersexual Selection: Mate Choice

Intersexual (between sexes) selection occurs when members of the choosy sex select a mate based on a trait or suite of traits, such as feather colors, the performance of a mating dance, or the building of an elaborate structure. There are several, non-exclusive models of how and why mating preferences evolve. Broadly, there are two types of fitness benefits that drive mate choice: **direct and indirect benefits.**

Direct Benefits

Direct benefits increase the fitness of choosy individuals through material resources. Members of the competing sex will sometimes provide members of the choosy sex with a food gift before mating. These resources, called **nuptial gifts**, provide nourishment to prospective mates that they may not otherwise get. For example, male great grey shrikes- a predatory bird- will present prey items (e.g., rodents, other birds, lizards) to females immediately before mating. A female great grey shrike will choose a mate according to the size of the prey item presented to her. Nuptial gifts are observed in many insects and spiders where males present nuptial food gifts to females in the hopes that she will choose to mate with him (Fig 3.3).

Figure 3.3 The male katydid transfers a type of nuptial gift called a spermatophore to a female during mating. Wikimedia CC BY-2.0

In extreme cases, the competing sex will even sacrifice parts or all of themselves to members of the choosy sex. For example, in some species of ground crickets, females receive a nuptial gift by chewing on a specialized spur structure on the male hind tibia (i.e. leg) while mating. Most predatory species of preying mantids practice a type of extreme nuptial feeding known as sexual cannibalism, in which a female will eat her mate prior to, during, or after copulation. Most often, a female mantid will begin feeding by biting off the head of a male, as they would with regular prey. Because copulatory movement in males is controlled by nerves in the abdomen, not the head, removal of a male's head does not affect mating, sperm transfer, or proper fertilization. The reason for sexual cannibalism has been heavily debated. Experiments show that females on low quality diets are more likely to cannibalize her mates, compared with females given high quality diets. Thus, nuptial gifts are typically considered a direct benefit, because they enhance a female's survival and reproduction. Some suggest that males that submit to females and are cannibalized gain a selective advantage by producing higher quality offspring. In any event, this type of sexual behavior is quite rare because the costs are often assumed to outweigh the benefits, particularly for males.

Question #2

What are nuptial gifts?

A. A form of indirect benefits to the choosy sex
B. Resources provided by the competitive sex to the choosy sex
C. Nourishing resources typically provided by the choosy sex to the competitive
D. A form of intrasexual competition

Indirect Benefits

Indirect benefits do not directly benefit the choosing individual, but rather, indirectly benefit them by increasing the fitness of their offspring . There are multiple hypothesized mechanisms of indirect benefits. Three of the most common and well-supported are the Sexy Sons, Good Genes and Handicap Hypotheses.

The Sexy Sons Hypothesis: The sexy sons hypothesis postulates that members of the choosy sex who select mates with attractive traits will benefit by producing offspring who also possess the attractive traits and thus will be reproductively successful. As such, the attractive (sexy) sons will be more likely to attract females, and thus the choosy female's genes will continue to spread.

The Good Genes Hypothesis. The good genes hypothesis states that males develop impressive ornaments to show off their efficient metabolism or their ability to fight disease. Females then choose males with the most impressive traits because it signals their genetic superiority, which they will then pass on to their offspring.

The Handicap Hypothesis. Exaggerated traits, such as the Peacock's train, that exist to attract mates can reduce the owner's survival. Why would females prefer to mate with males that have traits that reduce survival? The Handicap hypothesis poses that a male with a large, elaborate train must be especially strong and fast to escape predators while having a handicap, and thus makes an ideal mate.

In both the handicap principle and the good genes hypothesis, the trait is an honest signal of the males' quality, thus giving females a way to find the fittest mates— males that will pass the best genes to their offspring.

Question #3

Individuals with a large, elaborate traits are ideal mates because they must be especially strong and fast to escape predators despite having such an unwieldy trait. This describes which hypothesized mechanism of sexual selection?

A. Sexy Sons hypothesis
B. Good genes hypothesis
C. Handicap hypothesis
D. Direct benefits hypothesis

Post-Copulatory Sexual Selection

Remember that sexual selection does not come to a halt after animals have mated! If a female mates with multiple males, such that sperm from several individuals remains in her body for an extended period of time, sexual selection can continue long after a male and female have mated. Just like with sexual selection before mating, post-copulatory sexual selection occurs in two forms: **cryptic female choice**– an extension of mate choice; and **sperm competition**– an extension of mate competition.

Cryptic female choice

Using physical or chemical mechanisms, females can bias paternity and affect male reproductive success by choosing whether certain sperm are successful in fertilizing their eggs. The term "cryptic" is used to describe an internal, and thereby hidden, process that females employ to choose the sperm from males that they prefer. The research suggests that cryptic female choice is likely a consequence of sexual conflict regarding the frequency and mode of mating. While males increase their fitness by successfully mating with as many females as possible, and thereby fertilizing as many eggs as possible from different females, females can incur fitness costs associated with mating with many males. Cryptic female choice reduces these costs by allowing females to mate multiply (as males wish to do), but then only select sperm from the favorable males afterwards. Here, females benefit by influencing paternity in favor of the males they prefer- possibly because they provide some direct or indirect benefit to her.

Sperm competition

Sperm competition, an extension of intrasexual competition, is the process by which sperm from two or more males compete for fertilization of a female's eggs. Sperm competition is often compared to having tickets in a raffle: a male has a better chance of having their ticket drawn (i.e. fathering offspring) if he has more tickets in the raffle (i.e. he releases more sperm per ejaculate into a female's reproductive tract). Alternatively, males may not release more sperm, but instead they evolve faster, more motile sperm that allow an individual's sperm to reach a female's eggs first. Among the best evidence we have for sperm competition is the evolution of longer sperm tails in animals that have multiple partners (Fig 3.4).

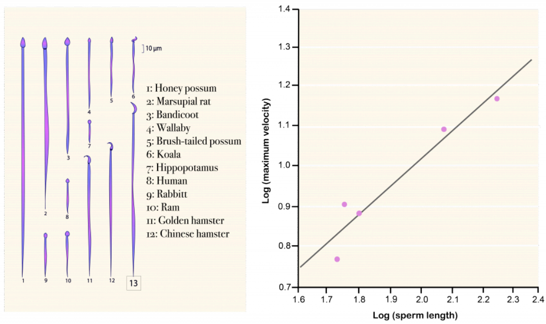

Figure 3.4 In animals where multiple matings are common, evolution has resulted in longer sperm tails, which allows sperm to swim more quickly. This provides evidence of sperm competition.

Sexual Dimorphism

Just as with natural selection, sexual selection can lead to changes in the genetic composition of a population that can be seen through physical changes to the way an organism looks. Both mate choice and mate competition can lead to the evolution of elaborate traits, termed secondary sexual traits, (secondary because they are not the primary traits involved in sexual reproduction or sperm transfer). Secondary sexual traits aid in sexual reproduction by improving an individual's ability to obtain mates. Typically, one sex possesses an elaborate secondary sexual trait or traits, but the other sex does not, a condition called **sexual dimorphism** (Fig 3.5). Both mate choice and mate competition can involve the evolution of secondary traits that are sexually dimorphic.

Figure 3.5 The stag beetle has horns that they use to stab rival males, helping them gain greater access to females. Wikimedia CC BY-SA 4.0

Traits that are subject to selection via mate choice are referred to as **ornaments** or **sexual signals**. Ornaments can involve different signal modalities, including visual signals like the bright colors of many birds and butterflies; olfactory (i.e. chemical) signals like the scent patches that many mammal species use to attract mates; auditory signals used by chorusing frogs and some insects like crickets; or even tactile signals like the vibratory signals used by some spiders when they tap their legs on the surface of a leaf to attract mates. Sexual signals can also involve multiple signal modalities. For example, male jumping spiders will often use both visual and vibratory signals when trying to attract females for mating.

Question #4

Which of the following correctly describes sexual dimorphism?

A. An evolutionary force that improves reproductive success in both males and females.
B. Traits related to sexual reproduction that are present in both males and females.
C. Traits that improve an individual's ability to survive.
D. Differences between males and females within a species resulting from sexual selection.

Question #5

What is the primary difference between natural and sexual selection?

A. Natural selection promotes traits enhancing the likelihood of reproduction whereas sexual selection promotes traits enhancing fitness.
B. Natural selection promotes traits enhancing survival whereas sexual selection promotes traits enhancing the likelihood of reproduction.
C. While natural selection occurs in individuals, sexual selection occurs on a population level.
D. There is no difference between them.

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4. Chapter 4: Non-adaptive mechanisms of evolution

ANASTASIA CHOUVALOVA AND LISA LIMERI

Mechanisms of Evolution

So far this semester we have focused on how natural and sexual selection drive **evolution.** Selection is the only mechanism of evolution that drives**adaptive evolution** – evolution that causes populations to become better adapted to their environments. However, not all evolution is adaptive. Evolution is changes in **allele frequencies i** populations over generations. The allele frequency describes the proportions of all of the possible alleles in the population's gene pool. The **gene pool** is the sum of all the alleles in a population. Changes in allele frequencies can be driven by more factors than just selection. Here we will investigate the three other mechanisms of evolution: gene flow, mutation, and genetic drift.

Gene Flow

Gene flow refers to the flow of alleles in and out of a population due to the migration of individuals or gametes (Fig 4.1). While some populations are fairly stable, others experience more flux. Many plants, for example, send their **pollen** far and wide, by wind or by pollinator, to **pollinate** other populations of the same species some distance away. Even a population that may initially appear to be stable, such as a pride of lions, experience immigration (coming into) and emigration (departing from) as developing males leave their mothers to seek out a new pride with genetically unrelated females. The flow of individuals in and out of populations changes the population's allele frequencies. When an individual migrates into a new population, it may sometimes carry alleles that were not **Gene flow**present in that population before, introducing new genetic variation into that population (Fig 4.1). Alternatively, if an individual emigrates from (leaves) a population where it was the only individual with a particular allele, it can result in its original population losing genetic diversity. Migration between populations causes them to become more genetically similar to each other. For example, alleles that may be present in one population but not the other can become present in both populations when a migrating individual introduces that allele to the new population.

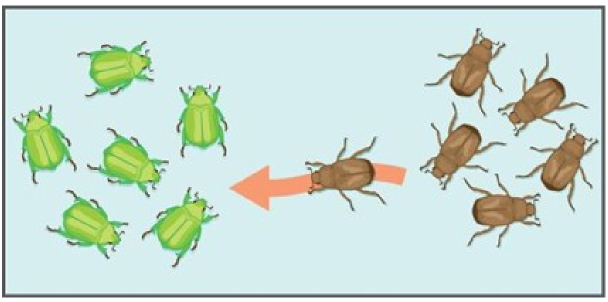

Figure 4.1 Gene flow occurs when an individual migrates from one population to another.

There are many examples of populations evolving through gene flow. An appreciation of gene flow can help us understand the global distribution of HIV resistance in humans. The CCR5 mutation confers resistance to some forms of HIV, yet is not most common in areas with a high prevalence of HIV and AIDS. The mutation is relatively new: biochemical and biogeographic evidence suggest an origin in Northern Europe approximately 1,200 years ago. However, the mutation was distributed globally long before HIV and AIDS were relevant to human health. In fact, the mutation's distribution pattern mirrors the Viking migration of the 9th through 11th centuries. Thus, we can hypothesize that Vikings carried the mutation with them as they conquered new territories, and passed the mutation to their descendants. But why was this genetic feature prevalent in Vikings? We'll develop that story further below.

Reading Question #1

What can result from an individual migrating to a new population?

A. The original population losing genetic diversity
B. The new population gaining genetic diversity
C. Allele frequencies in both populations changing
D. All of the above

Mutation

Mutation is a random change in the DNA sequence. Mutation is the ultimate source of genetic variation in all populations—new alleles, and, therefore, new genetic variations arise through mutation. A mutation creates a new allele, and thus by definition results in a small change in the allele frequencies within the population in which it occurs.

A mutation may produce an allele that is selected against, selected for, or selectively neutral. Harmful mutations (also called deleterious mutations) are removed from the population by selection and will generally only be found in very low frequencies equal to the mutation rate. Some are beneficial and will spread through the population. Whether a mutation is beneficial or harmful is determined by the environmental context in which it exists. If it helps an organism survive and reproduce in its environment, it is beneficial and therefore an adaptation. Some mutations do not do have any impact on fitness (called neutral mutations). The frequency of neutral mutations is unaffected by selection, and only subject to the other mechanisms of evolution.

Reading Question #2

Which of the following describes how mutations affect an individual's fitness.

A. All mutations are beneficial to an individual's fitness.
B. All mutations are harmful to an individual's fitness.
C. All mutations are neutral with respect to an individual's fitness.
D. Mutations can be beneficial, harmful, or neutral with respect to an individual's fitness.

Genetic Drift

Genetic drift refers to changes in allele frequencies across generations that occurs purely by random chance. The term "random" is key to an understanding of drift. Sometimes chance events, such a natural disaster, influence which individuals survive and reproduce and thus influence the allele frequencies in the next generation. Thus, evolution has occurred due only to random chance – this is genetic drift. While natural selection results from aspects of an organism's environment exerting "**selective pressure**" on the individual (e.g., the desert environment favors the spines of the cactus and the long ears of the fox), genetic drift is not a result of environmental pressures. Genetic drift, like natural selection, is occurring all of the time in all environments. Drift will influence every allele, even those that are being naturally selected. Thus, it can be difficult to determine which process dominates because it is often nearly impossible to determine the cause of change in allele frequencies at any given time.

Reading Question #3

Which of the following accurately describes genetic drift?

A. Adaptive changes in allele frequencies in a population
B. Random changes in allele frequencies in a population
C. Changes in allele frequencies due to migration of individuals to a new population
D. The random changes in DNA sequences creating new alleles

Genetic drift exerts a particularly strong effect in small populations, such as those that colonize islands or or the few individuals that remain after large-scale disruptions (e.g. earthquakes, fire). You are already familiar with the statistical principle (**sampling bias**) underlying this: the random loss of 20 iguanas from a large population of 1 million iguanas is bound to result in a smaller impact on allele frequencies than the random loss of 20 iguanas from an island population of 100 iguanas. Genetic drift occurs because the alleles in an offspring generation are a random sample of the alleles in the parent generation. Alleles may or may not make it into the next generation due to chance events including mortality of an individual, events affecting finding a mate, and even the events affecting which gametes end up in fertilizations. If one individual in a population of ten individuals happens to die before it leaves any offspring to the next generation, all of its genes—a tenth of the population's gene pool—will be suddenly lost. In a population of 100, that 1 individual represents only 1 percent of the overall gene pool; therefore, it has much less impact on the population's genetic structure and is unlikely to remove all copies of even a relatively rare allele.

Imagine a population of ten haploid individuals, half with allele A and half with allele a. In a **stable population**, the next generation will also have ten individuals. Choose that generation randomly by flipping a coin ten times and let heads be A and tails be a. It is unlikely that the next generation will have exactly half of each allele. There might be six of one and four of the other, or some different set of frequencies. Thus, the allele frequencies have changed and evolution has occurred. A coin will no longer work to choose the next generation (because the odds are no longer one half for each allele). The frequency in each generation will drift up and down on what is known as a random walk until at one point either all A or all a are chosen and that allele is fixed from that point on. This could take a very long time for a large population. This simplification is not very biological, but simulations and studies have shown that real populations behave this way. The effect of drift on frequencies is greater the smaller a population is. Its effect is also greater on an allele with a frequency far from one half. Genetic drift causes random changes in allele frequencies and these changes are larger when populations are small.

Reading Question #4

Where would you expect genetic drift to exert the strongest effects?

A. On an island with a small population.
B. On the mainland with a large population.
C. Genetic drift would have the same strength in both populations.

Bottleneck effect

Natural events, such as an earthquake disaster that randomly kills a large portion of the population, can magnify the effects of genetic drift. These situations, where a large portion of the gene pool is suddenly and randomly eliminated, is called the **bottleneck effect**(Fig 4.2). At once, the survivors' genetic structure (i.e., allele frequencies) becomes the entire population's genetic structure, which may be very different from the pre-disaster population. Almost certainly rare alleles are lost from the population, resulting in a decrease in the variability in the population. The survivors reproduce to create the next generation, which can have dramatically different allele frequencies compared to the population before the bottleneck event occurred. Bottleneck effects are a special case of genetic drift where the effects of drift are particularly strong because a population's size has been dramatically reduced.

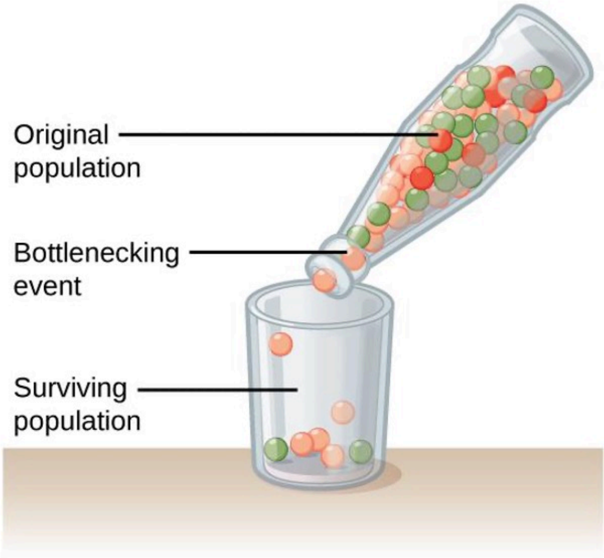

Figure 4.2 A chance event or catastrophe that dramatically reduces the population size can dramatically alter the allele frequencies in the population.

Founder Effect

Another scenario in which populations might experience a strong influence of genetic drift is if some portion of the population leaves to start a new population in a new location. It is likely that the small number of individuals who found the new population have different allele frequencies than the entire population due to random chance (sampling error). Thus, the new population can end up having very different allele frequencies than the original source population due to genetic drift – this is called the **founder effect**.

Reading Question #5

Which of the following are mechanisms of evolution? Select all that apply.

A. Acquired traits
B. Natural selection
C. Genetic drift
D. Gene flow
E. Mutation

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5. Chapter 5: Species Concepts

LISA LIMERI

Species Concepts

We will soon begin exploring how small evolutionary changes between generations (**microevolution**) can accumulate to result in large-scale changes, such as the evolution of new species (**macroevolution**). However, to discuss the evolution of new species over time, we need to be able to define what a species is. This is not as straight-forward as it seems. We would not expect all members of a species to be identical, so we must consider what magnitude and types of differences between individuals would lead us to consider them members of different species. A **species concept** is, therefore, a working definition of a species and/or a methodology for determining whether or not two organisms are members of the same species. In this chapter, we will consider three species concepts that are commonly used by scientists. All species concepts have limitations and work better for some organismal groups than others. Each section below considers the definition of the species concept, its assumptions and limitations, and examples of groups for which that species concept does, and does not, easily apply.

The Biological Species Concept

The most well-known species concept is the Biological Species Concept, which was proposed by evolutionary biologist Ernst Mayr.

The biological species concept states that a species is a group of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups. **Reproductive isolation** can be **prezygotic**, meaning that individuals of different groups do not mate with each other, or **postzygotic** , meaning that individuals of different groups mate together, but they are not able to produce offspring that are **viable** (able to survive) and **fertile** (able to reproduce).

In some cases, the biological species concept is straightforward and easy to apply. For instance, the western meadowlark (*Sturnella neglecta*) and the eastern meadowlark (*Sturnella magna*), both shown in Figure 5.1, respectively inhabit the western and eastern halves of North America. Despite the fact that their breeding ranges overlap throughout many upper midwestern states, including Michigan, Wisconsin, Illinois, Iowa, Missouri and Minnesota, the two groups do not interbreed. The courtship songs of the males of each species are distinctly different and females of each species respond to the songs of the males of their own species, leading to strong reproductive isolation between the two groups despite a high degree of similarity in appearance.

Figure 5.1 Males of the western meadowlark, Sturnella neglecta (left) and the eastern meadowlark Sturnella magna (right). Images from Wikimedia Commons

In many cases, however, the biological species concept is difficult or impossible to use. For example, the definition's focus on interbreeding means this concept cannot be applied to asexual organisms, such as bacteria. Additionally, it can only be applied to groups for which detailed reproductive data are available, or at least obtainable. It is therefore impossible to apply the biological species concept to long-extinct species for which reproductive data do not exist and can no longer be obtained. It can also be difficult to apply the biological species concept to groups for which little is known about their reproductive biology or behavior. In these cases, extensive research would be required to determine the degree to which individuals do or do not interbreed with other groups before being able to clearly identify species boundaries. Additionally, some groups have complex patterns of reproductive connectivity and isolation, such as the *Ensatina* salamander group shown in Fig 5.2. Systems like *Ensatina* are termed 'ring species' because they form a ring around a particular geographic barrier, in this case, California's Central Valley. As the group spread around the valley, populations maintained reproductive connectivity (ie. interbreeding) with nearby populations, but developed reproductive isolation from geographically distant populations. In the diagram below, interbreeding is shown as a gradation in color between two populations and reproductive isolation is shown as a solid line. For example, *E. oregonensis* (in red) can interbreed with *E. picta* (orange), *E. xanthoptica* (yellow), and *E. platensis* (pink), but none of the other species. Similarly, *E. xanthoptica* (yellow) can interbreed with *E. eschscholtzii* (green) and *E. oregonensis* (red), but none of the other species. In this case, the biological species concept leads to nonsensical and contradictory conclusions: *E. oregonensis*, *E. xanthoptica*, and *E. eschscholtzii* are members of the same species, but *E. oregonensis* and *E. eschscholtzii* are different species.

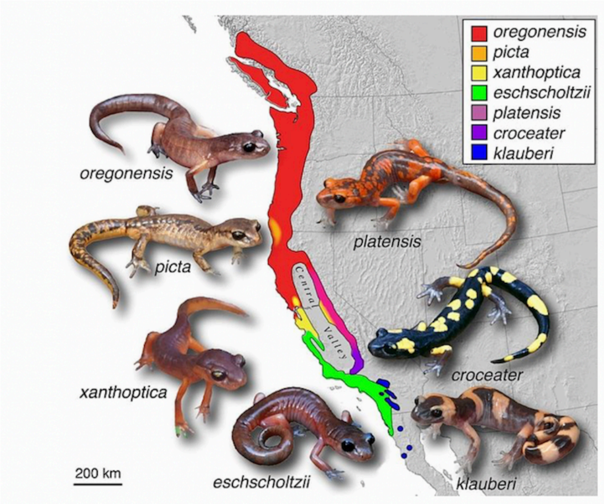

Figure 5.2 Range map for Ensatina species on the western coast of North America. Gradations in color (ex: E. oregonensis and E. picta) denote interbreeding between the two species, while solid lines (ex: E. klauberi and E. escholtzii) denote reproductive isolation. Image from Wikimedia Commons.

More philosophically, the biological species concept also considers species at only a single point in time (the present) and ignores the evolutionary and ecological processes that shaped reproductive isolation between groups.

Reading Question #1

The Biological Species Concept defines species based on

A. Whether individuals exist in the same geographic area
B. How similar individuals appear
C. How similar individuals' genomes are
D. Whether individuals can breed together

Reading Question #2

What are the types of reproductive isolation in the Biological Species Concept? Select all that apply.

A. Preferential reproductive isolation
B. Prezygotic reproductive isolation
C. Postzygotic reproductive isolation
D. Zygotic reproductive isolation

The Phylogenetic Species Concept

Due to the limitations of the biological species concept described above, other species concepts have been developed. The **phylogenetic species concept** defines species as groups of organisms that share a pattern of ancestry and descent and which form a single branch on the tree of life (Fig 5.3). This concept focuses more on the evolutionary history that has shaped the species as we see it today, and increasingly relies on genetic data to assign individuals to species. The phylogenetic species concept resolves some of the problems of the biological species concept since it can be applied to asexual species and those for which detailed reproductive behavioral data are unavailable. Its reliance on genetic data makes it also difficult to apply to long-extinct species; however, recent advances in genetic analysis have allowed scientists to extract DNA from recently extinct organisms such as Neanderthals and wooly mammoths. Scientists using the lineage species concept must still consider what type and magnitude of genetic differences, and in what portions of the genome, constitute different species and must employ modern computational tools to manage the increasingly large datasets produced in genetic analyses.

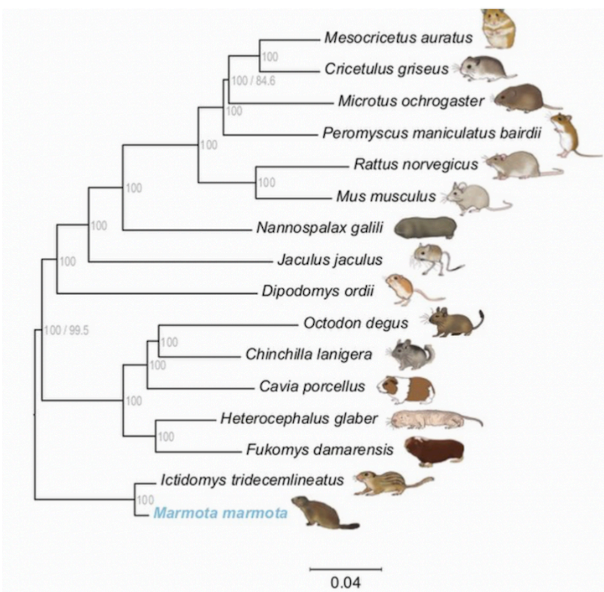

Figure 5.3 A *phylogenetic tree of the order Rodentia (rodents), representing the lineage species concept's focus on species being identified as unique branches on a phylogenetic tree. Image from Wikimedia Commons*

The Morphological Species Concept

How do scientists define species in groups where there is limited or unavailable data on reproductive behavior or genetic similarity? Consider, for example, the two trilobites shown in Figure 5.4. Both of the fossils shown in the figure are members of the Order Phacopidae, which went extinct during the end-Devonian mass extinction event that occurred approximately 360 million years ago. Consequently, the only evidence that remains of their existence is fossils; there is no behavioral data on reproductive isolation or connectivity with other trilobites and the fossils are old enough that their DNA has degraded beyond our current analytical capabilities. How then, do we define species in trilobites? The **morphological species concept** is frequently applied in such cases, as it relies entirely on morphology (the physical structures or traits of an organism).

As you look at two photos in Fig 5.4, you will notice clear morphological differences. The fossil on the right has large spines jutting from both its head and rear ends (in trilobites, these are termed the cephalon and pygidium, respectively). Additionally, the spines along the side of the trilobite's thorax are much larger and more pronounced in the fossil on the right. These morphological differences lead us to categorize these fossils as members of different species. In this case, the differences are large enough that we even categorize these fossils as members of different genera and families.

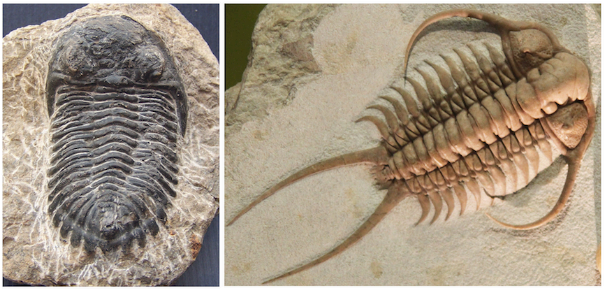

Figure 5.4 Two trilobites in the order Phacopidae; Hollardops mesocristata (left) and Cheirurus ingricus (right). Images from Wikimedia Commons

Since all organisms have physical traits, the morphological species can be used on any group of organisms on Earth. The major limitation to this species concept, however, is that morphology can be very misleading. Consider, for example, the shark and dolphin shown in Figure 5.5. These organisms have many morphological similarities in their body shape and coloration; however, we know from genetic analyses and more detailed morphological studies (on internal structures, etc) that sharks are more closely related to rays and other fish and dolphins are more closely related to whales and other mammals. The similarities that we first notice in these organisms are due to the similarities in the marine environment in which both organisms live and not to relatedness between the organisms. Consequently, the morphological species concept is often only used when other species concepts cannot be applied (for example, in the trilobate case) or in conjunction with other species concepts described above.

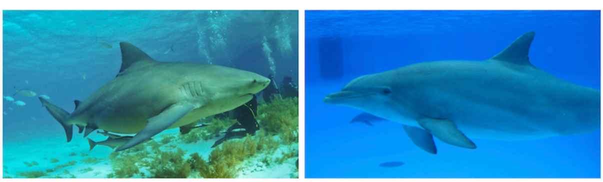

Figure 5.5 A bullshark (Carcharhinus leucas, left) and a bottlenose dolphin (Tursiops truncates, right). Images from Wikimedia Commons

Reading Question #4

A biologist using the morphological species concept to make an argument about whether two specimens are part of the same species or not would be using what evidence?

A. Genetic sequences
B. Mating behaviors
C. Physical traits
D. All of the above

Linking Species Concepts

Most scientists generally agree that a species is a group of organisms that share an evolutionary and ecological history and that are distinct from other groups. The primary difference in the species concepts described above is the forms of evidence used to quantify those differences and to categorize individuals as members of a particular species. The biological species concept relies on behavioral data and emphasizes reproductive isolation between groups. The lineage species concept relies on genetic data and emphasizes distinct evolutionary trajectories between groups, which result in distinct lineages (branches on a phylogenetic tree). The morphological species concept relies on morphological data and emphasizes groups of physical traits that are unique to each species. These lines of evidence are not mutually exclusive and so multiple species concepts may be used together to define species boundaries. Regardless of the species concept used, not all organisms are easily categorized into distinct groups and so conversations around species concepts, species boundaries, and the evidence used to define them are a dynamic field of evolutionary biology.

Reading Question #5

Which is the best species concept?

A. Biological Species Concept
B. Morphological Species Concept
C. Phylogenetic Species Concept
D. None are strictly better or worse, it depends on the situation

Naming Species

Carl Linnaeus began formally naming and categorizing species in 1735 in his publication *Systema Naturae*. Linnaeus developed the **binomial nomenclature** system for naming species, which is still used by scientists today. In this system, each species is given a two-word (binomial) Latin name. The first word is the generic name, which is shared among all the species in that genus. The second word is the specific epithet and is unique among species in that genus. For instance, all juniper trees have the genus name *Juniperus* and each species has a specific epithet that identifies which juniper species it is, such as western juniper (*Juniperus occidentalis*) or California juniper (*Juniperus californica*), etc. There are many species that have the genus name *Juniperus*, and many species that have the specific epithet *occidentalis* but only one *Juniperus occidentalis*. As you may have noted in this paragraph, species names are italicized and the genus name is capitalized while the specific epithet is not. The full formal name also includes the last name of the scientist who described the species and the year in which it was named. For example, the common limpets shown in Figure 6 carry the formal scientific name of *Patella vulgata* Linnaeus, 1758.

Figure 5.6 Common limpets, described by Carl Linnaeus in 1758 and named Patella vulgata. Image from Wikimedia Commons

Today, scientists have formalized guidelines they follow to choose names for new species. Scientists follow the guidelines of the International Code of Zoological Nomenclature (ICZN) or the International Code of Nomenclature for Algae, Fungi and Plants (ICN). These codes have strict rules for Latinizing names and descriptive terms to use in species names and for resolving conflicts in changes to scientific names. As our understanding of life on Earth expands, revisions to previous taxonomic groupings are often made and these guidelines help track changes and keep renaming or regrouping of organisms consistent.

References

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6. Chapter 6: Speciation

MASON TEDESCHI AND LISA LIMERI

Speciation

All of the extraordinary diversity of life on the planet arose from what was at one time a single common ancestor. Over time, new specie have arisen through **speciation**: the formation of two species from one original species. Darwin envisioned this process as a branching event and diagrammed the process in the only illustration in On the Origin of Species (Figure 3). Compare this illustration to the diagram of elephant evolution (Figure 3), which shows that as one species changes over time, it branches to form more than one new species, repeatedly, as long as the population survives or until the organism becomes extinct.

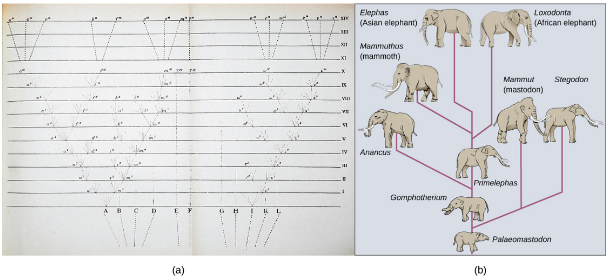

Figure 6.1 The only illustration in Darwin's On the Origin of Species is (a) a diagram showing speciation events leading to biological diversity. The diagram shows similarities to phylogenetic charts that today illustrate the relationships of species. (b) Modern elephants evolved from the Palaeomastodon, a species that lived in Egypt 35–50 million years ago.

For speciation to occur, two new populations must form from one original population and they must evolve in such a way that it becomes impossible for individuals from the two new populations to interbreed. Biologists have proposed mechanisms by which this could occur that fall into two broad categories. **Allopatric speciation** (allo- = "other"; -patric = "homeland") involves geographic separation of populations from a parent species and subsequent evolution. **Sympatric speciation** (sym- = "same"; -patric

= “homeland”) involves speciation occurring within a parent species remaining in one location.

Reading Question #1

What are the two types of speciation?

A. Evolutionary and non-evolutionary
B. Allopatric and sympatric
C. Adaptive and non-adaptive
D. Radiation and linear

Allopatric Speciation

A geographically continuous population typically has a gene pool that is relatively homogeneous. Gene flow, the movement of alleles across a species’ range due to migration, is relatively free because individuals can move and then mate with individuals in their new location. Thus, an allele’s frequency at one end of a distribution will be similar to the allele’s frequency at the other end. When populations become geographically discontinuous, it prevents alleles’ free-flow. When that separation lasts for a period of time, the two populations are able to evolve along different trajectories. Thus, their allele frequencies at numerous genetic loci gradually become increasingly different as new alleles independently arise by mutation in each population. Typically, environmental conditions, such as climate, resources, predators, and competitors for the two populations will differ causing natural selection to favor divergent adaptations in each group.

Isolation of populations leading to allopatric speciation can occur in a variety of ways: a river forming a new branch, erosion creating a new valley, a group of organisms traveling to a new location without the ability to return, or seeds floating over the ocean to an island. The nature of the geographic separation necessary to isolate populations depends entirely on the organism's biology and its potential for dispersal. If two flying insect populations took up residence in separate nearby valleys, chances are, individuals from each population would fly back and forth continuing gene flow. However, if a new lake divided two rodent populations continued gene flow would be unlikely; therefore, speciation would be more likely.

Biologists group allopatric processes into two categories:**dispersal** and **vicariance**. Dispersal is when a few members of a species move to a new geographical area, and vicariance is when a natural situation arises to physically divide organisms.

Scientists have documented numerous cases of allopatric speciation taking place. For example, along the west coast of the United States, two separate spotted owl subspecies exist. The northern spotted owl has genetic and phenotypic differences from its close relative: the Mexican spotted owl, which lives in the south (Fig 6.2).

Figure 6.2 The northern spotted owl and the Mexican spotted owl inhabit geographically separate locations with different climates and ecosystems. The owl is an example of allopatric speciation. (credit "northern spotted owl": modification of work by John and Karen Hollingsworth; credit "Mexican spotted owl": modification of work by Bill Radke)

Additionally, scientists have found that the further the distance between two groups that once were the same species, the more likely it is that speciation will occur. This seems logical because as the distance increases, the various environmental factors would likely have less in common than locations in close proximity. Consider the two owls: in the north, the climate is cooler than in the south. The types of organisms in each ecosystem differ, as do their behaviors and habits. Also, the hunting habits and prey choices of the southern owls vary from the northern owls. These variances can lead to evolved differences in the owls, and speciation likely will occur.

Reading Question #2

Allopatric speciation can occur due to…

A. Dispersal
B. Vicariance
C. Sympatric speciation
D. A and B
E. A, B, and C

Sympatric Speciation

Can divergence occur if no physical barriers are in place to separate individuals who continue to live and reproduce in the same habitat? The answer is yes. We call the process of speciation within the same space sympatric. The prefix "sym" means same, so "sympatric" means "same homeland" in contrast to "allopatric" meaning "other homeland." Scientists have proposed and studied many mechanisms.

One form of sympatric speciation can begin with a serious chromosomal error during cell division. In a normal cell division event chromosomes replicate, pair up, and then separate so that each new cell has the same number of chromosomes. However, sometimes the pairs separate and the end cell product has extra sets of chromosomes in a condition that we call polyploidy (Fig 6.3).

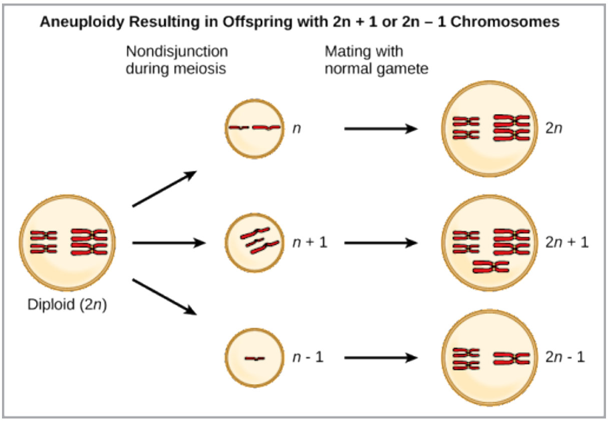

Figure 6.3 Aneuploidy results when the gametes have too many or too few chromosomes due to nondisjunction during meiosis. In this example, the resulting offspring will have 2n+1 or 2n-1 chromosomes.

Which is most likely to survive, offspring with 2n+1 chromosomes or offspring with 2n-1 chromosomes?

Polyploidy is a condition in which a cell or organism has an extra set, or sets, of chromosomes. Scientists have identified two main types of polyploidy that can lead to reproductive isolation of an individual in the polyploidy state. Reproductive isolation is the inability to interbreed. In some cases, a polyploid individual will have two or more complete sets of chromosomes from its own species in a condition that we call **autopolyploidy** (Fig 6.4). The prefix "auto-" means "self," so the term means multiple chromosomes from one's own species. Polyploidy results from an error in meiosis in which all of the chromosomes move into one cell instead of separating.

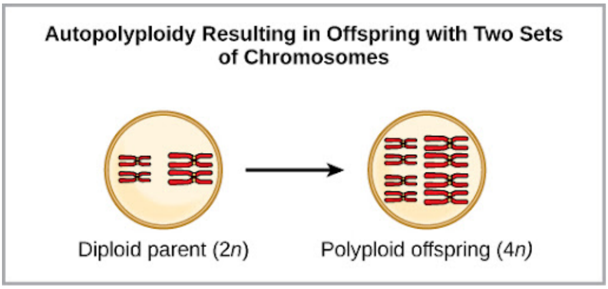

Figure 6.4 Autopolyploidy results when mitosis is not followed by cytokinesis.

For example, if a plant species with 2n = 6 produces autopolyploid gametes that are also diploid (2n = 6, when they should be n = 3), the gametes now have twice as many chromosomes as they should have. These new gametes will be incompatible with the normal gametes that this plant species produces. However, they could either self-pollinate or reproduce with other autopolyploid plants with gametes having the same diploid number. In this way, sympatric speciation can occur quickly by forming offspring with 4n that we call a tetraploid. These individuals would immediately be able to reproduce only with those of this new kind and not those of the ancestral species.

The other form of polyploidy occurs when individuals of two different species reproduce to form a viable offspring that we call an **allopolyploidy**. The prefix "allo-" means "other" (recall from allopatric): therefore, an allopolyploid occurs when gametes from two different species combine. Figure 6.5 illustrates one possible way an allopolyploid can form. Notice how it takes two generations, or two reproductive acts, before the viable fertile hybrid results.

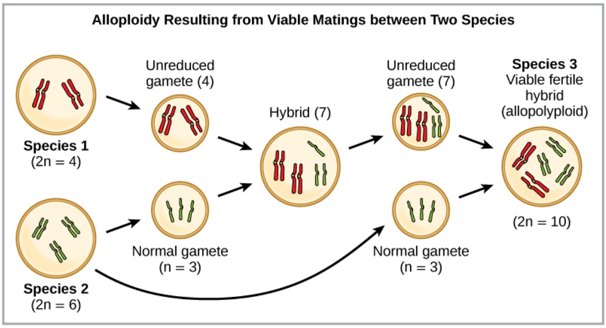

Figure 6.5 Alloploidy results when two species mate to produce viable offspring. In this example, a normal gamete from one species fuses with a polyploidy gamete from another. Two matings are necessary to produce viable offspring.

The cultivated forms of wheat, cotton, and tobacco plants are all allopolyploids. Although polyploidy occurs occasionally in animals, it takes place most commonly in plants. Scientists have discovered more than half of all plant species studied relate back to a species evolved through polyploidy. With such a high rate of polyploidy in plants, some scientists hypothesize that this mechanism takes place more as an adaptation than as an error.

Sympatric speciation may also take place in ways other than polyploidy. For example, consider a fish species that lives in a lake. As the population grows, competition for food increases. Under pressure to find food, suppose that a group of these fish had the genetic flexibility to discover and feed off another resource that other fish did not use. What if this new food source was located at a different depth of the lake? Over time, those feeding on the second food source would interact more with each other than the other fish; therefore, they would breed together as well. Offspring of these fish would likely behave as their parents: feeding and living in the same area and keeping separate from the original population.

If this group of fish continued to remain separate from the first population, eventually sympatric speciation might occur as more genetic differences accumulated between them.

This scenario does play out in nature, as do others that lead to reproductive isolation. One such place is Lake Victoria in Africa, famous for its sympatric speciation of cichlid fish. Researchers have found hundreds of sympatric speciation events in these fish, which have not only happened in great number, but also over a short period of time. Figure 13 shows this type of speciation among a cichlid fish population in Nicaragua. In this locale, two types of cichlids live in the same geographic location but have come to have different morphologies that allow them to eat various food sources.

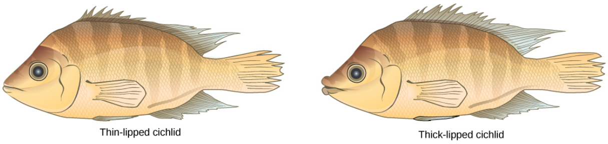

Figure 6.6 Cichlid fish from Lake Apoyeque, Nicaragua, show evidence of sympatric speciation. Lake Apoyeque, a crater lake, is 1800 years old, but genetic evidence indicates that a single population of cichlid fish populated the lake only 100 years ago. Nevertheless, two populations with distinct morphologies and diets now exist in the lake, and scientists believe these populations may be in an early stage of speciation.

Question #3

Sympatric speciation can occur due to…

A. Polyploidy
B. Populations adapting to use different parts of the habitat
C. Dispersal and vicariance
D. A and B
E. A, B, and C

Adaptive Radiation

In some cases, a population of one species disperses throughout an area, and each finds a distinct niche or isolated habitat. Over time, the varied demands of their new lifestyles lead to multiple speciation events originating from a single species. We call this **adaptive radiation** because many adaptations evolve from a single point of origin; thus, causing the species to radiate into several new ones. Island archipelagos like the Hawaiian Islands provide an ideal context for adaptive radiation events because water surrounds each island which leads to geographical isolation for many organisms. The Hawaiian honeycreeper illustrates one example of adaptive radiation. From a single species, the founder species, numerous species have evolved, including the six in Figure 6.7.

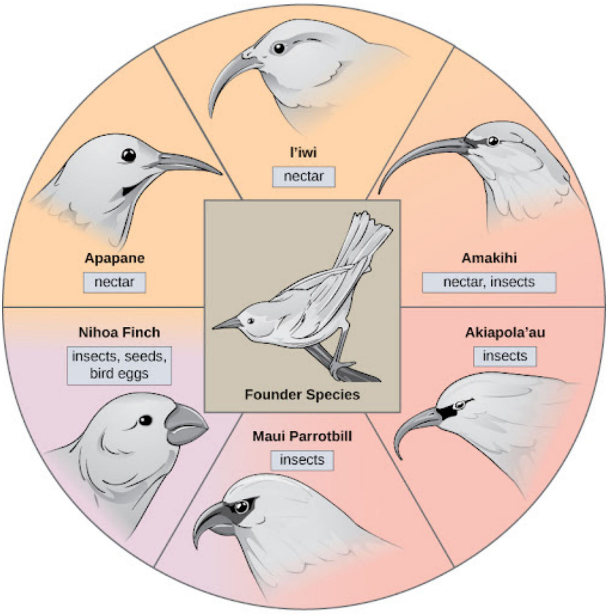

Figure 6.7 The honeycreeper birds illustrate adaptive radiation. From one original species of bird, multiple others evolved, each with its own distinctive characteristics.

Notice the differences in the species' beaks in Figure 6.7. Evolution in response to natural selection based on specific food sources in each new habitat led to evolution of a different beak suited to the specific food source. The seed-eating bird has a thicker, stronger beak which is suited to break hard nuts. The nectar-eating birds have long beaks to dip into flowers to reach the nectar. The insect-eating birds have beaks like swords, appropriate for stabbing and impaling insects. Darwin's finches are another example of adaptive radiation in an archipelago.

Link to Learning: The Origin of Birds

Watch this video to see how scientists use evidence to understand how birds evolved.

Reproductive Isolation

Given enough time, the genetic and phenotypic divergence between populations will affect characters that influence reproduction: if individuals of the two populations were brought together, mating would be less likely, but if mating occurred, offspring would be nonviable or infertile. Many types of diverging characters may affect the reproductive isolation, the ability to interbreed, of the two populations.

Reproductive isolation can take place in a variety of ways. Scientists organize them into two groups: **prezygotic** barriers and **postzygotic** barriers. Recall that a zygote is a fertilized egg: the first cell of an organism's development that reproduces sexually. Therefore, a prezygotic barrier is a mechanism that blocks reproduction from taking place. This includes barriers that prevent fertilization when organisms attempt reproduction. A postzygotic barrier occurs after zygote formation. This includes organisms that don't survive the embryonic stage and those that are born sterile.

Some types of prezygotic barriers prevent reproduction entirely. Many organisms only reproduce at certain times of the year, often just annually. Differences in breeding schedules, which we call **temporal isolation**, can act as a form of reproductive isolation. For example, two frog species inhabit the same area, but one reproduces from January to March; whereas, the other reproduces from March to May (Fig 6.8).

Figure 6.8 These two related frog species exhibit temporal reproductive isolation. (a) Rana aurora breeds earlier in the year than (b) Rana boylii. (credit a: modification of work by Mark R. Jennings, USFWS; credit b: modification of work by Alessandro Catenazzi)

In some cases, populations of a species move or are moved to a new habitat and take up residence in a place that no longer overlaps with the same species' other populations. We call this situation **habitat isolation**. Reproduction with the parent species ceases, and a new group exists that is now reproductively and genetically independent. For example, a cricket population that was divided after a flood could no longer interact with each other. Over time, natural selection forces, mutation, and genetic drift will likely result in the two groups diverging.

Behavioral isolation occurs when the presence or absence of a specific behavior prevents reproduction. For example, male fireflies use specific light patterns to attract females. Various firefly species display their lights differently. If a male of one species tried to attract the female of another, she would not recognize the light pattern and would not mate with the male.

Other prezygotic barriers work when differences in their gamete cells (eggs and sperm) prevent fertilization from taking place. We call this a **gametic barrier**.

Similarly, in some cases closely related organisms try to mate, but their reproductive structures simply do not fit together, which is called **mechanical isolation**. For example, damselfly males of different species have differently shaped reproductive organs. If one species tries to mate with the female of another, their body parts simply do not fit together. (Fig 6.9).

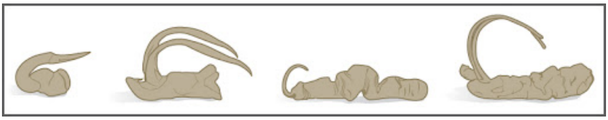

Figure 6.9 The shape of the male reproductive organ varies among male damselfly species, and is only compatible with the female of that species. Reproductive organ incompatibility keeps the species reproductively isolated.

In plants, certain structures aimed to attract one type of pollinator simultaneously prevent a different pollinator from accessing the pollen. The tunnel through which an animal must access nectar can vary widely in length and diameter, which prevents the plant from cross-pollinating with a different species (Fig 6.10).

(a) Honeybee drinking nectar from a foxglove flower

(b) Ruby-throated hummingbird drinking nectar from a trumpet creeper flower

Figure 6.10 Some flowers have evolved to attract certain pollinators. The (a) wide foxglove flower is adapted for pollination by bees, while the (b) long, tube-shaped trumpet creeper flower is adapted for pollination by hummingbirds.

When fertilization takes place and a zygote forms, **postzygotic** barriers can prevent reproduction. Hybrid individuals in many cases cannot form normally in the womb and simply do not survive past the embryonic stages. We call this **hybrid inviability** because the hybrid organisms simply are not viable. In another postzygotic situation, reproduction leads to hybrid birth and growth that is sterile. Therefore, the organisms are unable to reproduce offspring of their own. We call this **hybrid sterility**.

Reading Question #4

Which of the following reproductive isolation mechanisms are prezygotic? Select all that apply.

A. Behavioral isolation
B. Hybrid infertility
C. Mechanical isolation
D. Hybrid inviability
E. Gametic barrier

Reconnection

Speciation occurs over a span of evolutionary time, so when a new species arises, there is a transition period during which the closely related species continue to interact. After speciation, two species may recombine or even continue interacting indefinitely. Individual organisms will mate with any nearby individual with whom they are capable of breeding. We call an area where two closely related species continue to interact and reproduce, forming hybrids, a **hybrid zone**. Over time, the hybrid zone may change depending on the fitness of the hybrids and the reproductive barriers (Fig 6.11). If the hybrids are less fit than the parents, speciation **reinforcement** occurs, and the species continue to diverge until they can no longer mate and produce viable offspring. If reproductive barriers weaken, **fusion** occurs and the two species become one. Barriers remain the same if hybrids are fit and reproductive: **stability** may occur and hybridization continues.

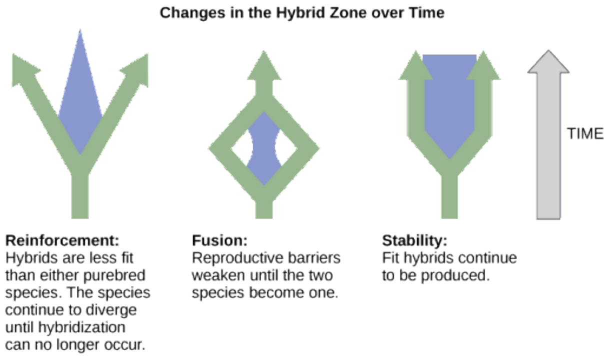

Figure 6.11 After speciation has occurred, the two separate but closely related species may continue to produce offspring in an area called the hybrid zone. Reinforcement, fusion, or stability may result, depending on reproductive barriers and the relative fitness of the hybrids.

If two species eat a different diet but one of the food sources is eliminated and both species are forced to eat the same foods, what change in the hybrid zone is most likely to occur?

Hybrids can be either less fit than the parents, more fit, or about the same. Usually hybrids tend to be less fit; therefore, such reproduction diminishes over time, nudging the two species to diverge further in a process we call reinforcement. Scientists use this term because the hybrids' low success reinforces the original speciation. If the hybrids are as fit or more fit than the parents, the two species may fuse back into one species (Fig 6.11). Scientists have also observed that sometimes two species will remain separate but also continue to interact to produce some individuals. Scientists classify this as stability because no real net change is taking place.

Reading Question #5

When populations come back into contact after a period of reproductive isolation, which of the following is not a possible outcome?

A. Cycling
B. Reinforcement
C. Fusion
D. Stability

Varying Rates of Speciation

Scientists around the world study speciation, documenting observations both of living organisms and those found in the fossil record. As their ideas take shape and as research reveals new details about how life evolves, they develop models to help explain speciation rates. In terms of how quickly speciation occurs, we can observe two current patterns: gradual speciation model and punctuated equilibrium model.

In the gradual speciation model, species diverge gradually over time in small steps. In the punctuated equilibrium model, a new species undergoes changes quickly from the parent species, and then remains largely unchanged for long periods of time afterward (Fig 6.12). We call this early change model punctuated equilibrium, because it begins with a punctuated or periodic change and then remains in balance afterward. While punctuated equilibrium suggests a faster tempo, it does not necessarily exclude gradualism.

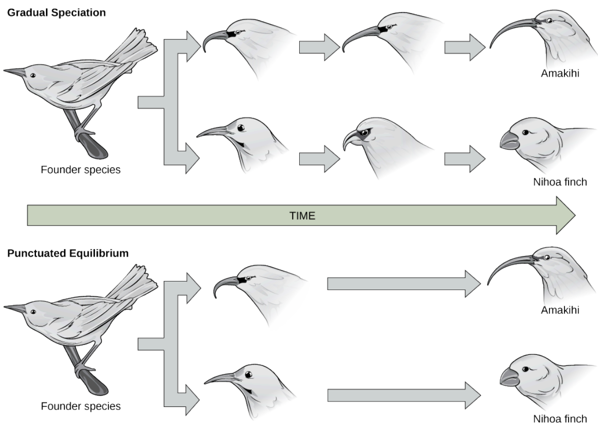

Figure 6.12 In (a) gradual speciation, species diverge at a slow, steady pace as traits change incrementally. In (b) punctuated equilibrium, species diverge quickly and then remain unchanged for long periods of time.

The primary influencing factor on changes in speciation rate is environmental conditions. Under some conditions, selection occurs quickly or radically. Consider a species of snails that had been living with the same basic form for many thousands of years. Layers of their fossils would appear similar for a long time. When a change in the environment takes place—such as a drop in the water level—a small number of organisms are separated from the rest in a brief period of time, essentially forming one large and one tiny population. The tiny population faces new environmental conditions. Because its gene pool quickly became so small, any variation that surfaces and that aids in surviving the new conditions becomes the predominant form.

References

Adapted from Clark, M.A., Douglas, M., and Choi, J. (2018). Biology

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7. Chapter 7: Phylogenies

ANASTASIA CHOUVALOVA AND LISA LIMERI

Introduction to Phylogenies

Biologists strive to understand the evolutionary history and relationships of living organisms. **Phylogeny** is the evolutionary history and relationship of an organism or group of organisms. A phylogeny describes the organism's relationships, such as from which organisms it may have evolved, or to which species it is most closely related. Phylogenetic relationships provide information on shared ancestry but not necessarily on how organisms are similar or different.

Evolutionary biologists could list many reasons why understanding phylogeny is important to everyday life in human society. For botanists, phylogeny acts as a guide to discovering new plants that can be used to benefit people. Think of all the ways humans use plants—food, medicine, and clothing are a few examples. If a plant contains a compound that is effective in treating cancer, scientists might want to examine all of the compounds for other useful drugs.

A research team in China identified a DNA segment that they thought to be common to some medicinal plants in the family Fabaceae (the legume family). They worked to identify which species had this segment (Fig 7.1). After testing plant species in this family, the team found a DNA marker (a known location on a chromosome that enabled them to identify the species) present. Then, using the DNA to uncover phylogenetic relationships, the team could identify whether a newly discovered plant was in this family and assess its potential medicinal properties.

Figure 7.1. Dalbergia sissoo is a member of the legume, or Fabaceae, family. It was discovered that this plant has a common DNA marker with other species in the Fabaceae family that possess anti-fungal properties. Then, scientists also discovered that D. sissoo has fungicidal properties – this supports the notion that DNA markers can be used to screen and detect plants that may possess useful medicinal properties.

Reading Question #1

What information does a phylogeny include?

A. Which lineage a currently-living species evolved from
B. Shared ancestry among currently-living groups
C. How similar organisms are
D. A and B
E. A, B, and C

Phylogenetic Trees

Scientists use a type of model called a **phylogenetic tree** to show the evolutionary pathways and connections among organisms. A phylogenetic tree is a diagram used to reflect evolutionary relationships among organisms or groups of organisms (Fig 7.2). Scientists consider phylogenetic trees to be a hypothesis of the evolutionary past since one cannot go back to confirm the proposed relationships. Many phylogenetic trees have a single lineage at the base representing a common ancestor. Scientists call such trees rooted, which means there is a single ancestral lineage (typically drawn from the bottom or left) to which all organisms represented in the diagram relate. Notice in the rooted phylogenetic tree that the three domains— Bacteria, Archaea, and Eukarya—diverge from a single point and branch off (Fig 7.2A). The small branch that plants and animals (including humans) occupy in this diagram shows how recent and miniscule these groups are compared with other organisms. Unrooted trees do not show a common ancestor but do show relationships among species.

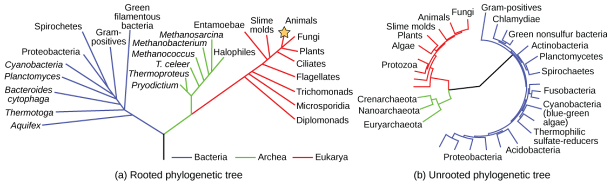

Figure 7.2 These two phylogenetic trees showcase the relationship among three life domains: Bacteria, Eukarya, and Archaea. A) features a rooted tree, which shows when different species came from a common ancestor, while b) is an unrooted tree.

The tips of the branches depict the current-day taxa that are the subject of the phylogenetic tree (Fig 7.3). A **taxon** (plural: taxa) is a broad term used for any group or rank in a biological classification into which related organisms are classified. Taxa at the tips of phylogenetic trees could be sub-species, species, genera, families, phyla, *et. cetera* – any level of biological grouping that is the focus of the phylogenetic tree. Each branching point, called a **node**, is the point at which a single taxon, such as a species, separates into two or more species – a.k.a speciation (Fig 7.3). In a phylogenetic tree, closely related organisms are joined by nodes. These nodes suggest common ancestry. We call two taxa stemming from the same most recent node **sister taxa**. In Figure 7.3 below, the kangaroo and lion are sister taxa because they are the two tips stemming from the most recent node. An important key to interpreting phylogenetic tree structure is to recognize that branch points could be rotated without changing the information. For example, if a branch point rotated and the taxon order changed, this would not alter the information because each taxon's evolution from the branch point was independent of the other. This means that in Figure 7.3 below, we could rotate the node between the lion and kangaroo, switching the location of the lion and kangaroo, and it would still depict the same information.

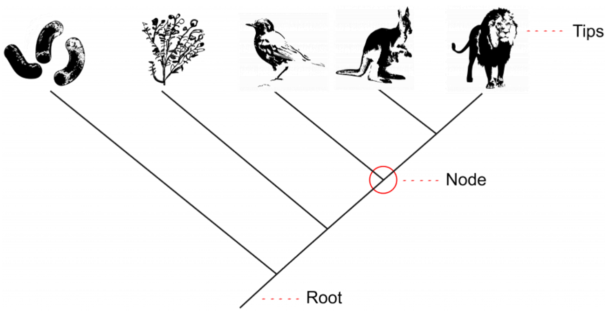

Figure 7.3 Phylogenetic trees demonstrate the evolutionary relationship between species. Nodes represent speciation events where a common ancestral lineage splits into separate lineages. Current-day taxa appear at the tips of the phylogenetic tree.

We can trace the pathway from the origin of life to any individual species by navigating through the evolutionary branches between the two points. Also, by starting with a single species and tracing back towards the "trunk" of the tree, one can discover species' ancestors, as well as where lineages share a common ancestry.

Reading Question #2

Where are currently-living species depicted on a phylogenetic tree?

A. Root
B. Tip
C. Node
D. Branch

Reading Question #3

What does a node in a phylogenetic tree represent?

A. Convergent evolution
B. The evolution of an ancestral trait
C. A speciation event
D. A species going extinct

Phyletic groups

Phylogenies help us group organisms in evolutionarily meaningful ways. **Clades** also called **monophyletic groups**, are groups of organisms that descended from a single ancestor. For example, in

Figure 7.4, all the organisms in the orange region evolved from a single ancestor that had amniotic eggs. Consequently, these organisms also have amniotic eggs and make a single clade, or a monophyletic group, called the Amniota. Clades must include all descendants from a branch point. Thus, rabbits and lizards would not make a clade because the most recent ancestor they have in common (the base of the Amniota) also includes humans as one of their descendants (Figure 7.4).

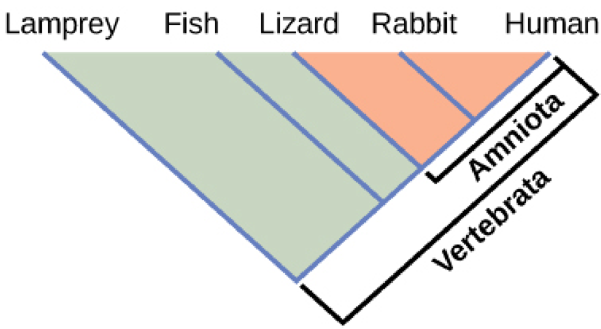

Figure 7.4 Lizards, rabbits, and humans all descended from a common ancestor that had an amniotic egg. Thus, lizards, rabbits, and humans all belong to the clade Amniota. Vertebrata is a larger clade that also includes fish and lamprey.

Clades can vary in size depending on which branch point one references. The important factor is that all organisms in the clade or monophyletic group stem from a single point on the tree. You can remember this because monophyletic breaks down into "mono," meaning one, and "phyletic," meaning evolutionary relationship. Figure 7.5 shows various clade examples. Notice how each clade comes from a single point; whereas, the non-clade groups, also called **paraphyletic groups,** show branches that do not share a single point.

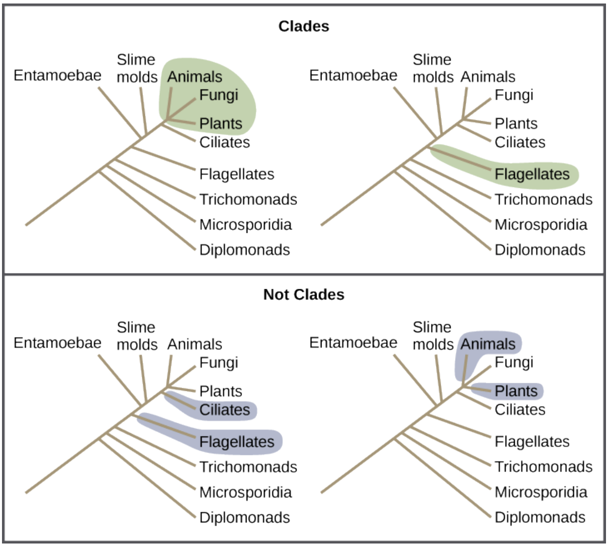

Figure 7.5 All the organisms within a clade stem from a single point on the tree. A clade may contain multiple groups, as in the case of animals, fungi and plants, or a single group, as in the case of flagellates. Groups that diverge at a different branch point, or that do not include all groups in a single branch point, are not clades.

Reading Question #4

What distinguishes a monophyletic group from a paraphyletic group?

A. The evolutionary relatedness of the taxa in the group
B. Which evolutionary forces acted on the group

C. The similarity of traits in the group
D. The terms are synonyms

Ancestral and derived traits

Taxa evolve from common ancestors and then diversify. Scientists use the phrase "descent with modification" because even though related organisms have many of the same characteristics and genetic codes, changes occur. This pattern repeats as one goes through the phylogenetic tree of life:

1. A change in an organism's genetic makeup leads to a new trait which becomes prevalent in the group.
2. Many organisms descend from this point and have this trait.
3. New variations continue to arise: some are adaptive and persist, leading to new traits.
4. With new traits, a new branch point is determined (go back to step 1 and repeat).

If a trait in a clade is found in the ancestor of a group, it is considered a shared **ancestral trait** because all of the organisms in the clade have that trait. The vertebrate in Figure 7.4 is a shared ancestral character. Now consider the amniotic egg characteristic in the same figure. Only some of the organisms in Figure 7.4 have this trait, and to those that do, it is called a shared **derived trait** because this trait derived at some point but does not include all of the ancestors in the tree.

The tricky aspect to shared ancestral and shared derived characters is that these terms are relative. We can consider the same trait one or the other depending on the particular diagram that we use. Returning to Figure 7.4, note that the amniotic egg is a shared ancestral character for lizards, rabbits, and humans, while having hair is a shared derived character only for humans and rabbits. For the Amniotes as a group, however, the amniotic egg is a shared derived character that is not seen in fish. These terms help scientists distinguish between clades in building phylogenetic trees.

Reading Question #5

What is the definition of an ancestral trait?

A. A trait that is at least 2 million years old.
B. A trait that evolved before the most recent speciation.
C. A trait that is only found in extinct species.
D. A trait that the ancestor of a clade had.

Building Phylogenetic Trees

Organizing the evolutionary relationships of all life on Earth is a very challenging task: scientists must span enormous blocks of time and work with information from long-extinct organisms. Trying to decipher the proper connections, especially given the presence of homologies and analogies, makes the task of building an accurate tree of life extraordinarily difficult. Advancing DNA technology provides large quantities of genetic sequences for researchers to use and analyze.

To aid in the tremendous task of describing phylogenies accurately, scientists often use the concept of**maximum parsimony**, which means defaulting to the assumption that events occurred in the simplest, most obvious way. In the context of building phylogenetic trees, this means that the most probable series of events is the one that includes the fewest major evolutionary events/changes. Starting with all of the homologous traits in a group of organisms, scientists look for the most obvious and simple order of evolutionary events that led to the occurrence of those traits. In other words, if two organisms have a trait in common, it's more likely that it evolved once and those two organisms share ancestry, rather than the trait evolving twice from separate ancestors.

Link to Learning

Head to this website to learn how researchers use maximum parsimony to create phylogenetic trees.

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Adapted from

Clark, M.A., Douglas, M., and Choi, J. (2018). Biology 2e. OpenStax. Retrieved from https://openstax.org/books/biology-2e/pages/1-introduction

8. Chapter 8: Convergent Evolution

MASON TEDESCHI AND LISA LIMERI

Convergent Evolution

The evolution of species has resulted in enormous variation in form and function. Sometimes, evolution gives rise to groups of organisms that become tremendously different from each other. When two species evolve in diverse directions from a common point, it is called **divergent evolution**. Such divergent evolution can be seen in the forms of the reproductive organs of flowering plants which share the same basic anatomies; however, they can look very different as a result of selection in different physical environments and adaptation to different kinds of pollinators (Fig 8.1).

Figure 8.1 Flowering plants evolved from a common ancestor. Notice that the (a) dense blazing star (Liatrus spicata) and the (b) purple coneflower (Echinacea purpurea) vary in appearance, yet both share a similar basic morphology. (credit a: modification of work by Drew Avery; credit b: modification of work by Cory Zanker)

In other cases, similar phenotypes evolve independently in distantly related species. For example, flight has evolved in both bats and insects, and they both have structures we refer to as wings, which are adaptations to flight (Fig 8.2). However, bat and insect wings have evolved from very different original structures. We call this phenomenon **convergent evolution**, where similar traits evolve independently in species that do not share a recent common ancestry. The trait in the two species came to be similar in structure and have the same function, flying, but did so separately from each other.

Reading Quiz #1

What causes convergent evolution?

A. Populations facing similar selection pressures
B. Populations facing different selection pressures
C. An increased mutation rate
D. Strong genetic drift

Reading Question #2

What is the result of convergent evolution?

A. Distantly related species have quite different traits
B. Closely related species have quite different traits
C. Distantly related species have similar traits
D. Closely related species have similar traits

Homologous and analogous structures

Some organisms may be very closely related, even though a minor genetic change caused a major morphological difference to make them look quite different. Similarly, unrelated organisms may be distantly related, but appear very much alike. This usually happens because both organisms share common adaptations that evolved within similar environmental conditions, called **convergent evolution**. When similar characteristics occur because of environmental constraints and not due to a close evolutionary relationship, it is an analogy or **homoplasy**. For example, insects use wings to fly like bats and birds, but the wing structure and embryonic origin is completely different. Thus, wings in bats and birds are a homoplasy (Fig 8.2).

Figure 8.2 The (c) wing of a honeybee is similar in shape to a (b) bird wing and (a) bat wing, and it serves the same function. However, the honeybee wing is not composed of bones and has a distinctly different structure and embryonic origin. These wing types (insect versus bat and bird) illustrate a homoplasy—similar structures that do not share an evolutionary history. (credit a: modification of work by U.S. DOI BLM; credit b: modification of work by Steve Hillebrand, USFWS; credit c: modification of work by Jon Sullivan)

Another example can be seen in arctic mammals such as foxes and snowshoe hares, which each grow white fur during the winter months. White fur allows these organisms to blend into the ice and snow that characterizes their polar home, and presumably protects them from predation. However, foxes and snowshoe hares do not share a common ancestor with white fur. Of course they ultimately share a common ancestor, as do all mammals, but the fox lineage is full of non-white animals, as is the group to which hares belong. The winter white of arctic foxes and snowshoe hares is thus a homoplasy, due to convergent evolution in a white, wintry landscape.

Similar traits can be either homologous or analogous. **Homologous structures** share a similar embryonic origin due to their deep evolutionary relationship. **Analogous structures** have a similar function, but often very different developmental pathways. For example, the bones in a whale's front flipper are homologous to the bones in the human arm. These structures are not analogous. A butterfly or bird's wings are analogous but not homologous. Scientists must determine which type of similarity a feature exhibits to decipher the organisms' phylogeny.

We use developmental/embryonic origin as an indicator of homology because development is a very complex process. The more complex the feature, the more likely any kind of overlap is due to a common evolutionary past. Imagine two people from different countries both inventing a car with all the same parts and in exactly the same arrangement without any previous or shared knowledge. That outcome would be highly improbable. However, if two people both invented a hammer, we can reasonably conclude that both could have the original idea without the help of the other. The same relationship between complexity and shared evolutionary history is true for homologous structures in organisms.

Reading Question #3

What are homologous structures?

A. Traits that have common evolutionary origin
B. Traits that serve a similar function
C. Both A and B

Reading Question #4

What do analogous structures have in common?
A. Evolutionary origin
B. Function
C. Embryonic development
D. A and B
E. A, B, and C

References

Adapted from Clark, M.A., Douglas, M., and Choi, J. (2018). Biology 2e. OpenStax. Retrieved from https://openstax.org/books/biology-2e/pages/1-introduction

9. Chapter 9: Biodiversity

MASON TEDESCHI; ANASTASIA CHOUVALOVA; AND LISA LIMERI

Introduction to Biodiversity

Biodiversity describes a community's biological complexity: it is measured by the number of different species (species richness) in a particular area and their relative abundance (species evenness). The area in question could be a habitat, a biome, or the entire biosphere.

Despite considerable effort, knowledge of the species that inhabit the planet is limited. A recent estimate suggests that the **eukaryote** species for which science has names, about 1.5 million species, account for less than 20% of the total number of eukaryote species present on the planet (8.7 million species, by one estimate). Estimates of numbers of prokaryotic species are largely guesses, but biologists agree that science has only begun to catalog their diversity. Even with what is known, there is no central repository of names or samples of the described species; therefore, there is no way to be sure that the 1.5 million descriptions is an accurate number. It is a best guess based on the opinions of experts in different taxonomic groups. Estimates suggest that at the current rate of species description, which according to the State of Observed Species Report is 17,000 to 20,000 new species per year, it will take close to 500 years to finish describing life on this planet.

One of the oldest observed patterns in ecology is that species biodiversity in almost every taxonomic group increases as latitude declines. In other words, biodiversity increases closer to the equator (Fig 9.1). There are a number of hypotheses to explain why biodiversity increases closer to the equator. One of these hypotheses is the greater age of the ecosystems in the tropics versus temperate regions that were largely devoid of life or drastically impoverished during the last glaciation. The idea is that greater age provides more time for **speciation**. Another possible explanation is the increased energy the tropics receive from the sun versus the decreased energy that temperate and polar regions receive. It is not entirely clear how greater energy input could translate into more species. Another hypothesis is that the complexity of tropical ecosystems may promote speciation by increasing the heterogeneity, or number of ecological niches, in the tropics relative to higher latitudes. The greater heterogeneity provides more opportunities for coevolution, specialization, and perhaps greater selection pressures leading to population differentiation. However, this hypothesis suffers from some circularity—ecosystems with more species encourage speciation, but how did they get more species to begin with? Another hypothesis is that the tropics are more more stable than temperate regions, which have a pronounced climate and day-length seasonality. The tropics have their own forms of seasonality, such as rainfall, but they are generally assumed to be more stable environments and this stability might promote speciation.

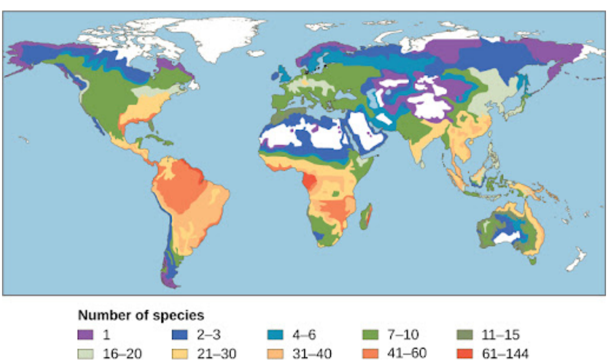

Figure 9.1 This map illustrates the number of amphibian species across the globe and shows the trend toward higher biodiversity at lower latitudes.

Regardless of the mechanisms, it is certainly true that all levels of biodiversity are greatest in the tropics. Additionally, there are more **endemic species** in the tropics. Endemic species are species that are found in only one location. However, this richness of diversity in the tropics also means that knowledge of species is lowest, and there is a high potential for biodiversity loss.

In 1988, British environmentalist Norman Myers developed a conservation concept to identify areas rich in species and at significant risk for species loss: **biodiversity hotspots**. Biodiversity hotspots are geographical areas that contain high numbers of endemic species. The purpose of the concept was to identify important locations on the planet for conservation efforts, a kind of conservation triage. By protecting hotspots, governments are able to protect a larger number of species. The original criteria for a hotspot included the presence of 1500 or more endemic plant species and 70 percent of the area disturbed by human activity. There are now 34 biodiversity hotspots (Fig 9.2) containing large numbers of endemic species, which include half of Earth's endemic plants.

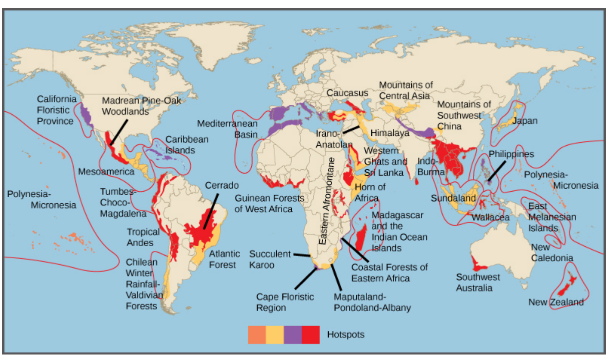

Figure 9.2 Conservation International has identified 34 biodiversity hotspots, which cover only 2.3% of the Earth's surface but have endemic to them 42% of the terrestrial vertebrate species and 50% of the world's plants.

Reading Question #1

Where is biodiversity the highest for all taxa?

A. Near the equator
B. Near the poles
C. At high latitudes
D. In the ocean

Measuring Biodiversity

Species richness (the number of species present in an area) varies across the globe (Fig 9.1). One factor in determining species richness is latitude, with the greatest species richness occurring in ecosystems near the equator, which often have warmer temperatures, large amounts of rainfall, and low seasonality. The lowest species richness occurs near the poles, which are much colder, drier, and thus less conducive to life. The predictability of climate or productivity is also an important factor. Other factors influence species richness as well. For example, the study of island biogeography attempts to explain the relatively high species richness found in certain isolated island chains, including the Galápagos Islands that inspired the young Darwin.

Relative species abundance, also known as **species evenness**, is the number of individuals in a species relative to the total number of individuals in all species within a habitat, ecosystem, or biome. Foundation species (primary producers) often have the highest relative abundance of species.

Traditionally, ecologists have measured biodiversity by taking into account both species richness and relative species abundance. Biodiversity can be estimated at a number of levels of organization of living things. These estimation indexes, which came from information theory, are most useful as a first step in quantifying biodiversity between and within ecosystems; they are less useful when the main concern among conservation biologists is simply the loss of biodiversity. However, biologists recognize that measures of biodiversity, in terms of species diversity, may help focus efforts to preserve the biologically or technologically important elements of biodiversity.

Reading Question #2

What is the difference between species richness and species evenness

A. Species richness is a more accurate measure of biodiversity
B. Species evenness is a more accurate measure of biodiversity
C. Species richness only counts the number of species present while species evenness accounts for the relative abundance
D. Species evenness only counts the number of species present while species richness includes the relative abundance

Biodiversity over spatial scales

Whittaker (1972) described three terms for measuring biodiversity over spatial scales: alpha, beta, and gamma diversity. **Alpha diversity** refers to the diversity within a particular area or ecosystem, and is usually expressed by the number of species (i.e., species richness) in that ecosystem. For example, if we are monitoring the effect that British farming practices have on the diversity of native birds in a particular region of the country, then we might want to compare species diversity within different ecosystems, such as an undisturbed deciduous wood, a well-established hedgerow bordering a small pasture, and a large arable field. We can walk a transect in each of these three ecosystems and count the number of species we see; this gives us the alpha diversity for each ecosystem (Table 9.1).

If we examine the change in species diversity between these ecosystems then we are measuring the **beta diversity** We are counting the total number of species that are unique to each of the ecosystems being compared. For example, the beta diversity between the woodland and the hedgerow habitats is 7 (representing the 5 species found in the woodland but not the hedgerow, plus the 2 species found in the hedgerow but not the woodland). Thus, beta diversity allows us to compare diversity between ecosystems (Table 9.1).

Gamma diversity is a measure of the overall diversity for the different ecosystems within a region. Hunter (2002: 448) defines gamma diversity as "geographic-scale species diversity". In the example in Table 9.1, the total number of species for the three ecosystems is 14, which represent the gamma diversity.

Hypothetical species	Woodland habitat	Hedgerow habitat	Open field habitat
A	X		
B	X		
C	X		
D	X		
E	X		
F	X	X	
G	X	X	
H	X	X	
I	X	X	
J	X	X	
K		X	
L		X	X
M			X
N			X
Alpha diversity	10	7	3
Beta diversity	Woodland vs. hedgerow: 7	Hedgerow vs. open field: 8	Woodland vs. open field: 13
Gamma diversity	14		

Table 9.1 Alpha, beta, and gamma diversity for hypothetical bird species in three different ecosystems.

Reading Question #3

Match the terms to their definitions.

Terms: Alpha diversity, beta diversity, gamma diversity

Definitions:

A. the species diversity between two communities or ecosystems.
B. the total species diversity in a landscape.
C. the species diversity in a site at a local scale.

Reading Question #4

What level of diversity would an ecologist use to describe the diversity of the entire planet?

A. Alpha
B. Beta
C. Gamma
D. Omega

Reading Question #5

What level of diversity would an ecologist use to describe the species richness of their backyard?

A. Alpha
B. Beta
C. Gamma
D. Omega

Types of Biodiversity

Scientists generally accept that the term biodiversity describes the number and kinds of species in a location or on the planet. Species can be difficult to define, but most biologists still feel comfortable with the concept and are able to identify and count eukaryotic species in most contexts. Biologists have also identified alternate measures of biodiversity, some of which are important for planning how to preserve biodiversity.

Genetic diversity is one of those alternate concepts. Genetic diversity or variation is the raw material for adaptation in a species. A species' future potential for adaptation depends on the genetic diversity held in the genomes of the individuals in populations that make up the species. The same is true for higher taxonomic categories. A genus with very different types of species will have more genetic diversity than a genus with species that look alike and have similar ecologies. If there were a choice between one of these genera of species being preserved, the one with the greatest potential for subsequent evolution is the most genetically diverse one. It would be ideal not to have to make such choices, but increasingly this may be the norm.

Many genes code for proteins, which in turn carry out the metabolic processes that keep organisms alive and reproducing. Genetic diversity can be measured as chemical diversity in that different species produce a variety of chemicals in their cells, both the proteins as well as the products and byproducts of metabolism. This chemical diversity has potential benefit for humans as a source of pharmaceuticals, so it provides one way to measure diversity that is important to human health and welfare.

Humans have generated diversity in domestic animals, plants, and fungi. This diversity is also suffering losses because of migration, market forces, and increasing globalism in agriculture, especially in heavily populated regions such as China, India, and Japan. The human population directly depends on this diversity as a stable food source, and its decline is troubling biologists and agricultural scientists.

It is also useful to define ecosystem diversity, meaning the number of different ecosystems on the planet or in a given geographic area (Fig 9.3). Whole ecosystems can disappear even if some of the species might survive by adapting to other ecosystems. The loss of an ecosystem means the loss of interactions between species, the loss of unique features of coadaptation, and the loss of biological productivity that an ecosystem is able to create. An example of a largely extinct ecosystem in North America is the prairie ecosystem. Prairies once spanned central North America from the boreal forest in northern Canada down into Mexico. They are now all but gone, replaced by crop fields, pasture lands, and suburban sprawl. Many of the species survive, but the hugely productive ecosystem that was responsible for creating the most productive agricultural soils is now gone. As a consequence, soils are disappearing or must be maintained at greater expense.

(a)

(b)

Figure 9.3 The variety of ecosystems on Earth—from (a) coral reef to (b) prairie—enables a great diversity of species to exist. (credit a: modification of work by Jim Maragos, USFWS; credit b: modification of work by Jim Minnerath, USFWS)

The 6th Mass Extinction

The Lake Victoria cichlids (Fig 9.4) provide an example through which we can begin to understand biodiversity. The biologists studying cichlids in the 1980s discovered hundreds of cichlid species representing a variety of specializations to particular habitat types and specific feeding strategies: eating plankton floating in the water, scraping and then eating algae from rocks, eating insect larvae from the bottom, and eating the eggs of other species of cichlid. The cichlids of Lake Victoria are the product of an adaptive radiation. An adaptive radiation is a rapid (less than three million years in the case of the Lake Victoria cichlids) branching through speciation of a phylogenetic tree into many closely related species; typically, the species "radiate" into different habitats and niches. The Galápagos finches are an example of a modest adaptive radiation with 15 species. The cichlids of Lake Victoria are an example of a spectacular adaptive radiation that includes about 500 species.

Figure 9.4 Both (a) Haplochromis nyererei and (b) Haplochromis vonlinnei are cichlids endemic to Lake Victoria. Haplochromis vonlinnei has not been seen in the lake for over two decades, and has likely gone extinct due to the presence of invasive species.

At the time biologists were making this discovery, some species began to quickly disappear. A culprit in these declines was a species of large fish that was introduced to Lake Victoria by fisheries to feed the people living around the lake. The Nile perch was introduced in 1963, but lay low until the 1980s when its populations began to surge. The Nile perch population grew by consuming cichlids, driving species after species to the point of **extinction** (the disappearance of a species). In fact, there were several factors that played a role in the extinction of perhaps 200 cichlid species in Lake Victoria: the Nile perch, declining lake water quality due to agriculture and land clearing on the shores of Lake Victoria, and increased fishing pressure. Scientists had not even catalogued all of the species present—so many were lost that were never named. The diversity is now a shadow of what it once was.

The cichlids of Lake Victoria are a thumbnail sketch of contemporary rapid species loss that occurs all over Earth and is caused by human activity. Extinction is a natural process of macroevolution that occurs at the rate of about one out of 1 million species becoming extinct per year. The fossil record reveals that there have been five periods of mass extinction in history with much higher rates of species loss, and the rate of species loss today is comparable to those periods of mass extinction. However, there is a major difference between the previous mass extinctions and the current extinction we are experiencing: human activity. Specifically, three human activities have a major impact: destruction of habitat, introduction of exotic species, and over-harvesting. Predictions of species loss within the next century, a tiny amount of time on geological timescales, range from 10 percent to 50 percent. Extinctions on this scale have only happened five other times in the history of the planet, and they have been caused by cataclysmic events that changed the course of the history of life in each instance. Earth is now in one of those times.

Lake Victoria contained almost 500 species of cichlids alone, ignoring the other fish families present in the lake. All of these species were found only in Lake Victoria; therefore, the 500 species of cichlids were **endemic**. Endemics with highly restricted distributions are particularly vulnerable to extinction. Higher taxonomic levels, such as genera and families, can also be endemic.

Career Connection: Biogeographer

Biogeography is the study of the distribution of the world's species—both in the past and in the present. The work of biogeographers is critical to understanding our physical environment, how the environment affects species, and how environmental changes impact the distribution of a species; it has also been critical to developing evolutionary theory. Biogeographers need to understand both biology and ecology. They also need to be well-versed in evolutionary studies, soil science, and climatology.

There are three main fields of study under the heading of biogeography: ecological biogeography, historical biogeography (called paleobiogeography), and conservation biogeography. Ecological biogeography studies the current factors affecting the distribution of plants and animals. Historical biogeography, as the name implies, studies the past distribution of species. Conservation biogeography, on the other hand, is focused on the protection and restoration of species based upon known historical and current ecological information. Each of these fields considers both zoogeography and phytogeography—the past and present distribution of animals and plants.

The Importance of Biodiversity to Human Life

It may not be clear why biologists are concerned about biodiversity loss. When biodiversity loss is thought of as the extinction of the passenger pigeon, the dodo bird, and even the wooly mammoth, the loss may appear to be an emotional one. Biodiversity may provide important psychological benefits to humans. Additionally, there are moral arguments for the maintenance of biodiversity.

But is the loss practically important for the welfare of the human species? From the perspective of evolution and ecology, the loss of a particular individual species is unimportant (however, the loss of a keystone species can lead to ecological disaster). Extinction is a normal part of macroevolution. But the accelerated extinction rate means the loss of tens of thousands of species within our lifetimes, and it is likely to have dramatic effects on human welfare through the collapse of ecosystems and in added costs to maintain food production, clean air and water, and human health.

Agriculture began after early hunter-gatherer societies first settled in one place and heavily modified their immediate environment. This cultural transition has made it difficult for humans to recognize their dependence on undomesticated living things on the planet. Biologists recognize the human species is embedded in ecosystems and is dependent on them, just as every other species on the planet is dependent. Technology smoothes out the extremes of existence, but ultimately the human species cannot exist without its ecosystem.

Humans use many compounds that were first discovered or derived from living organisms as medicines: secondary plant compounds, animal toxins, and antibiotics produced by bacteria and fungi. More medicines are expected to be discovered in nature. Loss of biodiversity will impact the number of pharmaceuticals available to humans.

Crop diversity is a requirement for food security, and it is being lost. The loss of wild relatives to crops also threatens breeders' abilities to create new varieties. Ecosystems provide ecosystem services that support human agriculture: pollination, nutrient cycling, pest control, and soil development and maintenance. Loss of biodiversity threatens these ecosystem services and risks making food production more expensive or impossible. Wild food sources are mainly aquatic, but few are being managed for sustainability. Fisheries' ability to provide protein to human populations is threatened when extinction occurs.

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10. Chapter 10: Disturbance and Succession

LISA LIMERI

Ecological Disturbance

Changes in community structure and composition over time are induced by **environmental disturbances** such as volcanoes, earthquakes, storms, fires, and climate change. Communities with a stable structure are said to be at equilibrium. Following a disturbance, the community may or may not return to the equilibrium state. In primary succession, newly exposed or newly formed land is colonized by living things; in secondary succession, part of an ecosystem is disturbed and remnants of the previous community remain. Thus, disturbance can initiate successional change.

Species that are well adapted for exploiting disturbance sites are referred to as **pioneers** or **early successional species.** In forests, these shade-intolerant species are able to photosynthesize at high rates and as a result grow quickly. Their fast growth is usually balanced by short life spans. Furthermore, although these species often dominate immediately following a disturbance, they are unable to compete with shade-tolerant species later on and are replaced by these species through succession. However these shifts may not reflect the progressive entry to the community of the taller long-lived forms, but instead, the gradual emergence and dominance of species that may have been present, but inconspicuous directly after the disturbance. Disturbances have also been shown to be important facilitators of non-native plant invasions.

While plants must deal directly with disturbances because of their lack of mobility, many animals are mobile and thus are not as immediately affected by disturbance. For example, some animals could successfully evade the initial destruction of a forest fire, but can later return to the burned area and thrive on new growth on the forest floor. Disturbed communities (such as a forest after a fire) often support a wider variety of plants compared to pre-disturbance vegetation. The plants in turn support a variety of wildlife, temporarily increasing biological diversity in the forest.

Reading Question #1

Which of the following terms describes the first species to colonize newly-formed land, such as the result of a volcanic eruption?

A. Climax community
B. Keystone species
C. Foundation species
D. Pioneer species

Intermediate Disturbance Hypothesis

The **intermediate disturbance hypothesis** (IDH) suggests that local species diversity is maximized when ecological disturbances are neither too rare nor too frequent (Figure 10.1). At low levels of disturbance, more competitive organisms will push **subordinate species** to extinction and dominate the ecosystem. At high levels of disturbance, due to frequent forest fires or human impacts like deforestation, all species are at risk of going extinct. According to IDH, at intermediate levels of disturbance, diversity is thus maximized because species that thrive at both early and late successional stages can coexist. IDH is a non-equilibrium model used to describe the relationship between disturbance and species diversity.

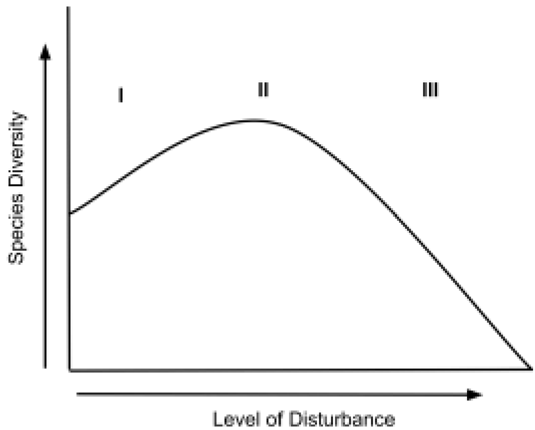

Figure 10.1 I. at low levels of ecological disturbance species richness decreases as competitive exclusion increases, II. at intermediate levels of disturbance, diversity is maximized because species that thrive at both early and late successional stages can coexist, III. at high levels of disturbance species richness is decreased due to an increase in species movement. (image from Wikimedia)

IDH is based on the following premises:

1. ecological disturbances have major effects on species richness (the total number of different species) within the area of disturbance,
2. interspecific competition results in one species driving a competitor to extinction and becoming dominant in the ecosystem, and
3. moderate ecological scale disturbances prevent interspecific competition.

Disturbances act to disrupt stable ecosystems and clear species' habitat. As a result, disturbances lead to species movement into the newly cleared area (secondary succession). Once an area is cleared there is a progressive increase in species richness and competition between species takes place. Once the conditions that create a disturbance are gone, and competition between species in the formerly disturbed area increases, species richness decreases as competitive exclusion increases.

Reading Question #2

When will biodiversity be highest?

A. Where there is no disturbance in the ecosystem
B. When there is an intermediate level of disturbance in the ecosystem
C. When there is a high level of disturbance in the ecosystem
D. When there are variable levels of disturbance in the ecosystem

Ecological Succession

Communities with a stable structure are said to be at equilibrium. Following a disturbance, the community may or may not return to the equilibrium state. **Succession** describes the sequential appearance and disappearance of species in a community over time. There are two types of ecological succession: primary and secondary. In primary succession, newly exposed or newly formed land is colonized by living things; in secondary succession, part of an ecosystem is disturbed and remnants of the previous community remain.

Primary Succession

Primary succession occurs when new land is formed or rock is exposed: for example, following the eruption of volcanoes, such as those on the Big Island of Hawaii. As lava flows into the ocean, new land is continually being formed. On the Big Island, approximately 32 acres of land are added each year. First, weathering and other natural forces break down the substrate enough for the establishment of pioneer species such as hearty plants and lichens with few soil requirements (Figure 10.2). These species help to further break down the mineral-rich lava into the soil where other, less hardy species will grow and eventually replace the pioneer species. In addition, as these early species grow and die, they add to an ever-growing layer of decomposing organic material and contribute to soil formation. Over time the area will reach an equilibrium state, with a set of organisms quite different from the pioneer species.

Figure 10.2. During primary succession in lava on Maui, Hawaii, succulent plants are the pioneer species. (credit: Forest and Kim Starr)

Secondary succession

A classic example of **secondary succession** occurs in oak and hickory forests cleared by wildfire (Figure 10.3). Wildfires will burn most vegetation and kill those animals unable to flee the area. Their nutrients, however, are returned to the ground in the form of ash. Thus, even when areas are devoid of life due to severe fires, the area will soon be ready for new life to take hold.

Before the fire, the vegetation was dominated by tall trees with access to the major plant energy resource: sunlight. Their height gave them access to sunlight while also shading the ground and other low-lying species. After the fire, though, these trees are no longer dominant. Thus, the first plants to grow back are usually annual plants followed within a few years by quickly growing and spreading grasses and other pioneer species. Due to, at least in part, changes in the environment brought on by the growth of the grasses and other species, over many years, shrubs will emerge along with small pine, oak, and hickory trees. These organisms are called intermediate species. Eventually, over 150 years, the forest will reach its equilibrium point where species composition is no longer changing and resembles the community before the fire. This equilibrium state is referred to as the climax community, which will remain stable until the next disturbance.

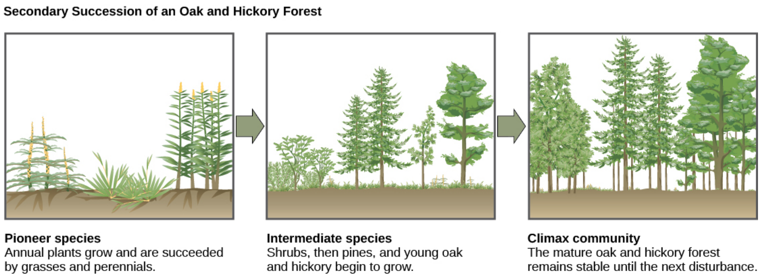

Figure 10.3. Secondary succession is shown in an oak and hickory forest after a forest fire.

Climatic factors may be very important, but on a much longer time-scale than any other. Changes in temperature and rainfall patterns will promote changes in communities. As the climate warmed at the end of each ice age, great successional changes took place. The tundra vegetation and bare glacial till deposits underwent succession to mixed deciduous forest. The greenhouse effect resulting in increase in temperature is likely to bring profound Allogenic changes in the next century. Geological and climatic catastrophes such as volcanic eruptions, earthquakes, avalanches, meteors, floods, fires, and high wind also bring allogenic changes.

In general, communities in early succession will be dominated by fast-growing, well-dispersed species (opportunist, fugitive, or r-selected life histories). As succession proceeds, these species will tend to be replaced by more competitive (K-selected) species. Trends in ecosystem and community properties in succession have been suggested, but few appear to be general. For example, species diversity almost necessarily increases during early succession as new species arrive, but may decline in later succession as competition eliminates opportunistic species and leads to dominance by locally superior competitors.

Reading Question #3

What is the difference between primary and secondary succession?

A. Primary succession always occurs before secondary succession
B. Primary succession occurs more often than secondary succession
C. In primary succession a brand new community is founded whereas in secondary succession the community is influenced by the pre-existing community
D. In primary succession, only pioneer species can establish whereas in secondary succession only climax species can establish.

Climax Communities

Ecological succession was formerly seen as having a stable end-stage called the climax, sometimes referred to as the 'potential vegetation' of a site, and shaped primarily by the local climate (Figure 10.4). This idea has been largely abandoned by modern ecologists in favor of non-equilibrium ideas of ecosystem dynamics. Most natural ecosystems experience disturbance at a rate that makes a "climax" community unattainable. Climate change often occurs at a rate and frequency sufficient to prevent arrival at a climax state. Additions to available species pools through range expansions and introductions can also continually reshape communities.

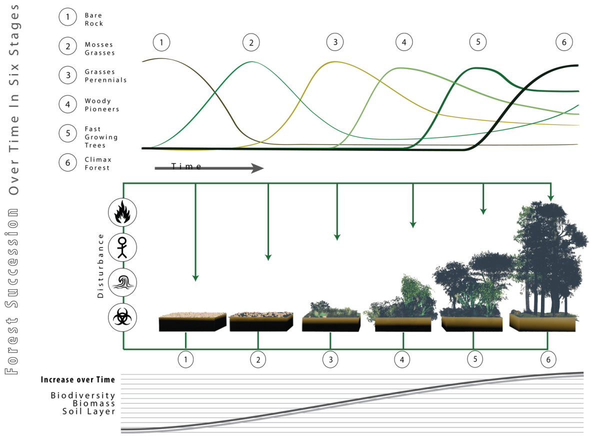

Figure 10.4: Trajectory of forest secondary succession following an intense disturbance, resulting in nearly no original biomass, to a mature forest state. Biodiversity, biomass, and soil depth all increase with time, and community composition changes. (CC-SA-BY *Wikimedia*)

Succession Mechanisms

The trajectory of successional change can be influenced by site conditions, by the type of events initiating succession, by the interactions of the species present, and by more stochastic factors such as availability of propagules or weather conditions at the time of disturbance. Some of these factors contribute to predictability of succession dynamics; others add more probabilistic elements.

Autogenic succession can be brought by changes in the soil caused by the organisms there. These changes include accumulation of organic matter in litter or humic layer, alteration of soil nutrients, or change in the pH of soil due to the plants growing there. The structure of the plants themselves can also alter the community. For example, when larger species like trees mature, they produce shade on to the developing forest floor that tends to exclude light-requiring species. Shade-tolerant species will invade the area.

Allogenic succession is caused by external environmental influences and not by the vegetation. For example, soil changes due to erosion, leaching or the deposition of silt and clays can alter the nutrient content and water relationships in the ecosystems. Animals also play an important role in allogenic changes as they are pollinators, seed dispersers and herbivores. They can also increase nutrient content of the soil in certain areas, or shift soil about (as termites, ants, and moles do) creating patches in the habitat. This may create regeneration sites that favor certain species.

Climatic factors may be very important, but on a much longer time-scale than any other. Changes in temperature and rainfall patterns will promote changes in communities. As the climate warmed at the end of each ice age, great successional changes took place. The tundra vegetation and bare glacial till deposits underwent succession to mixed deciduous forest. The greenhouse effect resulting in increase in temperature is likely to bring profound Allogenic changes in the next century. Geological and climatic catastrophes such as volcanic eruptions, earthquakes, avalanches, meteors, floods, fires, and high wind also bring allogenic changes.

Models of Successional Change

Joseph Connell and Ralph Slatyer further developed the understanding of successional mechanisms in their 1977 paper and proposed that there were 3 main modes of successional development: Facilitation, Tolerance, and Inhibition.

Facilitation model

The **facilitation model** is based on the assumption that only particular species with qualities ideal for "early succession" can colonize the newly exposed landforms after an ecological disturbance.

- These "colonizing" qualities include: highly effective methods of dispersal, the ability to remain dormant for long periods of time, and a rapid growth rate. However, the pioneer species are often subsequently less successful once an area has been heavily populated by surrounding species due to increased shade, litter or concentrated roots in the soil, etc.
- Thus, the presence of early successional species often changes the environment so that the habitat is less hospitable for the original species' own ecological demands and facilitates the invasion of later-successional species.

The facilitation model suggests that the presence of an initial species aids and increases the probability of the growth of a second species (Fig 10.5). For example, the presence of alder plants aids the growth of willow and poplar seedlings in an Alaskan floodplain. Alder roots contain nitrogen-fixing bacteria, which greatly increase the amount of inorganic nitrogen present in soils. This increased availability of nitrogen aids the growth of both willow and poplar seedlings in areas without other competition. Eventually, however, willow and poplar grow more rapidly than alder, leading to a reduction in the abundance of the pioneer species, and eventually, spruce becomes a later-succession species, due to its increased ability (over alder) to grow in shaded areas.

Another case of facilitation comes from the colonization of lakeshore sand dunes. Adjacent pioneer plants colonize the otherwise moving sands and alter the environmental constraints of the sandy environment to better suit other plant species, which can then allow for soil binding to take place. The giant saguaro cactus, in this respect, can only survive in the shade of other plants (or in some cases rocks) – pioneer species facilitate their existence by providing shade. (The argument has also been made that this type of interaction is exemplary of the tolerance model; see below).

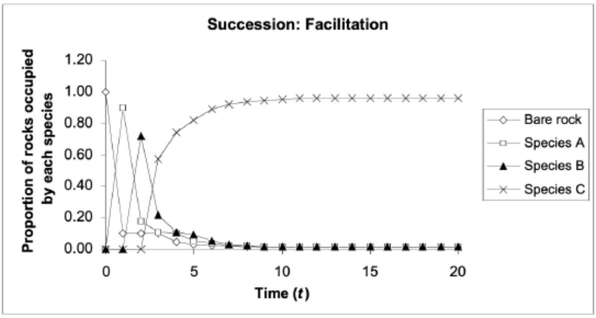

Figure 10.5: Bare rock is frequently replaced by species A, species A by species B, and species B by species C. All these species are equally likely to be replaced by bare rock. Species C is unique in that it is almost always replaced by itself, only rarely by bare rock, and never by other species.

Tolerance model

In the **tolerance model**, new pioneer species neither inhibit nor facilitate the growth and success of other species. The sequences of succession are thus entirely dependent on life-history characteristics such as the specific amount of energy a species allocates to growth.

- The climax community is composed of the most "tolerant" species that can co-exist with other species in a more densely populated area. Eventually, dominant species replace or reduce pioneer species abundance through competition.

The tolerance model is completely dependent upon life history characteristics. Each species has an equally likely chance to establish itself in the early stages of succession and their establishment results in no environmental changes or impacts on other species (Fig 10.6). Eventually, early species, typically dominated by r-selected species, which prioritize fast rates of reproduction, are out-competed by K-selected species (species that become more dominant when there is competition for limited resources).

For example, we can examine succession in the Loess Plateau in China, where there is initial dominance of the *Artemisia scoparia*, the pioneer species. Over time, however, the *Bothriochloa ischaemum* becomes the dominant species and the abundance of *A. scoparia* greatly declines. This is due to the rapid rate of reproduction of the *A. scoparia*, resulting in the species' early abundance, and the dominant competition from the K-selected *B. ischaemum*, resulting in that species' later abundance.

A characteristic that is often associated with the tolerance model and well documented in forest succession is survival in conditions of shade. As an uninhabited area becomes populated by different plant species, shade increases – which makes less light available for the next generation. Species that are better adapted to shady conditions will then become dominant.

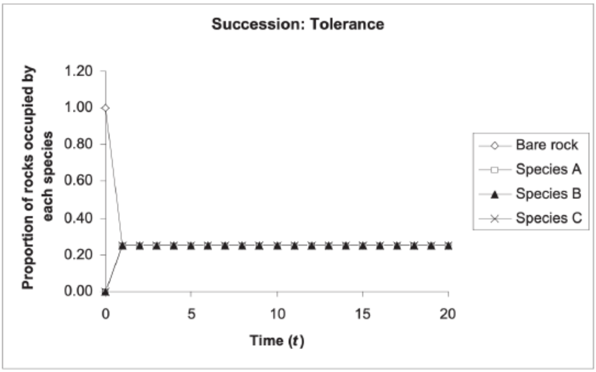

Figure 10.6 In the tolerance succession model, any species is equally likely to replace any other, and equally susceptible to disturbance.

Reading Question #4

In the tolerance model …

A. Earlier species make the environment more hospitable for other species
B. Earlier species make the environment more difficult for other species
C. Early species completely prevent other species from establishing
D. Earlier species do not directly affect the success of later species

Inhibition model

In the **inhibition model**, earlier successional species inhibit growth of later successional species and reduce growth of colonizing species already present.

- Pioneer species might modify the environment through rapid growth and make the area increasingly shady (essentially increasing competition for light).
- The environment is thus less hospitable to other potential colonizing species.
- The only possibility for new growth/colonization in this successional sequence arises when a disturbance leads to dominating species being destroyed, damaged, or removed. This frees up resources and allows for the invasion of other species that were not previously present

In this model, one species inhibits the presence of another, either through direct means, such as predation (by eating the other species or attacking them), or indirect means, such as competition for resources.

Sometimes in inhibition models, the time of establishment of a species determines which species becomes dominant (Fig 10.7). This phenomenon is referred to as the priority effect and suggests that the species that became established earlier are more likely to become the dominant species. One example of the inhibition model, and the priority effect, occurs in South Australia. In areas where bryozoans are established first, tunicates and sponges cannot grow.

The inhibition model has also been observed at work in forest ecosystems; in these systems the early arrivers hold a monopoly on the land, keeping other species out. Closed shrub canopies have been known to prevent tree growth and access to land for periods of up to 45 years – in an experimental study on inhibition it was found that areas occupied by large areas of Lantana sprawling shrubs excluded and inhibited the growth of tree species.

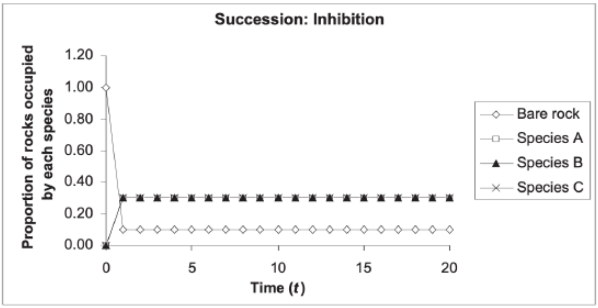

Figure 10.7: Each species is equally likely to colonize bare rock, and all species are equally susceptible to disturbance. Each species holds its site and inhibits occupancy by all others, so replacement occurs only by disturbance.

Reading Question #5

In the inhibition model, which species is most likely to become dominant?

A. The species that arrives first
B. The species that is the strongest competitor
C. The species that is the most shade-tolerant
D. The species that can survive with the fewest resources

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11. Chapter 11: Trophic interactions

ANASTASIA CHOUVALOVA AND LISA LIMERI

Food Chains

The term "food chain" is sometimes used metaphorically to describe human social situations. Individuals who are considered successful are seen as being at the top of the food chain, consuming all others for their benefit, whereas the less successful are seen as being at the bottom.

The scientific understanding of a **food chain** is more precise than in its everyday usage. In ecology, a food chain is a linear sequence of organisms through which nutrients and energy pass: primary producers, primary consumers, and higher-level consumers are used to describe ecosystem structure and dynamics. There is a single path through the chain. Each organism in a food chain occupies what is called a **trophic level.** Depending on their role as producers or consumers, species or groups of species can be assigned to various trophic levels.

In many ecosystems, the bottom of the food chain consists of photosynthetic organisms (plants and/or phytoplankton), which are called **primary producers.** The organisms that consume the primary producers are herbivores: the **primary consumers. Secondary consumers** are usually carnivores that eat the primary consumers. **Tertiary consumers** are carnivores that eat other carnivores. Higher-level consumers feed on the next lower trophic levels, and so on, up to the organisms at the top of the food chain: the **apex consumers.** In the Lake Ontario food chain shown in Figure 11.1, the Chinook salmon is the apex consumer at the top of this food chain.

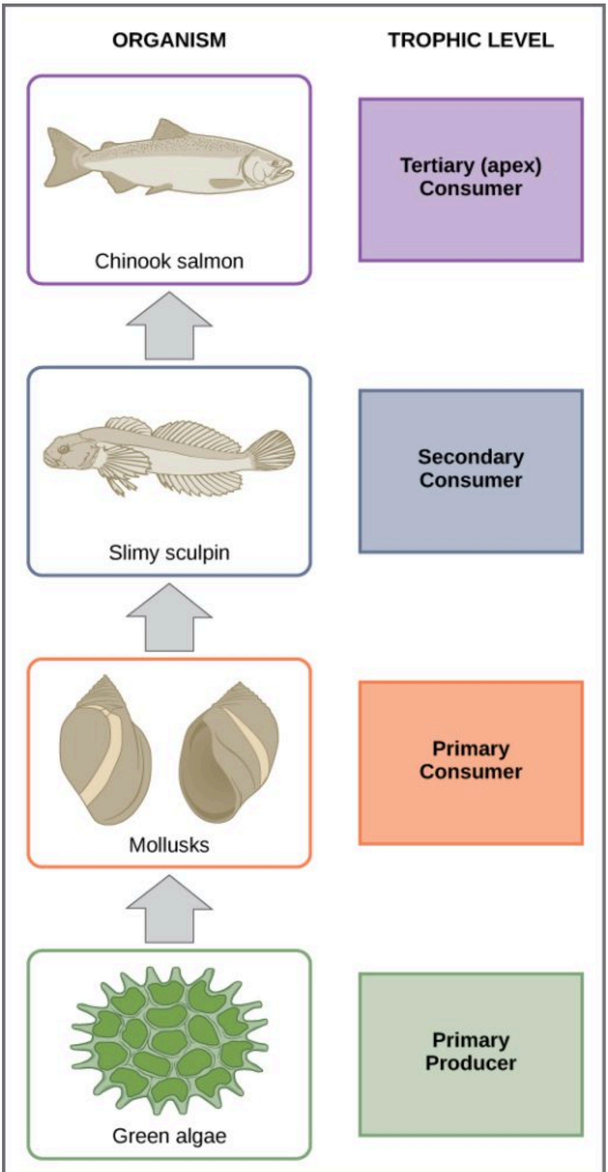

Figure 11.1 Trophic levels of a food chain in Lake Ontario at the United States-Canada border. Energy and nutrients flow from photosynthetic green algae at the bottom to the top of the food chain: the Chinook salmon.

One major factor that limits the length of food chains is energy. Energy is lost as heat between each trophic level due to the second law of thermodynamics. Thus, after a limited number of trophic energy transfers, the amount of energy remaining in the food chain may not be great enough to support viable populations at yet a higher trophic level.

The loss of energy between trophic levels is illustrated by the pioneering studies of Howard T. Odum in the Silver Springs, Florida, ecosystem in the 1940s (Fig 11.2). The primary producers generated 20,819 kcal/m^2/yr (kilocalories per square meter per year), the primary consumers generated 3368 kcal/m^2/yr, the secondary consumers generated 383 kcal/m^2/yr, and the tertiary consumers only generated 21 kcal/m^2/yr. Thus, there is little energy remaining for another level of consumers in this ecosystem.

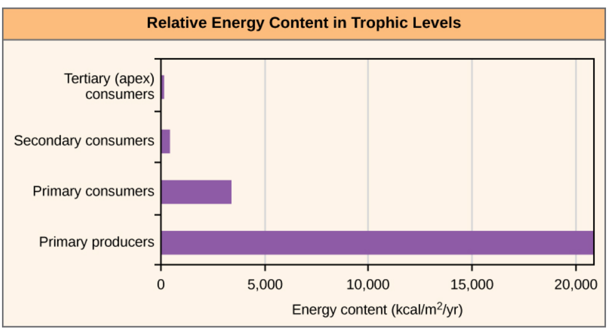

Figure 11.2 The relative energy in trophic levels in a Silver Springs, Florida, ecosystem is shown. Each trophic level has less energy available and supports fewer organisms at the next level.

Food Webs

Food chains are a simplified model that do not accurately describe most ecosystems. Even when all organisms are grouped into appropriate trophic levels, some of these organisms can feed on species from more than one trophic level; likewise, some of these organisms can be eaten by species from multiple trophic levels. In other words, the linear model of ecosystems, the food chain, is not completely descriptive of ecosystem structure. A holistic model—which accounts for all the interactions between different species and their complex interconnected relationships with each other and with the environment—is a more accurate and descriptive model for ecosystems.

A **food web** is a model of a holistic, nonlinear web of primary producers, primary consumers, and higher-level consumers used to describe ecosystem structure and dynamics (Fig 11.3). A food web accounts for the multiple trophic (feeding) interactions between each species and the many species it may feed on, or that feed on it. In a food web, the several trophic connections between each species and the other species that interact with it may cross multiple trophic levels. The matter and energy movements of virtually all ecosystems are more accurately described by food webs.

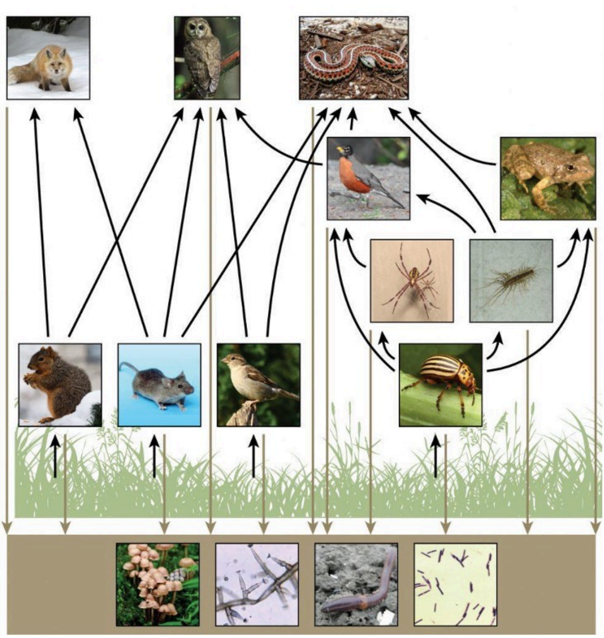

Figure 11.3 This food web shows the interactions between organisms across trophic levels. Arrows point from an organism that is consumed to the organism that consumes it. All the producers and consumers eventually become nourishment for the decomposers (fungi, mold, earthworms, and bacteria in the soil).

Two general types of food webs are often shown interacting within a single ecosystem. A **grazing food web** has plants or other photosynthetic organisms at its base, followed by herbivores and various carnivores. A **detrital food web** consists of a base of organisms that feed on decaying organic matter (dead organisms), including **decomposers** (which break down dead and decaying organisms) and **detritivores** (which consume organic detritus), as depicted in Figure 11.3. These organisms are usually bacteria or fungi that recycle organic material back into the biotic part of the ecosystem as they themselves are consumed by other organisms. As all ecosystems require a method to recycle material from dead organisms, most grazing food webs have an associated detrital food web. For example, in a meadow ecosystem, plants may support a grazing food web of different organisms, primary and other levels of consumers, while at the same time supporting a detrital food web of bacteria and fungi feeding off dead plants and animals. Simultaneously, a detrital food web can contribute energy to a grazing food web, as when a robin eats an earthworm (e.g., Fig 11.3).

Reading Question #1

In a grazing oceanic food web, who would likely be the primary producer?

A. Fungi
B. Protist
C. Krill
D. Phytoplankton

How Organisms Acquire Energy

All living things require energy in one form or another. It is important to understand how organisms acquire energy and how that energy is passed from one organism to another through food webs and their constituent food chains. Food webs illustrate how energy flows directionally through ecosystems, including how efficiently organisms acquire it, use it, and how much remains for use by other organisms of the food web.

Energy is acquired by living things in three ways: **photosynthesis**,

chemosynthesis, and the **consumption** and digestion of other living or previously living organisms by **heterotrophs.**

Photosynthetic and chemosynthetic organisms are both grouped into a category known as **autotrophs**: organisms capable of synthesizing their own food (more specifically, capable of using inorganic carbon as a carbon source). Photosynthetic autotrophs (**photoautotrophs**) use sunlight as an energy source, whereas chemosynthetic autotrophs (**chemoautotrophs**) use inorganic molecules as an energy source (Fig 11.4). Autotrophs are critical for all ecosystems. Without these organisms, energy would not be available to other living organisms and life itself would not be possible.

Figure 11.4 Swimming shrimp, a few squat lobsters, and hundreds of vent mussels are seen at a hydrothermal vent at the bottom of the ocean. As no sunlight penetrates to this depth, the ecosystem is supported by chemoautotrophic bacteria and organic material that sinks from the ocean's surface. This picture was taken in 2006 at the submerged NW Eifuku volcano off the coast of Japan by the National Oceanic and Atmospheric Administration (NOAA). The summit of this highly active volcano lies 1535 m below the surface.

Photoautotrophs, such as plants, algae, and photosynthetic bacteria, serve as the energy source for a majority of the world's ecosystems. The rate at which photosynthetic producers harness energy from the Sun is called **gross primary productivity**. However, not all of the energy incorporated by producers is available to the other organisms in the food web because producers must also grow and reproduce, which consumes energy, and some is lost as heat due to the second law of thermodynamics. **Net primary productivity** is the energy that remains in the producers after accounting for these organisms' respiration and heat loss. The net productivity is then available to the primary consumers at the next trophic level.

Chemoautotrophs are primarily bacteria that are found in rare ecosystems where sunlight is not available, such as in those associated with dark caves or hydrothermal vents at the bottom of the ocean (Fig 11.4). Many chemoautotrophs in hydrothermal vents use hydrogen sulfide (H_2S), which is released from the vents, as a source of chemical energy. This allows chemoautotrophs to synthesize complex organic molecules, such as glucose, for their own energy and in turn supplies energy to the rest of the ecosystem.

Reading Question #2

Which statement accurately contrasts heterotrophs from autotrophs?

A. Heterotrophs can photosynthesize, while autotrophs cannot.
B. Heterotrophs cannot photosynthesize, while autotrophs can.
C. Heterotrophs cannot obtain their own food, while

autotrophs can.
D. Both A and C
E. Both B and C

Biological Magnification

One of the most important environmental consequences of ecosystem dynamics is **biomagnification.**. Biomagnification is the increasing concentration of persistent, toxic substances in organisms at each trophic level, from the primary producers to the apex consumers. These are substances that are fat soluble, not water soluble, and are stored in the fat reserves of each organism. Many substances have been shown to bioaccumulate, including classical studies with the pesticide dichlorodiphenyltrichloroethane (DDT), which was published in the 1960s bestseller, Silent Spring, by Rachel Carson. DDT was a commonly-used pesticide before its dangers became known. In some aquatic ecosystems, organisms from each trophic level consumed many organisms of the lower level, which caused DDT to increase in birds (apex consumers) that ate fish. Thus, the birds accumulated sufficient amounts of DDT to cause fragility in their eggshells. This effect increased egg breakage during nesting and was shown to have adverse effects on these bird populations. The use of DDT was banned in the United States in the 1970s.

Other substances that biomagnify are polychlorinated biphenyls (PCBs), which were used in coolant liquids in the United States until their use was banned in 1979, and heavy metals, such as mercury, lead, and cadmium. These substances were best studied in aquatic ecosystems, where fish species at different trophic levels accumulate toxic substances brought through the ecosystem by the primary producers. As illustrated in a study performed by the National Oceanic and Atmospheric Administration (NOAA) in the Saginaw Bay of Lake Huron, PCB concentrations increased from the ecosystem's primary producers (phytoplankton) through the different trophic levels of fish species (Figure 11.5). The apex consumer (walleye) has more than four times the amount of PCBs compared to phytoplankton. Also, based on results from other studies, birds that eat these fish may have PCB levels at least one order of magnitude higher than those found in the lake fish.

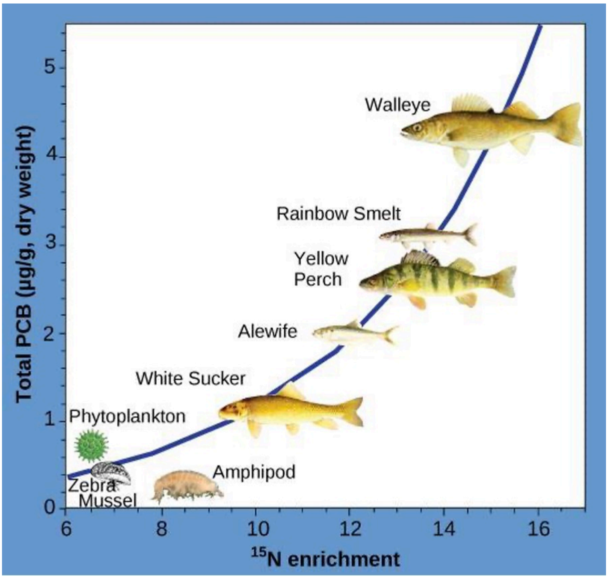

Figure 11.5 This chart shows the PCB concentrations found at the various trophic levels in the Saginaw Bay ecosystem of Lake Huron. Numbers on the x-axis reflect enrichment with heavy isotopes of nitrogen (^{15}N)*, which is a marker for increasing trophic level. Notice that the fish in the higher trophic levels accumulate more PCBs than those in lower trophic levels.* (credit: Patricia Van Hoof, NOAA, GLERL)

Other concerns have been raised by the accumulation of heavy metals, such as mercury and cadmium, in certain types of seafood. The United States Environmental Protection Agency (EPA) recommends that pregnant women and young children should not consume any swordfish, shark, king mackerel, or tilefish because of their high mercury content. These individuals are advised to eat fish low in mercury: salmon, tilapia, shrimp, pollock, and catfish. Biomagnification is a good example of how ecosystem dynamics can affect our everyday lives, even influencing the food we eat.

Productivity within Trophic Levels

Productivity within an ecosystem can be defined as the percentage of energy entering the ecosystem that becomes incorporated into biomass in a particular trophic level. Biomass is the total mass, in a unit area at the time of measurement, of living or previously living organisms within a trophic level. Ecosystems have characteristic amounts of biomass at each trophic level. For example, in the English Channel ecosystem the primary producers account for a biomass of 4 g/m^2 (grams per meter squared), while the primary consumers exhibit a biomass of 21 g/m^2.

The productivity of the primary producers is especially important in any ecosystem because these organisms bring energy to other living organisms by photoautotrophy or chemoautotrophy. The rate at which photosynthetic primary producers incorporate energy from the sun is called **gross primary productivity**. An example of gross primary productivity is shown in the compartment diagram of energy flow in Howard T. Odum's classical study of the Silver Springs, Florida, holistic ecosystem in the mid-twentieth century (Fig 11.6). This study shows the energy content and transfer between various ecosystem compartments. In this ecosystem, the total energy accumulated by the primary producers (gross primary productivity) was shown to be 20,810 kcal/m^2/yr.

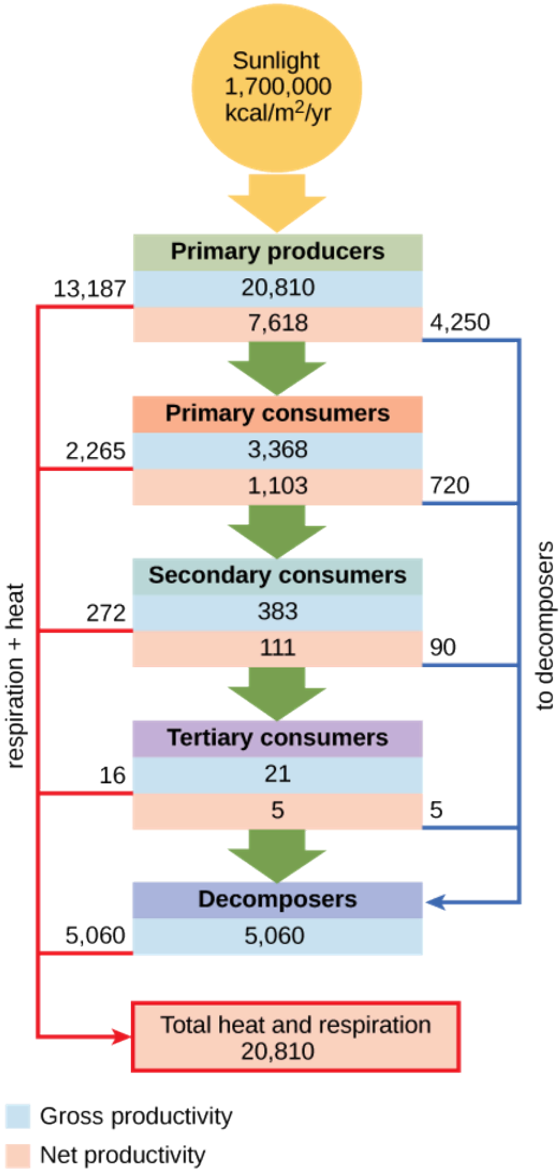

Figure 11.6 This conceptual model shows the flow of energy through a spring ecosystem in Silver Springs, Florida. Notice that the energy decreases with each increase in trophic levels.

Because all organisms need to use some of this energy for their own functions (like respiration and resulting metabolic heat loss) scientists often refer to the net primary productivity of an ecosystem. Net primary productivity is the energy that remains in the primary producers after accounting for the organisms' respiration and heat loss. The net productivity is then available to the primary consumers at the next trophic level. In our Silver Spring example, 13,187 of the 20,810 kcal/m2/yr were used for respiration or were lost as heat, leaving 7,632 kcal/m2/yr of energy for use by the primary consumers.

Reading Question #3

What happens to the amount of energy available as trophic level increases? At higher trophic levels, the amount of energy…

A. Increases
B. Decreases
C. Does not change

Ecological Efficiency

As illustrated in Figure 11.6, large amounts of energy are lost from the ecosystem from one trophic level to the next level as energy flows from the primary producers through the various trophic levels of consumers and decomposers. The main reason for this loss is the second law of thermodynamics, which states that whenever energy is converted from one form to another, there is a tendency toward disorder (entropy) in the system. In biologic systems, this means a great deal of energy is lost as metabolic heat when the organisms from one trophic level consume the next level. In the Silver Springs ecosystem example (Figure 11.6), we see that the primary consumers produced 1103 kcal/m^2/yr from the 7618 kcal/m^2/yr of energy available to them from the primary producers. The measurement of energy transfer efficiency between two successive trophic levels is termed the **trophic level transfer efficiency (TLTE)** and is defined by the formula:

$$\text{TLTE} = \frac{\text{production at present trophic level}}{\text{production at previous trophic level}} \times 100$$

In Silver Springs, the TLTE between the first two trophic levels was approximately 14.8%. The low efficiency of energy transfer between trophic levels is usually the major factor that limits the length of food chains observed in a food web. The fact is, after four to six energy transfers, there is not enough energy left to support another trophic level.

Ecologists have many different methods of measuring energy transfers within ecosystems. Some transfers are easier or more difficult to measure depending on the complexity of the ecosystem and how much access scientists have to observe the ecosystem. In other words, some ecosystems are more difficult to study than others, and sometimes the quantification of energy transfers has to be estimated.

Another main parameter that is important in characterizing energy flow within an ecosystem is the net production efficiency. **Net production efficiency** (NPE) allows ecologists to quantify how efficiently organisms of a particular trophic level incorporate the energy they receive into biomass; it is calculated using the following formula:

$$\text{NPE} = \frac{\text{net consumer productivity}}{\text{assimilation}} \times 100$$

Net consumer productivity is the energy content available to the organisms of the next trophic level. Assimilation is the biomass (energy content generated per unit area) of the present trophic level after accounting for the energy lost due to incomplete ingestion of food, energy used for respiration, and energy lost as waste. Incomplete ingestion refers to the fact that some consumers eat only a part of their food. For example, when a lion kills an antelope, it will eat everything except the hide and bones. The lion is missing the energy-rich bone marrow inside the bone, so the lion does not make use of all the calories its prey could provide.

Thus, NPE measures how efficiently each trophic level uses and incorporates the energy from its food into biomass to fuel the next trophic level. In general, cold-blooded animals (ectotherms), such as invertebrates, fish, amphibians, and reptiles, use less of the energy they obtain for respiration and heat than warm-blooded animals (endotherms), such as birds and mammals. The extra heat generated in endotherms, although an advantage in terms of the activity of these organisms in colder environments, is a major disadvantage in terms of NPE. Therefore, many endotherms have to eat more often than ectotherms to get the energy they need for survival. In general, NPE for ectotherms is an order of magnitude (10x) higher than for endotherms. For example, the NPE for a caterpillar eating leaves has been measured at 18%, whereas the NPE for a squirrel eating acorns may be as low as 1.6%.

The inefficiency of energy use by warm-blooded animals has broad implications for the world's food supply. It is widely accepted that the meat industry uses large amounts of crops to feed livestock, and because the NPE is low, much of the energy from animal feed is lost. For example, it costs about 1¢ to produce 1000 dietary calories (kcal) of corn or soybeans, but approximately $0.19 to produce a similar number of calories growing cattle for beef consumption.

The same energy content of milk from cattle is also costly, at approximately $0.16 per 1000 kcal. Much of this difference is due to the low NPE of cattle. Thus, there has been a growing movement worldwide to promote the consumption of non-meat and non-dairy foods so that less energy is wasted feeding animals for the meat industry.

Reading Question #4

Why is trophic level transfer efficiency less than 100%?

A. Heat loss
B. Imperfect ingestion
C. Cellular respiration
D. All of the above

Ecological Pyramids

The structure of ecosystems can be visualized with **ecological pyramids**, which were first described by the pioneering studies of Charles Elton in the 1920s. Ecological pyramids show the relative amounts of various parameters (such as number of organisms, energy, and biomass) across trophic levels (Fig 11.7).

Pyramids of numbers can be either upright or inverted, depending on the ecosystem. As shown in Figure 11.7B, typical grassland during the summer has a base of many plants and the numbers of organisms decrease at each trophic level. However, during the summer in a temperate forest, the base of the pyramid consists of few trees compared with the number of primary consumers, mostly insects. Because trees are large, they have great photosynthetic capability, and dominate other plants in this ecosystem to obtain sunlight. Even in smaller numbers, primary producers in forests are still capable of supporting other trophic levels.

Another way to visualize ecosystem structure is with pyramids of biomass. This pyramid measures the amount of energy converted into living tissue at the different trophic levels. Using the Silver Springs ecosystem example, this data exhibits an upright biomass pyramid (Figure 11.7A), whereas the pyramid from the English Channel example is inverted.

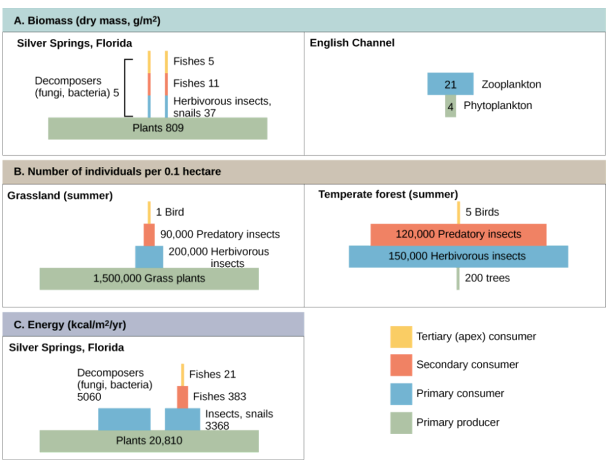

Figure 11.7 Ecological pyramids depict the (a) biomass, (b) number of organisms, and (c) energy in each trophic level.

The plants (primary producers) of the Silver Springs ecosystem make up a large percentage of the biomass found there. However, the phytoplankton in the English Channel example make up less biomass than the primary consumers, the zooplankton. As with inverted pyramids of numbers, this inverted pyramid is not due to a lack of productivity from the primary producers, but results from the high turnover rate of the phytoplankton. The phytoplankton are consumed rapidly by the primary consumers, thus, minimizing their biomass at any particular point in time. However, phytoplankton reproduce quickly, thus they are able to support the rest of the ecosystem.

Pyramid ecosystem modeling can also be used to show energy flow through the trophic levels. Notice that these numbers are the same as those used in the energy flow compartment diagram in Figure 11.6. Pyramids of energy are always upright, and an ecosystem without sufficient primary productivity cannot be supported. All types of ecological pyramids are useful for characterizing ecosystem structure. However, in the study of energy flow through the ecosystem, pyramids of energy are the most consistent and representative models of ecosystem structure (Fig 11.7).

Pyramids of organisms may be inverted or diamond-shaped because a large organism, such as a tree, can sustain many smaller organisms. Likewise, a low biomass of organisms can sustain a larger biomass at the next trophic level because the organisms reproduce rapidly and thus supply continuous nourishment. Energy pyramids, however, must always be upright because of the laws of thermodynamics. The first law of thermodynamics states that energy can neither be created nor destroyed; thus, each trophic level must acquire energy from the trophic level below. The second law of thermodynamics states that, during the transfer of energy, some energy is always lost as heat; thus, less energy is available at each higher trophic level.

Reading Question #5

Which of the following values can be greater at higher trophic levels?

A. Number of individuals
B. Biomass
C. Energy
D. A and B only
E. A, B, and C

Research into Ecosystem Dynamics: Ecosystem Experimentation and Modeling

The study of the changes in ecosystem structure caused by changes in the environment (disturbances) or by internal forces is called ecosystem dynamics. Ecosystems are characterized using a variety of research methodologies. Some ecologists study ecosystems using controlled experimental systems, while some study entire ecosystems in their natural state, and others use both approaches.

A holistic ecosystem model attempts to quantify the composition, interaction, and dynamics of entire ecosystems; it is the most representative of the ecosystem in its natural state. A food web is an example of a holistic ecosystem model. However, this type of study is limited by time and expense, as well as the fact that it is neither feasible nor ethical to do experiments on large natural ecosystems. It is difficult to quantify all different species in an ecosystem and the dynamics in their habitat, especially when studying large habitats such as the Amazon Rainforest.

For these reasons, scientists study ecosystems under more controlled conditions. Experimental systems usually involve either partitioning a part of a natural ecosystem that can be used for experiments, termed a **mesocosm**, or by recreating an ecosystem entirely in an indoor or outdoor laboratory environment, which is referred to as a **microcosm**. A major limitation to these approaches is that removing individual organisms from their natural ecosystem or altering a natural ecosystem through partitioning may change the dynamics of the ecosystem. These changes are often due to differences in species numbers and diversity and also to environment alterations caused by partitioning (mesocosm) or recreating (microcosm) the natural habitat. Thus, these types of experiments are not totally predictive of changes that would occur in the ecosystem from which they were gathered. As both of these approaches have their limitations, some ecologists suggest that results from these experimental systems should be used only in conjunction with holistic ecosystem studies to obtain the most representative data about ecosystem structure, function, and dynamics.

Scientists use the data generated by these experimental studies to develop ecosystem models that demonstrate the structure and dynamics of ecosystems. They use three basic types of ecosystem modeling in research and ecosystem management: a conceptual model, an analytical model, and a simulation model. A conceptual model is an ecosystem model that consists of flow charts to show interactions of different compartments of the living and nonliving components of the ecosystem. A conceptual model describes ecosystem structure and dynamics and shows how environmental disturbances affect the ecosystem; however, its ability to predict the effects of these disturbances is limited. Analytical and simulation models, in contrast, are mathematical methods of describing ecosystems that are indeed capable of predicting the effects of potential environmental changes without direct experimentation, although with some limitations as to accuracy. An analytical model is an ecosystem model that is created using simple mathematical formulas to predict the effects of environmental disturbances on ecosystem structure and dynamics. A simulation model is an ecosystem model that is created using complex computer algorithms to holistically model ecosystems and to predict the effects of environmental disturbances on ecosystem structure and dynamics. Ideally, these models are accurate enough to determine which components of the ecosystem are particularly sensitive to disturbances, and they can serve as a guide to ecosystem managers (such as conservation ecologists or fisheries biologists) in the practical maintenance of ecosystem health.

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12. Chapter 12: Niches and competition

ANASTASIA CHOUVALOVA AND LISA LIMERI

Introduction to Niches

A species' **niche** is the range of environmental factors that allow that species to survive and reproduce. A particular tree species, for example, may be able to live where temperatures do not drop below −40°, and where yearly precipitation is at least 750 mm. Perhaps it also needs open sunlight and an appropriate collection of root fungi. Such are the parameters of a niche.

G. Evelyn Hutchinson, one of the great ecologists of the twentieth century, envisioned the parameters that form a niche as an "n-dimensional hypervolume." The **Hutchinsonian niche** is an "n-dimensional hypervolume", where the dimensions are environmental conditions and resources, that define the requirements of an individual or a species to persist. The "**fundamental niche**" is the set of conditions allowing the species to survive if there are no other species interfering. Physical conditions are chief among those. The "**realized niche**" is the real life niche—where species are restricted by interactions with other species.

Niche overlap and interspecific competition

Interspecific competition may occur when individuals of two separate species share a limiting resource in the same area. When two species attempt to use the same resources or occupy the same space, it is described as niche overlap. Niche overlap results in **interspecific competition** (inter- means between species, as opposed to intraspecific, which is within-species competition). If the resource cannot support both populations, then lowered fecundity, growth, or survival may result in at least one species. Interspecific competition has the potential to alter populations, communities, and the evolution of interacting species.

Consider latitude on the earth's surface, which is connected to several parameters such as sunlight and temperature. And consider two species that can thrive anywhere between 40◦ and 60◦ latitude, and whose density drops slowly with increasing latitude (Fig 12.1).

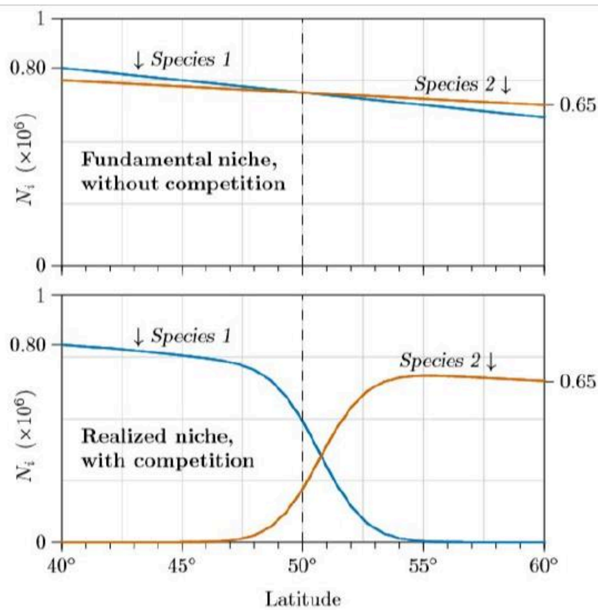

Figure 12.1 Species living apart along a spatial gradient (above) and living together along the same gradient (below).

At the top of Figure 12.1 are two nearly horizontal lines representing the abundance you might observe of the two species as you travel north. If free of Species 2 (its competitor), Species 1 (blue line) declines slowly in abundance in more northerly climates. Species 2 similarly declines in abundance (red line), but compared with Species 1 fares a little better in the north and a little worse in the south.

When these two species are together they compete with each other—each suppressing the other. In the south, where Species 1 fares better, it takes over and dominates. In the north, in contrast, where Species 2 fares better, it dominates instead (Fig 12.1 , bottom).

You see that there can be a sharp change in abundance even with only very slight changes in species characteristics. A range of one species can end and that of a new species can begin, even though you may not be able to discover anything from either species alone as to why they switch their dominance. And the switch-over point need not correspond to the exact place in which their dominance switches. Here the actual switch-over point is a few degrees to the north because of the migration simulated in the model. This phenomenon is called "competitive exclusion."

Reading Question #1

What is the difference between a fundamental and realized niche?

A. Fundamental niche is based on fewer variables than realized niche.
B. Fundamental niche is for animals and realized niche is for plants.
C. Realized niche is more complex than fundamental niche.
D. Realized niche accounts for competition whereas fundamental niche does not.

Competitive Exclusion Principle

Resources are often limited within a habitat and multiple species may compete to obtain them. All species have an ecological niche in the ecosystem, which describes how they acquire the resources they need and how they interact with other species in the community. Life in an ecosystem is often about competition for limited resources, a characteristic of the theory of natural selection. Competition in communities (all living things within specific habitats) is observed both within species and among different species. The resources for which organisms compete include organic material, sunlight, and mineral nutrients, which provide the energy for living processes and the matter to make up organisms' physical structures.

The **competitive exclusion principle** states that two species cannot occupy the same niche in a habitat. In other words, different species cannot coexist in a community if they are competing for all the same resources. An example of this principle is shown in Figure 12.2 with two protozoan species, *Paramecium aurelia* and *Paramecium caudatum*. When grown individually in the laboratory, they both thrive. But when they are placed together in the same test tube (habitat), *P. aurelia* outcompetes *P. caudatum* for food, leading to the latter's eventual extinction.

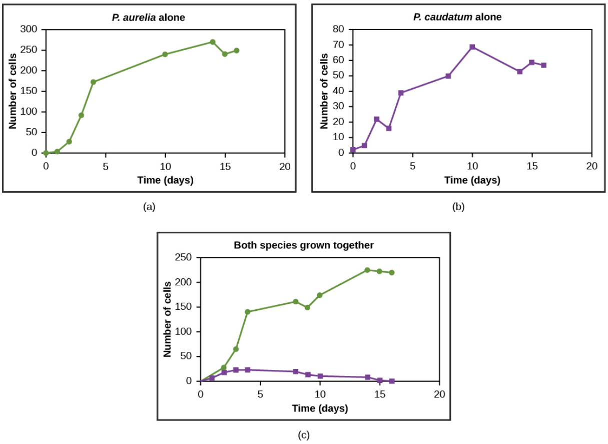

Figure 12.2 Paramecium aurelia and Paramecium caudatum grow well individually, but when they compete for the same resources, the P. aurelia outcompetes the P. caudatum.

Resource Partitioning

Competitive exclusion may be avoided if one or both of the competing species evolves to use a different resource, occupy a different area of the habitat, or feed during a different time of day. The result of this kind of evolution is that two similar species use largely non-overlapping resources and thus have different niches. This is called **resource partitioning** or **niche differentiation** and it helps the species coexist because there is less direct competition between them. When two species differentiate their niches, they tend to compete less strongly, and are thus more likely to coexist. Species can differentiate their niches in many ways, such as by consuming different foods, or using different areas of the environment.

The anole lizards found on the island of Puerto Rico are a good example of resource partitioning. These anoles share common diets—mainly insects. They avoid competition by occupying different physical locations within the same area. For example, some live on the ground while others are arboreal (tree-living). Species who live in different areas compete less for food and other resources, which minimizes competition between species. Figure 12.3 below shows resource partitioning among 11 species of anole lizards. Each species lives in its own preferred habitat, which is defined by type and height of vegetation (trees, shrubs, cactus, etc.), sunlight, and moisture, among other factors.

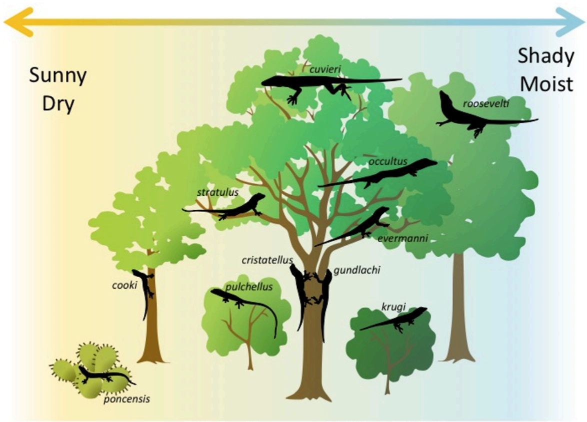

Figure 12.3 Resource partitioning among anole lizards.

Niche differentiation (also known as niche separation and niche partitioning) refers to the process by which competing species use the environment differently in a way that helps them to coexist. When two species differentiate their niches, they tend to compete less strongly, and are thus more likely to coexist. Species can differentiate their niches in many ways, such as by consuming different foods, or using different areas of the environment.

Reading Question #2

Which of the following best describes resource partitioning?

A. Dividing resources to avoid competition for limited resources in ecosystems
B. Sharing resources to avoid competition for limited resources in ecosystems
C. Dividing resources to promote competition for limited resources in ecosystems
D. Sharing resources to promote competition for limited resources in ecosystems

Reading Question #3

What causes niche partitioning to occur?

A. Competition
B. Niche overlap
C. Speciation
D. A and B
E. A, B, and C

Character displacement

Character displacement is trait differentiation that occurs when similar species that live in the same geographic region and occupy similar niches differentiate in order to minimize niche overlap and avoid competitive exclusion. Several species of Galapagos finches exhibit character displacement. Each closely related species differs in beak size and beak depth, allowing them to coexist in the same region since each species eats a different type of seed: the seed best fit for its unique beak. The finches with the deeper, stronger beaks consume large, tough seeds, while the finches with smaller beaks consume the smaller, softer seeds (Fig 12.4).

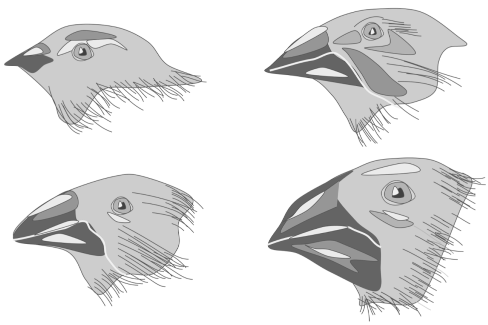

Figure 12.4 Character displacement exhibited by Galapagos finches

Character displacement is the phenomenon where differences among similar species whose distributions overlap geographically are accentuated in regions where the species co-occur, but are minimized or lost where the species' distributions do not overlap. This pattern results from evolutionary change driven by biological competition among species for a limited resource (e.g. food). The rationale for character displacement stems from the competitive exclusion principle, which contends that to coexist in a stable environment two competing species must differ in their respective ecological niche; without differentiation, one species will eliminate or exclude the other through competition.

For example, Darwin's finches can be found alone or together on the Galapagos Islands. Both species' populations actually have more individuals with intermediate-sized beaks when they live on islands without the other species present. However, when both species are present on the same island, competition is intense between individuals that have intermediate-sized beaks of both species because they all require intermediate sized seeds. Consequently, individuals with small and large beaks have greater survival and reproduction on these islands than individuals with intermediate-sized beaks. Different finch species can coexist if they have traits—for instance, beak size—that allow them to specialize on particular resources. When *Geospiza fortis* and *Geospiza fuliginosa* are present on the same island, G. *fuliginosa* tends to evolve a small beak and G. *fortis* a large beak. The observation that competing species' traits are more different when they live in the same area than when competing species live in different areas is called character displacement. For the two finch species, beak size was displaced: beaks became smaller in one species and larger in the other species.

Reading Question #4

Which of the following best describes character displacement?

A. Dividing resources to avoid competition for limited resources in ecosystems
B. Species occupy the same niche
C. Trait differentiation resulting from resource partitioning
D. Species feed on the same food

Reading Question #5

What causes character displacement to occur?

A. Competition
B. Niche overlap
C. Resource partitioning
D. A and B
E. A, B, and C

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13. Chapter 13: Invasive Species

MASON TEDESCHI; ANASTASIA CHOUVALOVA; AND LISA LIMERI

Introduction to Invasive Species

Imagine sailing down a river in a small motorboat on a weekend afternoon; the water is smooth and you are enjoying the warm sunshine and cool breeze when suddenly you are hit in the head by a 20-pound silver carp. This is now a risk on many rivers and canal systems in Illinois and Missouri because of the presence of Asian carp.

This fish—actually a group of species including the silver, black, grass, and big head carp—has been farmed and eaten in China for over 1000 years. It is one of the most important aquaculture food resources worldwide. In the United States, however, Asian carp is considered a dangerous invasive species that disrupts community structure and composition to the point of threatening native species.

Invasive species are nonnative organisms that, when introduced to an area out of their native range, threaten the ecosystem balance of that habitat. Many such species exist in the United States (Fig 13.1). Whether enjoying a forest hike, taking a summer boat trip, or simply walking down an urban street, you have likely encountered an invasive species.

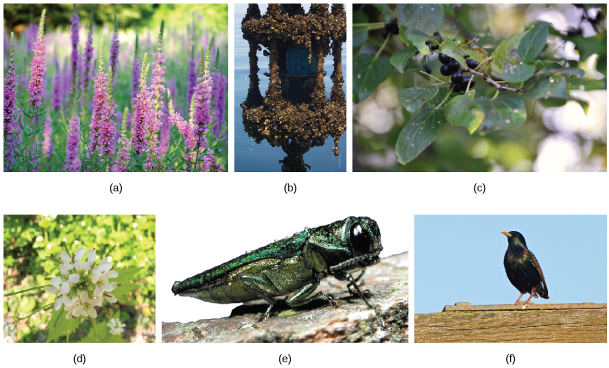

Figure 13.1 In the United States, invasive species like (a) purple loosestrife (Lythrum salicaria) and the (b) zebra mussel (Dreissena polymorpha) threaten certain aquatic ecosystems. Some forests are threatened by the spread of (c) common buckthorn (Rhamnus cathartica), (d) garlic mustard (Alliaria petiolata), and (e) the emerald ash borer (Agrilus planipennis). The (f) European starling (Sturnus vulgaris) may compete with native bird species for nest holes. (Photo credits: photo credits: a: modification of work by Liz West;

credit b: modification of work by M. McCormick, NOAA; credit c: modification of work by E. Dronkert; credit d: modification of work by Dan Davison; credit e: modification of work by USDA; credit f: modification of work by Don DeBold)

Introductions of species, particularly plants into new areas, by whatever means and for whatever reasons have brought about major and permanent changes to the environment over large areas. Examples include the introduction of *Caulerpa taxifolia* into the Mediterranean, the introduction of oat species into the California grasslands, and the introduction of privet, kudzu, and purple loosestrife to North America. Rats, cats, and goats have radically altered biodiversity in many islands. Additionally, introductions have resulted in genetic changes to native fauna where interbreeding has taken place, as with buffalo with domestic cattle, and wolves with domestic dogs.

Reading Question #1

What is an invasive species?

A. Any non-native species introduced to a new area.
B. Any species that becomes dominant in a community.
C. Any species that negatively impacts a community.
D. A non-native species that negatively impacts a community.

Example: Asian carp

One of the many recent proliferations of an invasive species concerns the growth of Asian carp populations. Asian carp were introduced to the United States in the 1970s by fisheries and sewage treatment facilities that used the fish's excellent filter feeding capabilities to clean their ponds of excess plankton. Some of the fish escaped, however, and by the 1980s they had colonized many waterways of the Mississippi River basin, including the Illinois and Missouri Rivers.

Voracious eaters and rapid reproducers, Asian carp may outcompete native species for food, potentially leading to their extinction. For example, black carp are voracious eaters of native mussels and snails, limiting this food source for native fish species. Silver carp eat plankton that native mussels and snails feed on, reducing this food source by a different alteration of the food web. In some areas of the Mississippi River, Asian carp species have become the most predominant, effectively outcompeting native fishes for habitat. In some parts of the Illinois River, Asian carp constitute 95% of the community's biomass. Although edible, the fish is bony and not a desired food in the United States. Moreover, their presence threatens the native fish and fisheries of the Great Lakes, which are important to local economies and recreational anglers. Asian carp have even injured humans. The fish, frightened by the sound of approaching motorboats, thrust themselves into the air, often landing in the boat or directly hitting the boaters.

The Great Lakes and their prized salmon and lake trout fisheries are also being threatened by these invasive fish. Asian carp have already colonized rivers and canals that lead into Lake Michigan. One infested waterway of particular importance is the Chicago Sanitary and Ship Channel, the major supply waterway linking the Great Lakes to the Mississippi River. To prevent the Asian carp from leaving the canal, a series of electric barriers have been successfully used to discourage their migration; however, the threat is significant enough that several states and Canada have sued to have the Chicago channel permanently cut off from Lake Michigan. Local and national politicians have weighed in on how to solve the problem, but no one knows whether the Asian carp will ultimately be considered a nuisance, like other invasive species such as the water hyacinth and zebra mussel, or whether it will be the destroyer of the largest freshwater fishery of the world.

The issues associated with Asian carp show how population and community ecology, fisheries management, and politics intersect on issues of vital importance to the human food supply and economy. Socio-political issues like this make extensive use of the sciences of population ecology (the study of members of a particular species occupying a particular area known as a habitat) and community ecology (the study of the interaction of all species within a habitat).

Exotic Species

Exotic species are species that have been intentionally or unintentionally introduced into an ecosystem in which they did not evolve. For example, Kudzu (*Pueraria lobata*), which is native to Japan, was introduced in the United States in 1876. It was later planted for soil conservation. Problematically, it grows too well in the southeastern United States—up to a foot a day. It is now an invasive pest species and covers over 7 million acres in the southeastern United States. If an introduced species is able to survive in its new habitat, that introduction is now reflected in the observed range of the species. Human transportation of people and goods, including the intentional transport of organisms for trade, has dramatically increased the introduction of species into new ecosystems, sometimes at distances that are well beyond the capacity of the species to ever travel itself and outside the range of the species' natural predators.

Most exotic species introductions probably fail because of the low number of individuals introduced or poor adaptation to the ecosystem they enter. Some species, however, possess **pre-adaptations** that can make them especially successful in a new ecosystem. These exotic species often undergo dramatic population increases in their new habitat and reset the ecological conditions in the new environment, threatening the species that exist there. When exotic species are successful in their introductions and damage their new ecosystem, they are called **invasive species.**. Invasive species can threaten other species through competition for resources, predation, or disease. For example, the Eurasian star thistle, also called spotted knapweed, has invaded and rendered useless some of the open prairies of the western states. However, it is a great nectar-bearing flower for the production of honey and supports numerous pollinating insects, including migrating monarch butterflies in the north-central states such as Michigan.

Lakes and islands are particularly vulnerable to extinction threats from introduced species. In Lake Victoria the intentional introduction of the Nile perch was largely responsible for the extinction of about 200 species of endemic cichlids. The accidental introduction of the brown tree snake via aircraft from the Solomon Islands to Guam in 1950 has led to the extinction of three species of birds and three to five species of reptiles endemic to the island. Several other species are still threatened. The brown tree snake is adept at exploiting human transportation as a means to migrate; one was even found on an aircraft arriving in Corpus Christi, Texas. Constant vigilance on the part of airport, military, and commercial aircraft personnel is required to prevent the snake from moving from Guam to other islands in the Pacific, especially Hawaii. Islands do not make up a large area of land on the globe, but they do contain a disproportionate number of endemic species because of their isolation from mainland ancestors.

Many introductions of aquatic species, both marine and freshwater, have occurred when ships have dumped ballast water taken on at a port of origin into waters at a destination port. Water from the port of origin is pumped into tanks on a ship empty of cargo to increase stability. The water is drawn from the ocean or estuary of the port and typically contains living organisms such as plant parts, microorganisms, eggs, larvae, or aquatic animals. The water is then pumped out before the ship takes on cargo at the destination port, which may be on a different continent. The zebra mussel was introduced to the Great Lakes from Europe prior to 1988 in ballast water. The zebra mussels in the Great Lakes have created millions of dollars in clean-up costs to maintain water intakes and other facilities. The mussels have also altered the ecology of the lakes dramatically. They threaten native mollusk populations, but have also benefited some species, such as smallmouth bass. The mussels are filter feeders and have dramatically improved water clarity, which in turn has allowed aquatic plants to grow along shorelines, providing shelter for young fish where it did not exist before. The European green crab, *Carcinus maenas*, was introduced to San Francisco Bay in the late 1990s, likely in ship ballast water, and has spread north along the coast to Washington. The crabs have been found to dramatically reduce the abundance of native clams and crabs with resulting increases in the prey species of those native crabs.

The crimes of fungal pathogens

In the 1990's, researchers became alarmed by the dramatic global decline of amphibian populations. It now appears that the global decline in amphibian species is, in some part, caused by the fungus *Batrachochytrium dendrobatidis*, which causes the disease chytridiomycosis (Figure 13.2). There is evidence that the fungus is native to Africa and may have been spread throughout the world by transport of a commonly used laboratory and pet species: the African clawed frog, *Xenopus laevis*. It may well be that biologists themselves are responsible for spreading this disease worldwide. The North American bullfrog, *Rana catesbeiana*, which has also been widely introduced as a food animal but which easily escapes captivity, survives most infections of *B. dendrobatidis* and can act as a reservoir for the disease.

Figure 13.2. This Limosa harlequin frog (Atelopus limosus), *an endangered species from Panama, died from a fungal disease called chytridiomycosis. The red lesions are symptomatic of the disease. (credit: Brian Gratwicke)*

Early evidence suggests that another fungal pathogen, *Geomyces destructans*, introduced from Europe is responsible for white-nose syndrome, which infects cave-hibernating bats in eastern North America and has spread from a point of origin in western New York State. The disease has decimated bat populations and threatens extinction of species already listed as endangered: the Indiana bat, *Myotis sodalis*, and potentially the Virginia big-eared bat, *Corynorhinus townsendii virginianus*. How the fungus was introduced is unknown, but one logical presumption would be that recreational cavers unintentionally brought the fungus on clothes or equipment from Europe.

Career Connection: Microbiologist

The most effective action anyone can take to prevent the spread of contagious **illness** is to wash their hands. Why? Because microbes (organisms so tiny that they can only be seen with microscopes) are ubiquitous. They live on doorknobs, money, your hands, and many other surfaces. If someone sneezes into his hand and touches a doorknob, and afterwards you touch that same doorknob, the microbes from the sneezer's mucus are now on your hands. If you touch your hands to your mouth, nose, or eyes, those microbes can enter your body and could make you sick.

However, not all microbes (also called microorganisms) cause disease; most are actually beneficial. You have microbes in your gut that make vitamin K. Other microorganisms are used to ferment beer and wine.

Microbiologists are scientists who study microbes. Microbiologists can pursue a number of careers. Not only do they work in the food industry, they are also employed in the veterinary and medical fields. They can work in the pharmaceutical sector, serving key roles in research and development by identifying new antibiotic sources that can treat bacterial infections.

Environmental microbiologists may look for new ways to use specially selected or genetically engineered microbes to remove pollutants from soil or groundwater, as well as hazardous elements from contaminated sites. We call using these microbes bioremediation technologies. Microbiologists can also work in the bioinformatics field, providing specialized knowledge and insight for designing, developing, and specificity of computer models of, for example, bacterial epidemics.

Reading Question #2

What are the possible outcomes of a species being introduced to a new continent it did not evolve on?

A. It could fail to establish and not impact the ecosystem
B. It could establish and alter the ecosystem dynamics
C. It could establish and outcompete native species and drive them to extinction
D. All of the above

Reading Question #3

How do exotic species get introduced to new regions?

A. On accident through human activity.
B. Intentionally by humans as pets.

C. Intentionally by humans as ornamental species.
D. All of the above.

Reading Question #4

How can invasive species impact their new ecosystems?

A. By causing disease
B. By outcompeting native species
C. By consuming native species
D. All of the above

References

Adapted from Clark, M.A., Douglas, M., and Choi, J. (2018). Biology 2e. OpenStax. Retrieved from https://openstax.org/books/biology-2e/pages/1-introduction

14. Chapter 14: Antagonistic Species Interactions: Consumption and Parasitism

ANASTASIA CHOUVALOVA AND LISA LIMERI

Consumption: Predation and Herbivory

Predation is a biological interaction where one organism, the predator, kills and eats another organism, its prey. It is distinct from scavenging on dead prey, though many predators also scavenge. Predation and herbivory overlap because seed predators and destructive frugivores kill their "prey." The concept of predation is broad, defined differently in different contexts, and includes a wide variety of feeding methods

Predation

Perhaps the classical example of species interaction is predation: the consumption of prey by its predator. Nature shows on television highlight the drama of one living organism killing another. Predators are adapted and often highly specialized for hunting, with acute senses such as vision, hearing, or smell. Many predatory animals, both vertebrate and invertebrate, have sharp claws or jaws to grip, kill, and cut up their prey. Other adaptations include stealth and aggressive mimicry that improve hunting efficiency. When prey is detected, the predator assesses whether to attack it. Predators may actively search for or pursue prey (pursuit predation) or sit and wait for prey (ambush predation), often concealed, prior to attack. If the attack is successful, the predator kills the prey, removes any inedible parts like the shell or spines, and eats it.

Modeling Predator/Prey Dynamics

Population sizes of predators and prey in a community are not constant over time: in most cases, they vary in cycles that appear to be related. The most often cited example of predator-prey dynamics is seen in the cycling of the lynx (predator) and the snowshoe hare (prey), using nearly 200 year-old trapping data from North American forests (Figure 14.1). Lotka and Volterra independently proposed in the 1920s a mathematical model for the population dynamics of a predator and prey that would explain this observation. These Lotka-Volterra predator-prey equations have since become an iconic model of mathematical biology. The Lotka-Volterra model predicts that as the hare numbers increase, there is more food available for the lynx, allowing the lynx population to increase as well. When the lynx population grows to a threshold level, however, they kill so many hares that hare population begins to decline, followed by a decline in the lynx population because of scarcity of food. When the lynx population is low, the hare population size begins to increase due to low predation pressure, starting the cycle anew. This cycle of predator and prey lasts approximately 10 years, with the predator population lagging 1–2 years behind that of the prey population.

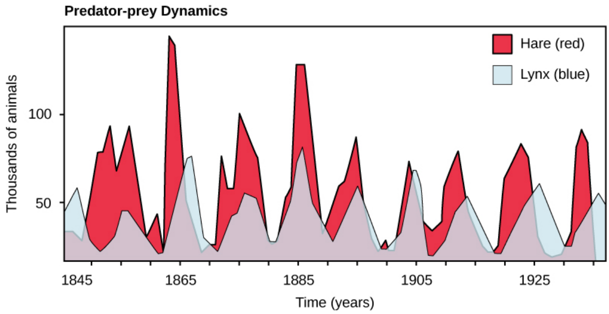

Figure 14.1 The cycling of lynx and snowshoe hare populations in Northern Ontario is an example of predator-prey dynamics.

Link to Learning

The Lotka-Volterra model equations are outside of the scope of this course, but you can find more information on them at this link: https://math.libretexts.org/Bookshelves/Applied_Mathematics/Mathematical_Biology_(Chasnov)/01%3A_Population_Dynamics/1.04%3A_The_Lotka-Volterra_Predator-Prey_Model

Like all mathematical models, the Lotka-Volterra model of predator-prey dynamics makes a number of assumptions that must be met in order for the model's predictions to be observed. These assumptions include that the number of prey grow exponentially in the absence of predators (there is unlimited food available to the prey), and that the number of predators decay exponentially in the absence of prey (predators must eat prey or starve). Contact between predators and prey increases the number of predators and decreases the number of prey.

The Lotka-Volterra model is one of the earliest predator-prey models to be based on sound mathematical principles. It forms the basis of many models used today in the analysis of population dynamics. Unfortunately, in its original form Lotka-Volterra has some significant problems. It predicts that there is no stable equilibrium point, but rather that the predator and prey populations will cycle endlessly. While this cycling has been observed in some situations in nature (such as the historical trapping data from lynxes and hares), it is not very common.

The Lotka-Volterra by itself is not sufficient to model many predator-prey systems because it assumes that the only factors influencing predator and prey populations are the population sizes of the predators and prey. However, there are other density-dependent factors that are important in influencing prey population size, in addition to predation. One possibility is that the cycling is inherent in the hare population due to density-dependent effects such as lower fecundity (maternal stress) caused by crowding when the hare population gets too dense. The hare cycling would then induce the cycling of the lynx because it is the lynxes' major food source. The more we study communities, the more complexities we find, allowing ecologists to derive more accurate and sophisticated models of population dynamics.

Reading Question #1

What is the primary prediction of the Lotka-Volterra models?

A. Predator population sizes will always be higher than prey population sizes.
B. Predator and prey population sizes do not affect

each other.
C. Predator and prey population sizes cyclically influence each other.
D. Predators influence prey population sizes but prey do not influence predator's population sizes.

Reading Question #2

What is an assumption of the Lotka-Volterra model?

A. Population sizes are constant over time.
B. Prey population size is unaffected by predator population size.
C. Mathematical equations cannot explain biological phenomena.
D. The number of prey grow exponentially in the absence of predators.

Herbivory

Herbivory is a form of consumption in which an organism principally eats autotrophs such as plants, algae and photosynthesizing bacteria. More generally, organisms that feed on autotrophs are known as primary consumers. Herbivory is usually limited to animals that eat plants. Fungi, bacteria, and protists that feed on living plants are usually termed plant pathogens (plant diseases), while fungi and microbes that feed on dead plants are described as saprotrophs. Flowering plants that obtain nutrition from other living plants are usually termed parasitic plants.

Two herbivore feeding strategies are grazing (e.g. cows) and browsing (e.g. moose). For a terrestrial mammal to be called a grazer, at least 90% of the forage has to be grass, and for a browser at least 90% tree leaves and twigs. An intermediate feeding strategy is called "mixed-feeding". In their daily need to take up energy from forage, herbivores of different body masses may be selective in choosing their food. "Selective" means that herbivores may choose their forage source depending on environmental conditions such as season or food availability, but also that they may choose high-quality (and consequently highly nutritious) forage before lower quality. The latter especially is determined by the body mass of the herbivore, with small herbivores selecting for high-quality forage, and with increasing body mass animals are less selective.

Defense Mechanisms against Predation and Herbivory

Predation has a powerful selective effect on prey, and prey evolve anti-predator adaptations such as warning coloration, alarm and other calls, camouflage, copying (mimicry) of well-defended species, and defensive spines and chemicals. Sometimes predator and prey find themselves in an evolutionary arms race, a cycle of adaptations and counter-adaptations. Unlike animals, most plants cannot outrun predators. However, plants have evolved a variety of mechanisms to defend against herbivory. Other species have developed mutualistic relationships; for example, herbivory provides a mechanism of seed distribution that aids in plant reproduction.

The study of communities must consider evolutionary forces that act on the members of the various populations contained within it.

Species are not static, but slowly changing and adapting to their environment by natural selection and other evolutionary forces. Species have evolved numerous mechanisms to escape predation and herbivory. These defenses may be mechanical, chemical, physical, or behavioral.

Mechanical defenses, such as the presence of thorns on plants or the hard shell on turtles, discourage animal predation and herbivory by causing physical pain to the predator or by physically preventing the predator from being able to eat the prey. Chemical defenses are produced by many animals as well as plants, such as the foxglove which is extremely toxic when eaten. Figure 14.2 shows some organisms' defenses against predation and herbivory.

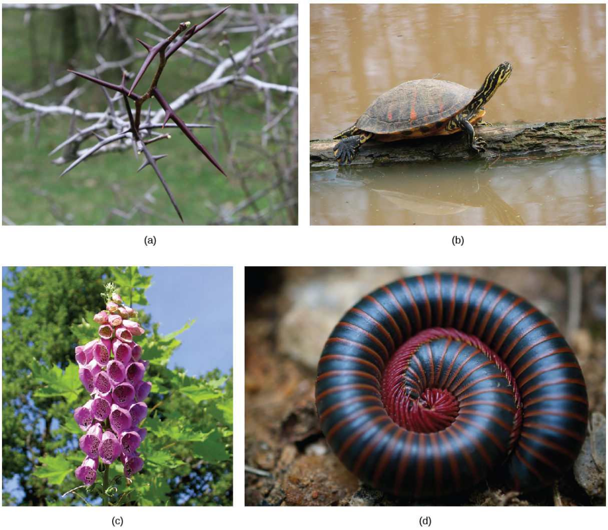

Figure 14.2. The (a) honey locust tree (Gleditsia triacanthos) uses thorns, a mechanical defense, against herbivores, while the (b) Florida red-bellied turtle (Pseudemys nelsoni) uses its shell as a mechanical defense against predators. (c) Foxglove (Digitalis spp.) uses a chemical defense: toxins produced by the plant can cause nausea, vomiting, hallucinations, convulsions, or death when consumed. (d) The North American millipede (Narceus americanus) uses both mechanical and chemical defenses: when threatened, the millipede curls into a

defensive ball and produces a noxious substance that irritates eyes and skin. (credit a: modification of work by Huw Williams; credit b: modification of work by "JamieS93"/ Flickr; credit c: modification of work by Philip Jägenstedt; credit d: modification of work by Cory Zanker)

Many species use physical appearance, such as body shape and coloration, to avoid being detected by predators. The tropical walking stick is an insect with the coloration and body shape of a twig which makes it very hard to see when stationary against a background of real twigs (Figure 14.3a). In another example, the chameleon can, within limitations, change its color to match its surroundings (Figure 14.3b). Both of these are examples of **camouflage**, or avoiding detection by blending in with the background. There are many behavioral adaptations to avoid or confuse predators. Playing dead and traveling in large groups, like schools of fish or flocks of birds, are both behaviors that reduce the risk of being eaten.

(a) (b)

Figure 14.3 (a) The tropical walking stick and (b) the chameleon use body shape and/ or coloration to prevent detection by predators. (credit a: modification of work by Linda Tanner; credit b: modification of work by Frank Vassen)

Some species use coloration as a way of warning predators that they are not good to eat. For example, the cinnabar moth caterpillar, the fire-bellied toad, and many species of beetle have bright colors that warn of a foul taste, the presence of toxic chemicals, and/or the ability to sting or bite, respectively. Predators that ignore this coloration and eat the organisms will experience their unpleasant taste or presence of toxic chemicals and learn not to eat them in the future. This type of defensive mechanism is called **aposematic coloration**, or **warning coloration** (Figure 14.4).

Figure 14.4 (a) The strawberry poison dart frog (Oophaga pumilio) uses aposematic coloration to warn predators that it is toxic, while the (b) striped skunk (Mephitis mephitis) uses aposematic coloration to warn predators of the unpleasant odor it produces. (credit a: modification of work by Jay Iwasaki; credit b: modification of work by Dan Dzurisin)

While some predators learn to avoid eating certain potential prey because of their coloration, other species have evolved mechanisms to mimic this coloration to avoid being eaten, even though they themselves may not be unpleasant to eat or contain toxic chemicals. In **Batesian mimicry**, a harmless species imitates the warning coloration of a harmful one. Assuming they share the same predators, this coloration then protects the harmless ones, even though they do not have the same level of physical or chemical defenses against predation as the organism they mimic. Many insect species mimic the coloration of wasps or bees, which are stinging, venomous insects, thereby discouraging predation (Figure 14.5).

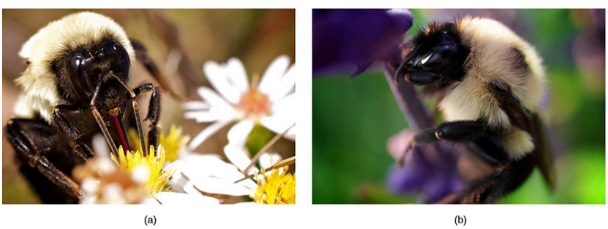

Figure 14.5 Batesian mimicry occurs when a harmless species mimics the coloration of a harmful species, as is seen with the (a) bumblebee and (b) bee-like robber fly. (credit a, b: modification of work by Cory Zanker)

In **Müllerian mimicry**, multiple species share the same warning coloration, but all of them actually have defenses. Figure 14.6 shows a variety of foul-tasting butterflies with similar coloration.

Figure 14.6 Several unpleasant-tasting Heliconius butterfly species share a similar color pattern with better-tasting varieties, an example of Müllerian mimicry. (credit: Joron M, Papa R, Beltrán M, Chamberlain N, Mavárez J, et al.)

Link to Learning

Go to this website to see stunning examples of mimicry.

Reading Question #3

In a region in Texas, biologists observed that two highly venomous snakes have similar markings deter owl predators. The biologists sequenced the genomes of the species and found that they are distantly related; they are separate species belonging to different genera. These snakes are an example of what predation defense?

A. Batesian mimicry, because it involves a nontoxic species that resembles a toxic species.
B. Bestesian mimicry because the two species are distantly related.
C. Mullerian mimicry because it involves an extremely toxic species that resembles a non-toxic species.
D. Mullerian mimicry because it involves different species that both produce toxins and display similar warning coloration.

Parasitism

Parasitism is a **symbiotic** between species, where one organism, the parasite, lives on or inside another organism, the host, causing it some harm, and is adapted structurally to this way of life. Like predation, parasitism is a type of consumer-resource interaction, but unlike predators, parasites are typically much smaller than their hosts, do not kill them, and often live in or on their hosts for an extended period. Parasites of animals are highly specialized, and reproduce at a faster rate than their hosts. Classic examples include interactions between vertebrate hosts and tapeworms, flukes, the malaria-causing Plasmodium species, and fleas.

Parasitism describes a relationship in which one member of the association benefits at the expense of the other. So, while the parasite itself benefits, the host organism is harmed. This is in contrast to **commensalism** in which one member benefits *without* affecting the other. The parasite typically weakens the host as it consumes resources that the host would normally benefit from. The parasite usually does not directly kill the host, but could indirectly contribute to the host's death by weakening it and robbing it of resources.

Parasites are classified in a variety of overlapping categories, based on their interactions with their hosts and on their life-cycles, which are sometimes very complex. An **obligate parasite** depends completely on the host to complete its life cycle and cannot survive without the host. In contrast, a **facultative** parasite benefits from parasitizing from a host but does not require its host for survival. An **endoparasite** lives inside the host's body; an **ectoparasite** lives outside, on the host's surface. **Mesoparasites** are in between endoparasites and ectoparasites—they enter an opening in the host's body and remain partly embedded there. Some parasites can be **generalists**, feeding on a wide range of hosts, but many parasites are **specialists** and extremely host-specific.

The reproductive cycles of parasites are often very complex, sometimes requiring more than one host species. A tapeworm is a parasite that causes disease in humans when contaminated, undercooked meat is consumed. The tapeworm can live inside the intestine of the host for several years, benefiting from the food the host is eating, and may grow to be over 50 ft long by adding segments. The parasite moves from species to species in a cycle, making two hosts necessary to complete its life cycle.

Many parasites that has multiple hosts are trophically-transmitted between their hosts. **Trophically-transmitted parasites** are transmitted by being eaten by a host. In their juvenile stages they infect a host termed the **intermediate host**. The intermediate host is a host the parasite can infect, but cannot complete its reproduction inside of. When the intermediate-host animal is eaten by a predator, the **definitive host**, the parasite survives the digestion process and matures into an adult; some live as intestinal parasites. When parasites have multiple hosts, the definitive host is the host that they can reproduce inside of. Many trophically-transmitted parasites modify the behavior of their intermediate hosts, increasing their chances of being eaten by a predator.

Connection to Evolution

Malaria is a parasitic disease in humans that is transmitted by infected female mosquitoes, including *Anopheles gambiae* (Figure 14.7a), and is characterized by cyclic high fevers, chills, flu-like symptoms, and severe anemia. *Plasmodium falciparum* and *P. vivax* are the most common causative agents of malaria, and *P. falciparum* is the most deadly (Figure 14.7b). When promptly and correctly treated, *P. falciparum* malaria has a mortality rate of 0.1%. However, in some parts of the world, the parasite has evolved resistance to commonly used malaria treatments, so the most effective malarial treatments can vary by geographic region.

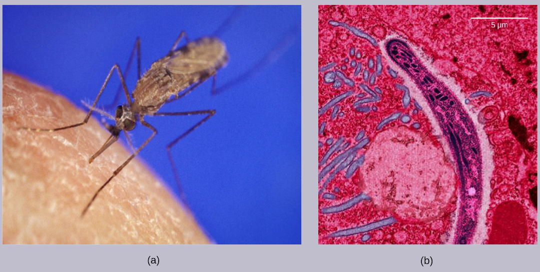

Figure 14.7 The (a) Anopheles gambiae, or African malaria mosquito, acts as a vector in the transmission to humans of the malaria-causing parasite (b) Plasmodium falciparum, here visualized using false-color transmission electron microscopy. (credit a: James D. Gathany; credit b: Ute Frevert; false color by Margaret Shear; scale-bar data from Matt Russell)

In Southeast Asia, Africa, and South America, *P. falciparum* has developed resistance to the anti-malarial drugs chloroquine, mefloquine, and sulfadoxine-pyrimethamine. *P. falciparum*, which is haploid during the life stage in which it is infectious to humans, has evolved multiple drug-resistant mutant alleles of the *dhps* gene. Varying degrees of sulfadoxine resistance are associated with each of these alleles. Being haploid, *P. falciparum* needs only one drug-resistant allele to express this trait.

In Southeast Asia, different sulfadoxine-resistant alleles of the *dhps* gene are localized to different geographic regions. This is a common evolutionary phenomenon that occurs because drug-resistant mutants arise in a population and interbreed with other *P. falciparum* isolates in close proximity. Sulfadoxine-resistant parasites cause considerable human hardship in regions where this drug is widely used as an over-the-counter malaria remedy. As is common with pathogens that multiply to large numbers within an infection cycle, *P. falciparum* evolves relatively rapidly (over a decade or so) in response to the selective pressure of commonly used anti-malarial drugs. For this reason, scientists must constantly work to develop new drugs or drug combinations to combat the worldwide malaria burden (Summit Vinayak et al., 2010).

Sumiti Vinayak, et al., "Origin and Evolution of Sulfadoxine Resistant *Plasmodium falciparum*," *Public Library of Science Pathogens* 6, no. 3 (2010): e1000830, doi:10.1371/journal.ppat.1000830.

Reading Question #4

Which of the following is NOT an example of parasitism?

A. Leeches attach to a salmon and suck its blood to obtain nutrients.
B. Barnacles attach themselves to the surface of whales to settle down and filter water.
C. Plasmodium enters a human's bloodstream via a mosquito bite and causes malaria.
D. A fungus colonizes a leaf surface and extracts nutrients from the leaf.

Variations on parasitism

Classic parasites live in or on the host's body. However, there are many interactions also described as parasitism where the parasite lives in close relationship with the host, but not directly in or on it.

Social parasitism

Social parasites take advantage of interspecific interactions between members of eusocial animals such as ants, termites, and bumblebees. An example is the large blue butterfly, *Phengaris arion*. Larvae (caterpillars) of this species mimic ants by emitting ant queen pheromones. Ant workers find larvae and care for them as they would their queen; they take it to an inner chamber in their nest and feed it. Another exampe is a bumblebee, *Bombus bohemicus*, which invades the hives of other bees and takes over reproduction while their young are raised by host workers.

Brood Parasitism

In brood parasitism, the hosts act as parents as they raise the young as their own. Brood parasites include birds in different families such as cowbirds, whydahs, cuckoos, and black-headed ducks. These birds do not build nests of their own, but leave their eggs in nests of other species. The eggs of some brood parasites mimic those of their hosts, while some cowbird eggs have tough shells, making them hard for the hosts to kill by piercing. The adult female European cuckoo further mimics a predator, the European sparrowhawk, giving her time to lay her eggs in the host's nest unobserved.

In brood parasitism, the host raises the young of another species, here a cowbird's egg, that has been laid in its nest.

Parasitoidism

Some relationships that result in the prey's death are not generally called predation. A **parasitoid**, such as an ichneumon wasp, lays its eggs in or on its host; the eggs hatch into larvae, which eat the host, and it inevitably dies. This is distinct from classic parasitism because parasites do not directly kill their hosts. A predator can be defined to differ from a parasitoid in that it has many prey, captured over its lifetime, where a parasitoid's larva has just one, or at least has its food supply provisioned for it on just one occasion.

Most parasitoids are parasitoid wasps or other hymenopterans. They can be divided into two groups, idiobionts and koinobionts, differing in their treatment of their hosts.

Idiobiont parasitoids sting their often large prey on capture, either killing them outright or paralyzing them immediately. The immobilized prey is then carried to a nest, sometimes alongside other prey if it is not large enough to support a parasitoid throughout its development. An egg is laid on top of the prey and the nest is then sealed. The parasitoid develops rapidly through its larval and pupal stages, feeding on the provisions left for it.

Idiobiont parasitoid wasps immediately paralyze their hosts for their larvae (Pimplinae, pictured) to eat (Poulin and Randhawa 2015).

Koinobiont parasitoids, which include flies as well as wasps, lay their eggs inside young hosts, usually larvae. These are allowed to go on growing, so the host and parasitoid develop together for an extended period, ending when the parasitoids emerge as adults, leaving the prey dead, eaten from inside. Some koinobionts regulate their host's development, for example preventing it from pupating or making it molt whenever the parasitoid is ready to molt. They may do this by producing hormones that mimic the host's molting hormones (ecdysteroids), or by regulating the host's endocrine system.

Koinobiont parasitoid wasps like this braconid lay their eggs inside their hosts, which continue to grow and moult.

Reading Question #5

A wasp lays its eggs in a caterpillar. For a while, the caterpillar is unaffected and grows normally. The wasp eggs hatch inside the caterpillar and when the wasp larvae reach a specific developmental stage, they consume the caterpillar from the inside out and burst from the caterpillar's body, killing it. This scenario best describes which of the following species interactions?

A. Predation
B. Herbivory
C. Parastism
D. Parasitoidism
E. Commensalism

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15. Chapter 15: Species Interactions: Symbioses

ANASTASIA CHOUVALOVA AND LISA LIMERI

Symbiosis

Symbiotic relationships, or **symbioses** (plural), are close interactions between individuals of different species over an extended period of time which impact the abundance and distribution of the associating populations. Symbioses can include relationships where one partner benefits and the other is unaffected (commensalism), one partner benefits while the other is harmed (parasitism), or both partners benefit (mutualism).

Commensalism

A **commensal** relationship occurs when one species benefits from the close, prolonged interaction, while the other neither benefits nor is harmed. Birds nesting in trees provide an example of a commensal relationship (Fig 15.1). The tree is not harmed by the presence of the nest among its branches. The nests are light and produce little strain on the structural integrity of the branch, and most of the leaves, which the tree uses to get energy by photosynthesis, are above the nest so they are unaffected. The bird, on the other hand, benefits greatly. If the bird had to nest in the open, its eggs and young would be vulnerable to predators. Another example of a commensal relationship is the pilot fish and the shark.

The pilot fish feed on the leftovers of the host's meals, and the host is not affected in any way.

Figure 15.1: The southern masked-weaver bird is starting to make a nest in a tree in Zambezi Valley, Zambia. This is an example of a commensal relationship, in which one species (the bird) benefits, while the other (the tree) neither benefits nor is harmed. (credit: "Hanay"/Wikimedia Commons)

Reading Question #1

Which of the following is the best example of commensalism?

A. A nematode is ingested by a human and attacks the intestinal lining in order to obtain nourishment.

B. An oxpecker (a type of bird) lands on a rhinoceros and eats parasites such as ticks from its body, getting nourishment in the process.
C. Barnacles settle on the body of a large whale, who remains undisturbed.
D. A shrimp constructs a burrow for goby fish and the fish defends the shrimp from higher-level consumers.

Mutualism

A **mutualism** is a symbiotic relationship where two species benefit from their interaction. For example, termites have a mutualistic relationship with protozoa that live in the insect's gut (Fig 15.2a). The termite benefits from the ability of bacterial **symbionts** within the protozoa to digest cellulose. The termite itself cannot do this, and without the protozoa, it would not be able to obtain energy from its food (cellulose from the wood it chews and eats). The **protozoa** and the bacterial symbionts benefit by having a protective environment and a constant supply of food from the wood chewing actions of the termite. Lichens are not an individual organism, but a mutualistic relationship between fungus and photosynthetic algae or bacteria (Fig 15.2b). As these symbionts grow together, the glucose produced by the algae provides nourishment for both organisms, whereas the physical structure of the lichen protects the algae from the elements and makes certain nutrients in the atmosphere more available to the algae.

Figure 15.2: (a) Termites form a mutualistic relationship with symbiotic protozoa in their guts, which allow both organisms to obtain energy from the cellulose the termite consumes. (b) Lichen is a fungus that has symbiotic photosynthetic algae living inside its cells. (credit a: modification of work by Scott Bauer, USDA; credit b: modification of work by Cory Zanker)

Reading Question #2

How is mutualism different from commensalism or parasitism?

A. Mutualism is where both interacting species benefit, while in commensalism, one species benefits and the other species is unaffected.
B. Mutualism is where both interacting species benefit, while in parasitism, one species benefits and the other species is unaffected.
C. Mutualism is where both interacting species benefit, while in parasitism, one species benefits and the other species is harmed.
D. Mutualism is where both interacting species are harmed, while in parasitism, one species benefits and the other species is harmed.
E. A) and C)

Fungus/Plant Mutualism

One of the most remarkable mutualisms in all of nature is the relationship between vascular plants and the fungus, *mycorrhizae*. **Mycorrhiza,** which is derived from the Greek words *myco* meaning fungus and *rhizo* meaning root, refers to the fungal partner of a mutualistic association between vascular plant roots and their symbiotic fungi. Nearly 90% of all vascular plant species have mycorrhizal partners. In a mycorrhizal association, the fungal mycelia use their extensive network of hyphae and large surface area in contact with the soil to channel water and minerals from the soil into the plant. In exchange, the plant supplies the products of photosynthesis to fuel the metabolism of the fungus.

There are several basic types

of mycorrhizae. **Ectomycorrhizae** (“outside” mycorrhizae) depend on fungi enveloping the roots in a sheath (called a mantle). Hyphae grow from the mantle into the root and envelope the outer layers of the root cells in a network of hyphae (Fig. 15.3). The fungal partner can belong to the Ascomycota, Basidiomycota or Zygomycota. **Endomycorrhizae** (“inside” mycorrhizae), also called *arbuscular mycorrhizae*, are produced when the fungi grow inside the root in a branched structure called an *arbuscule* (from the Latin for “little trees”). The fungal partners of endomycorrhizal associates all belong to the Glomeromycota. The fungal arbuscules penetrate root cells between the cell wall and the plasma membrane and are the site of the metabolic exchanges between the fungus and the host plant (Fig 15.3). Orchids rely on a third type of mycorrhiza. Orchids are epiphytes that typically produce very small airborne seeds without much storage to sustain germination and growth. Their seeds will not germinate without a mycorrhizal partner. After nutrients in the seed are depleted, fungal symbionts support the growth of the orchid by providing necessary carbohydrates and minerals. Some orchids continue to be mycorrhizal throughout their life cycle.

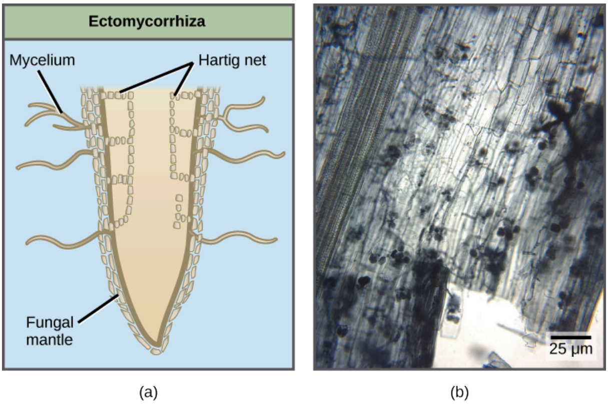

Figure 15.3: Two types of mycorrhizae. (a) Ectomycorrhizae and (b) arbuscular or endomycorrhizae have different mechanisms for interacting with the roots of plants. (credit b: MS Turmel, University of Manitoba, Plant Science Department)

Some plants are able to survive without an mycorrhizal partner, but they do better when they are benefitting from a mutualistic relationship with mycorrhizae. These plants are an example of a **facultative mutualism,** where the mutualism is beneficial, but partners are capable of surviving without the other. In contrast, other plants are completely unable to survive without mycorrhizae. These plants are an example of an **obligate mutualism,** a relationship where one or both partners requires the partnership to survive.

Other examples of fungus–plant mutualism include the endophytes: fungi that live inside tissue without damaging the host plant. Endophytes release toxins that repel herbivores, or confer resistance to environmental stress factors, such as infection by microorganisms, drought, or heavy metals in soil.

Evolution Connection: Coevolution of Land Plants and Mycorrhizae

As we have seen, mycorrhizae are the fungal partners of a mutually beneficial symbiotic association that coevolved between roots of vascular plants and fungi. A well-supported theory proposes that fungi were instrumental in the evolution of the root system in plants and contributed to the success of Angiosperms. The bryophytes (mosses and liverworts), which are considered the most ancestral plants and the first to survive and adapt on land, have simple underground rhizoids, rather than a true root system, and therefore cannot survive in dry areas. However, some bryophytes have arbuscular mycorrhizae and some do not.

True roots first appeared in the ancestral vascular plants: Vascular plants that developed a system of thin extensions from their roots would have had a selective advantage over nonvascular plants because they had a greater surface area of contact with the fungal partners than did the rhizoids of mosses and liverworts. The first true roots would have allowed vascular plants to obtain more water and nutrients in the ground.

Fossil records indicate that fungi actually preceded the invasion of ancestral freshwater plants onto dry land. The first association between fungi and photosynthetic organisms on land involved moss-like plants and endophytes. These early associations developed before roots appeared in plants. Slowly, the benefits of the endophyte and rhizoid interactions for both partners led to present-day mycorrhizae: About 90% of today's vascular plants have associations with fungi in their rhizosphere.

The fungi involved in mycorrhizae display many characteristics of ancestral fungi; they produce simple spores, show little diversification, do not have a sexual reproductive cycle, and cannot live outside of a mycorrhizal association. The plants benefited from the association because mycorrhizae allowed them to move into new habitats and allowed the increased uptake of nutrients, which gave them an enormous selective advantage over plants that did not establish symbiotic relationships.

Reading Question #3

A farmer is experimenting with different methods to get the best yield from their crops. They discover that their soybeans are capable of growing on their own, but when mycorrhizae are introduced, the soybeans grow larger and produce a greater crop yield. The relationship between the soybean and mycorrhizae is best described as:

A. Obligate mutualism
B. Facultative mutualism
C. Commensalism
D. facultative parasitism

Lichens

Lichens display a range of colors and textures (Fig. 15.4) and can survive in the most unusual and hostile habitats. They cover rocks, gravestones, tree bark, and the ground in the tundra where plant roots cannot penetrate. Lichens can survive extended periods of drought, when they become completely desiccated, and then rapidly become active once water is available again.

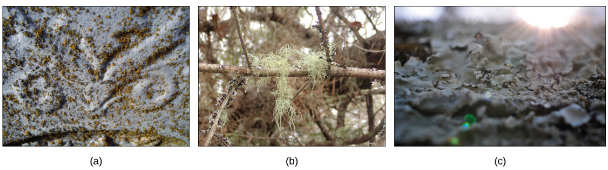

Figure 15.4 Lichens have many forms. They may be (a) crust-like, (b) hair-like, or (c) leaf-like. (credit a: modification of work by Jo Naylor; credit b: modification of work by "djpmaplefer ryman"/Flic kr; credit c: modification of work by Cory Zanker)

It is important to note that lichens are *not* a single organism, but rather another wonderful example of a mutualism, in which a fungus (usually a member of the Ascomycota or Basidiomycota) lives in a physical and physiological relationship with a photosynthetic organism (a eukaryotic alga or a prokaryotic cyanobacterium). Generally, neither the fungus nor the photosynthetic organism can survive alone outside of the symbiotic relationship. Thus, lichen is the result of an **obligate mutualism.** The body of a lichen, referred to as a thallus, is formed of hyphae wrapped around the photosynthetic partner. The photosynthetic organism provides carbon and energy in the form of carbohydrates. Some cyanobacteria additionally fix nitrogen from the atmosphere, contributing nitrogenous compounds to the association. In return, the fungus supplies minerals and protection from dryness and excessive light by encasing the algae in its mycelium. The fungus also attaches the lichen to its substrate.

The thallus of lichens grows very slowly, expanding its diameter a few millimeters per year. Both the fungus and the alga participate in the formation of dispersal units, called soredia—clusters of algal cells surrounded by mycelia. Soredia are dispersed by wind and water and form new lichens.

Lichens are extremely sensitive to air pollution, especially to abnormal levels of nitrogenous and sulfurous compounds. The U.S. Forest Service and National Park Service can monitor air quality by measuring the relative abundance and health of the lichen population in an area. Lichens fulfill many ecological roles. Caribou and reindeer eat lichens, and they provide cover for small invertebrates that hide in the mycelium. In the production of textiles, weavers used lichens to dye wool for many centuries until the advent of synthetic dyes. The pigments used in litmus paper are also extracted from lichens.

Reading Question #4

Which of the following describes lichens?

A. A mutualistic relationship between a fungus and an algae or bacteria
B. A commensalistic relationship between a fungus and an algae or bacteria

C. A fungus that parasitizes an algae or bacteria
D. A bacteria that parasitizes a fungus

Evolution Connection: Endosymbiosis

Symbiosis is a relationship in which organisms from two separate species depend on each other for their survival. Endosymbiosis (endo- = "within") is a mutually beneficial relationship in which one organism lives inside the other. Endosymbiotic relationships abound in nature. For example, microbes that live in our gut produce vitamin K. This relationship is beneficial for us because we are unable to synthesize vitamin K. It is also beneficial for the microbes because they are protected from other organisms and from drying out, and they receive abundant food from the environment of the large intestine.

Scientists have long noticed that bacteria, mitochondria, and chloroplasts are similar in size. We also know that bacteria have DNA and ribosomes, just like mitochondria and chloroplasts. Scientists believe that host cells and bacteria formed an endosymbiotic relationship when the host cells ingested both aerobic and autotrophic bacteria (cyanobacteria) but did not destroy them. Through many millions of years of evolution, these ingested bacteria became more specialized in their functions, with the aerobic bacteria becoming mitochondria and the autotrophic bacteria becoming chloroplasts.

Fungus/Animal Mutualism

Fungi have evolved mutualisms with numerous arthropods. Arthropods depend on the fungus for protection from predators and pathogens, while the fungus obtains nutrients and a way to disseminate spores into new environments.

One example is the leaf-cutter ants of Central and South America which literally farm fungi. They cut disks of leaves from plants and pile them up in subterranean gardens (Figure 15.5). Fungi are cultivated in these disk gardens, digesting the cellulose in the leaves that the ants cannot break down. Once smaller sugar molecules are produced and consumed by the fungi, the fungi in turn become a meal for the ants. The insects also patrol their garden, preying on competing fungi. Both ants and fungi benefit from this mutualistic association. The fungus receives a steady supply of leaves and freedom from competition, while the ants feed on the fungi they cultivate.

Figure 15.5 Leaf-cutter ant. A leaf-cutter ant transports a leaf that will feed a farmed fungus. (credit: Scott Bauer, USDA-ARS)

Reading Question #5

Typically, in plant-mycorrhizae relationships, the plants provide sugar to the mycorrhizae and the mycorrhizae provide water and nutrients to the plant. However, sometimes the plant may stop sharing sugar while continuing to receive water and nutrients. What is being described in this situation?

A. A mutualism becomes a parasitism
B. A parasitism becomes a mutualism
C. The relationship is a mutualism in both situations
D. A symbiosis ceases being symbiotic.

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16. Chapter 16: Population Growth

ANASTASIA CHOUVALOVA AND LISA LIMERI

Population Growth

Population ecologists make use of a variety of methods to model population dynamics mathematically. These more precise models can then be used to accurately describe changes occurring in a population and better predict future changes. Certain long-accepted models are now being modified or even abandoned due to their lack of predictive ability, and scholars strive to create effective new models.

The simplest models of population growth use deterministic equations (equations that do not account for random events) to describe the rate of change in the size of a population over time. The first of these models, **exponential growth**, describes populations that increase in numbers without any limits to their growth. The second model, **logistic growth**, introduces limits to reproductive growth that become more intense as the population size increases. Neither model adequately describes natural populations, but they provide points of comparison.

Exponential Growth

Charles Darwin, in his theory of natural selection, was greatly influenced by the work of Thomas Malthus. Malthus published a book in 1798 stating that populations with unlimited natural resources grow very rapidly, which represents an exponential growth, and then population growth decreases as resources become depleted, indicating a logistic growth.

The best example of exponential growth is seen in bacteria. Bacteria reproduce by prokaryotic fission. This division takes about an hour for many bacterial species. If 1000 bacteria are placed in a large flask with an unlimited supply of nutrients (so the nutrients will not become depleted), after an hour, there is one round of division and each organism divides, resulting in 2000 organisms—an increase of 1000. In another hour, each of the 2000 organisms will double, producing 4000, an increase of 2000 organisms. After the third hour, there should be 8000 bacteria in the flask, an increase of 4000 organisms. The important concept of exponential growth is the accelerating population growth rate—the number of organisms added in each reproductive generation—that is, it is increasing at a greater and greater rate. After 1 day and 24 of these cycles, the population would have increased from 1000 to more than 16 billion. When the population size, N, is plotted over time, a J-shaped growth curve is produced (Figure 16.1).

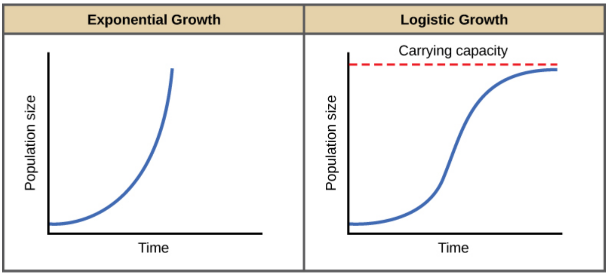

Figure 16.1 When resources are unlimited, populations exhibit exponential growth, resulting in a J-shaped curve. When resources are limited, populations exhibit logistic growth. In logistic growth, population expansion decreases as resources become scarce, and it levels off when the carrying capacity of the environment is reached, resulting in an S-shaped curve.

Reading Question #1

Why is the example about bacterial proliferation, given above, a good example of exponential growth? Select all that apply.

A. There is no limit in nutrient supply.

B. There is a strict limit in nutrient supply.

C. The rate at which the population grows increases over time.

D. The rate at which the population grows is constant over time.

E. The rate at which the population grows decreases over time.

F. Plotting the growth trend over time would result in an S-shaped curve.

G. Plotting the growth trend over time would result in an J-shaped curve.

The bacteria example is a poor representation of the real world, in which resources are limited. Furthermore, some bacteria will die during the experiment and thus not reproduce, lowering the growth rate. Therefore, when calculating the growth rate of a population, the death rate (*D*) (number organisms that die during a particular time interval) is subtracted from the birth rate (*B*) (number organisms that are born during that interval). This is shown in the following formula:

$$\frac{\Delta N \text{ (change in number)}}{\Delta T \text{ (change in time)}} = \boldsymbol{B} \text{ (birth rate) - } \boldsymbol{D} \text{ (death rate)}$$

The birth rate is usually expressed on a per capita (for each individual) basis. Thus, *B* (birth rate) = *bN* (the per capita birth rate "*b*" multiplied by the number of individuals "N") and *D* (death rate)

= *d*N (the per capita death rate "d" multiplied by the number of individuals "N"). Additionally, ecologists are interested in the population at a particular point in time, an infinitely small time interval. For this reason, the terminology of differential calculus is used to obtain the "instantaneous" growth rate, replacing the *change* in number and time with an instant-specific measurement of number and time.

$$\frac{dN}{dT} = bN \;-\; dN = (b \;-\; d)N$$

Notice that the "*d*" associated with the first term refers to the derivative (as the term is used in calculus) and is different from the death rate, also called "*d*." The difference between birth and death rates is further simplified by substituting the term "*r*" (intrinsic rate of increase) for the relationship between birth and death rates:

$$\frac{dN}{dT} = rN$$

The value "*r*" can be positive, meaning the population is increasing in size; or negative, meaning the population is decreasing in size; or zero, where the population's size is unchanging, a condition known as zero population growth. A further refinement of the formula recognizes that different species have inherent differences in their intrinsic rate of increase (often thought of as the potential for reproduction), even under ideal conditions. Obviously, a bacterium can reproduce more rapidly and have a higher intrinsic rate of growth than a human. The maximal growth rate for a species is its biotic potential, or r_{max}, thus changing the equation to:

$$\frac{dN}{dT} = r_{\mathrm{max}}N$$

Reading Question #2

What does the term r represent in exponential population growth equations? r represents the…

A. birth rate of the population
B. death rate of the population
C. number of individuals in the population
D. intrinsic rate of increase in the population

Logistic Growth

Exponential growth is possible only when infinite natural resources are available; this is not the case indefinitely in the real world. Charles Darwin recognized this fact in his description of the "struggle for existence," which states that individuals will compete (with members of their own or other species) for limited resources. The successful ones will survive to pass on their own characteristics and traits (which we know now are transferred by genes) to the next generation at a greater rate (natural selection). To model the reality of limited resources, population ecologists developed the logistic growth model.

Carrying Capacity and the Logistic Model

In the real world, with its limited resources, exponential growth cannot continue indefinitely. Exponential growth may occur in environments where there are few individuals and plentiful resources, but when the number of individuals gets large enough, resources will be depleted, slowing the growth rate. Eventually, the growth rate will plateau or level off (Figure 16.1). This population size, which represents the maximum population size that a particular environment can support, is called the carrying capacity, or *K*.

The formula we use to calculate logistic growth adds the carrying capacity as a moderating force in the growth rate. The expression "*K* – N" indicates how many individuals could be added to a population at a given stage, and "*K*– N" divided by "*K*" is the fraction of the carrying capacity available for further growth. Thus, the exponential growth model is restricted by this factor to generate the logistic growth equation:

$$\frac{dN}{dT} = r_{\max}\frac{dN}{dT} = r_{\max}N\frac{(K - N)}{K}$$

Notice that when N is very small, (*K*-N)/*K* becomes close to *K*/*K* or 1, and the right side of the equation reduces to r_{max}N, which means the population is growing exponentially and is not influenced by carrying capacity. On the other hand, when N is large, (K-N)/K comes close to zero, which means that population growth will be slowed greatly or even stopped. Thus, population growth is greatly slowed in large populations by the carrying capacity K. This model also allows for the population of a negative population growth, or a population decline. This occurs when the number of individuals in the population exceeds the carrying capacity (because the value of (K-N)/K is negative).

A graph of this equation yields an S-shaped curve (Figure 16.1), and it is a more realistic model of population growth than exponential growth. There are three different sections to an S-shaped curve. Initially, growth is exponential because there are few individuals and thus ample resources available. Then, as resources begin to become limited, the growth rate decreases. Finally, growth levels off at the carrying capacity of the environment, with little change in population size over time.

Role of Intraspecific Competition

The logistic model assumes that every individual within a population will have equal access to resources and, thus, an equal chance for survival. For plants, the amount of water, sunlight, nutrients, and the space to grow are the important resources, whereas in animals, important resources include food, water, shelter, nesting space, and mates.

In the real world, phenotypic variation among individuals within a population means that some individuals will be better adapted to their environment than others. The resulting competition between population members of the same species for resources is termed **intraspecific competition** (intra- = "within"; -specific = "species"). Intraspecific competition for resources may have little effect populations that are well below their carrying capacity—resources are plentiful and all individuals can obtain what they need. However, as population size increases, this competition intensifies. In addition, the accumulation of waste products can reduce an environment's carrying capacity.

Examples of Logistic Growth

Yeast, a microscopic fungus used to make bread and alcoholic beverages, exhibits the classical S-shaped curve when grown in a test tube (Figure 16.2a). Its growth levels off as the population depletes the nutrients. In the real world, however, there are variations to this idealized curve. Examples in wild populations include sheep and harbor seals (Figure 16.2b). In both examples, the population size exceeds the carrying capacity for short periods of time and then falls below the carrying capacity afterwards. This fluctuation in population size continues to occur as the population oscillates around its carrying capacity.

Reading Question #3

In the logistic population growth equations, what does K represent? Select all correct answers.

A. Rate at which the population changes over time
B. Carrying capacity
C. Biotic potential
D. The greatest population of a species that can be maintained by a given environment
E. The maximum rate at which a species can grow in a given environment.

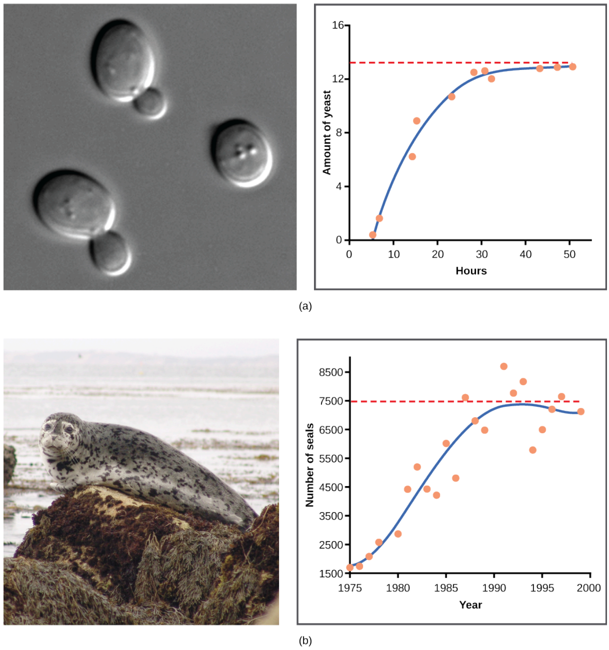

Figure 16.2 (a) Yeast grown in ideal conditions in a test tube show a classical S-shaped logistic growth curve, whereas (b) a natural population of seals shows real-world fluctuation.

Reading Question #4

What is the primary difference between exponential and logistic population growth models?

A. Exponential growth models account for resource limitations whereas logistic growth models do not.
B. Logistic growth models account for resource limitations whereas exponential growth models do

not.
C. The exponential growth model describes growth in bacteria whereas the logistic growth model describes growth in all other organisms.
D. The exponential growth model uses r while the logistic growth model uses r_{max}

Population dynamics and regulation

The logistic model of population growth, while valid in many natural populations and a useful model, is a simplification of real-world population dynamics. Implicit in the model is that the carrying capacity of the environment does not change, which is not the case. Carrying capacity for naturally occurring populations can vary annually: for example, some summers are hot and dry whereas others are cold and wet. In many areas, the carrying capacity during the winter is much lower than it is during the summer. Also, natural events such as earthquakes, volcanoes, and fires can alter an environment and hence its carrying capacity. Additionally, populations do not usually exist in isolation. They engage in interspecific competition: that is, they share the environment with other species competing for the same resources. These factors are also important to understanding how a specific population will grow.

Population growth is regulated in a variety of ways. These are grouped into **density-dependent factors**, in which the density of the population at a given time affects growth rate and mortality, and **density-independent factors**, which influence mortality in a population regardless of population density. Note that in the former, the effect of the factor on the population depends on the density of the population at onset. Conservation biologists want to understand both types because this helps them manage populations and prevent extinction or overpopulation.

Density-dependent Regulation

Most density-dependent factors are biological in nature (biotic), and include predation, inter- and intraspecific competition, accumulation of waste, and diseases such as those caused by parasites. Usually, the denser a population is, the greater its mortality rate. For example, during intra- and interspecific competition, the reproductive rates of the individuals will usually be lower, reducing their population's rate of growth. In addition, low prey density increases the mortality of its predator because it has more difficulty locating its food source.

An example of density-dependent regulation is shown in Figure 16.3 with results from a study focusing on the giant intestinal roundworm (*Ascaris lumbricoides*), a parasite of humans and other mammals. Denser populations of the parasite exhibited lower fecundity: they contained fewer eggs. One possible explanation for this is that females would be smaller in more dense populations (due to limited resources) and that smaller females would have fewer eggs. This hypothesis was tested and disproved in a 2009 study which showed that female weight had no influence. The actual cause of the density-dependence of fecundity in this organism is still unclear and awaiting further investigation.

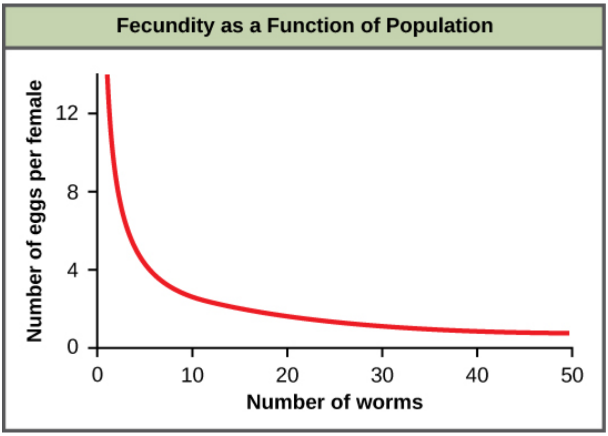

Figure 3. In this population of roundworms, fecundity (number of eggs) decreases with population density.

Density-Independent Regulation and Interaction with Density-Dependent Factors

Many factors, typically physical or chemical (abiotic), influence the mortality of a population regardless of its density, including weather, natural disasters, and pollution. An individual deer may be killed in a forest fire regardless of how many deer happen to be in that area. Its chances of survival are the same whether the population density is high or low. The same holds true for cold winter weather.

In real-life situations, population regulation is very complicated and density-dependent and independent factors can interact. A dense population that is reduced in a density-independent manner by some environmental factor(s) will be able to recover differently than a sparse population. For example, a population of deer affected by a harsh winter will recover faster if there are more deer remaining to reproduce.

Connection to Evolution

Why Did the Woolly Mammoth Go Extinct?

Figure 16.4. (a) 1916 mural of a mammoth herd from the American Museum of Natural History, (b) the only stuffed mammoth in the world, from the Museum of Zoology located in St. Petersburg, Russia, and (c) a one-month-old baby mammoth, named Lyuba, discovered in Siberia in 2007. (credit a: modification of work by Charles R. Knight; credit b: modification of work by "Tanapon"/Flickr; credit c:

modification of work by Matt Howry)

It's easy to get lost in the discussion about why dinosaurs went extinct 65 million years ago. Was it due to a meteor slamming into Earth near the coast of modern-day Mexico, or was it from some long-term weather cycle that is not yet understood? One hypothesis that will never be proposed is that humans had something to do with it. Mammals were small, insignificant creatures of the forest 65 million years ago, and no humans existed. Scientists are continually exploring these and other theories.

Woolly mammoths began to go extinct much more recently, about 10,000 years ago, when they shared the Earth with humans who were no different anatomically than humans today (Figure 16.4). Mammoths survived in isolated island populations as recently as 1700 BC. We know a lot about these animals from carcasses found frozen in the ice of Siberia and other regions of the north. Scientists have sequenced at least 50 percent of its genome and believe mammoths are between 98 and 99% identical to modern elephants.

It is commonly thought that climate change and human hunting led to their extinction. A 2008 study estimated that climate change reduced the mammoth's range from 3,000,000 square miles 42,000 years ago to 310,000 square miles 6,000 years ago (Nogués-Bravo et al. 2008). It is also well documented that humans hunted these animals. A 2012 study showed that no single factor was exclusively responsible for the extinction of these magnificent creatures. In addition to human hunting, climate change, and reduction of habitat, these scientists demonstrated another important factor in the mammoth's extinction was the migration of humans across the Bering Strait to North America during the last ice age 20,000 years ago.

The maintenance of stable populations was and is very complex, with many interacting factors determining the outcome. It is important to remember that humans are also part of nature. We once contributed to a species' decline using only primitive hunting technology.

Reading Question #5

It is thought that climate change contributed to the extinction of Wooly Mammoths. Which of the following describes climate change?

A. An exponential growth factor
B. A logistic growth factor
C. A density-dependent regulator
D. A density-independent regulator

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Adapted from

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17. Chapter 17: Life Histories

ANASTASIA CHOUVALOVA AND LISA LIMERI

Life History Patterns and Energy Budgets

Energy is required by all living organisms for their growth, maintenance, and reproduction; at the same time, energy is often a major limiting factor in determining an organism's survival. Plants, for example, acquire energy from the sun via photosynthesis, but must expend this energy to grow, maintain health, and produce energy-rich seeds to produce the next generation. Animals have the additional burden of using some of their energy reserves to acquire food. Furthermore, some animals must expend energy caring for their offspring. Thus, all species have an energy budget: they must balance energy intake with their use of energy for metabolism, reproduction, parental care, and energy storage (such as bears building up body fat for winter hibernation).

Parental Care and Fecundity

Fecundity is the potential reproductive capacity of an individual within a population. In other words, fecundity describes how many offspring could ideally be produced if an individual has as many offspring as possible, repeating the reproductive cycle as soon as possible after the birth of the offspring. In animals, fecundity is inversely related to the amount of parental care given to an individual offspring. Species, such as many marine invertebrates, that produce many offspring usually provide little if any care for the offspring (they would not have the energy or the ability to do so anyway). Most of their energy budget is used to produce many tiny offspring. Animals with this strategy are often self-sufficient at a very early age. This is because of the energy tradeoff these organisms have made to maximize their evolutionary fitness. Because their energy is used for producing offspring instead of parental care, it makes sense that these offspring have some ability to be able to move within their environment and find food and perhaps shelter. Even with these abilities, their small size makes them extremely vulnerable to predation, so the production of many offspring allows enough of them to survive to maintain the species.

Animal species that have few offspring during a reproductive event usually give extensive parental care, devoting much of their energy budget to these activities, sometimes at the expense of their own health. This is the case with many mammals, such as humans, kangaroos, and pandas. The offspring of these species are relatively helpless at birth and need to develop before they achieve self-sufficiency.

Plants with low fecundity produce few energy-rich seeds (such as coconuts and chestnuts) with each having a good chance to germinate into a new organism; plants with high fecundity usually have many small, energy-poor seeds (like orchids) that have a relatively poor chance of surviving. Although it may seem that coconuts and chestnuts have a better chance of surviving, the energy tradeoff of the orchid is also very effective. It is a matter of where the energy is used, for large numbers of seeds or for fewer seeds with more energy.

Early versus Late Reproduction

The timing of reproduction in a life history also affects species survival. Organisms that reproduce at an early age have a greater chance of producing offspring, but this is usually at the expense of their growth and the maintenance of their health. Conversely, organisms that start reproducing later in life often have greater fecundity or are better able to provide parental care, but they risk that they will not survive to reproductive age. Examples of this can be seen in fishes. Small fish, like guppies, use their energy to reproduce rapidly, but never attain the size that would give them defense against some predators. Larger fish, like the bluegill or shark, use their energy to attain a large size, but do so with the risk that they will die before they can reproduce or at least reproduce to their maximum. These different energy strategies and tradeoffs are key to understanding the evolution of each species as it maximizes its fitness and fills its niche. In terms of energy budgeting, some species "blow it all" and use up most of their energy reserves to reproduce early before they die. Other species delay having reproduction to become stronger, more experienced individuals and to make sure that they are strong enough to provide parental care if necessary.

K-selected and *r*-selected species

Some life history traits, such as fecundity, timing of reproduction, and parental care, can be grouped together into general strategies that are used by multiple species. Ecologists describe some of these strategies as **r-selection** and **K-selection**.

The regulation of population growth by resource limitation and reproductive potential can be used to introduce a classical concept in population biology: that of K-selected versus *r*-selected species. By the second half of the twentieth century, the concept of K- and r-selected species was used extensively and successfully to study populations. The concept relates not only to reproductive strategies, but also to a species' habitat and behavior. This includes the way they obtain resources and care for their young, as well as length of life and survivorship factors. For this analysis, population biologists have grouped species into the two large categories, *K*-selected and *r*-selected, although they are really two ends of a continuum. The first variable is *K* (the carrying capacity of a population; density dependent), and the second variable is *r* (the intrinsic rate of natural increase in population size, density independent).

K-selected species

K-selected species are species selected by stable, predictable environments. Populations of K-selected species tend to exist close to their carrying capacity (hence the term K-selected) where intraspecific competition is high. These species tend to have few, large offspring, a long gestation period, and often give long-term care to their offspring (see Table 17.1 for a comparison of K vs. r-selected species). While larger in size when born, the offspring are relatively helpless and immature at birth. By the time they reach adulthood, they must develop skills to compete for natural resources. In plants, scientists think of parental care more broadly: how long fruit takes to develop or how long it remains on the plant are determining factors in the time to the next reproductive event. Examples of K-selected species are primates (including humans), elephants, and plants such as oak trees (Figure 17.1).

Oak trees grow very slowly and take, on average, 20 years to produce their first seeds, known as acorns. As oak trees grow to a large size and for many years before they begin to produce acorns, they devote a large percentage of their energy budget to growth and maintenance. The tree's height and size allow it to dominate other plants in the competition for sunlight, the oak's primary energy resource. Furthermore, when it does reproduce, the oak produces large, energy-rich seeds that use their energy reserve to become quickly established (K-selection).

In summary, K-selected species tend to have few offspring, inhabit stable and unfluctuating environments, have longer gestation periods, provide their offspring with long-term care after they are born.

Reading Question #1

Which of the following traits of bison indicates that they are a K-selected species?

A. Bison are relatively large (30-70 pounds) when they are born.
B. Bison graze on grass
C. Bison have thick fur to protect from cold weather
D. Male bison physically compete with each other for mates.

r-selected species

In contrast, r-selected species tend to have a large number of small offspring (hence their r designation; Table 17.1). This strategy is often employed in unpredictable or changing environments. Animals that are r-selected tend to not give long-term parental care and the offspring are relatively mature and self-sufficient at birth. Examples of r-selected species are marine invertebrates, such as jellyfish, and plants, such as the dandelion (Figure 17.1b). Dandelions have small seeds that are wind dispersed long distances. Many seeds are produced simultaneously to ensure that at least some of them reach a hospitable environment. Seeds that land in inhospitable environments have little chance for survival since their seeds are low in energy content. Note that survival is not necessarily a function of energy stored in the seed itself.

In summary, r-selected species tend to have many offspring, inhabit unstable and fluctuating environments, have shorter gestation periods, do not provide their offspring with long-term care after they are born.

Table 17.1 Characteristics of K-selected vs. r-selected species

Characteristics of *K*-selected species	**Characteristics of *r*-selected species**
Mature late	Mature early
Greater longevity	Lower longevity
Increased parental care	Decreased parental care
Increased competition	Decreased competition
Fewer offspring	More offspring
Larger offspring	Smaller offspring

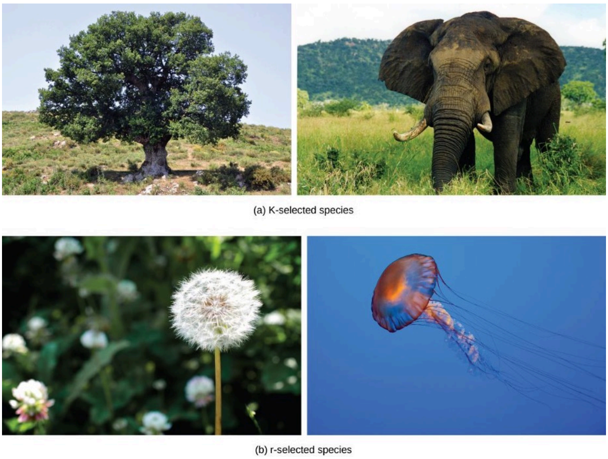

Figure 17.1 (a) Elephants are considered K-selected species as they live long, mature late, and provide long-term parental care to few offspring. Oak trees produce many offspring that do not receive parental care, but are considered K-selected species based on longevity and late maturation. (b) Dandelions and jellyfish are both considered r-selected species as they mature early, have short lifespans, and produce many offspring that receive no parental care.

Reading Question #2

Which of the following species is most likely to be an r-selected species?

A. A species in which the individuals reach sexual maturity relatively late in life.
B. A species that experiences intense intraspecific competition.
C. A species that produces a large number of offspring at one time.
D. A species that provides a lot of parental care to their offspring.

By the second half of the twentieth century, the concept of K- and r-selected species was used extensively and successfully to study populations. The r- and K-selection theory, although accepted for decades and used for much groundbreaking research, has now been reconsidered, and many population biologists have abandoned or modified it. One reason is that there are many species that do not fully conform to the predictions and r- and K-selection. For example, although oak trees live a long time and invest lots of energy into growth and maintenance (K-selected traits), they also produce huge numbers of offspring (thousands of acorns) which they invest minimally in each offspring and provide no care (r-selected traits).

Furthermore, r- vs. K-selection theory ignored the age-specific mortality of the populations which scientists now know is very important. New demographic-based models of life history evolution have been developed which incorporate many ecological concepts included in r- and K-selection theory as well as population age structure and mortality factors.

Reproductive Strategy

One important trait describing a species' life history is their reproductive strategy: semelparity or iteroparity.

Semelparity occurs when a species reproduces only once during its lifetime and then dies. Such species use most of their resource budget during a single reproductive event, sacrificing their health to the point that they do not survive. Examples of semelparity are bamboo, which flowers once and then dies, and the Chinook salmon (Figure 17.2a), which uses most of its energy reserves to migrate from the ocean to its freshwater nesting area, where it reproduces and then dies. Scientists have posited alternate explanations for the evolutionary advantage of the Chinook's post-reproduction death: a programmed suicide caused by a massive release of corticosteroid hormones, presumably so the parents can become food for the offspring, or simple exhaustion caused by the energy demands of reproduction; these are still being debated. Semelparity is consistent with r-selected strategies as many offspring are produced and there is low parental input, as one or both parents die after mating.

Iteroparity describes species that reproduce repeatedly during their lives. Some animals are able to mate only once per year, but survive multiple mating seasons. The pronghorn antelope is an example of an animal that goes into a seasonal estrus cycle ("heat"): a hormonally induced physiological condition preparing the body for successful mating (Fig 17.2b). Females of these species mate only during the estrus phase of the cycle. A different pattern is observed in primates, including humans and chimpanzees, which may attempt reproduction at any time during their reproductive years, even though their menstrual cycles make pregnancy likely only a few days per month during ovulation (Fig 17.2c). Iteroparity is consistent with K-selected strategies as individuals invest in their own growth and maintenance so that they can survive many reproductive events and care for their young after birth.

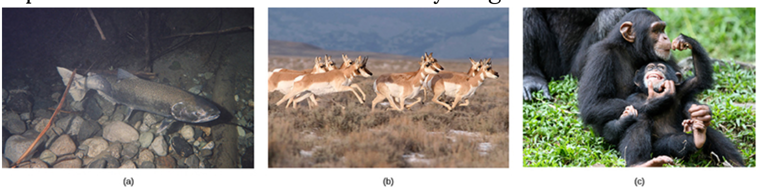

Figure 17.2 The (a) Chinook salmon mates once and dies. The (b) pronghorn antelope mates during specific times of the year during its reproductive life. Primates, such as humans and (c) chimpanzees, may mate on any day, independent of ovulation. (credit a: modification of work by Roger Tabor, USFWS; credit b: modification of work by Mark Gocke, USDA; credit c: modification of work by "Shiny Things"/Flickr)

Reading Question #3

What is the primary difference between iteroparity and semelparity?

A. The number of offspring produced.
B. The number of times an individual reproduces during its lifetime.
C. The amount of parental care provided to offspring.
D. The amount of resources invested in reproduction.

Survivorship Curves

Population ecologists describe mortality rates across organisms' life spans using **survivorship curves**. A survivorship curve is a graph of the number of individuals surviving at each age interval plotted versus time (usually with data compiled from a life table). These curves allow us to compare the life histories of different populations (Figure 17.3). There are 3 types of Survivorship curves which are distinguished by the ages at which mortality is highest in the population. Humans and most primates exhibit a **Type I survivorship curve** because a high percentage of offspring survive their early and middle years—death occurs predominantly in older individuals. These types of species usually have small numbers of offspring at one time, and they give a high amount of parental care to them to ensure their survival. Birds are an example of an intermediate or **Type II survivorship curve** because birds die more or less equally at each age interval. These organisms also may have relatively few offspring and provide significant parental care. Trees, marine invertebrates, and most fishes exhibit a **Type III survivorship curve** because very few of these organisms survive their younger years; however, those that make it to an old age are more likely to survive for a relatively long period of time. Organisms in this category usually have a very large number of offspring, but once they are born, little parental care is provided. Thus these offspring are "on their own" and vulnerable to predation, but their sheer numbers assure the survival of enough individuals to perpetuate the species.

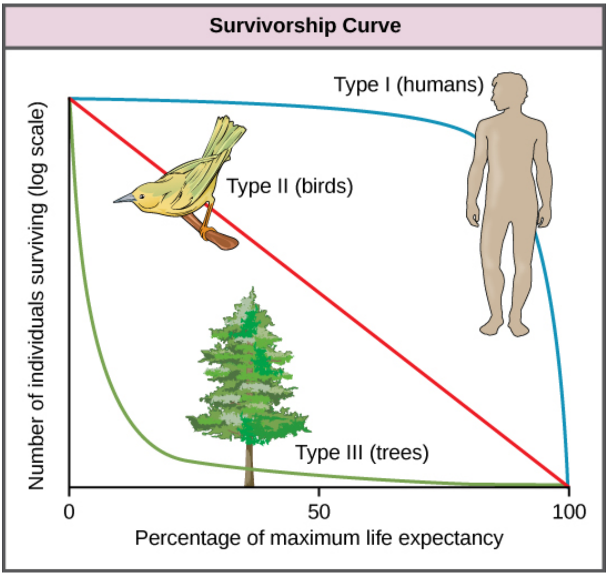

Figure 17.3 Survivorship curves show the distribution of individuals in a population according to age. Humans and most mammals have a Type I survivorship curve because death primarily occurs in the older years. Birds typically have a Type II survivorship curve, as death at any age is equally probable. Many trees have a Type III survivorship curve because very few survive the younger years, but after a certain age, individuals are much more likely to survive.

Reading Question #4

A turtle is equally likely to die at 10 years and at 100 years. Which type of survivorship curve are they most likely to exhibit, based on this statement?

A. Type I
B. Type II
C. Type III
D. Type IV

Reading Question #5

Female orange sulfur butterflies lay thousands of eggs, the vast majority of which die due to disease, competition, or predation. What survivorship curve best describes orange sulfur butterflies?

A. Type I
B. Type II
C. Type III
D. Not enough information to tell

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Adapted from

Clark, M.A., Douglas, M., and Choi, J. (2018). Biology 2e. OpenStax. Retrieved from https://openstax.org/books/biology-2e/pages/45-4-population-dynamics-and-regulation?query=K-selected%20species&target=%7B%22type%22%3A%22search%22%2C%22index%22%3A0%7D#fs-idm133176480

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18. Chapter 18: Introduction to Physiology

ANASTASIA CHOUVALOVA

Form follows Function

One of the overarching themes of biology is that **form follows function**; how something is arranged allows it to perform a specific job. We see this at all levels in the hierarchy of biological organization from atoms up to the biosphere.

Reading Question #1

What is meant by the phrase "form follows function"? Select the best answer.

A. How an organism or part of an organism is shaped is related to its purpose and use.

B. The shape and structure of an organism assists in its fitness and performance.

C. How an organism or part of an organism is structured produces its purpose and use.

D. The functionality of an organism assists in its fitness and performance.

Molecular level – proteins

The shape (structure) of a protein determines its function and the function of a protein often directs how it is shaped three-dimensionally (i.e., tertiary structure). For example, there are two basic shapes for proteins: fibrous and globular (round). Collagen is an example of a fibrous protein (Figure 18.1) that gives strength to our skin to prevent it from tearing and for this purpose, it is shaped like a rope. Fibrous proteins are structural proteins because they help give shape to and support the skin. This is an example of form follows function at the molecular level of proteins.

The function of globular proteins, such as hemoglobin (Figure 18.2), is to transport oxygen in the blood so that all cells of the body can receive oxygen to perform metabolic processes. Other examples of globular proteins that have different functions are enzymes (catalyze or speed up chemical reactions in the body) and plasma membrane proteins (can transport substances across the cell membrane, play a role in cell communication, act as enzymes, or help identify the cell to the rest of the body).

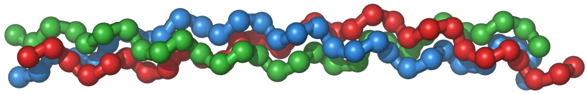

Figure 18.1 Collagen is a fibrous protein found in the skin and other connective tissues like cartilage. It is the most abundant bodily protein.

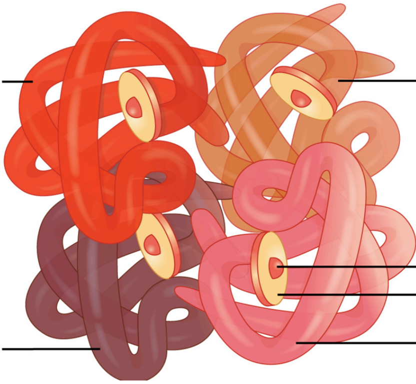

Figure 18.2 Hemoglobin is needed to convey oxygen from the lungs to all bodily tissues. Each hemoglobin molecule consists of four global proteins, granting this important polypeptide its quaternary structure. Each globe protein is bound to a molecule of heme, each of which contains iron (Fe). (credit: modified from Openstax Anatomy and Physiology)

Cellular level – skeletal muscle cells

The structure of skeletal muscle cells allows them to have the function of contraction, which allows us to move. But how a muscle is used also affects its structure and function – an overused muscle will often hypertrophy or in other words, have a larger cross-sectional area. A cell can change its shape and structure, and even its volume, if demands drastically change (e.g., more force production is needed).

Skeletal muscle cells that make up your biceps brachii muscle are attached to both ends of the humerus bone by tendons and are packed full of contractile proteins (actin and myosin) (Figure 18.3). When the contractile proteins contract, they shorten the muscle cell, which then pulls on the ends of the humerus and allows you to flex your forearm (Figure 18.4).

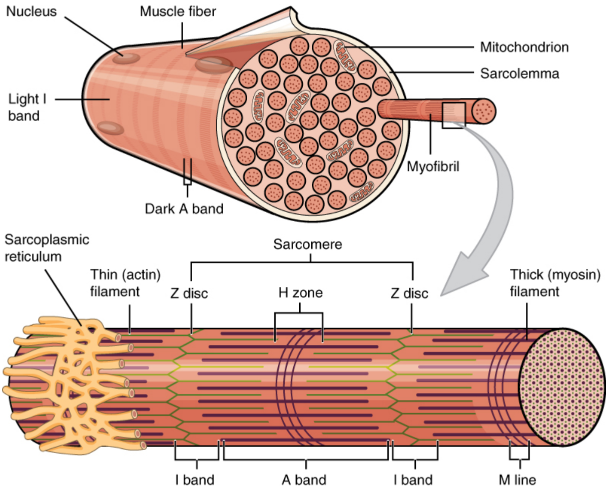

Figure 18.3 Muscle Fiber (Cell) A skeletal muscle fiber is surrounded by a plasma membrane called the sarcolemma, which contains sarcoplasm, the cytoplasm of muscle cells. A muscle fiber is composed of many fibrils, which give the cell its striated appearance. (credit: Openstax Anatomy and Physiology)

Figure 18.4 Biceps Brachii Muscle Contraction The large mass at the center of a muscle is called the belly. Tendons emerge from both ends of the belly and connect the muscle to the bones, allowing the skeleton to move. The tendons of the bicep connect to the upper arm and the forearm. (credit: Victoria Garcia)

Individual level – anatomy and physiology

In studying humans, **anatomy** is the study of the structure of the body (ex- where the quadriceps muscle is located) and **physiology** is the study of how the body functions (ex- how the quadriceps muscle contracts). Let's take a look at the function and anatomy of the heart, which pumps blood to the entire body. The heart consists of four hollow chambers (atria and ventricles) and is made of cardiac muscle cells (Figure 18.5). This structure allows the heart to have the function of pumping blood around the body. However, if the structure of the heart changes (ex- some of the heart chambers become stretched out or dilated), then the heart's function decreases as the heart can no longer pump as much blood, which will eventually cause congestive heart failure.

On the other hand, if one of the heart chambers loses functionality, it will affect that chamber's shape. For example, if the left ventricle stops pumping blood to the left atrium, its walls will thicken, leading to left ventricular hypertrophy. This is an example of form follows function, or more specifically, impaired form follows impaired function, in cardiac physiology.

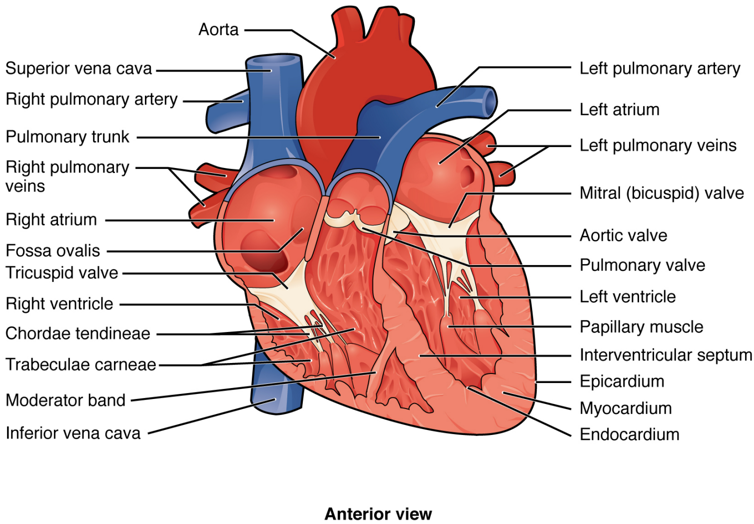

Figure 18.5 Internal anatomy of the heart. This anterior view of the heart shows the four chambers, the major vessels and their early branches, as well as the valves. (credit: Openstax Human Biology)

Ecosystem level. An ecosystem consists of a community of all the different species living in a particular geographic area as well as all of the nonliving components (ex- water, sand, light, oxygen). If we look at the structure of a coral reef ecosystem, we see that the corals, which are the foundation species, provide protection and habitat for other species (Figure 18.6). The coral reef protects other species, such as fish, from ocean waves and currents and gives them a place to hide from predators. If the coral reef's protective function is disrupted, the form of the overall ecosystem will change – the food web and food chain inherent to that ecosystem will be thrown off balance. For example, if the coral reef's structural integrity is damaged, fish at lower trophic levels will die since they are more vulnerable to the ocean waves, currents, and predators. This will deprive fish at higher trophic levels of prey. This is an example of form follows function at the broader ecosystem level. In this case, impaired function at lower trophic levels impacts the integrity of higher trophic levels.

Figure 18.6 By Fascinating Universe – Own work, CC BY-SA 3.0, https://commons.wikimedia.org/w/index.php?curid=16657833

Reading Question #2

Of the following, which is the best example of the phrase "form follows function" in the physiological context? (Hint: What happens if you lift greater weights?)

A. A weightlifter notices greater muscle mass in his arm muscles, which allows him to increase his load and do more repetitions of the increased load.

B. A weightlifter notices greater cross-sectional area of his arm muscles, which allows him to increase his load and do more repetitions of the increased load.

C. A weightlifter is increasing his load and doing more repetitions of the increased load, resulting in muscle hypertrophy and greater muscle mass.

D. A weightlifter is decreasing his load and doing less repetitions of the decreased load, resulting in muscle hypertrophy and greater muscle mass.

Biological Levels of Organization of Living Things

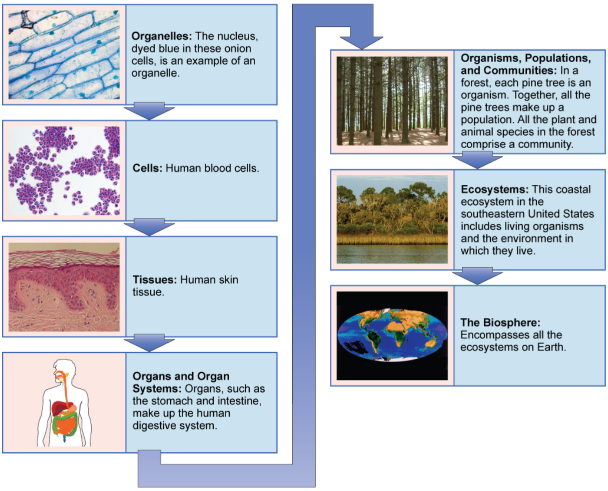

Figure 18.7 These are the biological levels of organization of living things. From a single organelle to the entire biosphere, living organisms are parts of a highly structured hierarchy. (credit "organelles": modification of work by Umberto Salvagnin; credit "cells": modification of work by Bruce Wetzel, Harry Schaefer/ National Cancer Institute; credit "tissues": modification of work by Kilbad; Fama Clamosa; Mikael Häggström; credit "organs": modification of work by Mariana Ruiz Villareal; credit "organisms": modification

of work by “Crystal”/Flickr; credit “ecosystems”: modification of work by US Fish and Wildlife Service Headquarters; credit “biosphere”: modification of work by NASA)

Reading Question #3

Of the following, identify the correct statement(s). Select all that apply.

A. Biospheres exist within organs which in turn, exist within organ systems.

B. Ecosystems are compromised of communities which in turn, are compromised of different populations.

C. Various cells exist within tissues which in turn, comprise organs.

D. Organs comprise cells which in turn, comprise tissues.

E. A community is made up of only animal species and excludes plant species.

F. Organs are comprised of various tissues which in turn, are made up of different cells.

G. The biosphere contains ecosystems which in turn, are made up of communities of populations.

Human Tissue Types

The term **tissue** is used to describe a group of similar cells found together in the body that act together to perform specific functions.

From the evolutionary perspective, tissues appear in more complex organisms.

Although there are many types of cells in the human body, they are organized into **four categories of tissues**: **epithelial, connective, muscle, and nervous**. Each of these categories is characterized by specific functions that contribute to the overall health and maintenance of the body. A disruption of the structure of a tissue is a sign of injury or disease. Such changes can be detected through histology, the microscopic study of tissue appearance, organization, and function.

The Four Types of Tissues

Epithelial tissue, also referred to as **epithelium**, refers to the sheets of cells that cover exterior surfaces of the body, line internal cavities and passageways, and form certain glands. Examples of epithelial tissue include skin, mucous membranes, endocrine glands, and sweat glands. **Connective tissue**, as its name implies, binds the cells and organs of the body together and functions in the protection, support, and integration of all parts of the body. Connective tissue is diverse and includes bone, tendons, ligaments, cartilage, fat, and blood. **Muscle tissue** is excitable, responding to stimulation and contracting to provide movement, and occurs as three major types: skeletal (voluntary) muscle, smooth muscle, and cardiac muscle in the heart. **Nervous tissue** is also excitable, allowing the propagation of electrochemical signals in the form of nerve impulses that communicate between different regions of the body (Figure 18.8).

The next level of organization is the **organ**, where two or more types of tissues come together to perform specific functions. Just as knowing the structure and function of cells helps you in your study of tissues, knowledge of tissues will help you understand how organs function.

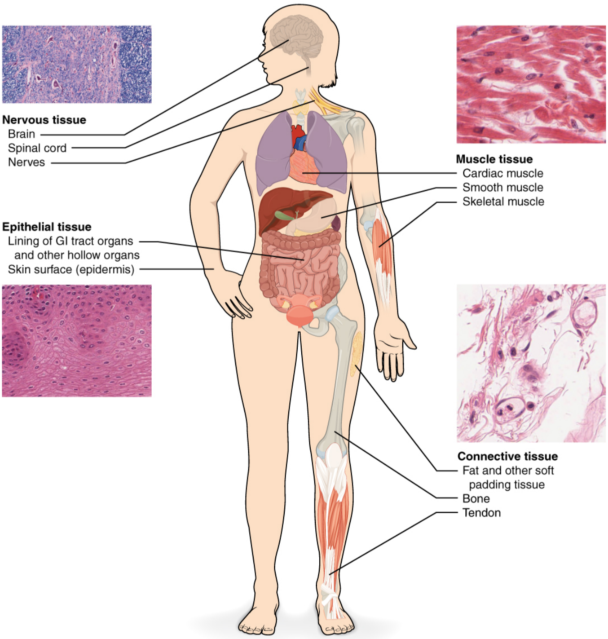

Figure 18.8 Four Types of Tissue: Body The four types of tissues are exemplified in nervous tissue, stratified squamous epithelial tissue, cardiac muscle tissue, and connective tissue in small intestine. Clockwise from nervous tissue, LM × 872, LM × 282, LM × 460, LM × 800. (Micrographs provided by the Regents of University of Michigan Medical School © 2012)

Reading Question #4

Of the four tissue types, which are excitable? Select all that apply.

A. Muscle

B. Epithelial

C. Nervous

D. Connective

Reading Question #5

Of the four tissue types, which one is used to form a protective barrier?

A. Nervous

B. Connective

C. Muscle

D. Epithelial

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19. Chapter 19: Homeostasis

ANASTASIA CHOUVALOVA

All living organisms share several key characteristics or functions: order, sensitivity or response to the environment, reproduction, adaptation, growth and development, regulation/homeostasis, energy processing, and evolution. In this chapter, we will focus on homeostasis in the context of organismal physiology.

Reading Question #1

Recall the homeostasis section of Chapter 19. What controls homeostasis?

A. Positive feedback loops

B. Negative feedback loops

C. Neuro-endocrine system

D. All of the above

Homeostasis

Even the smallest organisms are complex and require multiple regulatory mechanisms to coordinate internal functions, respond to stimuli, and cope with environmental stresses. Animal organs and organ systems constantly adjust to internal and external changes through a process called homeostasis ("steady state"). **Homeostasis** (literally, "steady state") refers to the relatively stable internal environment required to maintain life. Two examples of internal functions regulated in an organism are nutrient transport and blood flow. Organs (groups of tissues working together) perform specific functions, such as carrying oxygen throughout the body, removing wastes, delivering nutrients to every cell, and cooling the body. Homeostasis also aims to maintain proper levels of glucose or calcium in blood. Homeostasis means to maintain dynamic equilibrium in the body. It is dynamic because it is constantly adjusting to the changes that the body's systems encounter. It is equilibrium because body functions are kept within specific ranges. Even an animal that is apparently inactive is maintaining this homeostatic equilibrium.

Figure 19.1 Polar bears (Ursus maritimus) and other mammals living in ice-covered regions maintain their body temperature by generating heat and reducing heat loss through thick fur and a dense layer of fat under their skin. (credit: "longhorndave"/Flickr)

In order to function properly, cells require appropriate conditions such as proper temperature, pH, and appropriate concentration of diverse chemicals. These conditions may, however, change from one moment to the next. Organisms are able to maintain homeostatic internal conditions within a narrow range almost constantly, despite environmental changes, by activation of regulatory mechanisms. For example, an organism needs to regulate body temperature through the thermoregulation process. Organisms that live in cold climates, such as the polar bear (Figure 19.1), have body structures that help them withstand low temperatures and conserve body heat. Structures that aid in this type of insulation include fur, feathers, blubber, and fat. In hot climates, organisms have methods (such as perspiration in humans or panting in dogs) that help them to shed excess body heat.

Homeostatic Process

The goal of homeostasis is the maintenance of equilibrium around a point or value called a **set point.** While there are normal fluctuations from the set point, the body's systems will usually attempt to go back to this point. A change in the internal or external environment is called a stimulus and is detected by a receptor; the response of the system is to adjust the deviation parameter toward the set point. For instance, if the body becomes too warm, adjustments are made to cool the animal. If the blood's glucose rises after a meal, adjustments are made to lower the blood glucose level by getting the nutrient into tissues that need it or to store it for later use.

Control of Homeostasis

When a change occurs in an animal's environment, an adjustment must be made. The receptor senses the change in the environment, then sends a signal to the control center (in most cases, the brain) which in turn generates a response that is signaled to an effector. The effector is a muscle (that contracts or relaxes) or a gland that secretes. Homeostatsis is maintained by negative feedback loops. Positive feedback loops actually push the organism further out of homeostasis, but may be necessary for life to occur. Homeostasis is controlled by the nervous and endocrine system of mammals.

Negative Feedback Mechanisms

Any homeostatic process that changes the direction of the stimulus is a negative feedback loop. It may either increase or decrease the stimulus, but the stimulus is not allowed to continue as it did before the receptor sensed it. In other words, if a level is too high, the body does something to bring it down, and conversely, if a level is too low, the body does something to make it go up. Hence the term negative feedback. An example is animal maintenance of blood glucose levels. When an animal has eaten, blood glucose levels rise. This is sensed by the nervous system. Specialized cells in the pancreas sense this, and the hormone insulin is released by the endocrine system. Insulin causes blood glucose levels to decrease, as would be expected in a negative feedback system, as illustrated in Figure 19.2. However, if an animal has not eaten and blood glucose levels decrease, this is sensed in another group of cells in the pancreas, and the hormone glucagon is released causing glucose levels to increase. This is still a negative feedback loop, but not in the direction expected by the use of the term "negative." Another example of an increase as a result of the feedback loop is the control of blood calcium. If calcium levels decrease, specialized cells in the parathyroid gland sense this and release parathyroid hormone (PTH), causing an increased absorption of calcium through the intestines and kidneys and, possibly, the breakdown of bone in order to liberate calcium. The effects of PTH are to raise blood levels of the element. Negative feedback loops are the predominant mechanism used in homeostasis.

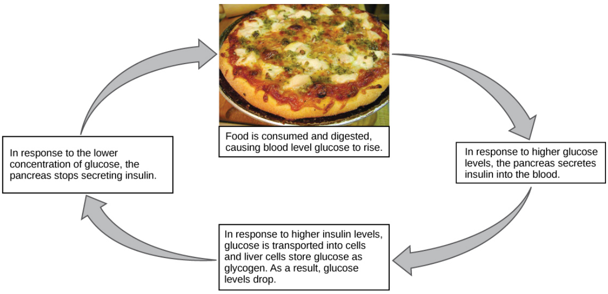

Figure 19.2 Blood sugar levels are controlled by a negative feedback loop. (credit: modification of work by Jon Sullivan)

Positive Feedback Loop

A positive feedback loop maintains the direction of the stimulus, possibly accelerating it. Few examples of positive feedback loops exist in animal bodies, but one is found in the cascade of chemical reactions that result in blood clotting, or coagulation. As one clotting factor is activated, it activates the next factor in sequence until a fibrin clot is achieved. The direction is maintained, not changed, so this is positive feedback. Another example of positive feedback is uterine contractions during childbirth, as illustrated in Figure 19.3. The hormone oxytocin, made by the endocrine system, stimulates the contraction of the uterus. This produces pain sensed by the nervous system. Instead of lowering the oxytocin and causing the pain to subside, more oxytocin is produced until the contractions are powerful enough to produce childbirth.

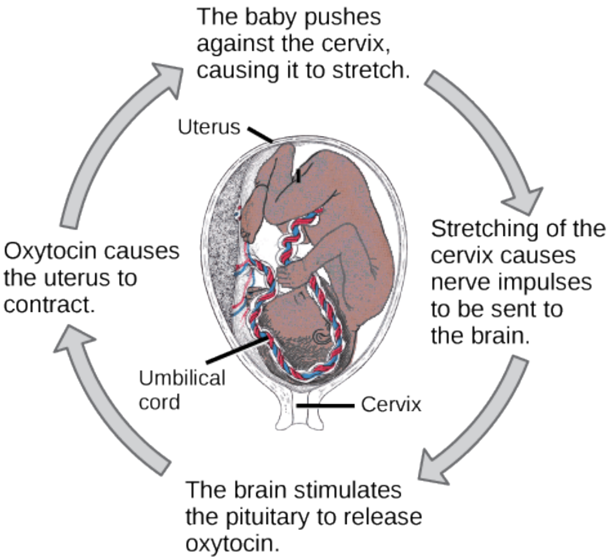

Figure 19.3 The birth of a human infant is the result of positive feedback.

Reading Question #2

Which statement correctly describes the difference between positive and negative feedback loops?

A. Positive feedback aims to reduce the change and reset back to homeostasis, while negative feedback amplifies the change and takes the system further away from homeostasis.

B. Negative feedback aims to reduce the change and reset back to homeostasis, while positive feedback amplifies the change and takes the system further away from homeostasis.

C. Positive feedback aims to reduce the change and take the system closer to homeostasis, while negative feedback amplifies the change and resets the system back to homeostasis.

D. Negative feedback aims to amplify the change and reset back to homeostasis, while positive feedback reduces the change and takes the system further away from homeostasis.

Set Point

It is possible to adjust a system's set point. When this happens, the feedback loop works to maintain the new setting. An example of this is blood pressure: over time, the normal or set point for blood pressure can increase as a result of continued increases in blood pressure. The body no longer recognizes the elevation as abnormal and no attempt is made to return to the lower set point. The result is the maintenance of an elevated blood pressure that can have harmful effects on the body. Medication can lower blood pressure and lower the set point in the system to a more healthy level. This is called a process of alteration of the set point in a feedback loop.

Changes can be made in a group of body organ systems in order to maintain a set point in another system. This is called acclimatization. This occurs, for instance, when an animal migrates to a higher altitude than that to which it is accustomed. In order to adjust to the lower oxygen levels at the new altitude, the body increases the number of red blood cells circulating in the blood to ensure adequate oxygen delivery to the tissues. Another example of acclimatization is animals that have seasonal changes in their coats: a heavier coat in the winter ensures adequate heat retention, and a light coat in summer assists in keeping body temperature from rising to harmful levels.

Link to Learning

Feedback mechanisms can be understood in terms of driving a race car along a track: watch a short video lesson on positive and negative feedback loops. Visit this link to view the video.

Reading Question #3

Match the following terms correctly to their definition.

A) Acclimatization. B) Set point. C) Homeostasis

1. A system's tendency to maintain internal stability.
2. When organ systems alter their function in response to environmental changes to maintain balance and order within the body.
3. The level at which a physiological parameter is most stable and conducive for proper bodily function.

Homeostasis: Thermoregulation

Body temperature affects body activities. Generally, as body temperature rises, enzyme activity rises as well. For every ten degree centigrade rise in temperature, enzyme activity doubles, up to a point. Body proteins, including enzymes, begin to denature and lose their function with high heat (around 50^{o}C for mammals). Enzyme activity will decrease by half for every ten degree centigrade drop in temperature, to the point of freezing, with a few exceptions. Some fish can withstand freezing solid and return to normal with thawing.

Link to Learning

Watch this Discovery Channel video on thermoregulation to see illustrations of this process in a variety of animals.

Endotherms and Ectotherms

Animals can be divided into two groups: some maintain a constant body temperature in the face of differing environmental temperatures, while others have a body temperature that is the same as their environment and thus varies with the environment. Animals that rely on external temperatures to set their body temperature are ectotherms. This group has been called cold-blooded, but the term may not apply to an animal in the desert with a very warm body temperature. In contrast to ectotherms, poikilotherms are animals with constantly varying internal temperatures. An animal that maintains a constant body temperature in the face of environmental changes is called a homeotherm. Endotherms are animals that rely on internal sources for maintenance of relatively constant body temperature in varying environmental temperatures. These animals are able to maintain a level of metabolic activity at cooler temperature, which an ectotherm cannot due to differing enzyme levels of activity. It is worth mentioning that some ectotherms and poikilotherms have relatively constant body temperatures due to the constant environmental temperatures in their habitats. These animals are so-called ectothermic homeotherms, like some deep sea fish species.

Heat can be exchanged between an animal and its environment through four mechanisms: radiation, evaporation, convection, and conduction (Figure 19.4). Radiation is the emission of electromagnetic "heat" waves. Heat comes from the sun in this manner and radiates from dry skin the same way. Heat can be removed with liquid from a surface during evaporation. This occurs when a mammal sweats. Convection currents of air remove heat from the surface of dry skin as the air passes over it. Heat will be conducted from one surface to another during direct contact with the surfaces, such as an animal resting on a warm rock.

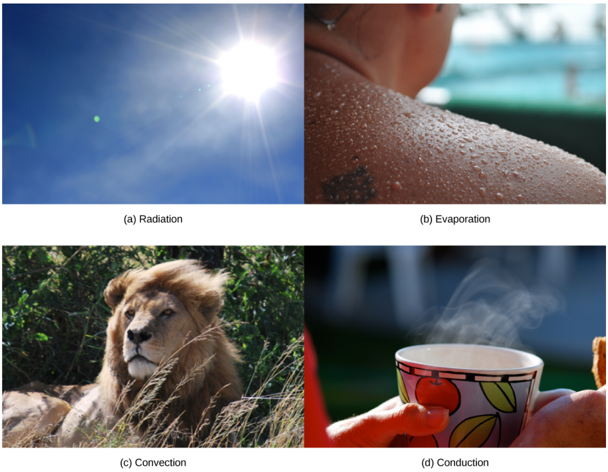

Figure 19.4 Heat can be exchanged by four mechanisms: (a) radiation, (b) evaporation, (c) convection, or (d) conduction. (credit b: modification of work by "Kullez"/Flickr; credit c: modification of work by Chad Rosenthal; credit d: modification of work by "stacey.d"/Flickr)

Heat Conservation and Dissipation

Animals conserve or dissipate heat in a variety of ways. In certain climates, endothermic animals have some form of insulation, such as fur, fat, feathers, or some combination thereof. Animals with thick fur or feathers create an insulating layer of air between their skin and internal organs. Polar bears and seals live and swim in a subfreezing environment and yet maintain a constant, warm, body temperature. The arctic fox, for example, uses its fluffy tail as extra insulation when it curls up to sleep in cold weather. Mammals have a residual effect from shivering and increased muscle activity: arrector pili muscles cause "goose bumps," causing small hairs to stand up when the individual is cold; this has the intended effect of increasing body temperature. Mammals use layers of fat to achieve the same end. Loss of significant amounts of body fat will compromise an individual's ability to conserve heat.

Endotherms use their circulatory systems to help maintain body temperature. Vasodilation brings more blood and heat to the body surface, facilitating radiation and evaporative heat loss, which helps to cool the body. Vasoconstriction reduces blood flow in peripheral blood vessels, forcing blood toward the core and the vital organs found there, and conserving heat. Some animals have adaptations to their circulatory system that enable them to transfer heat from arteries to veins, warming blood returning to the heart. This is called a countercurrent heat exchange; it prevents the cold venous blood from cooling the heart and other internal organs. This adaptation can be shut down in some animals to prevent overheating the internal organs. The countercurrent adaptation is found in many animals, including dolphins, sharks, bony fish, bees, and hummingbirds. In contrast, similar adaptations can help cool endotherms when needed, such as dolphin flukes and elephant ears.

Some ectothermic animals use changes in their behavior to help regulate body temperature. For example, a desert ectothermic animal may simply seek cooler areas during the hottest part of the day in the desert to keep from getting too warm. The same animals may climb onto rocks to capture heat during a cold desert night. Some animals seek water to aid evaporation in cooling them, as seen with reptiles. Other ectotherms use group activity such as the activity of bees to warm a hive to survive winter.

Many animals, especially mammals, use metabolic waste heat as a heat source. When muscles are contracted, most of the energy from the ATP used in muscle actions is wasted energy that translates into heat. Severe cold elicits a shivering reflex that generates heat for the body. Many species also have a type of adipose tissue called brown fat that specializes in generating heat.

Neural Control of Thermoregulation

The nervous system is important to thermoregulation, as illustrated in Figure 19.4. The processes of homeostasis and temperature control are centered in the hypothalamus of the advanced animal brain.

Visual Connection

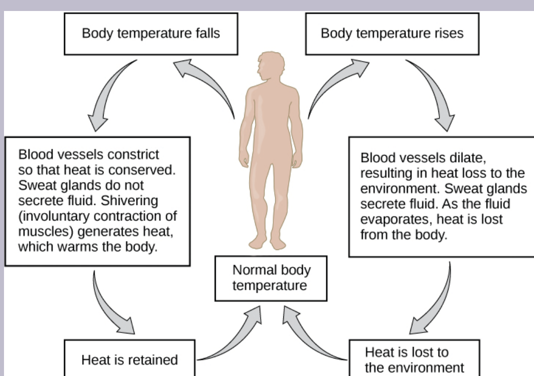

Figure 19.5 The body is able to regulate temperature in response to signals from the nervous system in various conditions, such as hypothermia (which occurs in very cold conditions) or infection.

When bacteria are destroyed by leukocytes, pyrogens are released into the blood. Pyrogens reset the body's thermostat to a higher temperature, resulting in fever. How might pyrogens cause the body temperature to rise? (Hint: Where in the brain does the thermostat reside?)

For more information and detailed answers, visit the embedded link.

El-Radhi A. S. (2019). Pathogenesis of Fever. *Clinical Manual of Fever in Children*, 53–68. https://doi.org/10.1007/978-3-319-92336-9_3

The hypothalamus maintains the set point for body temperature through reflexes that cause vasodilation and sweating when the body is too warm, or vasoconstriction and shivering when the body is too cold. It responds to chemicals from the body. When a bacterium is destroyed by phagocytic leukocytes, chemicals called endogenous pyrogens are released into the blood. These pyrogens circulate to the hypothalamus and reset the thermostat. This allows the body's temperature to increase in what is commonly called a fever. An increase in body temperature causes iron to be conserved, which reduces a nutrient needed by bacteria. An increase in body heat also increases the activity of the animal's enzymes and protective cells while inhibiting the enzymes and activity of the invading microorganisms. Finally, heat itself may also kill the pathogen. A fever that was once thought to be a complication of an infection is now understood to be a normal defense mechanism.

Reading Question #4

What is the most concerning effect of extremely hot or cold temperatures on organismal bodies?

A. Disruption in collagen integrity.

B. Disruption in enzyme shape and function.

C. Vasodilation may cause blood vessel rupturing.

D. Vasoconstriction may cause blood vessel collapse.

Reading Question #5

Which of the following statement(s) is/are true about fever?

A. Fevers have defensive purposes for the body because the heat can destroy causative pathogens.

B. Higher body temperatures induced by the fever decrease the activity of the affected organism's enzymes and protective cells.

C. Higher body temperatures induced by the fever increase the activity of the affected organism's enzymes and protective cells.

D. Higher body temperatures increase the availability of iron, which allows the causative pathogen to further proliferate.

E. Higher body temperatures induced by the fever decrease the activity of the pathogen's enzymes.

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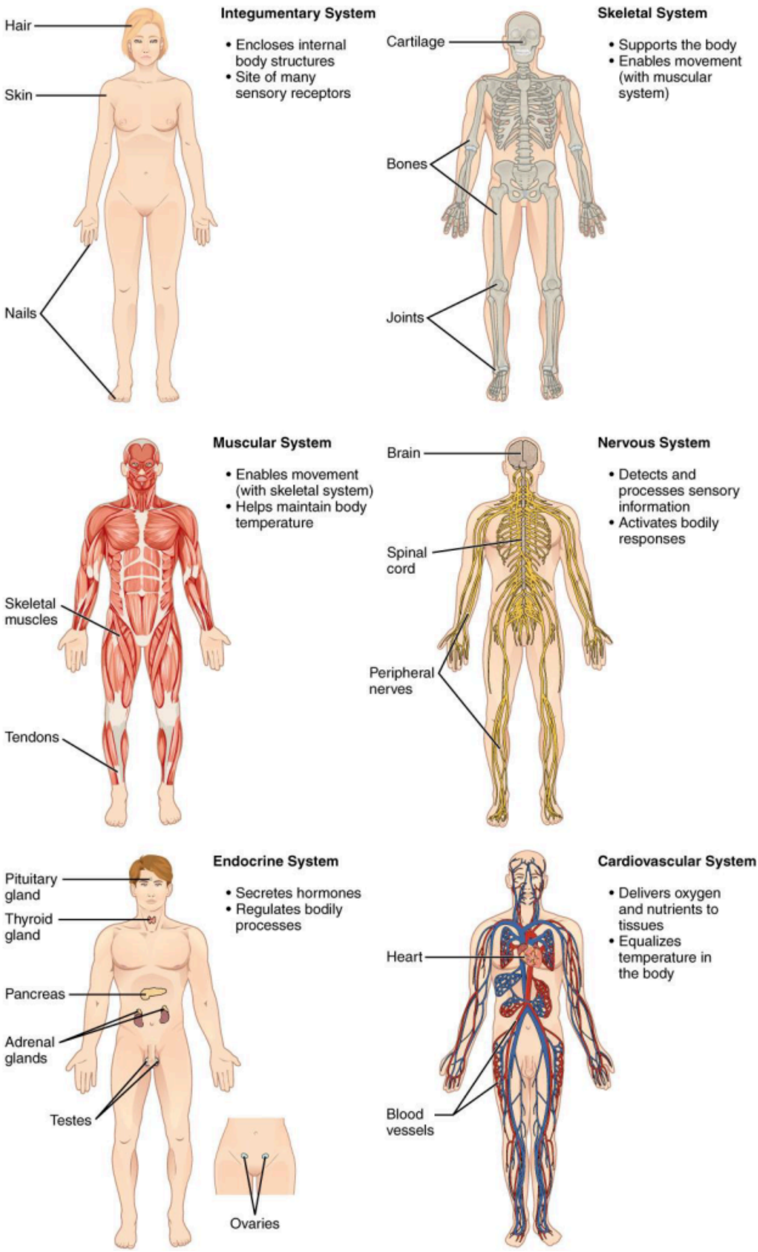
20. Chapter 20: Sensing and Responding to Stimuli: Body System Organization and Plant Responses

MASON TEDESCHI

Organs are collections of tissues grouped together performing a common function. Organs are present not only in animals but also in plants. An organ system is a group of organs that work together to perform major functions or meet physiological needs of the body. Mammals have many organ systems. For instance, the circulatory system transports blood through the body and to and from the lungs. It includes organs such as the heart and blood vessels. The digestive system consists of several organs, including the stomach, intestines, liver, and pancreas. Organ systems can come together to create an entire organism.

There are eleven distinct organ systems in the human body (Figure 20.1, 20.2). Assigning organs to organ systems can be imprecise since organs that "belong" to one system can also have functions integral to another system. In fact, most organs contribute to more than one system. In later chapters, we will discuss some of these organ systems in more depth.



Integumentary System
• Encloses internal body structures
• Site of many sensory receptors
Hair
Skin
Nails
Skeletal System
• Supports the body
• Enables movement (with muscular system)
Cartilage
Bones
Joints
Muscular System
• Enables movement (with skeletal system)
• Helps maintain body temperature
Skeletal muscles
Tendons
Nervous System
• Detects and processes sensory information
• Activates bodily responses
Brain
Spinal cord
Peripheral nerves
Endocrine System
• Secretes hormones
• Regulates bodily processes
Pituitary gland
Thyroid gland
Pancreas
Adrenal glands
Testes
Ovaries
Cardiovascular System
• Delivers oxygen and nutrients to tissues
• Equalizes temperature in the body
Heart
Blood vessels

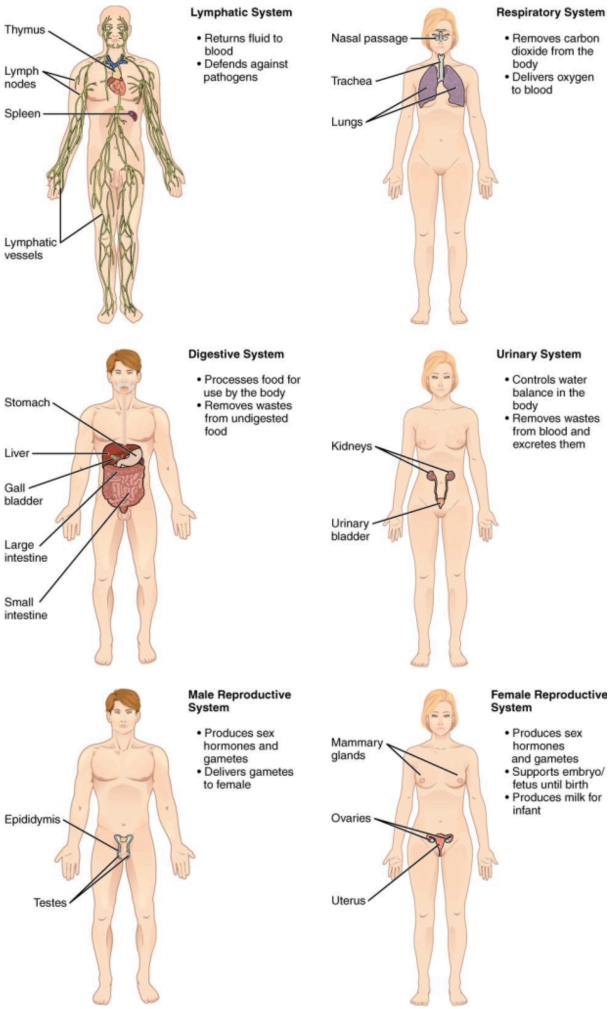


Fig 20.1–20.2 Each organ system works together to perform a specific function

Table 20.1

Organ System	Major Organs	Function
Skeletal	Bones, ligaments, cartilage	Support and protection
Muscular	Skeletal muscles, tendons	Voluntary movement
Circulatory	Heart, blood vessels	Transport substances
Respiratory	Nasal cavity, pharynx, larynx, lungs	Gas exchange and sound
Digestive	Mouth, stomach, intestines, liver, pancreas	Obtaining nutrients
Urinary	Kidneys, bladder	Filtering blood, water balance
Integumentary	Skin, hair, nails	Protection
Reproductive	Ovaries/testes, glands, uterus, vagina/penis	Reproduction
Lymphatic	Tonsils, spleen, lymph nodes	Immune protection
Nervous	Brain, spinal cord, nerves	Integration, communication, and control
Endocrine	Hypothalamus, pituitary, thyroid, adrenal, gonads	Integration, communication, and control

Reading Question #1

Which body system functions to deliver air to sites where gas exchange occur?

A. Reproductive

B. Urinary

C. Nervous

D. Respiratory

Reading Question #2

Which body system functions to provide communication within the body via hormones and directs long-term change in other organ systems to maintain homeostasis?

A. Reproductive

B. Endocrine

C. Integumentary

D. Digestive

Reading Question #3

Which body system functions break down and absorb food so the body can acquire the nutrients it needs?

A. Reproductive

B. Urinary

C. Digestive

D. Muscular

Plant Responses to Light

Plants have a number of sophisticated uses for light that go far beyond their ability to photosynthesize low-molecular-weight sugars using only carbon dioxide, light, and water. Phototropism is a directional response that allows plants to grow towards, or even away from, light. Positive phototropism is growth towards a light source (Figure 20.3), while negative phototropism (also called skototropism) is growth away from light. The sensing of light in the environment is important to plants; it can be crucial for competition and survival. The response of plants to light is mediated by different photoreceptors.

Figure 20.3 Azure bluets (Houstonia caerulea) display a phototropic response by bending toward the light. (credit: Cory Zanker)

Plant Responses to Gravity

Whether or not they germinate in the light or in total darkness, shoots usually sprout up from the ground, and roots grow downward into the ground. A plant laid on its side in the dark will send shoots upward when given enough time. Gravitropism ensures that roots grow into the soil and that shoots grow toward sunlight. Growth of the shoot apical tip upward is called negative gravitropism, whereas growth of the roots downward is called positive gravitropism.

Amyloplasts (also known as statoliths) are specialized plastids that contain starch granules and settle downward in response to gravity. Amyloplasts are found in shoots and in specialized cells of the root cap. When a plant is tilted, the statoliths drop to the new bottom cell wall. A few hours later, the shoot or root will show growth in the new vertical direction.

The mechanism that mediates gravitropism is reasonably well understood. When amyloplasts settle to the bottom of the gravity-sensing cells in the root or shoot, they physically contact the endoplasmic reticulum (ER), causing the release of calcium ions from inside the ER. This calcium signaling in the cells causes polar transport of the plant hormone IAA to the bottom of the cell. In roots, a high concentration of IAA inhibits cell elongation. The effect slows growth on the lower side of the root, while cells develop normally on the upper side. IAA has the opposite effect in shoots, where a higher concentration at the lower side of the shoot stimulates cell expansion, causing the shoot to grow up. After the shoot or root begin to grow vertically, the amyloplasts return to their normal position. Other hypotheses—involving the entire cell in the gravitropism effect—have been proposed to explain why some mutants that lack amyloplasts may still exhibit a weak gravitropic response.

Auxins

The term auxin is derived from the Greek word auxein, which means "to grow." Auxins are the main hormones responsible for cell elongation in phototropism and gravitropism. They also control the differentiation of meristem into vascular tissue, and promote leaf development and arrangement. While many synthetic auxins are used as herbicides, IAA is the only naturally occurring auxin that shows physiological activity. Apical dominance—the inhibition of lateral bud formation—is triggered by auxins produced in the apical meristem. Flowering, fruit setting and ripening, and inhibition of abscission (leaf falling) are other plant responses under the direct or indirect control of auxins.

Commercial use of auxins is widespread in plant nurseries and for crop production. IAA is used as a rooting hormone to promote growth of adventitious roots on cuttings and detached leaves. Applying synthetic auxins to tomato plants in greenhouses promotes normal fruit development. Outdoor application of auxin promotes synchronization of fruit setting and dropping to coordinate the harvesting season. Fruits such as seedless cucumbers can be induced to set fruit by treating unfertilized plant flowers with auxins.

Plant Responses to Wind and Touch

The shoot of a pea plant winds around a trellis, while a tree grows on an angle in response to strong prevailing winds. These are examples of how plants respond to touch or wind.

The movement of a plant subjected to constant directional pressure is called thigmotropism, from the Greek words thigma meaning “touch,” and tropism implying “direction.” Tendrils are one example of this. The meristematic region of tendrils is very touch sensitive; light touch will evoke a quick coiling response. Cells in contact with a support surface contract, whereas cells on the opposite side of the support expand. Application of jasmonic acid is sufficient to trigger tendril coiling without a mechanical stimulus.

A thigmonastic response is a touch response independent of the direction of stimulus. In the Venus flytrap, two modified leaves are joined at a hinge and lined with thin fork-like tines along the outer edges. Tiny hairs are located inside the trap. When an insect brushes against these trigger hairs, touching two or more of them in succession, the leaves close quickly, trapping the prey. Glands on the leaf surface secrete enzymes that slowly digest the insect. The released nutrients are absorbed by the leaves, which reopen for the next meal.

Thigmomorphogenesis is a slow developmental change in the shape of a plant subjected to continuous mechanical stress. When trees bend in the wind, for example, growth is usually stunted and the trunk thickens. Strengthening tissue, especially xylem, is produced to add stiffness to resist the wind’s force. Researchers hypothesize that mechanical strain induces growth and differentiation to strengthen the tissues. Ethylene and jasmonate are likely involved in thigmomorphogenesis.

Reading Question #4

Plant growth towards sunlight is best described as

A. Phototropism

B. Gravitropism

C. Negative feedback

D. Positive feedback

Reading Question #5

Plant roots growing downward is best described as

A. Phototropism

B. Gravitropism

C. Negative feedback

D. Positive feedback

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21. Chapter 21: Sensing and Responding to Stimuli: Nervous and Signaling Cascades

ANASTASIA CHOUVALOVA

Nervous system

When you're reading this book, your nervous system is performing several functions simultaneously. The visual system is processing what is seen on the page; the motor system controls the turn of the pages (or click of the mouse); the prefrontal cortex maintains attention. Even fundamental functions, like breathing and regulation of body temperature, are controlled by the nervous system. A nervous system is an organism's control center: it processes sensory information from outside (and inside) the body and controls all behaviors—from eating to sleeping to finding a mate.

Nervous systems throughout the animal kingdom vary in structure and complexity. Some organisms, like sea sponges, lack a true nervous system. Others, like jellyfish, lack a true brain and instead have a system of separate but connected nerve cells (neurons) called a "nerve net." Echinoderms such as sea stars have nerve cells that are bundled into fibers called nerves. Flatworms of the phylum *Platyhelminthes* have both a central nervous system (CNS), made up of a small "brain" and two nerve cords, and a peripheral nervous system (PNS) containing a system of nerves that extend throughout the body. The insect nervous system is more complex but also fairly decentralized. It contains a brain, ventral nerve cord, and ganglia (clusters of connected neurons). These ganglia can control movements and behaviors without input from the brain. Octopi may have the most complicated of invertebrate nervous systems—they have neurons that are organized in specialized lobes and eyes that are structurally similar to vertebrate species.

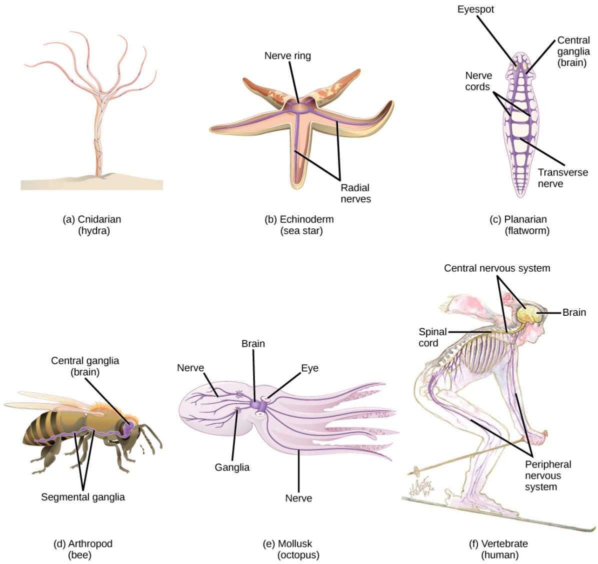


Figure 20.1 Nervous systems vary in structure and complexity. In (a) cnidarians, nerve cells form a decentralized nerve net. In (b) echinoderms, nerve cells are bundled into fibers called nerves. In animals exhibiting bilateral symmetry such as (c) planarians, neurons cluster into an anterior brain that processes information. In addition to a brain, (d) arthropods have clusters of nerve cell bodies, called peripheral ganglia, located along the ventral nerve cord. Mollusks such as squid and (e) octopi, which must hunt to survive, have complex brains containing

millions of neurons. In (f) vertebrates, the brain and spinal cord comprise the central nervous system, while neurons extending into the rest of the body comprise the peripheral nervous system. (credit e: modification of work by Michael Vecchione, Clyde F.E. Roper, and Michael J. Sweeney, NOAA; credit f: modification of work by NIH)

Compared to invertebrates, vertebrate nervous systems are more complex, centralized, and specialized. While there is great diversity among different vertebrate nervous systems, they all share a basic structure: a CNS that contains a brain and spinal cord and a PNS made up of peripheral sensory and motor nerves. One interesting difference between the nervous systems of invertebrates and vertebrates is that the nerve cords of many invertebrates are located ventrally whereas the vertebrate spinal cords are located dorsally. There is debate among evolutionary biologists as to whether these different nervous system plans evolved separately or whether the invertebrate body plan arrangement somehow "flipped" during the evolution of vertebrates.

Link to Learning

Watch this video of biologist Mark Kirschner discussing the "flipping" phenomenon of vertebrate evolution.

Reading Question #1

Which of the following statement(s) correctly describes invertebrate vs. vertebrae nervous systems?

A. In vertebrates, spinal cords are found on the ventral surface while in invertebrates, spinal cords are found on the dorsal surface.

B. Both types of organisms have a central and peripheral nervous system.

C. Invertebrate nervous systems tend to be more complex and specialized.

D. Invertebrate organisms don't have neurons, while vertebrate organisms do.

The nervous system is made up of neurons, specialized cells that can receive and transmit chemical or electrical signals, and glia, cells that provide support functions for the neurons by playing an information processing role that is complementary to neurons. A neuron can be compared to an electrical wire—it transmits a signal from one place to another. Glia can be compared to the workers at the electric company who make sure wires go to the right places, maintain the wires, and take down wires that are broken. Although glia have been compared to workers, recent evidence suggests that they also usurp some of the signaling functions of neurons.

There is great diversity in the types of neurons and glia that are present in different parts of the nervous system. There are four major types of neurons, and they share several important cellular components.

Neurons

The nervous system of the common laboratory fly, *Drosophila melanogaster*, contains around 100,000 neurons, the same number as a lobster. This number compares to 75 million in the mouse and 300 million in the octopus. A human brain contains around 86 billion neurons. Despite these very different numbers, the nervous systems of these animals control many of the same behaviors—from basic reflexes to more complicated behaviors like finding food and courting mates. The ability of neurons to communicate with each other as well as with other types of cells underlies all of these behaviors.

Most neurons share the same cellular components. But neurons are also highly specialized—different types of neurons have different sizes and shapes that relate to their functional roles.

Parts of a Neuron

Like other cells, each neuron has a cell body (or soma) that contains a nucleus, smooth and rough endoplasmic reticulum, Golgi apparatus, mitochondria, and other cellular components. Neurons also contain unique structures, illustrated in Figure 20.2 for receiving and sending the electrical signals that make neuronal communication possible. Dendrites are tree-like structures that extend away from the cell body to receive messages from other neurons at specialized junctions called synapses. Although some neurons do not have any dendrites, some types of neurons have multiple dendrites. Dendrites can have small protrusions called dendritic spines, which further increase surface area for possible synaptic connections.

Once a signal is received by the dendrite, it then travels passively to the cell body. The cell body contains a specialized structure, the axon hillock that integrates signals from multiple synapses and serves as a junction between the cell body and an axon. An axon is a tube-like structure that propagates the integrated signal to specialized endings called axon terminals. These terminals in turn synapse on other neurons, muscle, or target organs. Chemicals released at axon terminals allow signals to be communicated to these other cells. Neurons usually have one or two axons, but some neurons, like amacrine cells in the retina, do not contain any axons. Some axons are covered with myelin, which acts as an insulator to minimize dissipation of the electrical signal as it travels down the axon, greatly increasing the speed of conduction. This insulation is important as the axon from a human motor neuron can be as long as a meter—from the base of the spine to the toes. The myelin sheath is not actually part of the neuron. Myelin is produced by glial cells. Along the axon there are periodic gaps in the myelin sheath. These gaps are called nodes of Ranvier and are sites where the signal is "recharged" as it travels along the axon.

It is important to note that a single neuron does not act alone—neuronal communication depends on the connections that neurons make with one another (as well as with other cells, like muscle cells). Dendrites from a single neuron may receive synaptic contact from many other neurons. For example, dendrites from a Purkinje cell in the cerebellum are thought to receive contact from as many as 200,000 other neurons.

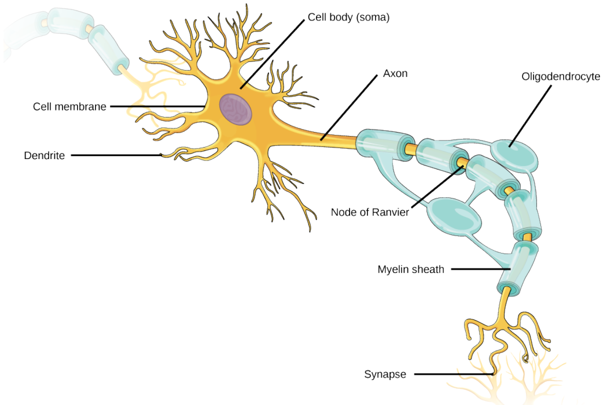


Figure 20.2 Neurons contain organelles common to many other cells, such as a nucleus and mitochondria. They also have more specialized structures, including dendrites and axons.

Types of Neurons

There are different types of neurons, and the functional role of a given neuron is intimately dependent on its structure. There is an amazing diversity of neuron shapes and sizes found in different parts of the nervous system(and across species), as illustrated by the neurons shown in Figure 20.3.

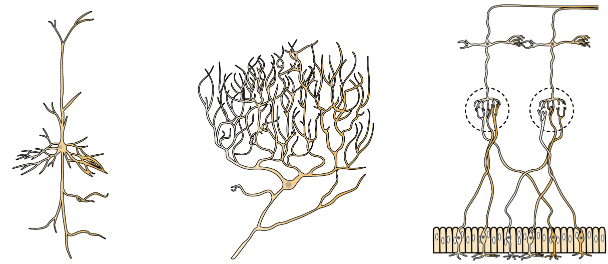


Figure 20.3 There is great diversity in the size and shape of neurons throughout the nervous system. Examples include (a) a pyramidal cell from the cerebral cortex, (b) a Purkinje cell from the cerebellar cortex, and (c) olfactory cells from the olfactory epithelium and olfactory bulb.

While there are many defined neuron cell subtypes, neurons are broadly divided into four basic types: unipolar, bipolar, multipolar, and pseudounipolar. Figure 20.4 illustrates these four basic neuron types. Unipolar neurons have only one structure that extends away from the soma. These neurons are not found in vertebrates but are found in insects where they stimulate muscles or glands. A bipolar neuron has one axon and one dendrite extending from the soma. An example of a bipolar neuron is a retinal bipolar cell, which receives signals from photoreceptor cells that are sensitive to light and transmits these signals to ganglion cells that carry the signal to the brain. Multipolar neurons are the most common type of neuron. Each multipolar neuron contains one axon and multiple dendrites. Multipolar neurons can be found in the central nervous system (brain and spinal cord). An example of a multipolar neuron is a

Purkinje cell in the cerebellum, which has many branching dendrites but only one axon. Pseudounipolar cells share characteristics with both unipolar and bipolar cells. A pseudounipolar cell has a single process that extends from the soma, like a unipolar cell, but this process later branches into two distinct structures, like a bipolar cell. Most sensory neurons are pseudounipolar and have an axon that branches into two extensions: one connected to dendrites that receive sensory information and another that transmits this information to the spinal cord.

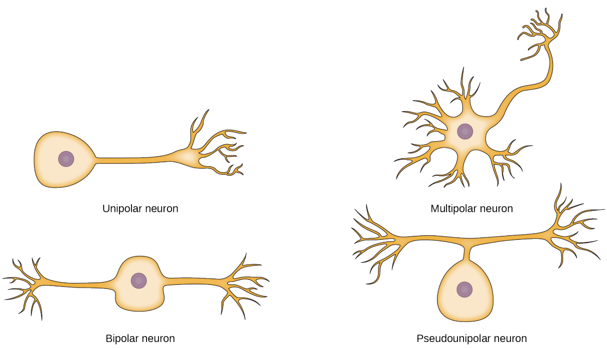


Figure 20.5 Neurons are broadly divided into four main types based on the number and placement of axons: (1) unipolar, (2) bipolar, (3) multipolar, and (4) pseudounipolar.

Everyday Connection

Neurogenesis

At one time, scientists believed that people were born with all the neurons they would ever have. Research performed during the last few decades indicates that neurogenesis, the birth of new neurons, continues into adulthood. Neurogenesis was first discovered in songbirds that produce new neurons while learning songs. For mammals, new neurons also play an important role in learning: about 1000 new neurons develop in the hippocampus (a brain structure involved in learning and memory) each day. While most of the new neurons will die, researchers found that an increase in the number of surviving new neurons in the hippocampus correlated with how well rats learned a new task. Interestingly, both exercise and some antidepressant medications also promote neurogenesis in the hippocampus. Stress has the opposite effect. While neurogenesis is quite limited compared to regeneration in other tissues, research in this area may lead to new treatments for disorders such as Alzheimer's, stroke, and epilepsy.

How do scientists identify new neurons? A researcher can inject a compound called bromodeoxyuridine (BrdU) into the brain of an animal. While all cells will be exposed to BrdU, BrdU will only be incorporated into the DNA of newly generated cells that are in S phase. A technique called immunohistochemistry can be used to attach a fluorescent label to the incorporated BrdU, and a researcher can use fluorescent microscopy to visualize the presence of BrdU, and thus new neurons, in brain tissue. Figure 20.6 is a micrograph which shows fluorescently labeled neurons in the hippocampus of a rat.

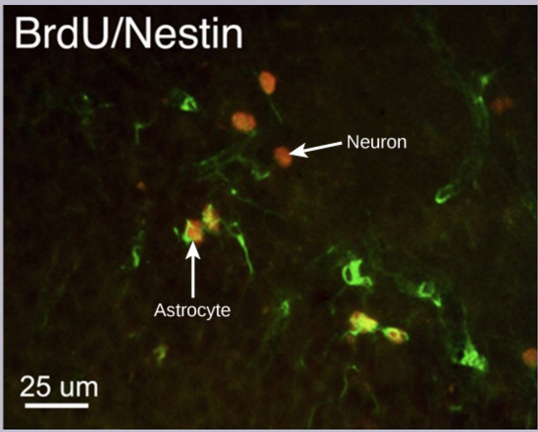


Figure 20.6 This micrograph shows fluorescently labeled new neurons in a rat hippocampus. Cells that are actively dividing have bromodeoxyuridine (BrdU) incorporated into their DNA and are labeled in red. Cells that express glial fibrillary acidic protein (GFAP) are labeled in green. Astrocytes, but not neurons, express GFAP. Thus, cells that are labeled both red and green

are actively dividing astrocytes, whereas cells labeled red only are actively dividing neurons. (credit: modification of work by Dr. Maryam Faiz, et. al., University of Barcelona; scale-bar data from Matt Russell)

Link to Learning

This site contains more information about neurogenesis, including an interactive laboratory simulation and a video that explains how BrdU labels new cells.

Reading Question #2

Which neuronal structure is responsible for releasing chemicals (e.g., neurotransmitters such as dopamine and serotonin)?

A. Dendrite

B. Axon

C. Axon terminal

D. Soma

Reading Question #3

Which of the following statement(s) about neurogenesis is **inaccurate**?

A. Neurogenesis is defined as the process of formation of new neurons.

B. The main brain area in which neurogenesis has been observed is the amygdala.

C. The first organism in which neurogenesis was discovered was mice.

D. Both stress and exercise have a negative effect on neurogenesis.

E. New neurons are identified using immunohistochemistry.

Glia

While glia are often thought of as the supporting cast of the nervous system, the number of glial cells in the brain actually outnumbers the number of neurons by a factor of ten. Neurons would be unable to function without the vital roles that are fulfilled by these glial cells. Glia guide developing neurons to their destinations, buffer ions and chemicals that would otherwise harm neurons, and provide myelin sheaths around axons. Scientists have recently discovered that they also play a role in responding to nerve activity and modulating communication between nerve cells. When glia do not function properly, the result can be disastrous—most brain tumors are caused by mutations in glia.

Types of Glia

There are several different types of glia with different functions, two of which are shown in Figure 20.7. Astrocytes, shown in Figure 20.8a make contact with both capillaries and neurons in the CNS. They provide nutrients and other substances to neurons, regulate the concentrations of ions and chemicals in the extracellular fluid, and provide structural support for synapses. Astrocytes also form the blood-brain barrier—a structure that blocks entrance of toxic substances into the brain. Astrocytes, in particular, have been shown through calcium imaging experiments to become active in response to nerve activity, transmit calcium waves between astrocytes, and modulate the activity of surrounding synapses. Satellite glia provide nutrients and structural support for neurons in the PNS. Microgliascavenge and degrade dead cells and protect the brain from invading microorganisms. Oligodendrocytes, shown in Figure 20.8b form myelin sheaths around axons in the CNS. One axon can be myelinated by several oligodendrocytes, and one oligodendrocyte can provide myelin for multiple neurons. This is distinctive from the PNS where a single Schwann cell provides myelin for only one axon as the entire Schwann cell surrounds the axon. Radial glia serve as scaffolds for developing neurons as they migrate to their end destinations. Ependymalcells line fluid-filled ventricles of the brain and the central canal of the spinal cord. They are involved in the production of cerebrospinal fluid, which serves as a cushion for the brain, moves the fluid between the spinal cord and the brain, and is a component for the choroid plexus.

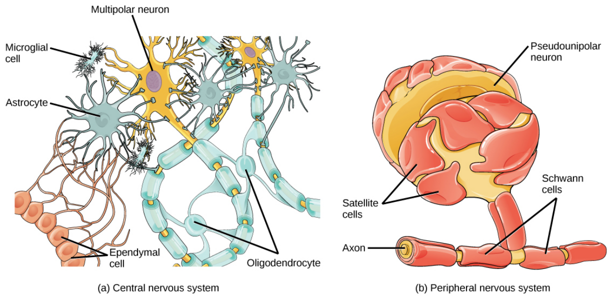


Figure 20.7 Glial cells support neurons and maintain their environment. Glial cells of the (a) central nervous system include oligodendrocytes, astrocytes, ependymal cells, and microglial cells. Oligodendrocytes form the myelin sheath around axons. Astrocytes provide nutrients to neurons, maintain their extracellular environment, and provide structural support. Microglia scavenge pathogens and dead cells. Ependymal cells produce cerebrospinal fluid that cushions the neurons. Glial cells of the (b) peripheral

nervous system include Schwann cells, which form the myelin sheath, and satellite cells, which provide nutrients and structural support to neurons.

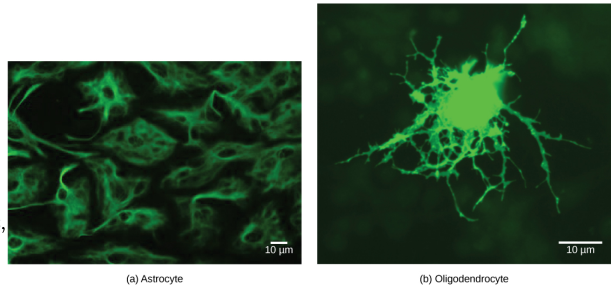


Figure 20.8 (a) Astrocytes and (b) oligodendrocytes are glial cells of the central nervous system. (credit a: modification of work by Uniformed Services University; credit b: modification of work by Jurjen Broeke; scale-bar data from Matt Russell).

All functions performed by the nervous system—from a simple motor reflex to more advanced functions like making a memory or a decision—require neurons to communicate with one another. While humans use words and body language to communicate, neurons use electrical and chemical signals. Just like a person in a committee, one neuron usually receives and synthesizes messages from multiple other neurons before "making the decision" to send the message on to other neurons.

Nerve Impulse Transmission within a Neuron

For the nervous system to function, neurons must be able to send and receive signals. These signals are possible because each neuron has a charged cellular membrane (a voltage difference between the inside and the outside), and the charge of this membrane can change in response to neurotransmitter molecules released from other neurons and environmental stimuli. To understand how neurons communicate, one must first understand the basis of the baseline or 'resting' membrane charge.

Neuronal Charged Membranes

The lipid bilayer membrane that surrounds a neuron is impermeable to charged molecules or ions. To enter or exit the neuron, ions must pass through special proteins called ion channels that span the membrane. Ion channels have different configurations: open, closed, and inactive, as illustrated in Figure 20.9. Some ion channels need to be activated in order to open and allow ions to pass into or out of the cell. These ion channels are sensitive to the environment and can change their shape accordingly. Ion channels that change their structure in response to voltage changes are called voltage-gated ion channels. Voltage-gated ion channels regulate the relative concentrations of different ions inside and outside the cell. The difference in total charge between the inside and outside of the cell is called the membrane potential.

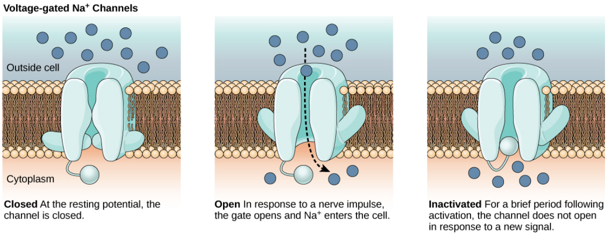


Figure 20.9 Voltage-gated ion channels open in response to changes in membrane voltage. After activation, they become inactivated for a brief period and will no longer open in response to a signal.

Link to Learning

This video discusses the basis of the resting membrane potential.

Resting Membrane Potential

A neuron at rest is negatively charged: the inside of a cell is approximately 70 millivolts more negative than the outside (–70 mV, note that this number varies by neuron type and by species). This voltage is called the resting membrane potential; it is caused by differences in the concentrations of ions inside and outside the cell. If the membrane were equally permeable to all ions, each type of ion would flow across the membrane and the system would reach equilibrium. Because ions cannot simply cross the membrane at will, there are different concentrations of several ions inside and outside the cell, as shown in Table 20.1. The difference in the number of positively charged potassium ions (K^+) inside and outside the cell dominates the resting membrane potential (Figure 20.10). When the membrane is at rest, K^+ ions accumulate inside the cell due to the activity of the Na/K pump, driving both ions against their concentration gradient. The negative resting membrane potential is created and maintained by increasing the concentration of cations outside the cell (in the extracellular fluid) relative to inside the cell (in the cytoplasm). The negative charge within the cell is created by the cell membrane being more permeable to potassium ion movement than sodium ion movement. In neurons, potassium ions are maintained at high concentrations within the cell while sodium ions are maintained at high concentrations outside of the cell. The cell possesses potassium and sodium leakage channels that allow the two cations to diffuse down their concentration gradient. However, the neurons have far more potassium leakage channels than sodium leakage channels. Therefore, potassium diffuses out of the cell at a much faster rate than sodium leaks in. Because more cations are leaving the cell than are entering, this causes the interior of the cell to be negatively charged relative to the outside of the cell. The actions of the sodium potassium pump help to maintain the resting potential, once established. Recall that sodium potassium pumps brings two K^+ ions into the cell while removing three Na^+ ions per ATP consumed. As more cations are expelled from the cell than taken in, the inside of the cell remains negatively charged relative to the extracellular fluid. It should be noted that chloride ions (Cl^-) tend to accumulate outside of the cell because they are repelled by negatively-charged proteins within the cytoplasm.

Ion Concentration Inside and Outside Neurons

Ion	Extracellular concentration (mM)	Intracellular concentration (mM)	Ratio outside/inside
Na^+	145	12	12
K+	4	155	0.026
Cl^-	120	4	30
Organic anions (A–)	–	100	

Table 20.1 The resting membrane potential is a result of different concentrations inside and outside the cell.

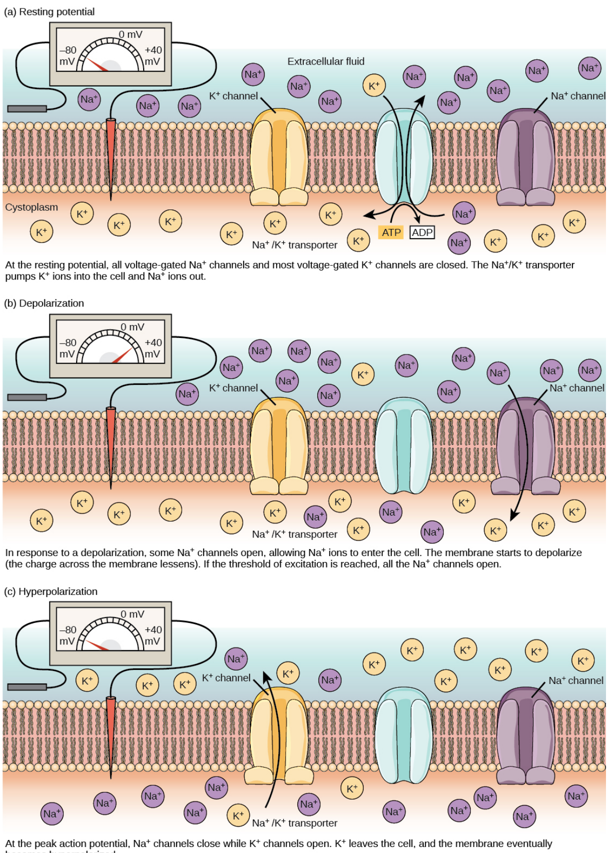


Figure 20.10 The (a) resting membrane potential is a result of different concentrations of Na^+ and K^+ ions inside and outside the cell. A nerve impulse causes Na^+ to enter the cell, resulting in (b) depolarization. At the peak action potential, K^+ channels open and the cell becomes (c) hyperpolarized.

Action Potential

A neuron can receive input from other neurons and, if this input is strong enough, send the signal to downstream neurons. Transmission of a signal between neurons is generally carried by a chemical called a neurotransmitter. Transmission of a signal within a neuron (from dendrite to axon terminal) is carried by a brief reversal of the resting membrane potential called an action potential. When neurotransmitter molecules bind to receptors located on a neuron's dendrites, ion channels open. At excitatory synapses, this opening allows positive ions to enter the neuron and results in depolarization of the membrane—a decrease in the difference in voltage between the inside and outside of the neuron. A stimulus from a sensory cell or another neuron depolarizes the target neuron to its threshold potential (-55 mV). Na^+ channels in the axon hillock open, allowing positive ions to enter the cell (Figure 20.10 and Figure 20.11). Once the sodium channels open, the neuron completely depolarizes to a membrane potential of about +40 mV. Action potentials are considered an "all-or nothing" event, in that, once the threshold potential is reached, the neuron always completely depolarizes. Once depolarization is complete, the cell must now "reset" its membrane voltage back to the resting potential. To accomplish this, the Na^+ channels close and cannot be opened. This begins the neuron's refractory period, in which it cannot produce another action potential because its sodium channels will not open. At the same time, voltage-gated K^+ channels open, allowing K^+ to leave the cell. As K^+ ions leave the cell, the membrane potential once again becomes negative and repolarizes. The diffusion of K+ out of the cell actually continues for a short period of time past the time of the achievement of the resting potential, and the membrane hyperpolarizes, in that the membrane potential becomes more negative than the cell's normal resting potential. This is the result of the slow closing of the K^+ channels. At this point, the sodium channels will return to their resting state, meaning they are ready to open again if the membrane potential again exceeds the threshold potential. Eventually all the K+ channels close, and the cell returns back to its resting membrane potential.

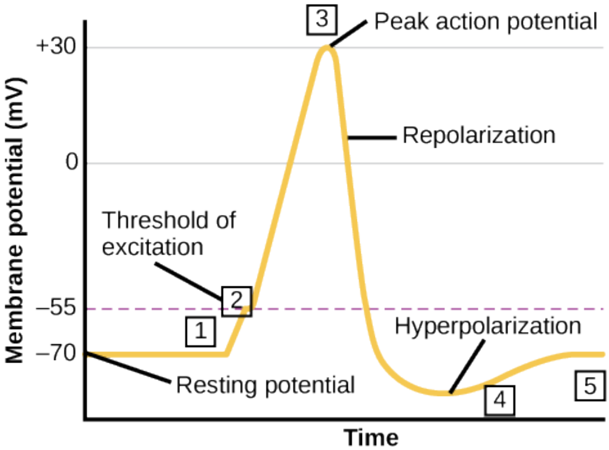


Figure 20.11 The (a) resting membrane potential is a result of different concentrations of Na^+ and K^+ ions inside and outside the cell. A nerve impulse causes Na^+ to enter the cell, resulting in (b) depolarization. At the peak action potential, K^+ channels open and the cell becomes (c) hyperpolarized.

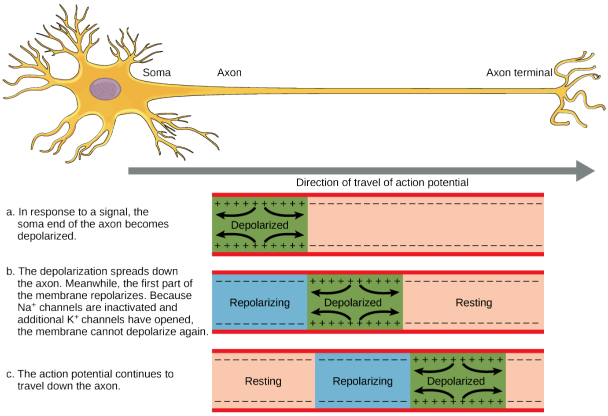


Figure 35.12 The action potential is conducted down the axon as the axon membrane depolarizes, then repolarizes.

Link to Learning

[This video](#) presents an overview of action potential.

Reading Question #4

Rank the order of the events in an action potential.

A) The cell repolarizes, wherein Na+ channels close and K+ channels open, resulting in K+ efflux.

B) The cell depolarizes, wherein Na+ channels open because of a stimulus, resulting in Na+ influx.

C) The cell hyperpolarizes due to continued K+ efflux.

D) The cell is at its resting potential of -70 mV.

Myelin and the Propagation of the Action Potential

For an action potential to communicate information to another neuron, it must travel along the axon and reach the axon terminals where it can initiate neurotransmitter release. The speed of conduction of an action potential along an axon is influenced by both the diameter of the axon and the axon's resistance to current leak. Myelin acts as an insulator that prevents current from leaving the axon; this increases the speed of action potential conduction. In demyelinating diseases like multiple sclerosis, action potential conduction slows because current leaks from previously insulated axon areas. The nodes of Ranvier, illustrated in Figure 20.13 are gaps in the myelin sheath along the axon. These unmyelinated spaces are about one micrometer long and contain voltage-gated Na^+ and K^+channels. Flow of ions through these channels, particularly the Na^+ channels, regenerates the action potential over and over again along the axon. This 'jumping' of the action potential from one node to the next is called saltatory conduction. If nodes of Ranvier were not present along an axon, the action potential would propagate very slowly since Na^+ and K^+ channels would have to continuously regenerate action potentials at every point along the axon instead of at specific points. Nodes of Ranvier also save energy for the neuron since the channels only need to be present at the nodes and not along the entire axon.

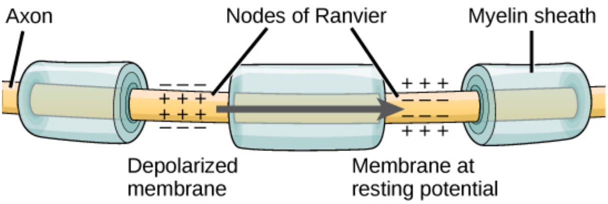


Figure 20.13 Nodes of Ranvier are gaps in myelin coverage along axons. Nodes contain voltage-gated K^+ and Na^+ channels. Action potentials travel down the axon by jumping from one node to the next.

Synaptic Transmission

The synapse or "gap" is the place where information is transmitted from one neuron to another. Synapses usually form between axon terminals and dendritic spines, but this is not universally true. There are also axon-to-axon, dendrite-to-dendrite, and axon-to-cell body synapses. The neuron transmitting the signal is called the presynaptic neuron, and the neuron receiving the signal is called the postsynaptic neuron. Note that these designations are relative to a particular synapse—most neurons are both presynaptic and postsynaptic. There are two types of synapses: chemical and electrical.

Chemical Synapse

When an action potential reaches the axon terminal it depolarizes the membrane and opens voltage-gated Na^+channels. Na^+ ions enter the cell, further depolarizing the presynaptic membrane. This depolarization causes voltage-gated Ca^{2+} channels to open. Calcium ions entering the cell initiate a signaling cascade that causes small membrane-bound vesicles, called synaptic vesicles, containing neurotransmitter molecules to fuse with the presynaptic membrane. Synaptic vesicles are shown in Figure 20.14, which is an image from a scanning electron microscope.

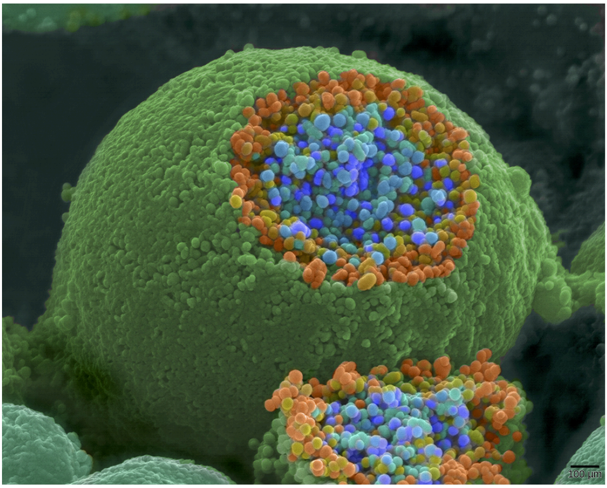


Figure 20.14 This pseudocolored image taken with a scanning electron microscope shows an axon terminal that was broken open to reveal synaptic vesicles (blue and orange) inside the neuron. (credit: modification of work by Tina Carvalho, NIH-NIGMS; scale-bar data from Matt Russell)

Fusion of a vesicle with the presynaptic membrane causes neurotransmitter to be released into the synaptic cleft, the extracellular space between the presynaptic and postsynaptic membranes, as illustrated in Figure 20.15. The neurotransmitter diffuses across the synaptic cleft and binds to receptor proteins on the postsynaptic membrane.

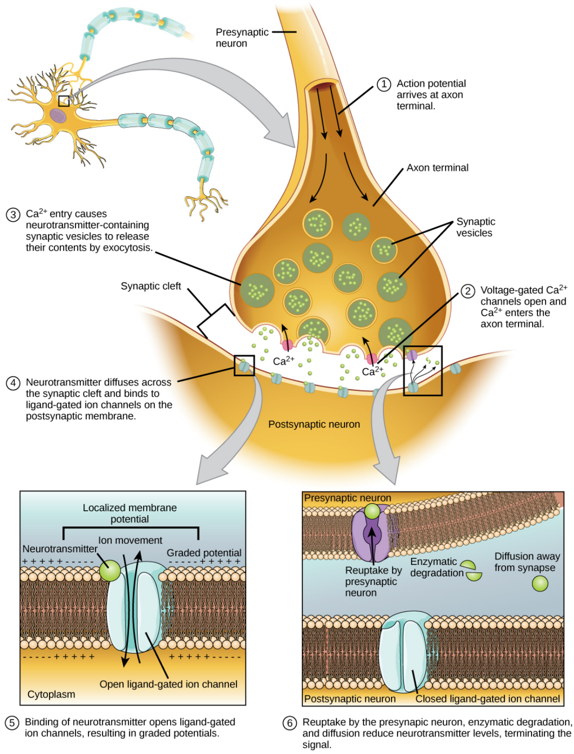


Figure 20.15 Communication at chemical synapses requires release of neurotransmitters. When the presynaptic membrane is depolarized, voltage-gated Ca^{2+} channels open and allow Ca^{2+} to enter the cell. The calcium entry causes synaptic vesicles to fuse with the membrane and release neurotransmitter molecules into the synaptic cleft. The neurotransmitter diffuses across the synaptic cleft and binds to ligand-gated ion channels in the postsynaptic membrane, resulting in a localized depolarization or hyperpolarization of the postsynaptic neuron.

The binding of a specific neurotransmitter causes particular ion channels, in this case ligand-gated channels, on the postsynaptic membrane to open. Neurotransmitters can either have excitatory or inhibitory effects on the postsynaptic membrane. For example, when acetylcholine is released at the synapse between a nerve and muscle (called the neuromuscular junction) by a presynaptic neuron, it causes postsynaptic Na^+ channels to open. Na^+enters the postsynaptic cell and causes the postsynaptic membrane to depolarize. This depolarization is called an excitatory postsynaptic potential (EPSP) and makes the postsynaptic neuron more likely to fire an action potential. Release of neurotransmitter at inhibitory synapses causes inhibitory postsynaptic potentials (IPSPs), a hyperpolarization of the presynaptic membrane. For example, when the neurotransmitter GABA (gamma-aminobutyric acid) is released from a presynaptic neuron, it binds to and opens Cl^- channels. Cl^- ions enter the cell and hyperpolarizes the membrane, making the neuron less likely to fire an action potential.

Once neurotransmission has occurred, the neurotransmitter must be removed from the synaptic cleft so the postsynaptic membrane can "reset" and be ready to receive another signal. This can be accomplished in three ways: the neurotransmitter can diffuse away from the synaptic cleft, it can be degraded by enzymes in the synaptic cleft, or it can be recycled (sometimes called reuptake) by the presynaptic neuron. Several drugs act at this step of neurotransmission. For example, some drugs that are given to Alzheimer's patients work by inhibiting acetylcholinesterase, the enzyme that degrades acetylcholine. This inhibition of the enzyme essentially increases neurotransmission at synapses that release acetylcholine. Once released, the acetylcholine stays in the cleft and can continually bind and unbind to postsynaptic receptors.

Electrical Synapse

While electrical synapses are fewer in number than chemical synapses, they are found in all nervous systems and play important and unique roles. The mode of neurotransmission in electrical synapses is quite different from that in chemical synapses. In an electrical synapse, the presynaptic and postsynaptic membranes are very close together and are actually physically connected by channel proteins forming gap junctions. Gap junctions allow current to pass directly from one cell to the next. In addition to the ions that carry this current, other molecules, such as ATP, can diffuse through the large gap junction pores.

There are key differences between chemical and electrical synapses. Because chemical synapses depend on the release of neurotransmitter molecules from synaptic vesicles to pass on their signal, there is an approximately one millisecond delay between when the axon potential reaches the presynaptic terminal and when the neurotransmitter leads to opening of postsynaptic ion channels. Additionally, this signaling is unidirectional. Signaling in electrical synapses, in contrast, is virtually instantaneous (which is important for synapses involved in key reflexes), and some electrical synapses are bidirectional. Electrical synapses are also more reliable as they are less likely to be blocked, and they are important for synchronizing the electrical activity of a group of neurons. For example, electrical synapses in the thalamus are thought to regulate slow-wave sleep, and disruption of these synapses can cause seizures.

Signal Summation

Sometimes a single EPSP is strong enough to induce an action potential in the postsynaptic neuron, but often multiple presynaptic inputs must create EPSPs around the same time for the postsynaptic neuron to be sufficiently depolarized to fire an action potential. This process is called summation and occurs at the axon hillock, as illustrated in Figure 20.16. Additionally, one neuron often has inputs from many presynaptic neurons—some excitatory and some inhibitory—so IPSPs can cancel out EPSPs and vice versa. It is the net change in postsynaptic membrane voltage that determines whether the postsynaptic cell has reached its threshold of excitation needed to fire an action potential. Together, synaptic summation and the threshold for excitation act as a filter so that random "noise" in the system is not transmitted as important information.

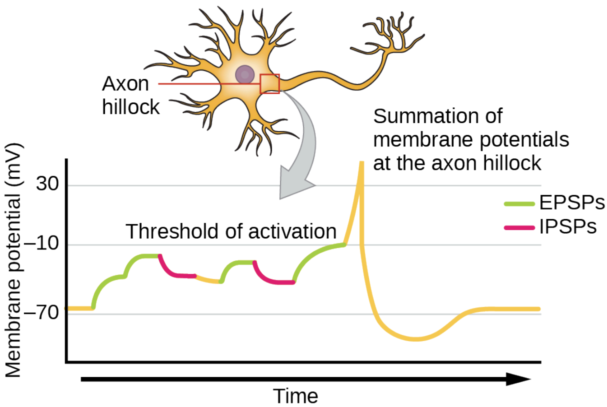


Figure 20.16 A single neuron can receive both excitatory and inhibitory inputs from multiple neurons, resulting in local membrane depolarization (EPSP input) and hyperpolarization (IPSP input). All these inputs are added together at the axon hillock. If the EPSPs are strong enough to overcome the IPSPs and reach the threshold of excitation, the neuron will fire.

Synaptic Plasticity

Synapses are not static structures. They can be weakened or strengthened. They can be broken, and new synapses can be made. Synaptic plasticity allows for these changes, which are all needed for a functioning nervous system. In fact, synaptic plasticity is the basis of learning and memory. Two processes in particular, long-term potentiation (LTP) and long-term depression (LTD) are important forms of synaptic plasticity that occur in synapses in the hippocampus, a brain region that is involved in storing memories.

Long-term Potentiation (LTP)

Long-term potentiation (LTP) is a persistent strengthening of a synaptic connection. LTP is based on the Hebbian principle: cells that fire together wire together. There are various mechanisms, none fully understood, behind the synaptic strengthening seen with LTP. One known mechanism involves a type of postsynaptic glutamate receptor, called NMDA (N-Methyl-D-aspartate) receptors, shown in Figure 20.18. These receptors are normally blocked by magnesium ions; however, when the postsynaptic neuron is depolarized by multiple presynaptic inputs in quick succession (either from one neuron or multiple neurons), the magnesium ions are forced out allowing calcium ions to pass into the postsynaptic cell. Next, Ca^{2+} ions entering the cell initiate a signaling cascade that causes a different type of glutamate receptor, called AMPA (α-amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid) receptors, to be inserted into the postsynaptic membrane, since activated AMPA receptors allow positive ions to enter the cell. So, the next time glutamate is released from the presynaptic membrane, it will have a larger excitatory effect (EPSP) on the postsynaptic cell because the binding of glutamate to these AMPA receptors will allow more positive ions into the cell. The insertion of additional AMPA receptors strengthens the synapse and means that the postsynaptic neuron is more likely to fire in response to presynaptic neurotransmitter release. Some drugs of abuse co-opt the LTP pathway, and this synaptic strengthening can lead to addiction.

Long-term Depression (LTD)

Long-term depression (LTD) is essentially the reverse of LTP: it is a long-term weakening of a synaptic connection. One mechanism known to cause LTD also involves AMPA receptors. In this situation, calcium that enters through NMDA receptors initiates a different signaling cascade, which results in the removal of AMPA receptors from the postsynaptic membrane, as illustrated in Figure 20.18. The decrease in AMPA receptors in the membrane makes the postsynaptic neuron less responsive to glutamate released from the presynaptic neuron. While it may seem counterintuitive, LTD may be just as important for learning and memory as LTP. The weakening and pruning of unused synapses allows for unimportant connections to be lost and makes the synapses that have undergone LTP that much stronger by comparison.

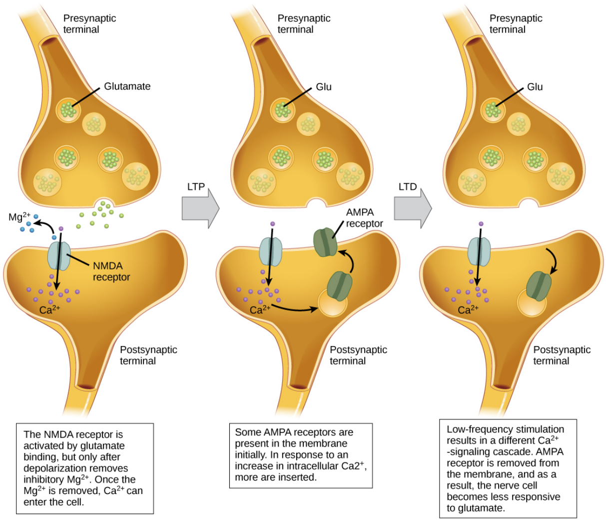


Figure 20.18 Calcium entry through postsynaptic NMDA receptors can initiate two different forms of synaptic plasticity: long-term potentiation (LTP) and long-term depression (LTD). LTP arises when a single synapse is repeatedly stimulated. This stimulation causes a calcium- and CaMKII-dependent cellular cascade, which results in the insertion of more AMPA receptors into the postsynaptic membrane. The next time glutamate is released from the presynaptic cell, it will bind to both NMDA and the newly inserted AMPA

receptors, thus depolarizing the membrane more efficiently. LTD occurs when few glutamate molecules bind to NMDA receptors at a synapse (due to a low firing rate of the presynaptic neuron). The calcium that does flow through NMDA receptors initiates a different calcineurin and protein phosphatase 1-dependent cascade, which results in the endocytosis of AMPA receptors. This makes the postsynaptic neuron less responsive to glutamate released from the presynaptic neuron.

Reading Question #5

Caffeine inhibits the action of adenosine (an inhibitory neurotransmitter). Therefore, caffeine is referred to as a

A. Stimulant

B. Depressant

C. Inhibitory neurotransmitter

D. Excitatory neurotransmitter

References

Adapted from Clark, M.A., Douglas, M., and Choi, J. (2018). Biology 2e. OpenStax. Retrieved from https://openstax.org/books/biology-2e/pages/35-introduction?query=nervous%20system&target=%7B%22index%22%3A0%2C%22type%22%3A%22search%22%7D#fig-ch35_00_01

22. Chapter 22: Sensing and Responding to Stimuli: Endocrine and Hormones

ANASTASIA CHOUVALOVA

Introduction to the Endocrine System

An animal's endocrine system controls body processes through the production, secretion, and regulation of hormones, which serve as chemical "messengers" functioning in cellular and organ activity and, ultimately, maintaining the body's homeostasis. The endocrine system plays a role in growth, metabolism, and sexual development. In humans, common endocrine system diseases include thyroid disease and diabetes mellitus. In organisms that undergo metamorphosis, the process is controlled by the endocrine system. The transformation from tadpole to frog, for example, is complex and nuanced to adapt to specific environments and ecological circumstances.

Figure 21.1 The process of amphibian metamorphosis, as seen in the tadpole-to-frog stages shown here, is hormone-driven. This constitutes one of many examples of how hormone-driven processes are essential for the survival and proper development of many organisms. (credit "tadpole": modification of work by Brian Gratwicke)

Different Types of Hormones

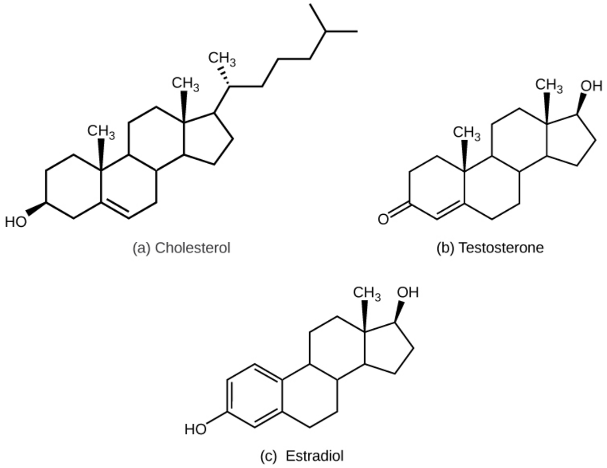
Maintaining homeostasis within the body requires the coordination of many different systems and organs. Communication between neighboring cells, and between cells and tissues in distant parts of the body, occurs through the release of chemicals called hormones. Hormones are released into body fluids (usually blood) that carry these chemicals to their target cells. At the target cells, which are cells that have a receptor for a signal or ligand from a signal cell, the hormones elicit a response. The cells, tissues, and organs that secrete hormones make up the endocrine system. Examples of glands of the endocrine system include the adrenal glands, which produce hormones such as epinephrine and norepinephrine that regulate responses to stress, and the thyroid gland, which produces thyroid hormones that regulate metabolic rates.

Although there are many different hormones in the human body, they can be divided into three classes based on their chemical structure: lipid-derived, amino acid-derived, and peptide (peptide and proteins) hormones. One of the key distinguishing features of lipid-derived hormones is that they can diffuse across plasma membranes whereas the amino acid-derived and peptide hormones cannot.

Lipid-Derived Hormones (or Lipid-soluble Hormones)

Most **lipid hormones** are derived from cholesterol and thus are structurally similar to it, as illustrated in Figure 21.2. The primary class of lipid hormones in humans is the steroid hormones. Chemically, these hormones are usually ketones or alcohols; their chemical names will end in "-ol" for alcohols or "-one" for ketones. Examples of steroid hormones include estrogens (such as estradiol) and androgens (such as testosterone), both of which regulate bone and tissue development in all humans.

Figure 21.2



Gonadal hormones, produced by the gonads, include both steroid and peptide hormones. Androgens and estrogens resemble one another in chemical structure and originate from the same molecule. Estrogens are chief drivers of sexual development in an ovarian reproductive system, while androgens drive development in a testicular reproductive system. The ovaries produce steroid hormones such as estradiol and progesterone. When androgens are produced, some of them are later converted to estrogens. Minute amounts of estrogen occur through aromatase actions in adipose, brain, skin, and bone, which convert testosterone to estrogen. The testes and the adrenal cortex both secrete testosterone.

Other steroid hormones include aldosterone and cortisol, which are released by the adrenal glands along with some other types of androgens. Steroid hormones are insoluble in water, and they are transported by transport proteins in blood. As a result, they remain in circulation longer than peptide hormones. For example, cortisol has a half-life of 60 to 90 minutes, while epinephrine, an amino acid derived-hormone, has a half-life of approximately one minute.

Reading Question #1

Which of the following is not a class of hormone?

A. Peptide

B. Amino-acid derived

C. Lipid-soluble hormone

D. Cortisol

Amino Acid-Derived Hormones

The **amino acid-derived hormones** are relatively small molecules that are derived from the amino acids tyrosine and tryptophan, shown in Figure 21.3. If a hormone is amino acid-derived, its chemical name will end in "-ine". Examples of amino acid-derived hormones include epinephrine and norepinephrine, which are synthesized in the medulla of the adrenal glands, and thyroxine, which is produced by the thyroid gland. The pineal gland in the brain makes and secretes melatonin which regulates sleep cycles.

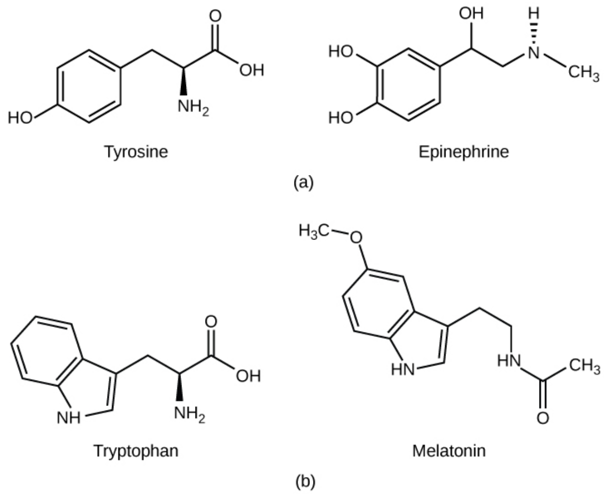


Figure 21.3 (a) The hormone epinephrine, which triggers the fight-or-flight response, is derived from the amino acid tyrosine. (b) The hormone melatonin, which regulates circadian rhythms, is derived from the amino acid tryptophan.

Peptide Hormones

The structure of **peptide hormones** is that of a polypeptide chain (chain of amino acids). The peptide hormones include molecules that are short polypeptide chains, such as antidiuretic hormone and oxytocin produced in the brain and released into the blood in the posterior pituitary gland. This class also includes small proteins, like growth hormones produced by the pituitary, and large glycoproteins such as follicle-stimulating hormone produced by the pituitary. Figure 21.4 illustrates these peptide hormones.

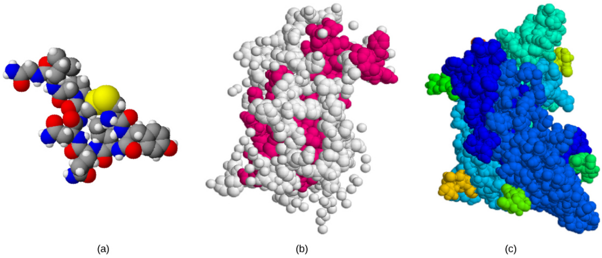


Figure 21.4 The structures of peptide hormones (a) oxytocin, (b) growth hormone, and (c) follicle-stimulating hormone are shown. These peptide hormones are much larger than those derived from cholesterol or amino acids.

Reading Question #2

Researchers at Texas Tech University Health Sciences Centre may have discovered a novel hormone that they have called Hormone X. Here are some of its properties:

- It is a steroid hormone that resembles testosterone.
- This hormone is produced by the testes.
- When detected in the bloodstream, it is attached to transport proteins.
- It has a long half-life.

Based on this description, which of the following is Hormone X most likely to be an example of? Choose all that apply.

A. Lipid-soluble hormone

B. Peptide

C. Amino-acid derived

D. Gonadal

Career Connection

Endocrinologist

An endocrinologist is a medical doctor who specializes in treating disorders of the endocrine glands, hormone systems, and glucose and lipid metabolic pathways. An endocrine surgeon specializes in the surgical treatment of endocrine diseases and glands. Some of the diseases that are managed by endocrinologists: disorders of the pancreas (diabetes mellitus), disorders of the pituitary (gigantism, acromegaly, and pituitary dwarfism), disorders of the thyroid gland (goiter and Graves' disease), and disorders of the adrenal glands (Cushing's disease and Addison's disease).

Endocrinologists are required to assess patients and diagnose endocrine disorders through extensive use of laboratory tests. Many endocrine diseases are diagnosed using tests that stimulate or suppress endocrine organ functioning. Blood samples are then drawn to determine the effect of stimulating or suppressing an endocrine organ on the production of hormones. For example, to diagnose diabetes mellitus, patients are required to fast for 12 to 24 hours. They are then given a sugary drink, which stimulates the pancreas to produce insulin to decrease blood glucose levels. A blood sample is taken one to two hours after the sugar drink is consumed. If the pancreas is functioning properly, the blood glucose level will be within a normal range. Another example is the A1C test, which can be performed during blood screening. The A1C test measures average blood glucose levels over the past two to three months by examining how well the blood glucose is being managed over a long time.

Once a disease has been diagnosed, endocrinologists can prescribe lifestyle changes and/or medications to treat the disease. Some cases of diabetes mellitus can be managed by exercise, weight loss, and a healthy diet; in other cases, medications may be required to enhance insulin release. If the disease cannot be controlled by these means, the endocrinologist may prescribe insulin injections.

In addition to clinical practice, endocrinologists may also be involved in primary research and development activities. For example, ongoing islet transplant research is investigating how healthy pancreas islet cells may be transplanted into diabetic patients. Successful islet transplants may allow patients to stop taking insulin injections.

How hormones work

Hormones mediate changes in target cells by binding to specific **hormone receptors.** In this way, even though hormones circulate throughout the body and come into contact with many different cell types, they only affect cells that possess the necessary receptors. Receptors for a specific hormone may be found on many different cells or may be limited to a small number of specialized cells. For example, thyroid hormones act on many different tissue types, stimulating metabolic activity throughout the body. Cells can have many receptors for the same hormone but often also possess receptors for different types of hormones. The number of receptors that respond to a hormone determines the cell's sensitivity to that hormone, and the resulting cellular response. Additionally, the number of receptors that respond to a hormone can change over time, resulting in increased or decreased cell sensitivity. In up-regulation, the number of receptors increases in response to rising hormone levels, making the cell more sensitive to the hormone and allowing for more cellular activity. When the number of receptors decreases in response to rising hormone levels, called **down-regulation,** cellular activity is reduced.

Receptor binding alters cellular activity and results in an increase or decrease in normal body processes. Depending on the location of the protein receptor on the target cell and the chemical structure of the hormone, hormones can mediate changes directly by binding to **intracellular hormone receptors** and modulating gene transcription, or indirectly by binding to cell surface receptors and stimulating signaling pathways.

Intracellular Hormone Receptors

Lipid-derived (soluble) hormones such as steroid hormones diffuse across the membranes of the endocrine cell. Once outside the cell, they bind to transport proteins that keep them soluble in the bloodstream. At the target cell, the hormones are released from the carrier protein and diffuse across the lipid bilayer of the plasma membrane of cells. The steroid hormones pass through the plasma membrane of a target cell and adhere to intracellular receptors residing in the cytoplasm or in the nucleus. The cell signaling pathways induced by the steroid hormones regulate specific genes on the cell's DNA. The hormones and receptor complex act as transcription regulators by increasing or decreasing the synthesis of mRNA molecules of specific genes. This, in turn, determines the amount of corresponding protein that is synthesized by altering gene expression. This protein can be used either to change the structure of the cell or to produce enzymes that catalyze chemical reactions. In this way, the steroid hormone regulates specific cell processes as illustrated in Figure 21.5.

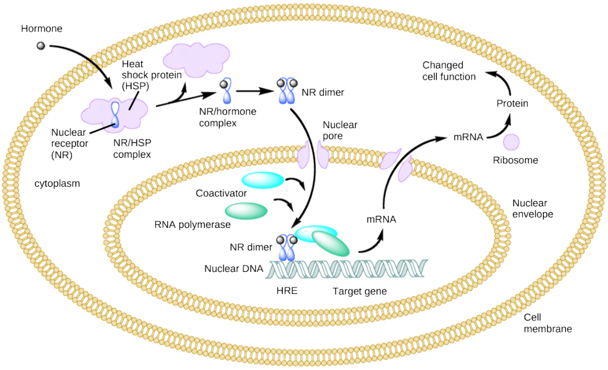


Figure 21.5 An intracellular nuclear receptor (NR) *is located in the cytoplasm bound to a heat shock protein* (HSP). *Upon hormone binding, the receptor dissociates from the heat shock protein and translocates to the nucleus. In the nucleus, the hormone-receptor complex binds to a DNA sequence called a hormone response element* (HRE), *which triggers gene transcription and translation. The corresponding protein product can then mediate changes in cell function.*

Plasma Membrane Hormone Receptors

Amino acid-derived hormones (with the exception of thyroxine) and polypeptide hormones are not lipid-derived (lipid-soluble) and therefore cannot diffuse through the plasma membrane of cells. Lipid insoluble hormones bind to receptors on the outer surface of the plasma membrane, via **plasma membrane hormone receptors.** Unlike steroid hormones, lipid insoluble hormones do not directly affect the target cell because they cannot enter the cell and act directly on DNA. Binding of these hormones to a cell surface receptor results in activation of a signaling pathway; this triggers intracellular activity and carries out the specific effects associated with the hormone. In this way, nothing passes through the cell membrane; the hormone that binds at the surface remains at the surface of the cell while the intracellular product remains inside the cell.

Reading Question #3

Which type of hormone is epinephrine; which hormone receptor does it bind to?

A. Lipid-soluble hormone; plasma membrane hormone receptor

B. Peptide derived hormone; plasma membrane hormone receptor

C. Amino acid derived hormone; plasma membrane hormone receptor

D. Lipid-soluble hormone; intracellular hormone receptor

E. Peptide derived hormone; intracellular hormone receptor

F. Amino acid derived hormone; intracellular hormone receptor

Role of hormones in physiological processes

Hormones have a wide range of effects and modulate many different body processes. The key regulatory processes that will be examined here are those affecting the growth process and the stress response.

Hormonal Regulation of Growth

Hormonal regulation is required for the growth and replication of most cells in the body. Growth hormone (GH), produced by the anterior portion of the pituitary gland, accelerates the rate of protein synthesis, particularly in skeletal muscle and bones. Growth hormone has direct and indirect mechanisms of action. The first direct action of GH is stimulation of triglyceride breakdown (lipolysis) and release into the blood by adipocytes. This results in a switch by most tissues from utilizing glucose as an energy source to utilizing fatty acids. This process is called a glucose-sparing effect. In another direct mechanism, GH stimulates glycogen breakdown in the liver; the glycogen is then released into the blood as glucose. Blood glucose levels increase as most tissues are utilizing fatty acids instead of glucose for their energy needs. The GH mediated increase in blood glucose levels is called a diabetogenic effectbecause it is similar to the high blood glucose levels seen in diabetes mellitus.

The indirect mechanism of GH action is mediated by insulin-like growth factors (IGFs) or somatomedins, which are a family of growth-promoting proteins produced by the liver, which stimulates tissue growth. IGFs stimulate the uptake of amino acids from the blood, allowing the formation of new proteins, particularly in skeletal muscle cells, cartilage cells, and other target cells, as shown in Figure 21.6. This is especially important after a meal, when glucose and amino acid concentration levels are high in the blood. GH levels are regulated by two hormones produced by the hypothalamus. GH release is stimulated by growth hormone-releasing hormone (GHRH) and is inhibited by growth hormone-inhibiting hormone (GHIH), also called somatostatin.

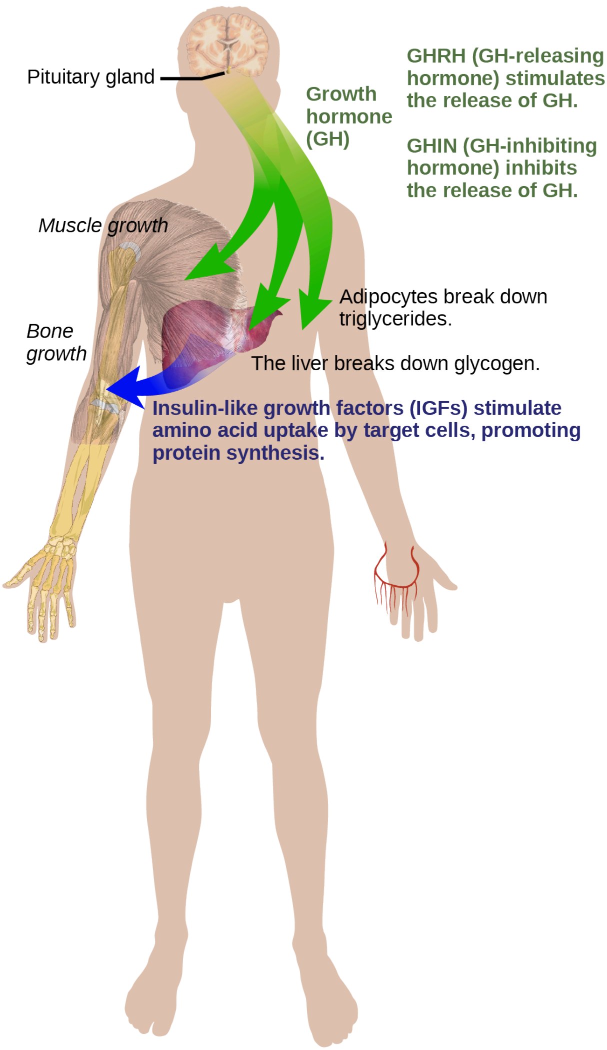


Figure 21.6 Growth hormone directly accelerates the rate of protein synthesis in skeletal muscle and bones. Insulin-like growth factor 1 (IGF-1) is activated by growth hormone and also allows formation of new proteins in muscle cells and bone. (credit: modification of work by Mikael Häggström)

A balanced production of growth hormone is critical for proper development. Underproduction of GH in adults does not appear to cause any abnormalities, but in children it can result in pituitary dwarfism, in which growth is reduced. Pituitary dwarfism is characterized by symmetric body formation. In some cases, individuals are under 30 inches in height. Oversecretion of growth hormone can lead to gigantism in children, causing excessive growth. In some documented cases, individuals can reach heights of over eight feet. In adults, excessive GH can lead to acromegaly, a condition in which there is enlargement of bones in the face, hands, and feet that are still capable of growth.

Hormonal Regulation of Stress

When a threat or danger is perceived, the body responds by releasing hormones that will ready it for the "fight-or-flight" response. The effects of this response are familiar to anyone who has been in a stressful situation: increased heart rate, dry mouth, and hair standing up.

Evolution Connection

Fight-or-Flight Response

Interactions of the endocrine hormones have evolved to ensure the body's internal environment remains stable. Stressors are stimuli that disrupt homeostasis. The sympathetic division of the vertebrate autonomic nervous system has evolved the fight-or-flight response to counter stress-induced disruptions of homeostasis. In the initial alarm phase, the sympathetic nervous system stimulates an increase in energy levels through increased blood glucose levels. This prepares the body for physical activity that may be required to respond to stress: to either fight for survival or to flee from danger.

However, some stresses, such as illness or injury, can last for a long time. Glycogen reserves, which provide energy in the short-term response to stress, are exhausted after several hours and cannot meet long-term energy needs. If glycogen reserves were the only energy source available, neural functioning could not be maintained once the reserves became depleted due to the nervous system's high requirement for glucose. In this situation, the body has evolved a response to counter long-term stress through the actions of the glucocorticoids, which ensure that long-term energy requirements can be met. The glucocorticoids mobilize lipid and protein reserves, stimulate gluconeogenesis, conserve glucose for use by neural tissue, and stimulate the conservation of salts and water. The mechanisms to maintain homeostasis that are described here are those observed in the human body. However, the fight-or-flight response exists in some form in all vertebrates.

The sympathetic nervous system regulates the stress response via the hypothalamus. Stressful stimuli cause the hypothalamus to signal the adrenal medulla (which mediates short-term stress responses) via nerve impulses, and the adrenal cortex, which mediates long-term stress responses, via the hormone adrenocorticotropic hormone (ACTH), which is produced by the anterior pituitary.

Short-term Stress Response

When presented with a stressful situation, the body responds by calling for the release of hormones that provide a burst of energy. The hormones **epinephrine** (also known as adrenaline) and **norepinephrine** (also known as noradrenaline) are released by the adrenal medulla. How do these hormones provide a burst of energy? Epinephrine and norepinephrine increase blood glucose levels by stimulating the liver and skeletal muscles to break down glycogen and by stimulating glucose release by liver cells. Additionally, these hormones increase oxygen availability to cells by increasing the heart rate and dilating the bronchioles. The hormones also prioritize body function by increasing blood supply to essential organs such as the heart, brain, and skeletal muscles, while restricting blood flow to organs not in immediate need, such as the skin, digestive system, and kidneys. Epinephrine and norepinephrine are collectively called catecholamines.

Long-term Stress Response

Long-term stress response differs from short-term stress response. The body cannot sustain the bursts of energy mediated by epinephrine and norepinephrine for long times. Instead, other hormones come into play. In a long-term stress response, the hypothalamus triggers the release of ACTH from the anterior pituitary gland. The adrenal cortex is stimulated by ACTH to release steroid hormones called **corticosteroids.** Corticosteroids turn on transcription of certain genes in the nuclei of target cells. They change enzyme concentrations in the cytoplasm and affect cellular metabolism. There are two main corticosteroids: glucocorticoids such as **cortisol,** and mineralocorticoids such as aldosterone. These hormones target the breakdown of fat into fatty acids in the adipose tissue. The fatty acids are released into the bloodstream for other tissues to use for ATP production. The glucocorticoids primarily affect glucose metabolism by stimulating glucose synthesis. Glucocorticoids also have anti-inflammatory properties through inhibition of the immune system. For example, cortisone is used as an anti-inflammatory medication; however, it cannot be used long term as it increases susceptibility to disease due to its immune-suppressing effects.

Mineralocorticoids function to regulate ion and water balance of the body. The hormone aldosterone stimulates the reabsorption of water and sodium ions in the kidney, which results in increased blood pressure and volume.

Hypersecretion of glucocorticoids can cause a condition known as **Cushing's disease**, characterized by a shifting of fat storage areas of the body. This can cause the accumulation of adipose tissue in the face and neck, and excessive glucose in the blood. Hyposecretion of the corticosteroids can cause **Addison's disease,** which may result in bronzing of the skin, hypoglycemia, and low electrolyte levels in the blood.

Regulation of Hormone Production

Hormone production and release are primarily controlled by negative feedback. In negative feedback systems, a stimulus elicits the release of a substance; once the substance reaches a certain level, it sends a signal that stops further release of the substance. In this way, the concentration of hormones in blood is maintained within a narrow range. For example, the anterior pituitary signals the thyroid to release thyroid hormones. Increasing levels of these hormones in the blood then give feedback to the hypothalamus and anterior pituitary to inhibit further signaling to the thyroid gland, as illustrated in Figure 21.7. There are three mechanisms by which endocrine glands are stimulated to synthesize and release hormones: humoral stimuli, hormonal stimuli, and neural stimuli.

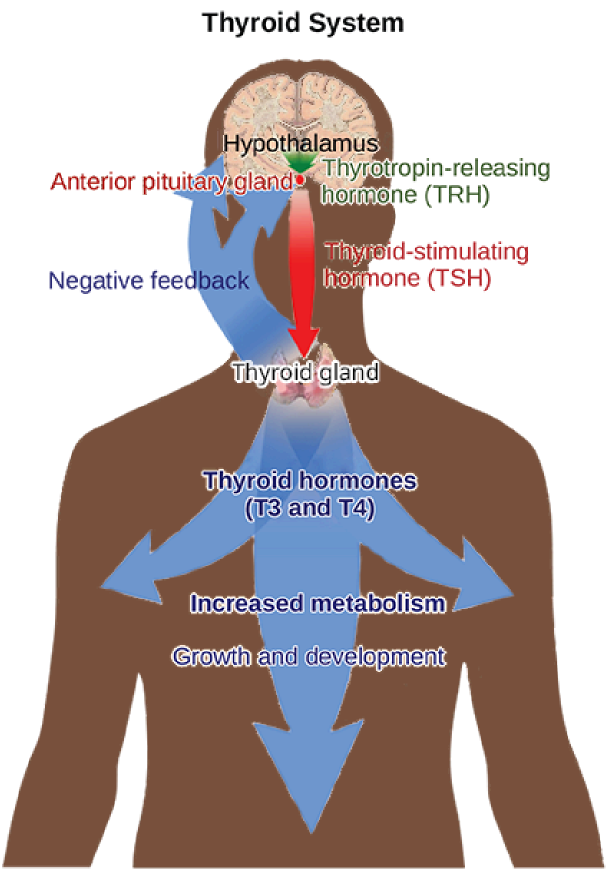


Figure 21.7

Humoral Stimuli

The term "humoral" is derived from the term "humor," which refers to bodily fluids such as blood. A **humoral stimulus** refers to the control of hormone release in response to changes in extracellular fluids such as blood or the ion concentration in the blood. For example, a rise in blood glucose levels triggers the pancreatic release of insulin. Insulin causes blood glucose levels to drop, which signals the pancreas to stop producing insulin in a negative feedback loop.

Hormonal Stimuli

Hormonal stimuli refers to the release of a hormone in response to another hormone. A number of endocrineglands release hormones when stimulated by hormones released by other endocrine glands. For example, the hypothalamus produces hormones that stimulate the anterior portion of the pituitary gland. The anterior pituitary in turn releases hormones that regulate hormone production by other endocrine glands. The anterior pituitary releases the thyroid-stimulating hormone, which then stimulates the thyroid gland to produce the hormones T_3 and T_4. As blood concentrations of T_3 and T_4 rise, they inhibit both the pituitary and the hypothalamus in a negative feedback loop.

Neural Stimuli

In some cases, the nervous system directly stimulates endocrine glands to release hormones, which is referred to as **neural stimuli**. Recall that in a short-term stress response, the hormones epinephrine and norepinephrine are important for providing the bursts of energy required for the body to respond. Here, neuronal signaling from the sympathetic nervous system directly stimulates the adrenal medulla to release the hormones epinephrine and norepinephrine in response to stress.

Reading Question #4

Which hormone is primarily responsible for calcium homeostasis when blood calcium levels are too high?

A. Glucagon

B. Insulin

C. Calcitonin

D. Parathyroid hormone

Endocrine Glands

Both the endocrine and nervous systems use chemical signals to communicate and regulate the body's physiology. The endocrine system releases hormones that act on target cells to regulate development, growth, energy metabolism, reproduction, and many behaviors. The nervous system releases neurotransmitters or neurohormones that regulate neurons, muscle cells, and endocrine cells. Because the neurons can regulate the release of hormones, the nervous and endocrine systems work in a coordinated manner to regulate the body's physiology.

Hypothalamic-Pituitary Axis

The hypothalamus in vertebrates integrates the endocrine and nervous systems. The hypothalamus is an endocrine organ located in the diencephalon of the brain. It receives input from the body and other brain areas and initiates endocrine responses to environmental changes. The hypothalamus acts as an endocrine organ, synthesizing hormones and transporting them along axons to the posterior pituitary gland. It synthesizes and secretes regulatory hormones that control the endocrine cells in the anterior pituitary gland. The hypothalamus contains autonomic centers that control endocrine cells in the adrenal medulla via neuronal control.

The **pituitary gland**, sometimes called the hypophysis or "master gland" is located at the base of the brain in the sella turcica, a groove of the sphenoid bone of the skull, illustrated in Figure 21.8. It is attached to the hypothalamus via a stalk called the **pituitary stalk** (or infundibulum). The anterior portion of the pituitary gland is regulated by releasing or release-inhibiting hormones produced by the hypothalamus, and the posterior pituitary receives signals via neurosecretory cells to release hormones produced by the hypothalamus. The pituitary has two distinct regions—the anterior pituitary and the posterior pituitary—which between them secrete nine different peptide or protein hormones. The posterior lobe of the pituitary gland contains axons of the hypothalamic neurons.

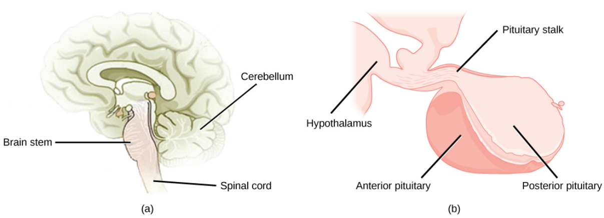


Figure 21.8 The pituitary gland is located at (a) the base of the brain and (b) connected to the hypothalamus by the pituitary stalk. (credit a: modification of work by NCI; credit b: modification of work by Gray's Anatomy)

Anterior Pituitary

The **anterior pituitary gland**, or adenohypophysis, is surrounded by a capillary network that extends from the hypothalamus, down along the infundibulum, and to the anterior pituitary. This capillary network is a part of the **hypophyseal portal system** that carries substances from the hypothalamus to the anterior pituitary and hormones from the anterior pituitary into the circulatory system. A portal system carries blood from one capillary network to another; therefore, the hypophyseal portal system allows hormones produced by the hypothalamus to be carried directly to the anterior pituitary without first entering the circulatory system.

The anterior pituitary produces seven hormones: growth hormone (GH), prolactin (PRL), thyroid-stimulating hormone (TSH), melanin-stimulating hormone (MSH), adrenocorticotropic hormone (ACTH), follicle-stimulating hormone (FSH), and luteinizing hormone (LH). Anterior pituitary hormones are sometimes referred to as tropic hormones, because they control the functioning of other organs. While these hormones are produced by the anterior pituitary, their production is controlled by regulatory hormones produced by the hypothalamus. These regulatory hormones can be releasing hormones or inhibiting hormones, causing more or less of the anterior pituitary hormones to be secreted. These travel from the hypothalamus through the hypophyseal portal system to the anterior pituitary where they exert their effect. Negative feedback then regulates how much of these regulatory hormones are released and how much anterior pituitary hormone is secreted.

Posterior Pituitary

The **posterior pituitary** is significantly different in structure from the anterior pituitary. It is a part of the brain, extending down from the hypothalamus, and contains mostly nerve fibers and neuroglial cells, which support axons that extend from the hypothalamus to the posterior pituitary. The posterior pituitary and the infundibulum together are referred to as the neurohypophysis.

The hormones antidiuretic hormone (ADH), also known as vasopressin, and oxytocin are produced by neurons in the hypothalamus and transported within these axons along the infundibulum to the posterior pituitary. They are released into the circulatory system via neural signaling from the hypothalamus. These hormones are considered to be posterior pituitary hormones, even though they are produced by the hypothalamus, because that is where they are released into the circulatory system. The posterior pituitary itself does not produce hormones, but instead stores hormones produced by the hypothalamus and releases them into the bloodstream.

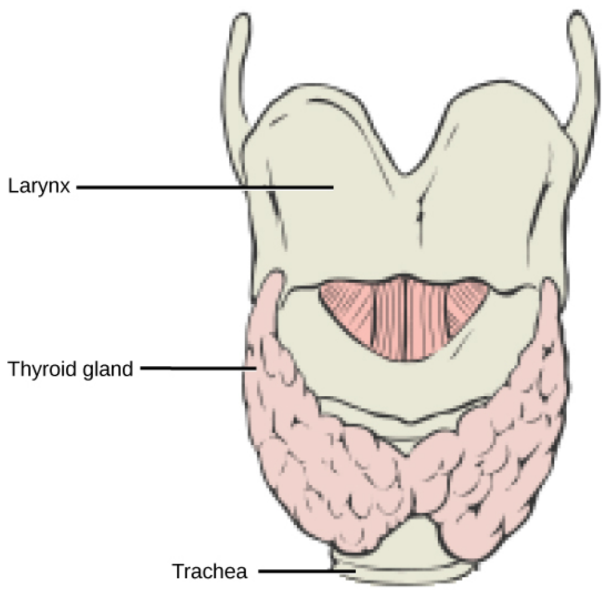
Endocrine Gland	Associated Hormones	Effect
Hypothalamus	releasing and inhibiting hormones	regulate hormone release from pituitary gland; produce oxytocin; produce uterine contractions and milk secretion in breast tissue
	antidiuretic hormone (ADH)	water reabsorption from kidneys; vasoconstriction to increase blood pressure
Pituitary (Anterior)	growth hormone (GH)	promotes growth of body tissues, protein synthesis; metabolic functions
	prolactin (PRL)	promotes milk production
	thyroid stimulating hormone (TSH)	stimulates thyroid hormone release
	adrenocorticotropic hormone (ACTH)	stimulates hormone release by adrenal cortex, glucocorticoids
	follicle-stimulating hormone (FSH)	stimulates gamete production (both ova and sperm); secretion of estradiol
	luteinizing hormone (LH)	stimulates androgen production by gonads; ovulation, secretion of progesterone
	melanocyte-stimulating hormone (MSH)	stimulates melanocytes of the skin increasing melanin pigment production.
Pituitary (Posterior)	antidiuretic hormone (ADH)	stimulates water reabsorption by kidneys
	oxytocin	stimulates uterine contractions during childbirth; milk ejection; stimulates ductus deferens and prostate gland contraction during emission

Table 21.1 Summary of the hormones secreted by the hypothalamus, anterior pituitary, and posterior pituitary.

Thyroid Gland

The **thyroid gland** is located in the neck, just below the larynx and in front of the trachea, as shown in Figure 21.9. It is a butterfly-shaped gland with two lobes that are connected by the isthmus. It has a dark red color due to its extensive vascular system. When the thyroid swells due to dysfunction, it can be felt under the skin of the neck.

Figure 21.9



Thyroid follicle cells synthesize the hormone thyroxine, which is also known as T_4 because it contains four atoms of iodine, and triiodothyronine, also known as T_3 because it contains three atoms of iodine. Follicle cells are stimulated to release stored T_3 and T_4 by thyroid stimulating hormone (TSH), which is produced by the anterior pituitary. These thyroid hormones increase the rates of mitochondrial ATP production.

Adrenal Glands

The **adrenal glands** are associated with the kidneys; one gland is located on top of each kidney as illustrated in Figure 21.10. The adrenal glands consist of an outer adrenal cortex and an inner adrenal medulla. These regions secrete different hormones.

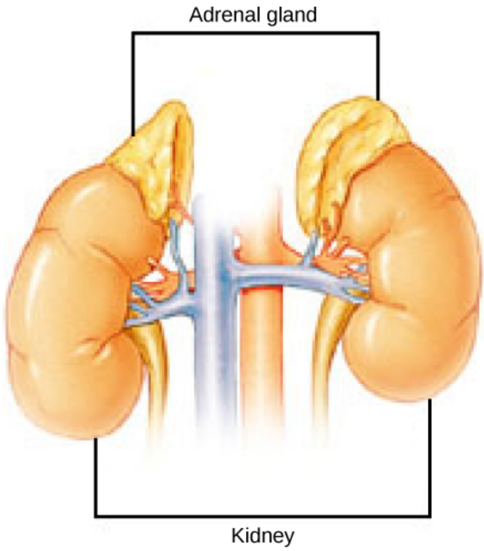


Figure 21.10 The location of the adrenal glands on top of the kidneys is shown. (credit: modification of work by NCI)

Adrenal Cortex

The **adrenal cortex** is made up of layers of epithelial cells and associated capillary networks. These layers form three distinct regions: an outer zona glomerulosa that produces mineralocorticoids, a middle zona fasciculata that produces glucocorticoids, and an inner zona reticularis that produces androgens.

The main mineralocorticoid is aldosterone, which regulates the concentration of Na^+ ions in urine, sweat, pancreas, and saliva.

Aldosterone release from the adrenal cortex is stimulated by a decrease in blood concentrations of sodium ions, blood volume, or blood pressure, or by an increase in blood potassium levels.

The three main glucocorticoids are cortisol, corticosterone, and cortisone. The glucocorticoids stimulate the synthesis of glucose and gluconeogenesis (converting a non-carbohydrate to glucose) by liver cells and they promote the release of fatty acids from adipose tissue. These hormones increase blood glucose levels to maintain levels within a normal range between meals. These hormones are secreted in response to ACTH and levels are regulated by negative feedback.

The adrenal cortex also produces small amounts of testosterone precursor, although the role of this additional hormone production is not fully understood. Testosterone is a type of androgen that is mainly produced by the gonads in both males and females, and promotes a suite of characteristics such as the growth and development of the testes and penis, increased skeletal and muscular growth, enlargement of the larynx, increased growth and redistribution of body hair, and increased sexual drive. Testosterone secretion is regulated by both the hypothalamus and the anterior pituitary gland. The hypothalamus sends releasing hormones that stimulate the release of gonadotropins from the anterior pituitary gland. Testosterone produced in small amounts in the adrenal cortex may work with sex hormones released from the gonads.

Adrenal Medulla

The **adrenal medulla** contains large, irregularly shaped cells that are closely associated with blood vessels. These cells are innervated by preganglionic autonomic nerve fibers from the central nervous system.

The adrenal medulla contains two types of secretory cells: one that produces epinephrine (adrenaline) and another that produces norepinephrine (noradrenaline). Epinephrine is the primary adrenal medulla hormone accounting for 75 to 80 percent of its secretions. Epinephrine and norepinephrine increase heart rate, breathing rate, cardiac muscle contractions, blood pressure, and blood glucose levels. They also accelerate the breakdown of glucose in skeletal muscles and stored fats in adipose tissue.

The release of epinephrine and norepinephrine is stimulated by neural impulses from the sympathetic nervous system. Secretion of these hormones is stimulated by acetylcholine release from preganglionic sympathetic fibers innervating the adrenal medulla. These neural impulses originate from the hypothalamus in response to stress to prepare the body for the fight-or-flight response.

Other notable endocrine glands

Some other notable endocrine glands include the **parathyroid gland**, **pancreas**, **pineal glands,** and **gonads.** You will find brief summaries of each of these glands, respectively, below.

Let's start with the parathyroid gland, which most people have two to six of. The parathyroid gland, fittingly, secretes a hormone called parathyroid hormone which is responsible for increasing blood calcium levels. Parathyroid hormone (1) enhances reabsorption of Ca^{2+} by the kidneys, (2) stimulates osteoclast activity and inhibits osteoblast activity, and (3) it stimulates synthesis and secretion of calcitriol by the kidneys, which enhances Ca^{2+} absorption by the digestive system.

Next we also have the pancreas which secretes two key hormones responsible for regulating blood glucose levels. The pancreatic islets contain two primary cell types: alpha cells, which produce the hormone glucagon, and beta cells, which produce the hormone insulin. These hormones regulate blood glucose levels. As blood glucose levels decline, alpha cells release glucagon to raise the blood glucose levels by increasing rates of glycogen breakdown and glucose release by the liver. When blood glucose levels rise, such as after a meal, beta cells release insulin to lower blood glucose levels by increasing the rate of glucose uptake in most body cells, and by increasing glycogen synthesis in skeletal muscles and the liver. Together, glucagon and insulin regulate blood glucose levels.

Thirdly, we have the pineal gland which secretes melatonin (Note that melatonin and serotonin are both derived from an essential amino acid called tryptophan). In some mammals, melatonin has an inhibitory affect on reproductive functions by decreasing production and maturation of sperm, oocytes, and reproductive organs. Melatonin is an effective antioxidant, protecting the CNS from free radicals such as nitric oxide and hydrogen peroxide. Lastly, melatonin is involved in biological rhythms, particularly circadian rhythms such as the sleep-wake cycle and eating habits.

Lastly, we will briefly discuss the gonads. The gonads—the testes and ovaries in males and females, respectively—produce steroid hormones. The testes produce androgens, testosterone being the most prominent, which allow for the growth and development of the testes and penis, increased skeletal and muscular growth, enlargement of the larynx, increased growth and redistribution of body hair, and the production of sperm cells. The ovaries produce some testosterone, estradiol and progesterone, which cause secondary sex characteristics and prepare the body for childbirth.

Reading Question #5

An individual with Diabetes Type I cannot produce _________ and therefore, may experience high blood glucose levels. Which hormone is not produced in individuals with Type I diabetes?

A. Insulin

B. Glucagon

C. Parathyroid hormone

D. Thyroid hormone

References

Adapted from Clark, M.A., Douglas, M., and Choi, J. (2018). Biology 2e. OpenStax. Retrieved from https://openstax.org/books/biology-2e/pages/1-introduction

23. Chapter 23: Obtain and Use Energy: Circulatory and Water/Nutrient Transport

MASON TEDESCHI

Animals: Circulation

In all animals, except a few simple types, the circulatory system is used to transport nutrients and gases through the body. Simple diffusion allows some water, nutrient, waste, and gas exchange into primitive animals that are only a few cell layers thick; however, bulk flow is the only method by which the entire body of larger more complex organisms is accessed.

Circulatory System Architecture

The circulatory system is effectively a network of cylindrical vessels: the arteries, veins, and capillaries that emanate from a pump, the heart. In all vertebrate organisms, as well as some invertebrates, this is a closed-loop system, in which the blood is not free in a cavity. In a closed circulatory system, blood is contained inside blood vessels and circulates unidirectionally from the heart around the systemic circulatory route, then returns to the heart again, as illustrated in Figure 22.1 a. As opposed to a closed system, arthropods—including insects, crustaceans, and most mollusks—have an open circulatory system, as illustrated in Figure 22.1 b. In an open circulatory system, the blood is not enclosed in the blood vessels but is pumped into a cavity called a hemocoel and is called hemolymph because the blood mixes with the interstitial fluid. As the heart beats and the animal moves, the hemolymph circulates around the organs within the body cavity and then reenters the hearts through openings called ostia. This movement allows for gas and nutrient exchange. An open circulatory system does not use as much energy as a closed system to operate or to maintain; however, there is a trade-off with the amount of blood that can be moved to metabolically active organs and tissues that require high levels of oxygen. In fact, one reason that insects with wing spans of up to two feet wide (70 cm) are not around today is probably because they were outcompeted by the arrival of birds 150 million years ago. Birds, having a closed circulatory system, are thought to have moved more agilely, allowing them to get food faster and possibly to prey on the insects.

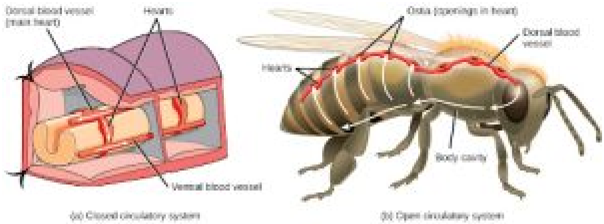


Figure 22.1 In (a) closed circulatory systems, the heart pumps blood through vessels that are separate from the interstitial fluid of the body. Most vertebrates and some invertebrates, like this annelid earthworm, have a closed circulatory system. In (b) open circulatory systems, a fluid called hemolymph is pumped through a blood vessel that empties into the body cavity. Hemolymph returns to the blood vessel through openings called ostia. Arthropods like this bee and most mollusks have open circulatory systems.

Reading Question #1

All of the following have blood vessels except:

A. Birds

B. Humans

C. Fish

D. Crabs

Circulatory System Variation in Animals

The circulatory system varies from simple systems in invertebrates to more complex systems in vertebrates. The simplest animals, such as the sponges (Porifera) and rotifers (Rotifera), do not need a circulatory system because diffusion allows adequate exchange of water, nutrients, and waste, as well as dissolved gases, as shown in Figure 22.2 a. Organisms that are more complex but still only have two layers of cells in their body plan, such as jellies (Cnidaria) and comb jellies (Ctenophora) also use diffusion through their epidermis and internally through the gastrovascular compartment. Both their internal and external tissues are bathed in an aqueous environment and exchange fluids by diffusion on both sides, as illustrated in Figure 22.2 b. Exchange of fluids is assisted by the pulsing of the jellyfish body.

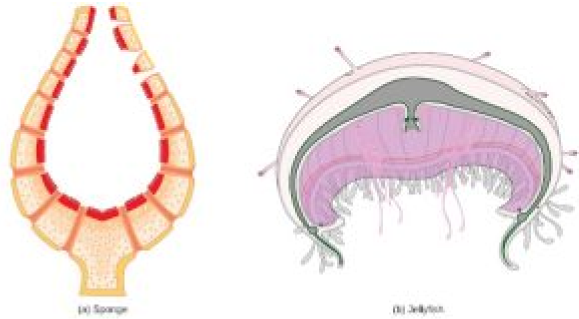


Figure 22.2 Simple animals consisting of a single cell layer such as the (a) sponge or only a few cell layers such as the (b) jellyfish do not have a circulatory system. Instead, gases, nutrients, and wastes are exchanged by diffusion.

For more complex organisms, diffusion is not efficient for cycling gases, nutrients, and waste effectively through the body; therefore, more complex circulatory systems evolved. Most arthropods and many mollusks have open circulatory systems. In an open system, an elongated beating heart pushes the hemolymph through the body and muscle contractions help to move fluids. The larger more complex crustaceans, including lobsters, have developed arterial-like vessels to push blood through their bodies, and the most active mollusks, such as squids, have evolved a closed circulatory system and are able to move rapidly to catch prey. Closed circulatory systems are a characteristic of vertebrates; however, there are significant differences in the structure of the heart and the circulation of blood between the different vertebrate groups due to adaptation during evolution and associated differences in anatomy. Figure 22.3 illustrates the basic circulatory systems of some vertebrates: fish, amphibians, reptiles, and mammals.

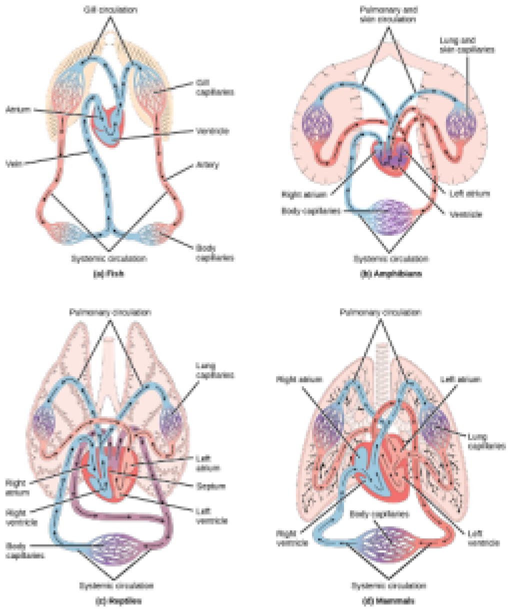


Figure 22.3 (a) Fish have the simplest circulatory systems of the vertebrates: blood flows unidirectionally from the two-chambered heart through the gills and then the rest of the body. (b) Amphibians have two circulatory routes: one for oxygenation of the blood through the lungs and skin, and the other to take oxygen to the rest of the body. The blood is pumped from a three-chambered heart with two atria and a single ventricle. (c) Reptiles also have two circulatory routes; however, blood is only oxygenated through the lungs. The heart is three chambered,

but the ventricles are partially separated so some mixing of oxygenated and deoxygenated blood occurs except in crocodilians and birds. (d) Mammals and birds have the most efficient heart with four chambers that completely separate the oxygenated and deoxygenated blood; it pumps only oxygenated blood through the body and deoxygenated blood to the lungs.

As illustrated in Figure 22.3 a. Fish have a single circuit for blood flow and a two-chambered heart that has only a single atrium and a single ventricle. The atrium collects blood that has returned from the body and the ventricle pumps the blood to the gills where gas exchange occurs and the blood is re-oxygenated; this is called gill circulation. The blood then continues through the rest of the body before arriving back at the atrium; this is called systemic circulation. This unidirectional flow of blood produces a gradient of oxygenated to deoxygenated blood around the fish's systemic circuit. The result is a limit in the amount of oxygen that can reach some of the organs and tissues of the body, reducing the overall metabolic capacity of fish.

In amphibians, reptiles, birds, and mammals, blood flow is directed in two circuits: one through the lungs and back to the heart, which is called pulmonary circulation, and the other throughout the rest of the body and its organs including the brain (systemic circulation). In amphibians, gas exchange also occurs through the skin during pulmonary circulation and is referred to as pulmocutaneous circulation.

As shown in Figure 22.3 b, amphibians have a three-chambered heart that has two atria and one ventricle rather than the two-chambered heart of fish. The two atria (superior heart chambers) receive blood from the two different circuits (the lungs and the systems), and then there is some mixing of the blood in the heart's ventricle (inferior heart chamber), which reduces the efficiency of oxygenation. The advantage to this arrangement is that high pressure in the vessels pushes blood to the lungs and body. The mixing is mitigated by a ridge within the ventricle that diverts oxygen-rich blood through the systemic circulatory system and deoxygenated blood to the pulmocutaneous circuit. For this reason, amphibians are often described as having double circulation.

Most reptiles also have a three-chambered heart similar to the amphibian heart that directs blood to the pulmonary and systemic circuits, as shown in Figure 22.3 c. The ventricle is divided more effectively by a partial septum, which results in less mixing of oxygenated and deoxygenated blood. Some reptiles (alligators and crocodiles) are the most primitive animals to exhibit a four-chambered heart. Crocodilians have a unique circulatory mechanism where the heart shunts blood from the lungs toward the stomach and other organs during long periods of submergence, for instance, while the animal waits for prey or stays underwater waiting for prey to rot. One adaptation includes two main arteries that leave the same part of the heart: one takes blood to the lungs and the other provides an alternate route to the stomach and other parts of the body. Two other adaptations include a hole in the heart between the two ventricles, called the foramen of Panizza, which allows blood to move from one side of the heart to the other, and specialized connective tissue that slows the blood flow to the lungs. Together these adaptations have made crocodiles and alligators one of the most evolutionarily successful animal groups on earth.

In mammals and birds, the heart is also divided into four chambers: two atria and two ventricles, as illustrated in Figure 22.3 d. The oxygenated blood is separated from the deoxygenated blood, which improves the efficiency of double circulation and is probably required for the warm-blooded lifestyle of mammals and birds. The four-chambered heart of birds and mammals evolved independently from a three-chambered heart. The independent evolution of the same or a similar biological trait is referred to as convergent evolution.

Osmosis is the diffusion of water across a membrane in response to osmotic pressure caused by an imbalance of molecules on either side of the membrane. Osmoregulation is the process of maintenance of salt and water balance (osmotic balance) across membranes within the body's fluids, which are composed of water, plus electrolytes and non-electrolytes. An electrolyte is a solute that dissociates into ions when dissolved in water. A non-electrolyte, in contrast, doesn't dissociate into ions during water dissolution. Both electrolytes and non-electrolytes contribute to the osmotic balance. The body's fluids include blood plasma, the cytosol within cells, and interstitial fluid, the fluid that exists in the spaces between cells and tissues of the body. The membranes of the body (such as the pleural, serous, and cell membranes) are semi-permeable membranes. Semi-permeable membranes are permeable (or permissive) to certain types of solutes and water. Solutions on two sides of a semi-permeable membrane tend to equalize in solute concentration by movement of solutes and/or water across the membrane. As seen in Figure 22.4, a cell placed in water tends to swell due to gain of water from the hypotonic or "low salt" environment. A cell placed in a solution with higher salt concentration, on the other hand, tends to make the membrane shrivel up due to loss of water into the hypertonic or "high salt" environment. Isotonic cells have an equal concentration of solutes inside and outside the cell; this equalizes the osmotic pressure on either side of the cell membrane which is a semi-permeable membrane.

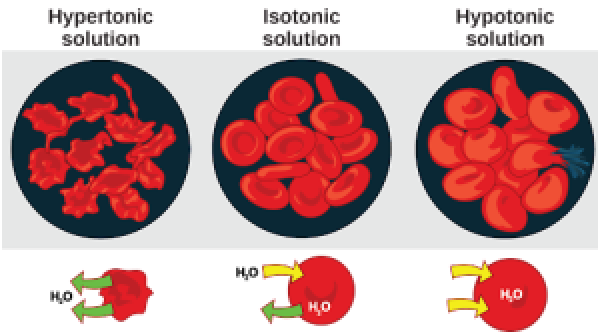


Figure 22.4 Cells placed in a hypertonic environment tend to shrink due to loss of water. In a hypotonic environment, cells tend to swell due to intake of water. The blood maintains an isotonic environment so that cells neither shrink nor swell. (credit: Mariana Ruiz Villareal)

The body does not exist in isolation. There is a constant input of water and electrolytes into the system. While osmoregulation is achieved across membranes within the body, excess electrolytes and wastes are transported to the kidneys and excreted, helping to maintain osmotic balance.

Reading Question #2

Osmoregulation is the process of maintaining the balance of:

A. Water and electrolytes only

B. Water, electrolytes, and non-electrolytes

C. Water and non-electrolytes only

D. Water only

Need for Osmoregulation

Biological systems constantly interact and exchange water and nutrients with the environment by way of consumption of food and water and through excretion in the form of sweat, urine, and feces. Without a mechanism to regulate osmotic pressure, or when a disease damages this mechanism, there is a tendency to accumulate toxic waste and water, which can have dire consequences.

Mammalian systems have evolved to regulate not only the overall osmotic pressure across membranes, but also specific concentrations of important electrolytes in the three major fluid compartments: blood plasma, extracellular fluid, and intracellular fluid. Since osmotic pressure is regulated by the movement of water across membranes, the volume of the fluid compartments can also change temporarily. Because blood plasma is one of the fluid components, osmotic pressures have a direct bearing on blood pressure.

Osmoregulators and Osmoconformers

Persons lost at sea without any freshwater to drink are at risk of severe dehydration because the human body cannot adapt to drinking seawater, which is hypertonic in comparison to body fluids. Organisms such as goldfish that can tolerate only a relatively narrow range of salinity are referred to as stenohaline. About 90 percent of all bony fish are restricted to either freshwater or seawater. They are incapable of osmotic regulation in the opposite environment. It is possible, however, for a few fishes like salmon to spend part of their life in freshwater and part in seawater. Organisms like the salmon and molly that can tolerate a relatively wide range of salinity are referred to as euryhaline organisms. This is possible because some fish have evolved osmoregulatory mechanisms to survive in all kinds of aquatic environments. When they live in freshwater, their bodies tend to take up water because the environment is relatively hypotonic, as illustrated in Figure 22.5 a. In such hypotonic environments, these fish do not drink much water. Instead, they pass a lot of very dilute urine, and they achieve electrolyte balance by active transport of salts through the gills. When they move to a hypertonic marine environment, these fish start drinking seawater; they excrete the excess salts through their gills and their urine, as illustrated in Figure 22.5 b. Most marine invertebrates, on the other hand, may be isotonic with seawater (osmoconformers). Their body fluid concentrations conform to changes in seawater concentration. Cartilaginous fishes' salt composition of the blood is similar to bony fishes; however, the blood of sharks contains the organic compounds urea and trimethylamine oxide (TMAO). This does not mean that their electrolyte composition is similar to that of seawater. They achieve isotonicity with the sea by storing large concentrations of urea. These animals that secrete urea are called ureotelic animals. TMAO stabilizes proteins in the presence of high urea levels, preventing the disruption of peptide bonds that would occur in other animals exposed to similar levels of urea. Sharks are cartilaginous fish with a rectal gland to secrete salt and assist in osmoregulation.

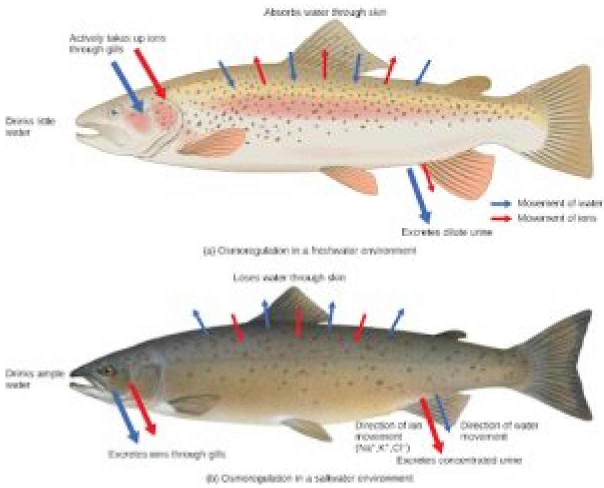


Figure 22.5 Fish are osmoregulators, but must use different mechanisms to survive in (a) freshwater or (b) saltwater environments. (credit: modification of work by Duane Raver, NOAA)

Plants: Water Transport

Plant Organ Systems

In plants, just as in animals, similar cells working together form a tissue. When different types of tissues work together to perform a unique function, they form an organ; organs working together form organ systems. Vascular plants have two distinct organ systems: a shoot system, and a root system. The shoot system consists of two portions: the vegetative (non-reproductive) parts of the plant, such as the leaves and the stems, and the reproductive parts of the plant, which include flowers and fruits. The shoot system generally grows above ground, where it absorbs the light needed for photosynthesis. The root system, which supports the plants and absorbs water and minerals, is usually underground. Figure 22.6 shows the organ systems of a typical plant.

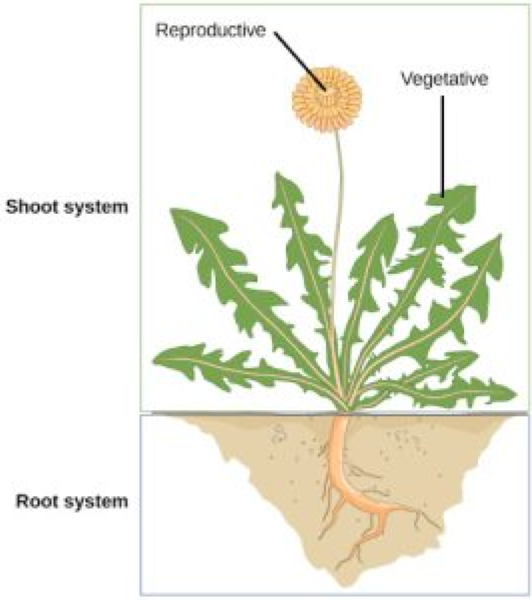


Figure 22.6 The shoot system of a plant consists of leaves, stems, flowers, and fruits. The root system anchors the plant while absorbing water and minerals from the soil.

Plant Tissues

Plants are multicellular eukaryotes with tissue systems made of various cell types that carry out specific functions.

Dermal tissue, for example, is a simple tissue that covers the outer surface of the plant and controls gas exchange. Vascular tissue is an example of a complex tissue, and is made of two specialized conducting tissues: xylem and phloem. Xylem tissue transports water and nutrients from the roots to different parts of the plant, and includes three different cell types: vessel elements and tracheids (both of which conduct water), and xylem parenchyma. Phloem tissue, which transports organic compounds from the site of photosynthesis to other parts of the plant, consists of four different cell types: sieve cells (which conduct photosynthates), companion cells, phloem parenchyma, and phloem fibers. Unlike xylem conducting cells, phloem conducting cells are alive at maturity. The xylem and phloem always lie adjacent to each other (Figure 22.7). In stems, the xylem and the phloem form a structure called a vascular bundle; in roots, this is termed the vascular stele or vascular cylinder.

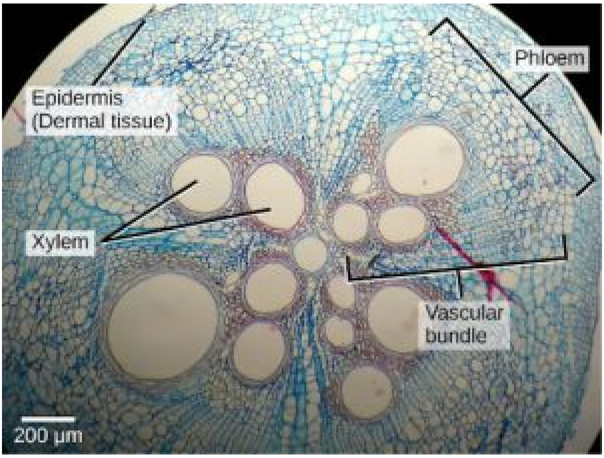


Figure 22.7 This light micrograph shows a cross section of a squash (Curcurbita maxima) root. Each teardrop-shaped vascular bundle consists of large xylem vessels toward the inside and smaller phloem cells toward the outside. Xylem cells, which transport water and nutrients from the roots to the rest of the plant, are dead at functional maturity. Phloem cells, which transport sugars and other organic compounds from photosynthetic tissue to the rest of the plant, are living. The vascular bundles are encased in ground tissue and

surrounded by dermal tissue. (credit: modification of work by "(biophotos)" /Flickr; scale-bar data from Matt Russell)

Reading Question #3

Xylem tissue:

A. Transports water and nutrients from the roots to other parts of the plant

B. Transports sugar from the site of photosynthesis to other parts of the plant

C. Transports fertilizer from the roots to other parts of the plant

D. Transports organic compounds from the site of photosynthesis to other parts of the plant

Reading Question #4

Phloem tissue:

A. Transports water and nutrients from the roots to other parts of the plant

B. Transports sugar from the site of photosynthesis to other parts of the plant

C. Transports fertilizer from the roots to other parts of the plant

D. Transports organic compounds from the site of photosynthesis to other parts of the plant

Stems and Plant Vascular Tissue

The stem of the plant connects the roots to the leaves, helping to transport absorbed water and minerals to different parts of the plant. It also helps to transport the products of photosynthesis, namely sugars, from the leaves to the rest of the plant.

The stem and other plant organs arise from the ground tissue, and are primarily made up of simple tissues formed from three types of cells: parenchyma, collenchyma, and sclerenchyma cells.

Parenchyma cells are the most common plant cells (Figure 22.8). They are found in the stem, the root, the inside of the leaf, and the pulp of the fruit. Parenchyma cells are responsible for metabolic functions, such as photosynthesis, and they help repair and heal wounds. Some parenchyma cells also store starch.

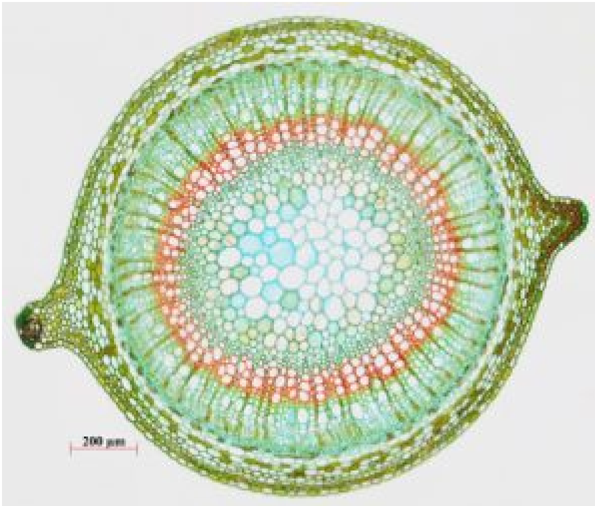


Figure 22.8 The stem of common St John's Wort (Hypericum perforatum) is shown in cross section in this light micrograph. The central pith (greenish-blue, in the center) and peripheral cortex (narrow zone 3–5 cells thick just inside the epidermis) are composed of parenchyma cells. Vascular tissue composed of xylem (red) and phloem tissue (green, between the xylem and cortex) surrounds the pith. (credit: Rolf-Dieter Mueller)

The xylem and phloem that make up the vascular tissue of the stem are arranged in distinct strands called vascular bundles, which run up and down the length of the stem. When the stem is viewed in cross section, the vascular bundles of dicot stems are arranged in a ring. In plants with stems that live for more than one year, the individual bundles grow together and produce the characteristic growth rings. In monocot stems, the vascular bundles are randomly scattered throughout the ground tissue.

(Figure 22.9).

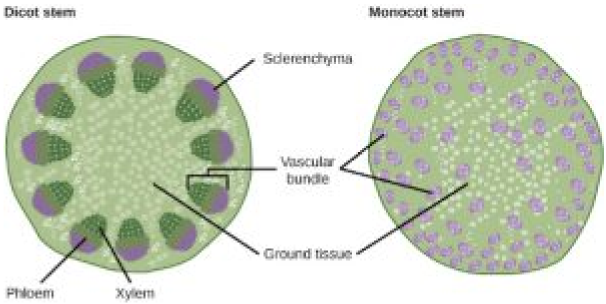


Figure 22.9 In (a) dicot stems, vascular bundles are arranged around the periphery of the ground tissue. The xylem tissue is located toward the interior of the vascular bundle, and phloem is located toward the exterior. Sclerenchyma fibers cap the vascular bundles. In (b) monocot stems, vascular bundles composed of xylem and phloem tissues are scattered throughout the ground tissue.

Xylem tissue has three types of cells: xylem parenchyma, tracheids, and vessel elements. The latter two types conduct water and are dead at maturity. Tracheids are xylem cells with thick secondary cell walls that are lignified. Water moves from one tracheid to another through regions on the side walls known as pits, where secondary walls are absent. Vessel elements are xylem cells with thinner walls; they are shorter than tracheids. Each vessel element is connected to the next by means of a perforation plate at the end walls of the element. Water moves through the perforation plates to travel up the plant.

Phloem tissue is composed of sieve-tube cells, companion cells, phloem parenchyma, and phloem fibers. A series of sieve-tube cells (also called sieve-tube elements) are arranged end to end to make up a long sieve tube, which transports organic substances such as sugars and amino acids. The sugars flow from one sieve-tube cell to the next through perforated sieve plates, which are found at the end junctions between two cells. Although still alive at maturity, the nucleus and other cell components of the sieve-tube cells have disintegrated. Companion cells are found alongside the sieve-tube cells, providing them with metabolic support. The companion cells contain more ribosomes and mitochondria than the sieve-tube cells, which lack some cellular organelles.

Reading Question #5

The main difference between dicot and monocot stems is:

A. Dicot stems have a dual structure

B. Dicot stems have vascular bundles around the periphery of the ground tissue, while monocots have vascular bundles distributed throughout

C. Monocot stems only have xylem tissue and not phloem tissue

D. Monocots don’t have vascular tissue

Growth in Stems

Growth in plants occurs as the stems and roots lengthen. Some plants, especially those that are woody, also increase in thickness during their lifespan. The increase in length of the shoot and the root is referred to as primary growth, and is the result of cell division in the shoot apical meristem. Secondary growth is characterized by an increase in thickness or girth of the plant, and is caused by cell division in the lateral meristem. Figure 22.10 shows the areas of primary and secondary growth in a plant. Herbaceous plants mostly undergo primary growth, with hardly any secondary growth or increase in thickness. Secondary growth or “wood” is noticeable in woody plants; it occurs in some dicots, but occurs very rarely in monocots.

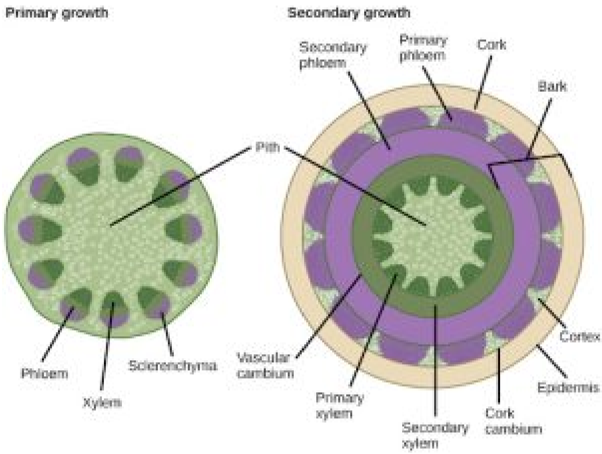


Figure 22.10 In woody plants, primary growth is followed by secondary growth, which allows the plant stem to increase in thickness or girth. Secondary vascular tissue is added as the plant grows, as well as a cork layer. The bark of a tree extends from the vascular cambium to the epidermis.

Water Transport

Figure 22.11 With heights nearing 116 meters, (a) coastal redwoods (Sequoia sempervirens) are the tallest trees in the world. Plant roots can easily generate enough force to (b) buckle and break concrete sidewalks, much to the dismay of homeowners and city maintenance departments. (credit a: modification of work by Bernt Rostad; credit b: modification of work by Pedestrians Educating Drivers on Safety, Inc.)

Movement of Water and Minerals in the Xylem

Solutes, pressure, and gravity are all important for the transport of water in plants. Transpiration is the loss of water from the plant through evaporation at the leaf surface. It is the main driver of water movement in the xylem. Transpiration is caused by the evaporation of water at the leaf–atmosphere interface. Water from the roots is pulled up by this tension. At night, when stomata shut and transpiration stops, the water is held in the stem and leaf by the adhesion of water to the cell walls of the xylem vessels and tracheids, and the cohesion of water molecules to each other. This is called the cohesion–tension theory of sap ascent.

Inside the leaf at the cellular level, water on the surface of mesophyll cells saturates the cellulose microfibrils of the primary cell wall. The leaf contains many large intercellular air spaces for the exchange of oxygen for carbon dioxide, which is required for photosynthesis. The wet cell wall is exposed to this leaf internal air space, and the water on the surface of the cells evaporates into the air spaces, decreasing the thin film on the surface of the mesophyll cells. This decrease creates a greater tension on the water in the mesophyll cells (Figure 22.12), thereby increasing the pull on the water in the xylem vessels. The xylem vessels and tracheids are structurally adapted to cope with large changes in pressure. Rings in the vessels maintain their tubular shape, much like the rings on a vacuum cleaner hose keep the hose open while it is under pressure. Small perforations between vessel elements reduce the number and size of gas bubbles that can form via a process called cavitation. The formation of gas bubbles in xylem interrupts the continuous stream of water from the base to the top of the plant, causing a break termed an embolism in the flow of xylem sap. The taller the tree, the greater the tension forces needed to pull water, and the more cavitation events. In larger trees, the resulting embolisms can plug xylem vessels, making them nonfunctional.

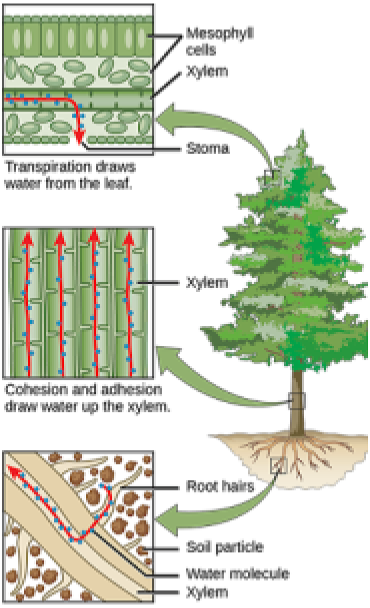


Figure 22.12 The cohesion–tension theory of sap ascent is shown. Evaporation from the mesophyll cells produces a negative water potential gradient that causes water to move upwards from the roots through the xylem.

Transpiration—the loss of water vapor to the atmosphere through stomata—is a passive process, meaning that metabolic energy in the form of ATP is not required for water movement. The energy driving transpiration is the difference in energy between the water in the soil and the water in the atmosphere. However, transpiration is tightly controlled.

Control of Transpiration

The atmosphere to which the leaf is exposed drives transpiration, but also causes massive water loss from the plant. Up to 90 percent of the water taken up by roots may be lost through transpiration.

Leaves are covered by a waxy cuticle on the outer surface that prevents the loss of water. Regulation of transpiration, therefore, is achieved primarily through the opening and closing of stomata on the leaf surface. Stomata are surrounded by two specialized cells called guard cells, which open and close in response to environmental cues such as light intensity and quality, leaf water status, and carbon dioxide concentrations. Stomata must open to allow air containing carbon dioxide and oxygen to diffuse into the leaf for photosynthesis and respiration.

Figure 22.13 Visualized at 500x with a scanning electron microscope, several stomata are clearly visible on (a) the surface of this sumac (Rhus glabra) leaf. At 5,000x magnification, the guard cells of (b) a single stoma from lyre-leaved sand cress (Arabidopsis lyrata). In this (c) light micrograph cross-section of an A. lyrata leaf, the guard cell pair is visible along with the large, sub-stomatal air space in the leaf. (credit: modification of work by Robert R. Wise; part c scale-bar data from Matt Russell)

When stomata are open, however, water vapor is lost to the external environment, increasing the rate of transpiration. Therefore, plants must maintain a balance between efficient photosynthesis and water loss.

Plants have evolved over time to adapt to their local environment and reduce transpiration (Figure 22.14). Desert plant and plants that grow on other plants have limited access to water. Such plants usually have a much thicker waxy cuticle than those growing in more moderate, well-watered environments. Aquatic plants also have their own set of anatomical and morphological leaf adaptations.

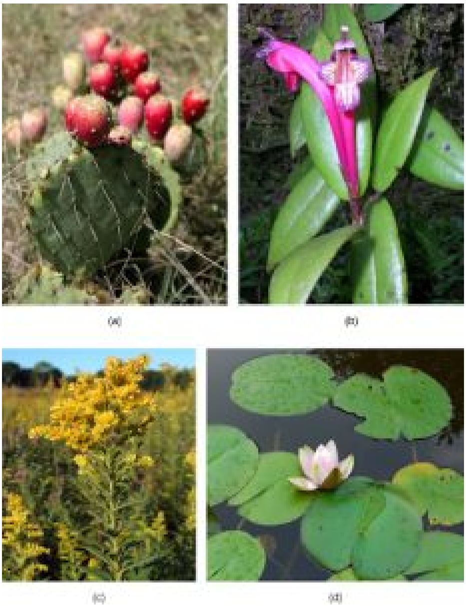


Figure 22.14 Plants are suited to their local environment. (a) This prickly pear cactus (Opuntia sp.) and (b) this tropical Aeschynanthus perrottetii have adapted to very limited water resources. The leaves of a prickly pear are modified into spines, which lowers the surface-to-volume ratio and reduces water loss. Photosynthesis takes place in the stem, which also stores water. (b) A. perottetii leaves have a waxy cuticle that prevents water loss. (c) Goldenrod (Solidago sp.) is well suited for moderate environments. (d) This fragrant water lily (Nymphaea odorata) is adapted to

thrive in aquatic environments. (credit a: modification of work by Jon Sullivan; credit b: modification of work by L. Shyamal/ Wikimedia Commons; credit c: modification of work by Huw Williams; credit d: modification of work by Jason Hollinger)

Transportation of Photosynthates in the Phloem

Plants need an energy source to grow. In seeds and bulbs, food is stored in polymers (such as starch) that are converted by metabolic processes into sucrose for newly developing plants. Once green shoots and leaves are growing, plants are able to produce their own food by photosynthesizing. The products of photosynthesis are called photosynthates, which are usually in the form of simple sugars such as sucrose.

Structures that produce photosynthates for the growing plant are referred to as sources. Sugars produced in sources, such as leaves, need to be delivered to growing parts of the plant via the phloem in a process called translocation. The points of sugar delivery, such as roots, young shoots, and developing seeds, are called sinks. Seeds, tubers, and bulbs can be either a source or a sink, depending on the plant's stage of development and the season.

The products from the source are usually translocated to the nearest sink through the phloem. For example, the highest leaves will send photosynthates upward to the growing shoot tip, whereas lower leaves will direct photosynthates downward to the roots. Intermediate leaves will send products in both directions, unlike the flow in the xylem, which is always unidirectional (soil to leaf to atmosphere). The pattern of photosynthate flow changes as the plant grows and develops. Photosynthates are directed primarily to the roots early on, to shoots and leaves during vegetative growth, and to seeds and fruits during reproductive development. They are also directed to tubers for storage.

Translocation: Transport from Source to Sink

Photosynthates, such as sucrose, are produced in the mesophyll cells of photosynthesizing leaves. From there they are translocated through the phloem to where they are used or stored. Mesophyll cells are connected by cytoplasmic channels. Photosynthates move through these channels to reach phloem sieve-tube elements (STEs) in the vascular bundles. From the mesophyll cells, the photosynthates are loaded into the phloem STEs. The sucrose is actively transported against its concentration gradient (a process requiring ATP) into the phloem cells using the electrochemical potential of the proton gradient. This is coupled to the uptake of sucrose with a carrier protein called the sucrose-H^+ symporter.

Phloem STEs have reduced cytoplasmic contents, and are connected by a sieve plate with pores that allow for pressure-driven bulk flow, or translocation, of phloem sap. Companion cells are associated with STEs. They assist with metabolic activities and produce energy for the STEs (Figure 22.15).

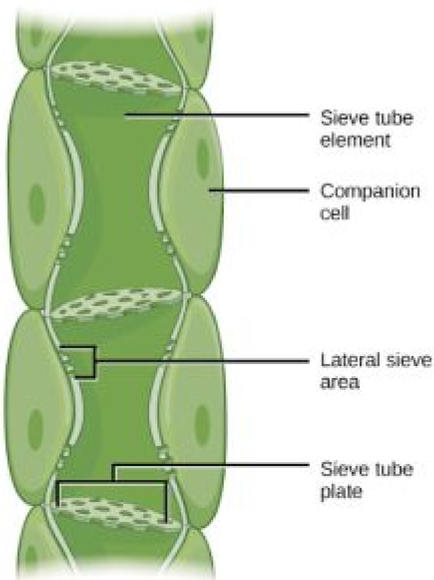


Figure 22.15 Phloem is comprised of cells called sieve-tube elements. Phloem sap travels through perforations called sieve tube plates. Neighboring companion cells carry out metabolic functions for the sieve-tube elements and provide them with energy. Lateral sieve areas connect the sieve-tube elements to the companion cells.

Figure 22.15 Phloem is comprised of cells called sieve-tube elements. Phloem sap travels through perforations called sieve tube plates. Neighboring companion cells carry out metabolic functions for the sieve-tube elements and provide them with energy. Lateral sieve areas connect the sieve-tube elements to the companion cells.

Once in the phloem, the photosynthates are translocated to the closest sink. Phloem sap is an aqueous solution that contains up to 30 percent sugar, minerals, amino acids, and plant growth regulators. Sucrose concentration in the sink cells is lower than in the phloem STEs because the sink sucrose has been metabolized for growth, or converted to starch for storage or other polymers, such as cellulose, for structural integrity. Unloading at the sink end of the phloem tube occurs by either diffusion or active transport of sucrose molecules from an area of high concentration to one of low concentration. Water diffuses from the phloem by osmosis and is then transpired or recycled via the xylem back into the phloem sap.

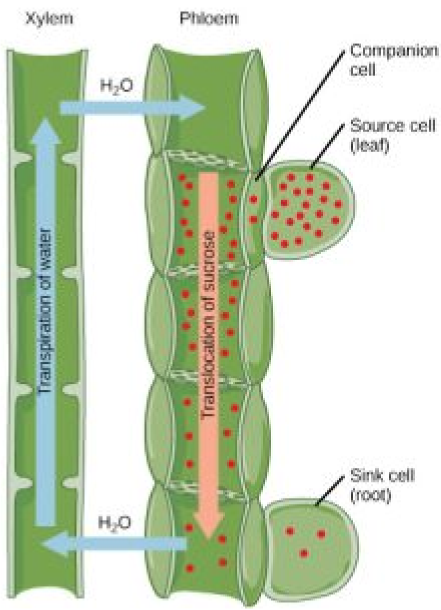


Figure 22.16 Sucrose is actively transported from source cells into companion cells and then into the sieve-tube elements. This reduces the water potential, which causes water to enter the phloem from the xylem. The resulting positive pressure forces the sucrose-water mixture down toward the roots, where sucrose is unloaded. Transpiration causes water to return to the leaves through the xylem vessels.

24. Chapter 24: Obtain and Use Energy: Respiration

ANASTASIA CHOUVALOVA

Review of cellular respiration

Let's think back to the metabolism unit of BIOL 1403, where we discussed cellular respiration and photosynthesis.

Cellular respiration is the process of oxidizing food molecules, like glucose, to carbon dioxide and water.

The equation of cellular respiration is: $C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O$.

The energy released is trapped in the form of **ATP** for use by all the energy-consuming activities of the cell. The process occurs in two phases:

- **glycolysis**, the breakdown of glucose to pyruvic acid
- the complete **oxidation of pyruvic acid** to carbon dioxide and water

In eukaryotes, glycolysis occurs in the cytosol and the remaining processes take place in **mitochondria**.

Mitochondria

Mitochondria are membrane-enclosed organelles distributed through the cytosol of most eukaryotic cells. Their number within the cell ranges from a few hundred to, in very active cells, thousands. Their main function is the conversion of the potential energy of food molecules into ATP.

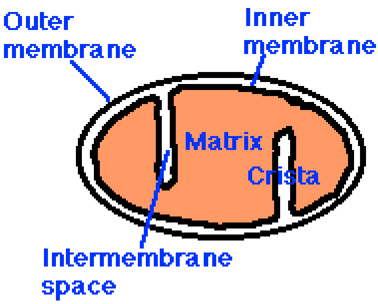


Figure 23.1. This is a simplified schematic diagram of the mitochondrion.

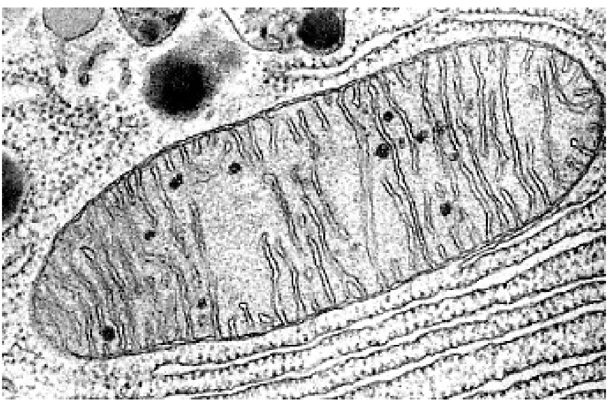


Figure 23.2 This image was obtained from an electron microscope – it depicts a mitochondrion found in a bat pancreatic cell.

Mitochondria have:

- an **outer membrane** that encloses the entire structure
- an **inner membrane** that encloses a fluid-filled **matrix**
- between the two is the **intermembrane space**
- the inner membrane is elaborately folded with shelflike **cristae** projecting into the **matrix**.
- a small number (some 5–10) circular molecules of **DNA**

This electron micrograph in Figure 23.2, shows a single mitochondrion from a bat pancreas cell. Note the double membrane and the way the inner membrane is folded into cristae. The dark, membrane-bounded objects above the mitochondrion are lysosomes. The number of mitochondria in a cell can increase either by their fission (e.g. following mitosis) or decrease by their fusing together. Defects in either process can produce serious, even fatal, illness.

The Outer Membrane

The outer membrane contains many complexes of integral membrane proteins that form channels through which a variety of molecules and ions move in and out of the mitochondrion.

The Inner Membrane

The inner membrane contains 5 complexes of integral membrane proteins:

- **NADH dehydrogenase** (Complex I)
- succinate dehydrogenase (Complex II)
- **cytochrome c reductase** (Complex III; also known as the cytochrome b-c1 complex)
- **cytochrome c oxidase** (Complex IV)
- **ATP synthase** (Complex V)

The Matrix

The matrix contains a complex mixture of soluble enzymes that catalyze the respiration of pyruvic acid and other small organic molecules. Here pyruvic acid is

- oxidized by NAD^+ producing NADH + H^+
- decarboxylated producing a molecule of
    - carbon dioxide (CO_2) and
    - a 2-carbon fragment of acetate bound to **coenzyme A** forming acetyl-CoA

The Citric Acid Cycle

This 2-carbon fragment is donated to a molecule of **oxaloacetic acid**. The resulting molecule of **citric acid** (which gives its name to the process) undergoes the series of enzymatic steps shown in the diagram. The final step regenerates a molecule of oxaloacetic acid and the cycle is ready to turn again. Note that the citric acid cycle is also referred to as Krebs cycle or the TCA (tricarboxylic acid) cycle.

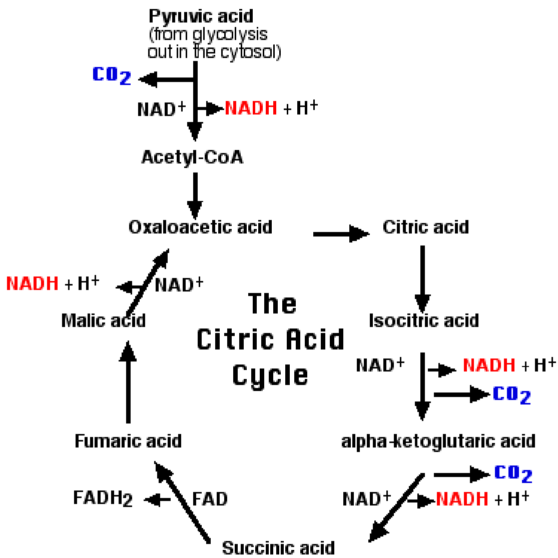


Figure 23.3 A flow chart depicting the citric acid cycle, also known as Krebs cycle.

A brief summary of the cycle is as follows:

- Each of the 3 carbon atoms present in the pyruvate that entered the mitochondrion leaves as a molecule of carbon dioxide (**CO_2**).
- At 4 steps, a pair of electrons (**$2e^-$**) is removed and transferred to **NAD^+** reducing it to **$NADH + H^+$**.
- At one step, a pair of electrons is removed from succinic acid and reduces the prosthetic group flavin adenine dinucleotide (**FAD**) to **$FADH_2$**.
- The electrons of NADH and $FADH_2$ are transferred to the **electron transport chain**.

The Electron Transport Chain

The electron transport chain consists of 3 complexes of integral membrane proteins

- the **NADH dehydrogenase** complex (I)
- the **cytochrome c reductase** complex (III)
- the **cytochrome c oxidase** complex (IV)

and two freely-diffusible molecules **ubiquinone, cytochrome c,** that shuttle electrons from one complex to the next.

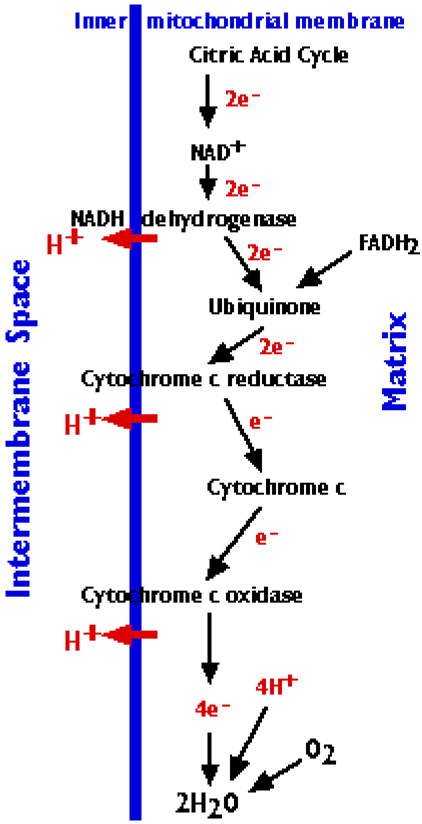


Figure 23.4 A flow chart depicting the electron transport chain (ETC), also called the respiratory chain. This process occurs exclusively within various compartments of the mitochondrion.

The electron transport chain accomplishes:

- The stepwise transfer of electrons from **NADH** (and **FADH2**) to **oxygen** molecules to form (with the aid of protons) water molecules (**H2O**). Cytochrome c can only transfer one electron at a time, so cytochrome c oxidase must wait until it has accumulated 4 of them before it can react with oxygen.
- Harnessing the energy released by this transfer to the pumping of protons (**H^+**) from the **matrix** to the **intermembrane space**.
- Approximately 20 protons are pumped into the intermembrane space as the 4 electrons needed to reduce oxygen to water pass through the respiratory chain.
- The gradient of protons formed across the inner membrane by this process of active transport forms a miniature battery.
- The protons can flow back down this gradient only by reentering the matrix through **ATP synthase**, another complex (complex V) of 16 integral membrane proteins in the inner membrane. The process is called chemiosmosis.

Chemiosmosis in mitochondria

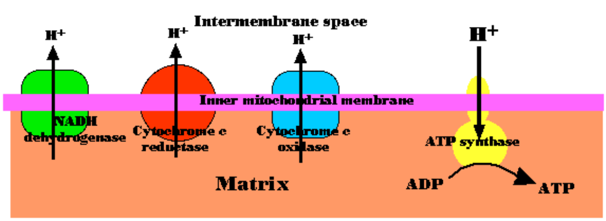


Figure 23.5 A schematic depicting the four protein complexes of the ETC. ATP synthase is an enzyme which utilizes the proton gradient, ultimately to produce ATP.

The energy released as electrons pass down the gradient from NADH to oxygen is harnessed by three enzyme complexes of the respiratory chain (I, III, and IV) to pump **protons** (**H^+**) **against** their concentration gradient **from the matrix** of the mitochondrion **into the intermembrane space.**

As their concentration increases there (which is the same as saying that the pH decreases), a strong diffusion gradient is set up. The only exit for these protons is through the **ATP synthase** complex. As in chloroplasts, the energy released as these protons flow down their gradient is harnessed to the synthesis of **ATP**. The process is called **chemiosmosis** and is an example of facilitated diffusion. One-half of the 1997 Nobel Prize in Chemistry was awarded to Paul D. Boyer and John E. Walker for their discovery of how ATP synthase works.

Fun fact!

Why do mitochondria have their own genome?

Many of the features of the mitochondrial genetic system resemble those found in bacteria. This has strengthened the theory that mitochondria are the evolutionary descendants of a bacterium that established an endosymbiotic relationship with the ancestors of eukaryotic cells early in the history of life on earth. However, many of the genes needed for mitochondrial function have since moved to the nuclear genome. The recent sequencing of the complete genome of *Rickettsia prowazekii* has revealed a number of genes closely related to those found in mitochondria. Perhaps rickettsias are the closest living descendants of the endosymbionts that became the mitochondria of eukaryotes.

Now that we have reviewed the complex process of cellular respiration responsible for producing

ATP, let's come back to the physiological aspects of cellular respiration, where the focus will be on the respiratory system.

Introducing the respiratory system

Examine the cellular respiration equation again: $\mathbf{C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O}$.

Recall that the production of ATP using the process of chemiosmosis in mitochondria is called oxidative phosphorylation. The overall result of these reactions is the production of ATP from the energy of the electrons removed from hydrogen atoms. These atoms were originally part of a glucose molecule. At the end of the pathway, the electrons are used to reduce an oxygen molecule to oxygen ions. The extra electrons on the oxygen attract hydrogen ions (protons) from the surrounding medium, and water is formed. Thus, oxygen is the final electron acceptor in the electron transport chain.

But how do humans obtain oxygen and what structures are involved in gas exchange? The key player is the lungs and the respiratory system, which are specifically designed for efficient gas exchange via tiny structures called the alveoli. In this section, we will explore the respiratory system in great detail to obtain a greater appreciation for this incredible organ system. In short, the lungs inspire (inspiration is also referred to as inhalation) oxygen and expire (expiration is also referred to as exhalation) carbon dioxide as a byproduct of cellular respiration. This exchange of oxygen and carbon dioxide is referred to as respiration.

Breathing is an involuntary event. How often a breath is taken and how much air is inhaled or exhaled are tightly regulated by the respiratory center in the brain. Humans, when they aren't exerting themselves, breathe approximately 15 times per minute on average. Canines, like the dog in Figure 39.1, have a respiratory rate of about 15–30 breaths per minute. With every inhalation, air fills the lungs, and with every exhalation, air rushes back out. That air is doing more than just inflating and deflating the lungs in the chest cavity. The air contains oxygen that crosses the lung tissue, enters the bloodstream, and travels to organs and tissues. Oxygen (O_2) enters the cells where it is used for metabolic reactions that produce ATP, a high-energy compound. At the same time, these reactions release carbon dioxide (CO_2) as a by-product. CO_2 is toxic and must be eliminated. Carbon dioxide exits the cells, enters the bloodstream, travels back to the lungs, and is expired out of the body during exhalation.

Exploring lung anatomy and function

The primary function of the respiratory system is to deliver oxygen to the cells of the body's tissues and remove carbon dioxide, a cell waste product. The main structures of the human respiratory system are the nasal cavity, the trachea, and lungs.

All aerobic organisms require oxygen to carry out their metabolic functions. Along the evolutionary tree, different organisms have devised different means of obtaining oxygen from the surrounding atmosphere. The environment in which the animal lives greatly determines how an animal respires. The complexity of the respiratory system is correlated with the size of the organism. As animal size increases, diffusion distances increase and the ratio of surface area to volume drops. In unicellular organisms, diffusion across the cell membrane is sufficient for supplying oxygen to the cell (Figure 23.6). Diffusion is a slow, passive transport process. In order for diffusion to be a feasible means of providing oxygen to the cell, the rate of oxygen uptake must match the rate of diffusion across the membrane. In other words, if the cell were very large or thick, diffusion would not be able to provide oxygen quickly enough to the inside of the cell. Therefore, dependence on diffusion as a means of obtaining oxygen and removing carbon dioxide remains feasible only for small organisms or those with highly-flattened bodies, such as many flatworms (Platyhelminthes). Larger organisms had to evolve specialized respiratory tissues, such as gills, lungs, and respiratory passages accompanied by complex circulatory systems, to transport oxygen throughout their entire body.

Figure 23.6 The cell of the unicellular alga Ventricaria ventricosa is one of the largest known, reaching one to five centimeters in diameter. Like all single-celled organisms, V. ventricosa exchanges gases across the cell membrane.

Direct Diffusion

For small multicellular organisms, diffusion across the outer membrane is sufficient to meet their oxygen needs. Gas exchange by direct diffusion across surface membranes is efficient for organisms less than 1 mm in diameter. In simple organisms, such as cnidarians and flatworms, every cell in the body is close to the external environment. Their cells are kept moist and gases diffuse quickly via direct diffusion. Flatworms are small, literally flat worms, which 'breathe' through diffusion across the outer membrane (Figure 23.7). The flat shape of these organisms increases the surface area for diffusion, ensuring that each cell within the body is close to the outer membrane surface and has access to oxygen. If the flatworm had a cylindrical body, then the cells in the center would not be able to get oxygen.

Figure 23.7 In the flatworm, respiration is fairly simple. They rely on direct diffusion through the outer membrane. Their flat shape, rather than a cylindrical shape, allows for highly efficient diffusion to occur to fuel all the cells of their little bodies. (credit: Stephen Childs)

Skin and Gills

Earthworms and amphibians use their skin (integument) as a respiratory organ. A dense network of capillaries lies just below the skin and facilitates gas exchange between the external environment and the circulatory system. The respiratory surface must be kept moist in order for the gases to dissolve and diffuse across cell membranes.

Organisms that live in water need to obtain oxygen from the water. Oxygen dissolves in water but at a lower concentration than in the atmosphere. The atmosphere has roughly 21 percent oxygen. In water, the oxygen concentration is much lower than that. Fish and many other aquatic organisms have evolved gills to take up the dissolved oxygen from water (Figure 23.8). Gills are thin tissue filaments that are highly branched and folded. When water passes over the gills, the dissolved oxygen in water rapidly diffuses across the gills into the bloodstream. The circulatory system can then carry the oxygenated blood to the other parts of the body. In animals that contain coelomic fluid instead of blood, oxygen diffuses across the gill surfaces into the coelomic fluid. Gills are found in mollusks, annelids, and crustaceans.

Reading Question #1

Gills in fish are analogous structures to ____.

A. Skin in humans

B. Mouth of crocodiles

C. Lungs in humans

D. Scales on crocodiles

Figure 23.8. This common carp, like many other aquatic organisms, has gills that allow it to obtain oxygen from water. (credit: "Guitardude 012"/Wikimedia Commons)

The folded surfaces of the gills provide a large surface area to ensure that the fish gets sufficient oxygen. Diffusion is a process in which material travels from regions of high concentration to low concentration until equilibrium is reached. In this case, blood with a low concentration of oxygen molecules circulates through the gills. The concentration of oxygen molecules in water is higher than the concentration of oxygen molecules in gills. As a result, oxygen molecules diffuse from water (high concentration) to blood (low concentration), as shown in Figure 23.9. Similarly, carbon dioxide molecules in the blood diffuse from the blood (high concentration) to water (low concentration).

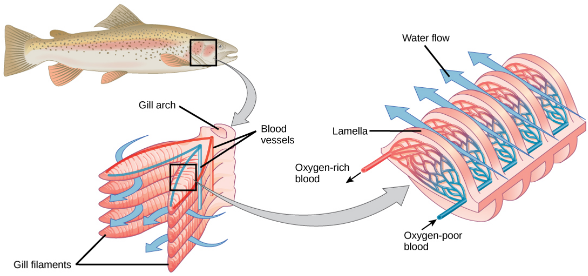


Figure 23.9 As water flows over the gills, oxygen is transferred to blood via the veins. (credit "fish": modification of work by Duane Raver, NOAA)

Tracheal Systems

Insect respiration is independent of its circulatory system; therefore, the blood does not play a direct role in oxygen transport. Insects have a highly specialized type of respiratory system called the tracheal system, which consists of a network of small tubes that carries oxygen to the entire body. The tracheal system is the most direct and efficient respiratory system in active animals. The tubes in the tracheal system are made of a polymeric material called chitin.

Insect bodies have openings, called spiracles, along the thorax and abdomen. These openings connect to the tubular network, allowing oxygen to pass into the body (Figure 23.10) and regulating the diffusion of CO_2 and water vapor. Air enters and leaves the tracheal system through the spiracles. Some insects can ventilate the tracheal system with body movements.

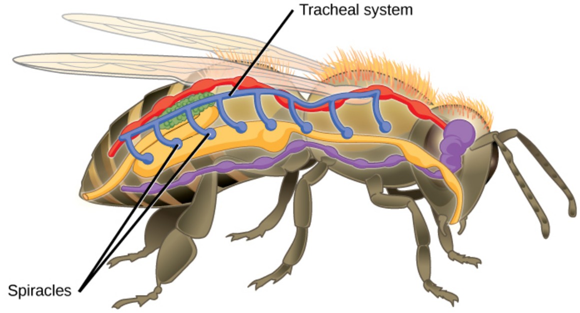


Figure 23.10

Mammalian Systems

In mammals, pulmonary ventilation occurs via inhalation (breathing). During inhalation, air enters the body through the nasal cavity located just inside the nose (Figure 29.11). As air passes through the nasal cavity, the air is warmed to body temperature and humidified. The respiratory tract is coated with mucus to seal the tissues from direct contact with air. Mucus is high in water. As air crosses these surfaces of the mucous membranes, it picks up water. These processes help equilibrate the air to the body conditions, reducing any damage that cold, dry air can cause. Particulate matter that is floating in the air is removed in the nasal passages via mucus and cilia. The processes of warming, humidifying, and removing particles are important protective mechanisms that prevent damage to the trachea and lungs. Thus, inhalation serves several purposes in addition to bringing oxygen into the respiratory system.

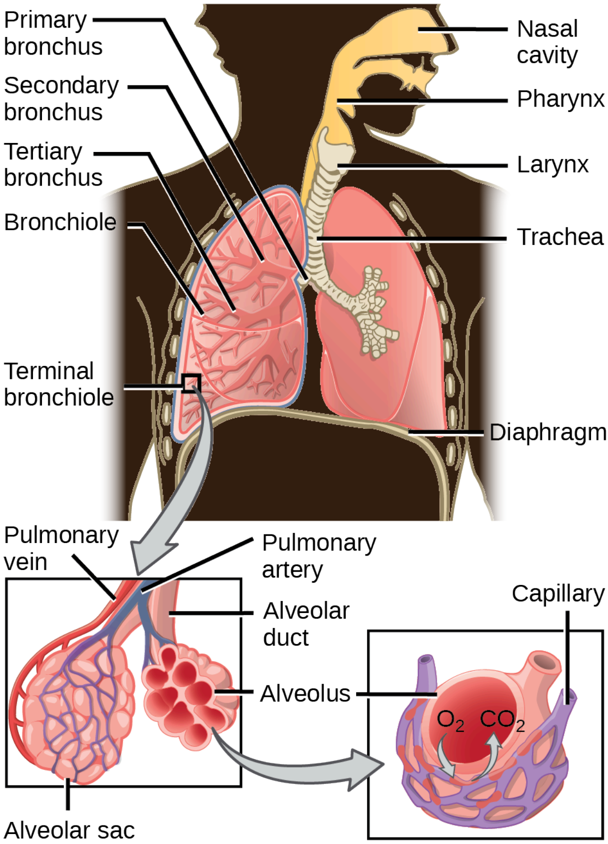


Figure 23.11 Air enters the respiratory system through the nasal cavity and pharynx, and then passes through the trachea and into the bronchi, which bring air into the lungs. (credit: modification of work by NCI)

From the nasal cavity, air passes through the pharynx (throat) and the larynx (voice box), as it makes its way to the trachea (Figure 23.11). The main function of the trachea is to funnel the inhaled air to the lungs and the exhaled air back out of the body. The human trachea is a cylinder about 10 to 12 cm long and 2 cm in diameter that sits in front of the esophagus and extends from the larynx into the chest cavity where it divides into the two primary bronchi at the midthorax. It is made of incomplete rings of hyaline cartilage and smooth muscle (Figure 23.12). The trachea is lined with mucus-producing goblet cells and ciliated epithelia. The cilia propel foreign particles trapped in the mucus toward the pharynx. The cartilage provides strength and support to the trachea to keep the passage open. The smooth muscle can contract, decreasing the trachea's diameter, which causes expired air to rush upwards from the lungs at a great force. The forced exhalation helps expel mucus when we cough. Smooth muscle can contract or relax, depending on stimuli from the external environment or the body's nervous system.

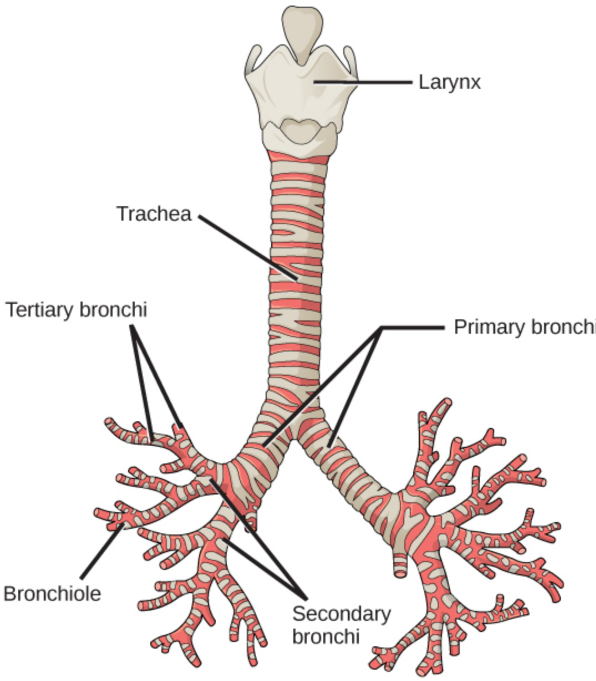


Figure 23.12 The trachea and bronchi are made of incomplete rings of cartilage. (credit: modification of work by Gray's Anatomy)

Lungs: Bronchi and Alveoli

The end of the trachea bifurcates (divides) to the right and left lungs. The lungs are not identical. The right lung is larger and contains three lobes, whereas the smaller left lung contains two lobes (Figure 23.13). The muscular diaphragm, which facilitates breathing, is inferior to (below) the lungs and marks the end of the thoracic cavity.

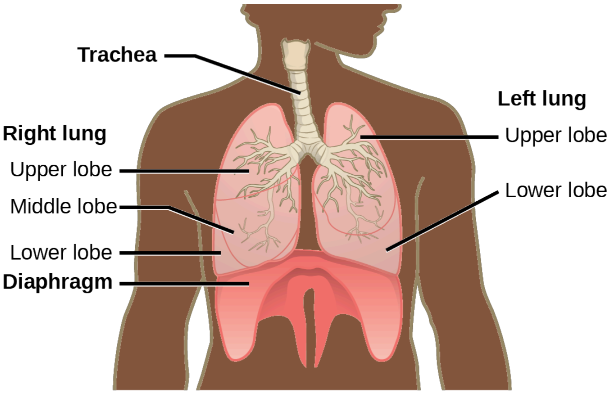


Figure 23.13 The trachea bifurcates into the right and left bronchi in the lungs. The right lung is made of three lobes and is larger. To accommodate the heart, the left lung is smaller and has only two lobes.

In the lungs, air is diverted into smaller and smaller passages, or bronchi. Air enters the lungs through the two primary (main) bronchi (singular: bronchus). Each bronchus divides into secondary bronchi, then into tertiary bronchi, which in turn divide, creating smaller and smaller diameter bronchioles as they split and spread through the lung. Like the trachea, the bronchi are made of cartilage and smooth muscle. At the bronchioles, the cartilage is replaced with elastic fibers. Bronchi are innervated by nerves of both the parasympathetic and sympathetic nervous systems that control muscle contraction (parasympathetic) or relaxation (sympathetic) in the bronchi and bronchioles, depending on the nervous system's cues. In humans, bronchioles with a diameter smaller than 0.5 mm are the respiratory bronchioles. They lack cartilage and therefore rely on inhaled air to support their shape. As the passageways decrease in diameter, the relative amount of smooth muscle increases.

The terminal bronchioles subdivide into microscopic branches called respiratory bronchioles. The respiratorybronchioles subdivide into several alveolar ducts. Numerous alveoli and alveolar sacs surround the alveolar ducts. The alveolar sacs resemble bunches of grapes tethered to the end of the bronchioles (Figure 23.14). In the acinar region, the alveolar ducts are attached to the end of each bronchiole. At the end of each duct are approximately 100 alveolar sacs, each containing 20 to 30 alveoli that are 200 to 300 microns in diameter. Gas exchange occurs only in alveoli. Alveoli are made of thin-walled parenchymal cells, typically one-cell thick, that look like tiny bubbles within the sacs. Alveoli are in direct contact with capillaries (one-cell thick) of the circulatory system. Such intimate contact ensures that oxygen will diffuse from alveoli into the blood and be distributed to the cells of the body. In addition, the carbon dioxide that was produced by cells as a waste product will diffuse from the blood into alveoli to be exhaled. The anatomical arrangement of capillaries and alveoli emphasizes the structural and functional relationship of the respiratory and circulatory systems. Because there are so many alveoli (~300 million per lung) within each alveolar sac and so many sacs at the end of each alveolar duct, the lungs have a sponge-like consistency. This organization produces a very large surface area that is available for gas exchange. The surface area of alveoli in the lungs is approximately 75 m^2. This large surface area, combined with the thin-walled nature of the alveolar parenchymal cells, allows gases to easily diffuse across the cells.

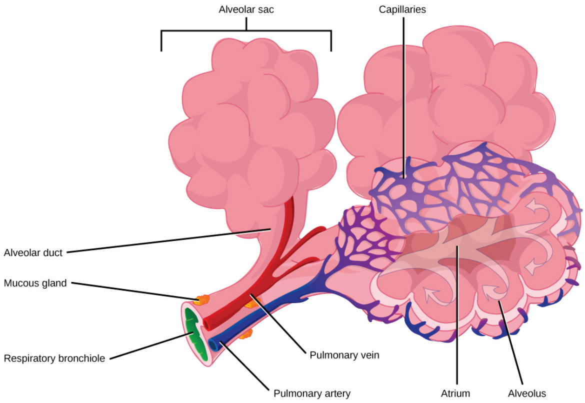


Figure 23.14 Terminal bronchioles are connected by respiratory bronchioles to alveolar ducts and alveolar sacs. Each alveolar sac contains 20 to 30 spherical alveoli and has the appearance of a bunch of grapes. Air flows into the atrium of the alveolar sac, then circulates into alveoli where gas exchange occurs with the capillaries. Mucous glands secrete mucous into the airways, keeping them moist and flexible. (credit: modification of work by Mariana Ruiz Villareal)

Protective Mechanisms

The air that organisms breathe contains particulate matter such as dust, dirt, viral particles, and bacteria that can damage the lungs or trigger allergic immune responses. The respiratory system contains several protective mechanisms to avoid problems or tissue damage. In the nasal cavity, hairs and mucus trap small particles, viruses, bacteria, dust, and dirt to prevent their entry.

If particulates do make it beyond the nose, or enter through the mouth, the bronchi and bronchioles of the lungs also contain several protective devices. The lungs produce mucus—a sticky substance made of mucin, a complex glycoprotein, as well as salts and water—that traps particulates. The bronchi and bronchioles contain cilia, small hair-like projections that line the walls of the bronchi and bronchioles (Figure 23.15). These cilia beat in unison and move mucus and particles out of the bronchi and bronchioles back up to the throat where it is swallowed and eliminated via the esophagus.

In humans, for example, tar and other substances in cigarette smoke destroy or paralyze the cilia, making the removal of particles more difficult. In addition, smoking causes the lungs to produce more mucus, which the damaged cilia are not able to move. This causes a persistent cough, as the lungs try to rid themselves of particulate matter, and makes smokers more susceptible to respiratory ailments.

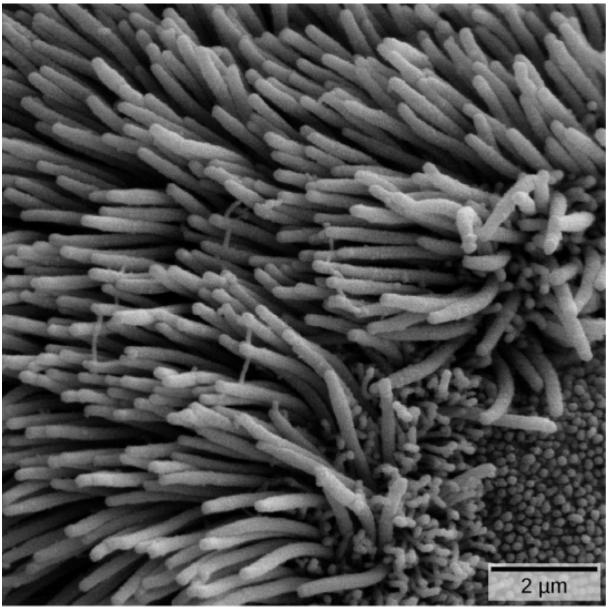


Figure 23.15 The bronchi and bronchioles contain cilia that help move mucus and other particles out of the lungs. (credit: Louisa Howard, modification of work by Dartmouth Electron Microscope Facility)

Reading Questions #2

Of the following statements, which is true about the mammalian respiratory system?

A. The bronchioles are the site of gas exchange between the lungs and the bloodstream.

B. The bronchi branch out into bronchioles.

C. Air travels from the trachea to the pharynx and larynx.

D. The small surface area of the alveoli optimizes the efficiency of gas exchange.

Reading Question #3

Which one of the following is not a protective mechanism of the human respiratory system?

A, Mucus in the alveoli

B. Hairs in the nasal cavity.

C. Cilia on the bronchi and bronchioles

d. Mucus in the lungs

Metabolomics

Metabolomics is the scientific study of chemical processes involving **metabolites.** The metabolome represents the collection of all metabolites, which are the end products of cellular processes, in a biological cell, tissue, organ, or organism. Thus, while mRNA gene expression data and proteomic analyses do not tell the whole story of what might be happening in a cell, metabolic profiling can give an instantaneous snapshot of the physiology of that cell. One of the challenges of systems biology and functional genomics is to integrate proteomic, transcriptomic, and metabolomic information to give a more complete picture of living organisms.

History and Development

The idea that biological fluids reflect the health of an individual has existed for a long time. The term “metabolic profile” was introduced by Horning, et al. in 1971, after they demonstrated that gas chromatography- mass spectrometry (GC-MS;) could be used to measure compounds present in human urine and tissue extracts. GC-MS is a method that combines the features of gas-liquid chromatography and mass spectrometry to identify different substances within a test sample. Concurrently, NMR spectroscopy, which was discovered in the 1940s, was also undergoing rapid advances. In 1974, Seeley et al. demonstrated the utility of using NMR to detect metabolites in unmodified biological samples. This first study on muscle tissue highlighted the value of NMR, in that it was determined that 90% of cellular ATP is complexed with magnesium. As sensitivity has improved with the evolution of higher magnetic field strengths and magic-angle spinning, NMR continues to be a leading analytical tool to investigate metabolism.

Figure –. Gas chromatography–mass spectrometry (GC-MS) is a method that combines the features of gas-liquid chromatography and mass spectrometry to identify different substances within a test sample.

In 2005, the first metabolomics web database for characterizing human metabolites, METLIN, was developed in the Siuzdak laboratory at The Scripps Research Institute. METLIN contained over 10,000 metabolites and tandem mass spectral data. On January 23, 2007, the Human Metabolome Project, led by Dr. David Wishart of the University of Alberta, Canada, completed the first draft of the human metabolome, consisting of a database of approximately 2500 metabolites, 1200 drugs and 3500 food components.

As late as mid-2010, metabolomics was still considered an "emerging field". Further, it was noted that further progress in the field was in large part the result of addressing otherwise "irresolvable technical challenges" through technical evolution of mass spectrometry instrumentation. The word was coined in analogy with transcriptomics and proteomics. Like the transcriptome and the proteome, the metabolome is dynamic, changing from second to second. Although the metabolome can be defined readily enough, it is not currently possible to analyse the entire range of metabolites by a single analytical method.

Metabolites are the intermediates and products of metabolism. Within the context of metabolomics, a metabolite is usually defined as any molecule less than 1 kDa in size. However, there are exceptions to this, depending on the sample and detection method. Macromolecules such as lipoproteins and albumin are reliably detected in NMR-based metabolomics studies of blood plasma. In plant-based metabolomics, it is common to refer to "primary metabolites," which are directly involved in growth, development and reproduction, and "secondary metabolites," which are indirectly involved in growth, development and reproduction. In contrast, in human-based metabolomics it is more common to describe metabolites as being either endogenous (produced by the host organism) or exogenous. The metabolome forms a large network of metabolic reactions, where outputs from one enzymatic chemical reaction are inputs to other chemical reactions. Such systems have been described as hypercycles.

Separation methods: Gas chromatography, especially when interfaced with mass spectrometry (GC-MS), is one of the most widely used and powerful methods. It offers very high chromatographic resolution, but requires chemical derivatization for many biomolecules: only volatile chemicals can be analysed without derivatization.

Detection methods: Mass spectrometry (MS) is used to identify and to quantify metabolites after separation. Surface-based mass analysis has seen a resurgence in the past decade, with new MS technologies focused on increasing sensitivity, minimizing background, and reducing sample preparation.

Statistical methods: The data generated in metabolomics usually consist of measurements performed on subjects under various conditions. These measurements may be digitized spectra, or a list of metabolite levels. In its simplest form this generates a matrix with rows corresponding to subjects and columns corresponding to metabolite levels.

Key applications

- *Toxicity assessment/toxicology*. Metabolic profiling, especially of urine or blood plasma samples, can be used to detect the physiological changes caused by toxic insult of a chemical or mixture of chemicals. This is of particular relevance to pharmaceutical companies wanting to test the toxicity of potential drug candidates.
- *Functional genomics*. Metabolomics can be an excellent tool for determining the phenotype caused by a genetic manipulation, such as gene deletion or insertion. Sometimes this can be a sufficient goal in itself—for instance, to detect any phenotypic changes in a genetically-modified plant intended for human or animal consumption. More exciting is the prospect of predicting the function of unknown genes by comparison with the metabolic perturbations caused by deletion/insertion of

known genes.

Key Points

- The metabolome represents the collection of all metabolites in a biological cell, tissue, organ or organism, which are the end products of cellular processes.
- Metabolites are the intermediates and products of metabolism.
- The metabolome forms a large network of metabolic reactions, where outputs from one enzymatic chemical reaction are inputs to other chemical reactions.
- NMR and Mass Spectroscopy are the most widely used techniques to identify metabolites.

Reading Question #4

Which molecule is responsible for the transport of oxygen in the blood?

A. Hemoglobin

B. Myoglobin

C. Testosterone

D. Auxin

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25. Chapter 25: Obtain and Use Energy: Digestion

MASON TEDESCHI

Invertebrate Digestive Systems

Animals have evolved different types of digestive systems to aid in the digestion of the different foods they consume. The simplest example is that of a gastrovascular cavity and is found in organisms with only one opening for digestion. Platyhelminthes (flatworms), Ctenophora (comb jellies), and Cnidaria (coral, jelly fish, and sea anemones) use this type of digestion. Gastrovascular cavities, as shown in Figure 24.1 a, are typically a blind tube or cavity with only one opening, the "mouth", which also serves as an "anus". Ingested material enters the mouth and passes through a hollow, tubular cavity. Cells within the cavity secrete digestive enzymes that breakdown the food. The food particles are engulfed by the cells lining the gastrovascular cavity.

The alimentary canal, shown in Figure 24.1b, is a more advanced system: it consists of one tube with a mouth at one end and an anus at the other. Earthworms are an example of an animal with an alimentary canal. Once the food is ingested through the mouth, it passes through the esophagus and is stored in an organ called the crop; then it passes into the gizzard where it is churned and digested. From the gizzard, the food passes through the intestine, the nutrients are absorbed, and the waste is eliminated as feces, called castings, through the anus.

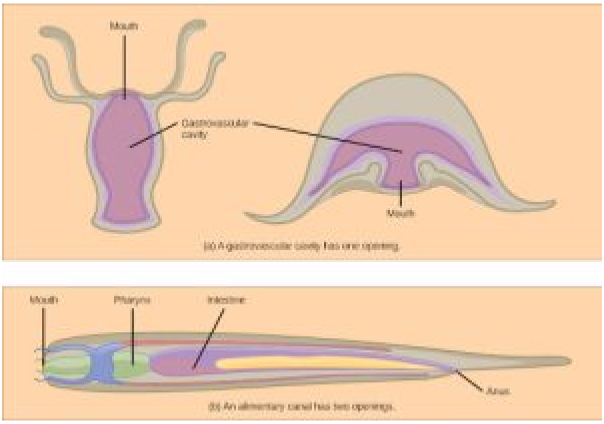


Figure 24.1 (a) A gastrovascular cavity has a single opening through which food is ingested and waste is excreted, as shown in this hydra and in this jellyfish medusa. (b) An alimentary canal has two openings: a mouth for ingesting food, and an anus for eliminating waste, as shown in this nematode.

Vertebrate Digestive Systems

Vertebrates have evolved more complex digestive systems to adapt to their dietary needs. Some animals have a single stomach, while others have multi-chambered stomachs. Birds have developed a digestive system adapted to eating unmasticated food.

Monogastric: Single-chambered Stomach

As the word monogastric suggests, this type of digestive system consists of one ("mono") stomach chamber ("gastric"). Humans and many animals have a monogastric digestive system as illustrated in Figure 24.2ab. The process of digestion begins with the mouth and the intake of food. The teeth play an important role in masticating (chewing) or physically breaking down food into smaller particles. The enzymes present in saliva also begin to chemically breakdown food. The esophagus is a long tube that connects the mouth to the stomach. Using peristalsis, or wave-like smooth muscle contractions, the muscles of the esophagus push the food towards the stomach. In order to speed up the actions of enzymes in the stomach, the stomach is an extremely acidic environment, with a pH between 1.5 and 2.5. The gastric juices, which include enzymes in the stomach, act on the food particles and continue the process of digestion. Further breakdown of food takes place in the small intestine where enzymes produced by the liver, the small intestine, and the pancreas continue the process of digestion. The nutrients are absorbed into the bloodstream across the epithelial cells lining the walls of the small intestines. The waste material travels on to the large intestine where water is absorbed and the drier waste material is compacted into feces; it is stored until it is excreted through the rectum.

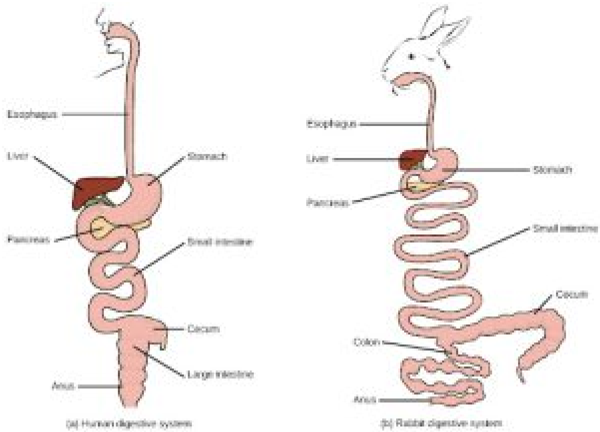
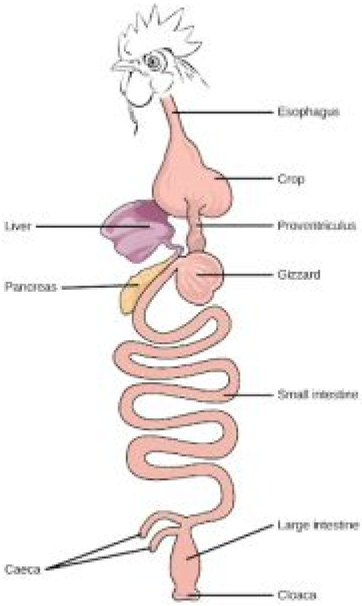


Figure 24.2 (a) Humans and herbivores, such as the (b) rabbit, have a monogastric digestive system. However, in the rabbit the small intestine and cecum are enlarged to allow more time to digest plant material. The enlarged organ provides more surface area for absorption of nutrients. Rabbits digest their food twice: the first time food passes through the digestive system, it collects in the cecum, and then it passes as soft feces called cecotrophes. The rabbit re-ingests these cecotrophes to further digest them.

Avian

Birds face special challenges when it comes to obtaining nutrition from food. They do not have teeth and so their digestive system, shown in Figure 24.3 must be able to process un-masticated food. Birds have evolved a variety of beak types that reflect the vast variety in their diet, ranging from seeds and insects to fruits and nuts. Because most birds fly, their metabolic rates are high in order to efficiently process food and keep their body weight low. The stomach of birds has two chambers: the proventriculus, where gastric juices are produced to digest the food before it enters the stomach, and the gizzard, where the food is stored, soaked, and mechanically ground. The undigested material forms food pellets that are sometimes regurgitated. Most of the chemical digestion and absorption happens in the intestine and the waste is excreted through the cloaca.



Evolution Connection

Birds have a highly efficient, simplified digestive system. Recent fossil evidence has shown that the evolutionary divergence of birds from other land animals was characterized by streamlining and simplifying the digestive system. Unlike many other animals, birds do not have teeth to chew their food. In place of lips, they have sharp pointy beaks. The beak, lack of jaws, and the smaller tongue of the birds can be traced back to their dinosaur ancestors. The emergence of these changes seems to coincide with the inclusion of seeds in the bird diet. Seed-eating birds have beaks that are shaped for grabbing seeds and the two-compartment stomach allows for delegation of tasks. Since birds need to remain light in order to fly, their metabolic rates are very high, which means they digest their food very quickly and need to eat often. Contrast this with the ruminants, where the digestion of plant matter takes a very long time

Ruminants

Ruminants are mainly herbivores like cows, sheep, and goats, whose entire diet consists of eating large amounts of roughage or fiber. They have evolved digestive systems that help them digest vast amounts of cellulose. An interesting feature of the ruminants' mouth is that they do not have upper incisor teeth. They use their lower teeth, tongue and lips to tear and chew their food. From the mouth, the food travels to the esophagus and on to the stomach.

To help digest the large amount of plant material, the stomach of the ruminants is a multi-chambered organ, as illustrated in Figure 24.4. The four compartments of the stomach are called the rumen, reticulum, omasum, and abomasum. These chambers contain many microbes that breakdown cellulose and ferment ingested food. The abomasum is the "true" stomach and is the equivalent of the monogastric stomach chamber where gastric juices are secreted. The four-compartment gastric chamber provides larger space and the microbial support necessary to digest plant material in ruminants. The fermentation process produces large amounts of gas in the stomach chamber, which must be eliminated. As in other animals, the small intestine plays an important role in nutrient absorption, and the large intestine helps in the elimination of waste.

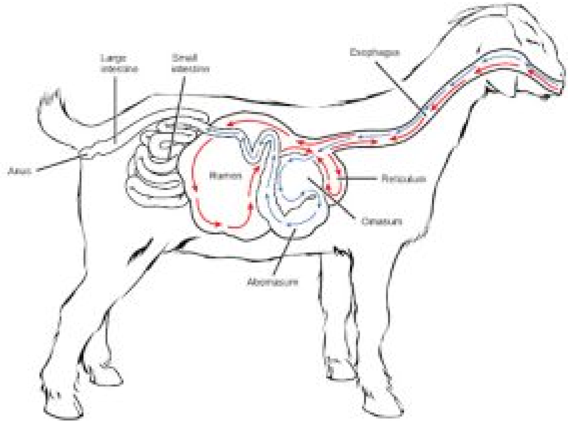


Figure 24.4 Ruminant animals, such as goats and cows, have four stomachs. The first two stomachs, the rumen and the reticulum, contain prokaryotes and protists that are able to digest cellulose fiber. The ruminant regurgitates cud from the reticulum, chews it, and swallows it into a third stomach, the omasum, which removes water. The cud then passes onto the fourth stomach, the abomasum, where it is digested by enzymes produced by the ruminant

Pseudo-ruminants

Some animals, such as camels and alpacas, are pseudo-ruminants.

They eat a lot of plant material and roughage. Digesting plant material is not easy because plant cell walls contain the polymeric sugar molecule cellulose. The digestive enzymes of these animals cannot breakdown cellulose, but microorganisms present in the digestive system can. Therefore, the digestive system must be able to handle large amounts of roughage and breakdown the cellulose. Pseudo-ruminants have a three-chamber stomach in the digestive system. However, their cecum—a pouched organ at the beginning of the large intestine containing many microorganisms that are necessary for the digestion of plant materials—is large and is the site where the roughage is fermented and digested. These animals do not have a rumen but have an omasum, abomasum, and reticulum.

Parts of the Digestive System

The vertebrate digestive system is designed to facilitate the transformation of food matter into the nutrient components that sustain organisms.

Oral Cavity

The oral cavity, or mouth, is the point of entry of food into the digestive system, illustrated in Figure 24.5. The food consumed is broken into smaller particles by mastication, the chewing action of the teeth. All mammals have teeth and can chew their food.

The extensive chemical process of digestion begins in the mouth. As food is being chewed, saliva, produced by the salivary glands, mixes with the food. Saliva is a watery substance produced in the mouths of many animals. There are three major glands that secrete saliva—the parotid, the submandibular, and the sublingual. Saliva contains mucus that moistens food and buffers the pH of the food. Saliva also contains immunoglobulins and lysozymes, which have antibacterial action to reduce tooth decay by inhibiting growth of some bacteria. Saliva also contains an enzyme called salivary amylase that begins the process of converting starches in the food into a disaccharide called maltose. Another enzyme called lipase is produced by the cells in the tongue. Lipases are a class of enzymes that can breakdown triglycerides. The lingual lipase begins the breakdown of fat components in the food. The chewing and wetting action provided by the teeth and saliva prepare the food into a mass called the bolus for swallowing. The tongue helps in swallowing—moving the bolus from the mouth into the pharynx. The pharynx opens to two passageways: the trachea, which leads to the lungs, and the esophagus, which leads to the stomach. The trachea has an opening called the glottis, which is covered by a cartilaginous flap called the epiglottis. When swallowing, the epiglottis closes the glottis and food passes into the esophagus and not the trachea. This arrangement allows food to be kept out of the trachea.

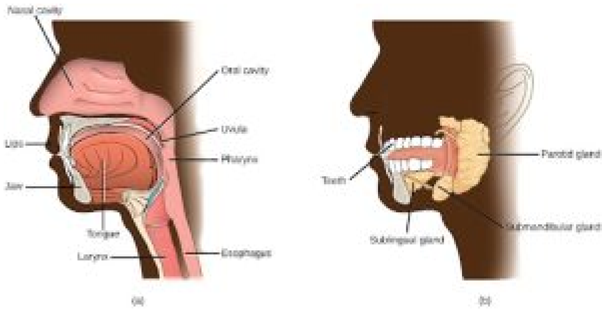


Figure 24.5 Digestion of food begins in the (a) oral cavity. Food is masticated by teeth and moistened by saliva secreted from the (b) salivary glands. Enzymes in the saliva begin to digest starches and fats. With the help of the tongue, the resulting bolus is moved into the esophagus by swallowing. (credit: modification of work by the National Cancer Institute)

Reading Question #1

Chewing (masticating) is an important part of the digestion process, except in:

A. Rabbits

B. Goats

C. Birds

D. Humans

Esophagus

The esophagus is a tubular organ that connects the mouth to the stomach. The chewed and softened food passes through the esophagus after being swallowed. The smooth muscles of the esophagus undergo a series of wave like movements called peristalsis that push the food toward the stomach, as illustrated in Figure 24.6. The peristalsis wave is unidirectional—it moves food from the mouth to the stomach, and reverse movement is not possible. The peristaltic movement of the esophagus is an involuntary reflex; it takes place in response to the act of swallowing.

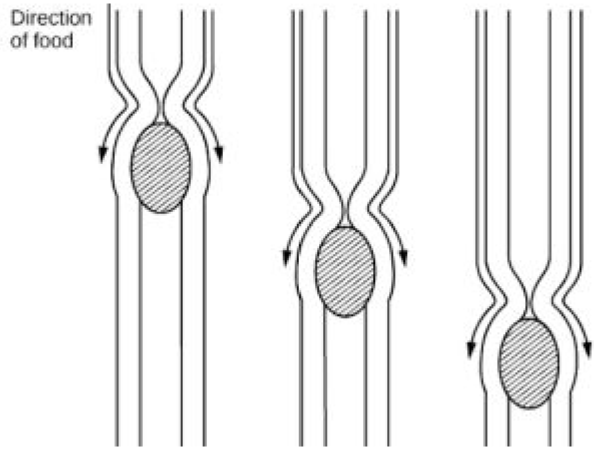


Figure 24.6 The esophagus transfers food from the mouth to the stomach through peristaltic movements.

A ring-like muscle called a sphincter forms valves in the digestive system. The gastro-esophageal sphincter is located at the stomach end of the esophagus. In response to swallowing and the pressure exerted by the bolus of food, this sphincter opens, and the bolus enters the stomach. When there is no swallowing action, this sphincter is shut and prevents the contents of the stomach from traveling up the esophagus. Many animals have a true sphincter; however, in humans, there is no true sphincter, but the esophagus remains closed when there is no swallowing action. Acid reflux or "heartburn" occurs when the acidic digestive juices escape into the esophagus.

Stomach

A large part of digestion occurs in the stomach, shown in Figure 24.7. The stomach is a saclike organ that secretes gastric digestive juices. The pH in the stomach is between 1.5 and 2.5. This highly acidic environment is required for the chemical breakdown of food and the extraction of nutrients. When empty, the stomach is a rather small organ; however, it can expand to up to 20 times its resting size when filled with food. This characteristic is particularly useful for animals that need to eat when food is available.

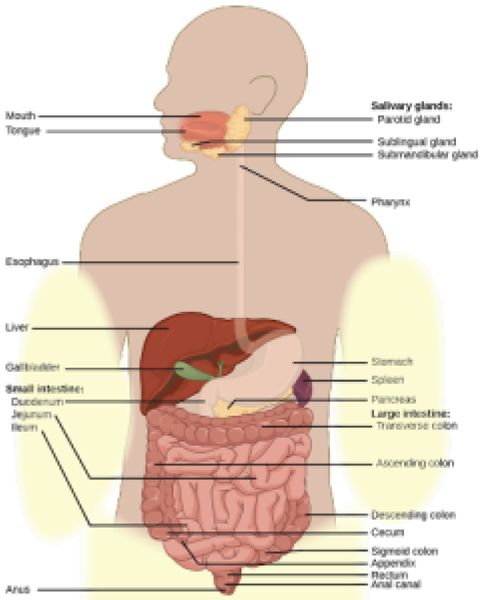


Figure 24.7 The human stomach has an extremely acidic environment where most of the protein gets digested. (credit: modification of work by Mariana Ruiz Villareal)

The stomach is also the major site for protein digestion in animals other than ruminants. Protein digestion is mediated by an enzyme called pepsin in the stomach chamber. Pepsin is secreted by the chief cells in the stomach in an inactive form called pepsinogen. Pepsin breaks peptide bonds and cleaves proteins into smaller polypeptides; it also helps activate more pepsinogen, starting a positive feedback mechanism that generates more pepsin. Another cell type—parietal cells—secrete hydrogen and chloride ions, which combine in the lumen to form hydrochloric acid, the primary acidic component of the stomach juices. Hydrochloric acid helps to convert the inactive pepsinogen to pepsin. The highly acidic environment also kills many microorganisms in the food and, combined with the action of the enzyme pepsin, results in the hydrolysis of protein in the food. Chemical digestion is facilitated by the churning action of the stomach. Contraction and relaxation of smooth muscles mixes the stomach contents about every 20 minutes. The partially digested food and gastric juice mixture is called chyme. Chyme passes from the stomach to the small intestine. Further protein digestion takes place in the small intestine. Gastric emptying occurs within two to six hours after a meal. Only a small amount of chyme is released into the small intestine at a time. The movement of chyme from the stomach into the small intestine is regulated by the pyloric sphincter.

When digesting protein and some fats, the stomach lining must be protected from getting digested by pepsin. There are two points to consider when describing how the stomach lining is protected. First, as previously mentioned, the enzyme pepsin is synthesized in the inactive form. This protects the chief cells, because pepsinogen does not have the same enzyme functionality of pepsin. Second, the stomach has a thick mucus lining that protects the underlying tissue from the action of the digestive juices. When this mucus lining is ruptured, ulcers can form in the stomach. Ulcers are open wounds in or on an organ caused by bacteria (Helicobacter pylori) when the mucus lining is ruptured and fails to reform.

Small Intestine

Chyme moves from the stomach to the small intestine. The small intestine is the organ where the digestion of protein, fats, and carbohydrates is completed. The small intestine is a long tube-like organ with a highly folded surface containing finger-like projections called the villi. The apical surface of each villus has many microscopic projections called microvilli. These structures, illustrated in Figure 24.8, are lined with epithelial cells on the luminal side and allow for the nutrients to be absorbed from the digested food and absorbed into the bloodstream on the other side. The villi and microvilli, with their many folds, increase the surface area of the intestine and increase absorption efficiency of the nutrients. Absorbed nutrients in the blood are carried into the hepatic portal vein, which leads to the liver. There, the liver regulates the distribution of nutrients to the rest of the body and removes toxic substances, including drugs, alcohol, and some pathogens.

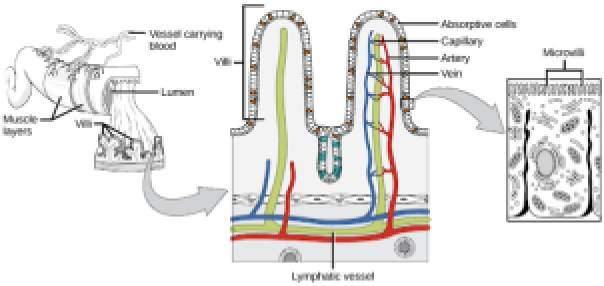


Figure 24.8 Villi are folds on the small intestine lining that increase the surface area to facilitate the absorption of nutrients.

The human small intestine is over 6m long and is divided into three parts: the duodenum, the jejunum, and the ileum. The “C-shaped,” fixed part of the small intestine is called the duodenum and is shown in [Figure 24.](#)8. The duodenum is separated from the stomach by the pyloric sphincter which opens to allow chyme to move from the stomach to the duodenum. In the duodenum, chyme is mixed with pancreatic juices in an alkaline solution rich in bicarbonate that neutralizes the acidity of chyme and acts as a buffer. Pancreatic juices also contain several digestive enzymes. Digestive juices from the pancreas, liver, and gallbladder, as well as from gland cells of the intestinal wall itself, enter the duodenum. Bile is produced in the liver and stored and concentrated in the gallbladder. Bile contains bile salts which emulsify lipids while the pancreas produces enzymes that catabolize starches, disaccharides, proteins, and fats. These digestive juices breakdown the food particles in the chyme into glucose, triglycerides, and amino acids. The bulk of chemical digestion of food takes place in the duodenum. Absorption of fatty acids also takes place in the duodenum.

The second part of the small intestine is called the jejunum, shown in [Figure 24.](#)8. Here, hydrolysis of nutrients is continued while most of the carbohydrates and amino acids are absorbed through the intestinal lining. Some chemical digestion and the bulk of nutrient absorption occurs in the jejunum.

The ileum, also illustrated in Figure 24.8 is the last part of the small intestine and here the bile salts and vitamins are absorbed into the bloodstream. The undigested food is sent to the colon from the ileum via peristaltic movements of the muscle. The ileum ends and the large intestine begins at the ileocecal valve. The vermiform, "worm-like," appendix is located at the ileocecal valve. The appendix of humans secretes no enzymes and has an insignificant role in immunity.

Large Intestine

The large intestine, illustrated in Figure 24.9, reabsorbs the water from the undigested food material and processes the waste material. The human large intestine is much smaller in length compared to the small intestine but larger in diameter. It has three parts: the cecum, the colon, and the rectum. The cecum joins the ileum to the colon and is the receiving pouch for the waste matter. The colon is home to many bacteria or "intestinal flora" that aid in the digestive processes. The colon can be divided into four regions, the ascending colon, the transverse colon, the descending colon, and the sigmoid colon. The main functions of the colon are to extract the water and mineral salts from undigested food, and to store waste material. Carnivorous mammals have a shorter large intestine compared to herbivorous mammals due to their diet.

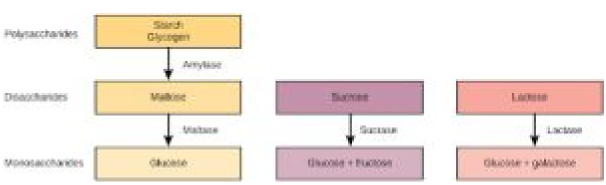


Figure 24.9 The large intestine reabsorbs water from undigested food and stores waste material until it is eliminated.

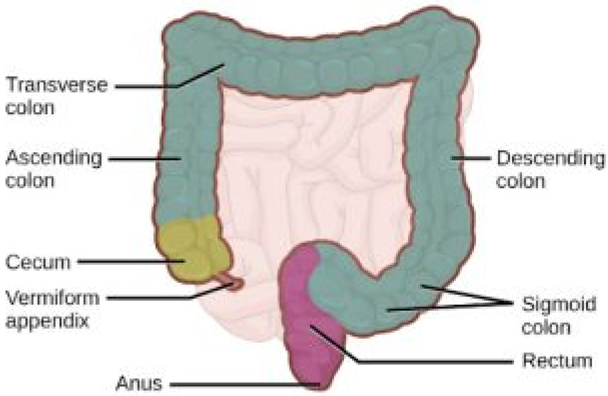


Figure 24.9 The large intestine reabsorbs water from undigested food and stores waste material until it is eliminated.

Rectum and Anus

The rectum is the terminal end of the large intestine, as shown in Figure 24.9. The primary role of the rectum is to store the feces until defecation. The feces are propelled using peristaltic movements during elimination. The anus is an opening at the far-end of the digestive tract and is the exit point for the waste material. Two sphincters between the rectum and anus control elimination: the inner sphincter is involuntary and the outer sphincter is voluntary.

Accessory Organs

The organs discussed above are the organs of the digestive tract through which food passes. Accessory organs are organs that add secretions (enzymes) that catabolize food into nutrients. Accessory organs include salivary glands, the liver, the pancreas, and the gallbladder. The liver, pancreas, and gallbladder are regulated by hormones in response to the food consumed.

The liver is the largest internal organ in humans and it plays a very important role in digestion of fats and detoxifying blood.

The liver produces bile, a digestive juice that is required for the breakdown of fatty components of the food in the duodenum. The liver also processes the vitamins and fats and synthesizes many plasma proteins.

The pancreas is another important gland that secretes digestive juices. The chyme produced from the stomach is highly acidic in nature; the pancreatic juices contain high levels of bicarbonate, an alkali that neutralizes the acidic chyme. Additionally, the pancreatic juices contain a large variety of enzymes that are required for the digestion of protein and carbohydrates.

The gallbladder is a small organ that aids the liver by storing bile and concentrating bile salts. When chyme containing fatty acids enters the duodenum, the bile is secreted from the gallbladder into the duodenum.

Reading Question #2

Food gets to the stomach through the

A. Trachea

B. Esophagus

C. Gastrovascular cavity

D. Intestines

Ingestion

The large molecules found in intact food cannot pass through the cell membranes. Food needs to be broken into smaller particles so that animals can harness the nutrients and organic molecules. The first step in this process is ingestion. Ingestion is the process of taking in food through the mouth. In vertebrates, the teeth, saliva, and tongue play important roles in mastication (preparing the food into bolus). While the food is being mechanically broken down, the enzymes in saliva begin to chemically process the food as well. The combined action of these processes modifies the food from large particles to a soft mass that can be swallowed and can travel the length of the esophagus.

Digestion and Absorption

Digestion is the mechanical and chemical breakdown of food into small organic fragments. It is important to breakdown macromolecules into smaller fragments that are of suitable size for absorption across the digestive epithelium. Large, complex molecules of proteins, polysaccharides, and lipids must be reduced to simpler particles such as simple sugar before they can be absorbed by the digestive epithelial cells. Different organs play specific roles in the digestive process. The animal diet needs carbohydrates, protein, and fat, as well as vitamins and inorganic components for nutritional balance. How each of these components is digested is discussed in the following sections.

Carbohydrates

The digestion of carbohydrates begins in the mouth. The salivary enzyme amylase begins the breakdown of food starches into maltose, a disaccharide. As the bolus of food travels through the esophagus to the stomach, no significant digestion of carbohydrates takes place. The esophagus produces no digestive enzymes but does produce mucous for lubrication. The acidic environment in the stomach stops the action of the amylase enzyme.

The next step of carbohydrate digestion takes place in the duodenum. Recall that the chyme from the stomach enters the duodenum and mixes with the digestive secretion from the pancreas, liver, and gallbladder. Pancreatic juices also contain amylase, which continues the breakdown of starch and glycogen into maltose, a disaccharide. The disaccharides are broken down into monosaccharides by enzymes called maltases, sucrases, and lactases, which are also present in the brush border of the small intestinal wall. Maltase breaks down maltose into glucose. Other disaccharides, such as sucrose and lactose are broken down by sucrase and lactase, respectively. Sucrase breaks down sucrose (or "table sugar") into glucose and fructose, and lactase breaks down lactose (or "milk sugar") into glucose and galactose. The monosaccharides (glucose) thus produced are absorbed and then can be used in metabolic pathways to harness energy. The monosaccharides are transported across the intestinal epithelium into the bloodstream to be transported to the different cells in the body. The steps in carbohydrate digestion are summarized in Figure 24.10.

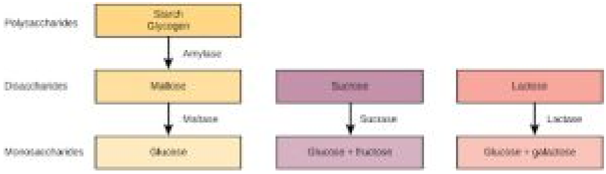


Figure 24.10 Digestion of carbohydrates is performed by several enzymes. Starch and glycogen are broken down into glucose by amylase and maltase. Sucrose (table sugar) and lactose (milk sugar) are broken down by sucrase and lactase, respectively.

Protein

A large part of protein digestion takes place in the stomach. The enzyme pepsin plays an important role in the digestion of proteins by breaking down the intact protein to peptides, which are short chains of four to nine amino acids. In the duodenum, other enzymes—trypsin, elastase, and chymotrypsin—act on the peptides reducing them to smaller peptides. Trypsin elastase, carboxypeptidase, and chymotrypsin are produced by the pancreas and released into the duodenum where they act on the chyme. Further breakdown of peptides to single amino acids is aided by enzymes called peptidases (those that breakdown peptides). Specifically, carboxypeptidase, dipeptidase, and aminopeptidase play important roles in reducing the peptides to free amino acids. The amino acids are absorbed into the bloodstream through the small intestines. The steps in protein digestion are summarized in Figure 24.11.

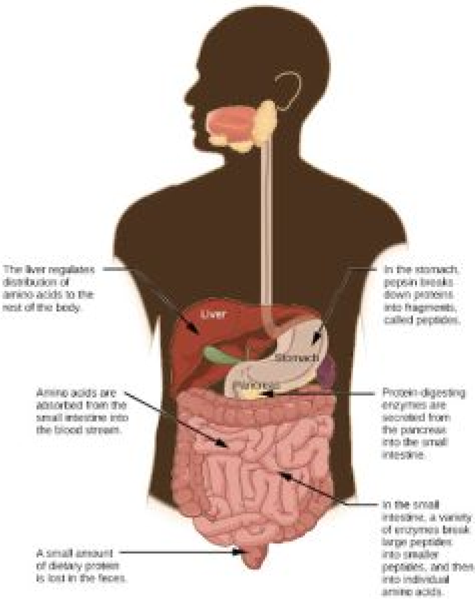


Figure 24.11 Protein digestion is a multistep process that begins in the stomach and continues through the intestines.

Lipids

Lipid digestion begins in the stomach with the aid of lingual lipase and gastric lipase. However, the bulk of lipid digestion occurs in the small intestine due to pancreatic lipase. When chyme enters the duodenum, the hormonal responses trigger the release of bile, which is produced in the liver and stored in the gallbladder. Bile aids in the digestion of lipids, primarily triglycerides by emulsification. Emulsification is a process in which large lipid globules are broken down into several small lipid globules. These small globules are more widely distributed in the chyme rather than forming large aggregates. Lipids are hydrophobic substances: in the presence of water, they will aggregate to form globules to minimize exposure to water. Bile contains bile salts, which are amphipathic, meaning they contain hydrophobic and hydrophilic parts. Thus, the bile salts hydrophilic side can interface with water on one side and the hydrophobic side interfaces with lipids on the other. By doing so, bile salts emulsify large lipid globules into small lipid globules.

Why is emulsification important for digestion of lipids? Pancreatic juices contain enzymes called lipases (enzymes that breakdown lipids). If the lipid in the chyme aggregates into large globules, very little surface area of the lipids is available for the lipases to act on, leaving lipid digestion incomplete. By forming an emulsion, bile salts increase the available surface area of the lipids many fold. The pancreatic lipases can then act on the lipids more efficiently and digest them. Lipases breakdown the lipids into fatty acids and glycerides. These molecules can pass through the plasma membrane of the cell and enter the epithelial cells of the intestinal lining. The bile salts surround long-chain fatty acids and monoglycerides forming tiny spheres called micelles. The micelles move into the brush border of the small intestine absorptive cells where the long-chain fatty acids and monoglycerides diffuse out of the micelles into the absorptive cells leaving the micelles behind in the chyme. The long-chain fatty acids and monoglycerides recombine in the absorptive cells to form triglycerides, which aggregate into globules and become coated with proteins. These large spheres are called chylomicrons. Chylomicrons contain triglycerides, cholesterol, and other lipids and have proteins on their surface. The surface is also composed of the hydrophilic phosphate “heads” of phospholipids. Together, they enable the chylomicron to move in an aqueous environment without exposing the lipids to water. Chylomicrons leave the absorptive cells via exocytosis. Chylomicrons enter the lymphatic vessels, and then enter the blood in the subclavian vein.

Vitamins

Vitamins can be either water-soluble or lipid-soluble. Fat soluble vitamins are absorbed in the same manner as lipids. It is important to consume some amount of dietary lipid to aid the absorption of lipid-soluble vitamins. Water-soluble vitamins can be directly absorbed into the bloodstream from the intestine.

Reading Question #3

Emulsification is important for the digestion of:

A. Carbohydrates

B. Proteins

C. Lipids

D. All of the above

Link to Learning

This website has an overview of the digestion of protein, fat, and carbohydrates.

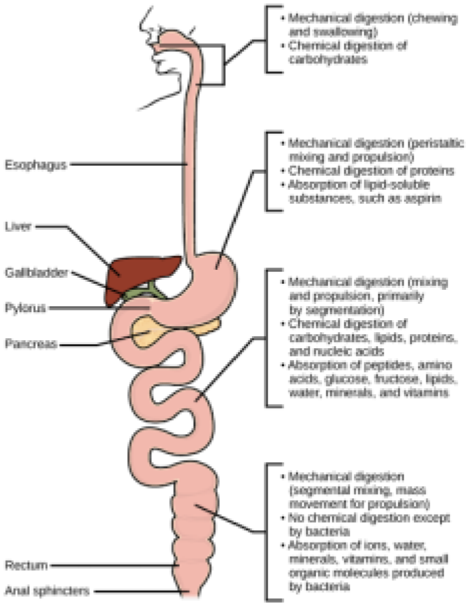


Figure 24.12 Mechanical and chemical digestion of food takes place in many steps, beginning in the mouth and ending in the rectum.

Elimination

The final step in digestion is the elimination of undigested food content and waste products. The undigested food material enters the colon, where most of the water is reabsorbed. Recall that the colon is also home to the microflora called “intestinal flora” that aid in the digestion process. The semi-solid waste is moved through the colon by peristaltic movements of the muscle and is stored in the rectum. As the rectum expands in response to storage of fecal matter, it triggers the neural signals required to set up the urge to eliminate. The solid waste is eliminated through the anus using peristaltic movements of the rectum.

Common Problems with Elimination

Diarrhea and constipation are some of the most common health concerns that affect digestion. Constipation is a condition where the feces are hardened because of excess water removal in the colon. In contrast, if enough water is not removed from the feces, it results in diarrhea. Many bacteria, including the ones that cause cholera, affect the proteins involved in water reabsorption in the colon and result in excessive diarrhea.

Emesis

Emesis, or vomiting, is elimination of food by forceful expulsion through the mouth. It is often in response to an irritant that affects the digestive tract, including but not limited to viruses, bacteria, emotions, sights, and food poisoning. This forceful expulsion of the food is due to the strong contractions produced by the stomach muscles. The process of emesis is regulated by the medulla.

Reading Question #4

In humans, mechanical digestion includes:

A. Mixing and propulsion

B. Breaking down carbohydrates and proteins

C. Bacteria aiding in the digestive process

D. Emesis

Reading Question #5

Water is absorbed in the ______, which passes waste into the rectum

A. Esophagus

B. Stomach

C. Gastrovascular cavity

D. Colon

26. Chapter 26: Asexual reproduction

ANASTASIA CHOUVALOVA

Animals produce offspring through asexual and/or sexual reproduction. Both methods have advantages and disadvantages. **Asexual reproduction** produces offspring that are genetically identical to the parent because the offspring are all clones of the original parent. A single individual can produce offspring asexually and large numbers of offspring can be produced quickly. In a stable or predictable environment, asexual reproduction is an effective means of reproduction because all the offspring will be adapted to that environment. In an unstable or unpredictable environment asexually-reproducing species may be at a disadvantage because all the offspring are genetically identical and may not have the genetic variation to survive in new or different conditions. On the other hand, the rapid rates of asexual reproduction may allow for a speedy response to environmental changes if individuals have mutations. An additional advantage of asexual reproduction is that colonization of new habitats may be easier when an individual does not need to find a mate to reproduce.

During sexual reproduction the genetic material of two individuals is combined to produce genetically diverse offspring that differ from their parents. The genetic diversity of sexually produced offspring is thought to give species a better chance of surviving in an unpredictable or changing environment. Species that reproduce sexually must maintain two different types of individuals, males and females, which can limit the ability to colonize new habitats as both sexes must be present.

Reading Question #1

Which of the following is not an advantage of asexual reproduction?

A. Easier colonization of new habitats

B. Fast rate of offspring production

C. Many offspring produced

D. A more diverse gene pool

Asexual Reproduction

Asexual reproduction occurs in prokaryotic microorganisms (bacteria) and in some eukaryotic single-celled and multi-celled organisms. There are a number of ways that animals reproduce asexually – fission, budding, fragmentation, and parthenogenesis.

Fission

Fission, also called binary fission, occurs in prokaryotic microorganisms and in some invertebrate, multi-celled organisms. After a period of growth, an organism splits into two separate organisms. Some unicellular eukaryotic organisms undergo binary fission by mitosis. In other organisms, part of the individual separates and forms a second individual. This process occurs, for example, in many asteroid echinoderms through splitting of the central disk. Some sea anemones and some coral polyps (Figure 25.1) also reproduce through fission.

Figure 25.1 Coral polyps reproduce asexually by fission. (credit: G. P. Schmahl, NOAA FGBNMS Manager)

Budding

Budding is a form of asexual reproduction that results from the outgrowth of a part of a cell or body region leading to a separation from the original organism into two individuals. Budding occurs commonly in some invertebrate animals such as corals and hydras. In hydras, a bud forms that develops into an adult and breaks away from the main body, as illustrated in Figure 25.2, whereas in coral budding, the bud does not detach and multiplies as part of a new colony. Visit this link to view a video of hydra budding.

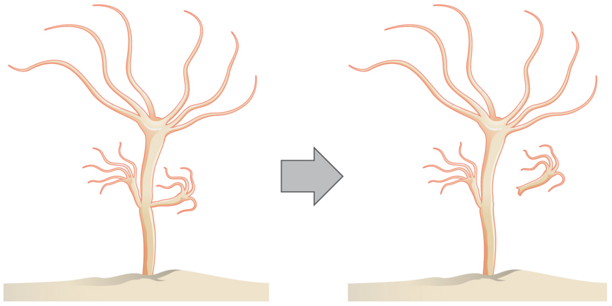


Figure 25.2 Hydra reproduce asexually through budding.

Fragmentation

Fragmentation is the breaking of the body into two parts with subsequent regeneration. If the animal is capable of fragmentation, and the part is big enough, a separate individual will regrow.

For example, in many sea stars, asexual reproduction is accomplished by fragmentation. Figure 25.3 illustrates a sea star for which an arm of the individual is broken off and regenerates a new sea star. Fisheries workers have been known to try to kill the sea stars eating their clam or oyster beds by cutting them in half and throwing them back into the ocean. Unfortunately for the workers, the two parts can each regenerate a new half, resulting in twice as many sea stars to prey upon the oysters and clams. Fragmentation also occurs in annelid worms, turbellarians, and poriferans.

Figure 25.3 Sea stars can reproduce through fragmentation. The large arm, a fragment from another sea star, is developing into a new individual.

Note that in fragmentation, there is generally a noticeable difference in the size of the individuals, whereas in fission, two individuals of approximate size are formed.

Parthenogenesis

Parthenogenesis is a form of asexual reproduction where an egg develops into a complete individual without being fertilized. The resulting offspring can be either haploid or diploid, depending on the process and the species. Parthenogenesis occurs in invertebrates such as water fleas, rotifers, aphids, stick insects, some ants, wasps, and bees. Bees use parthenogenesis to produce haploid males (drones). If eggs are fertilized, diploid females develop, and if the fertilized eggs are fed a special diet (so called royal jelly), a queen is produced.

Some vertebrate animals—such as certain reptiles, amphibians, and fish—also reproduce through parthenogenesis. Although more common in plants, parthenogenesis has been observed in animal species that were segregated by sex in terrestrial or marine zoos. Two female Komodo dragons, a hammerhead shark, and a blacktop shark have produced parthenogenic young when the females have been isolated from males.

Reading Question #2

Match the following definitions of different types of asexual reproduction to their terms.

A) Fission B) Budding C) Fragmentation D) Parthenogenesis

1. An unfertilized egg becomes a fully-functioning organism
2. One body separates into two separate bodies.
3. A portion of the parental organism splits into smaller parts.
4. Some outgrowth of the parental organism produces the offspring.

Fertilization methods in sexual reproduction

Sexual reproduction starts with the combination of a sperm and an egg in a process called fertilization. This can occur either inside (internal fertilization) or outside (external fertilization) the body of the female. Humans provide an example of the former whereas seahorse reproduction is an example of the latter.

External Fertilization

External fertilization usually occurs in aquatic environments where both eggs and sperm are released into the water. After the sperm reaches the egg, fertilization takes place. Most external fertilization happens during the process of spawning where one or several females release their eggs and the male(s) release sperm in the same area, at the same time. The release of the reproductive material may be triggered by water temperature or the length of daylight. Nearly all fish spawn, as do crustaceans (such as crabs and shrimp), mollusks (such as oysters), squid, and echinoderms (such as sea urchins and sea cucumbers). Figure 25.4 shows salmon spawning in a shallow stream. Frogs, like those shown in Figure 25.5, corals, mollusks, and sea cucumbers also spawn.

Figure 25.4 Salmon reproduce through spawning. (credit: Dan Bennett)

Figure 25.5 During sexual reproduction in toads, the male grasps the female from behind and externally fertilizes the eggs as they are deposited. (credit: "OakleyOriginals"/Flickr)

Pairs of fish that are not broadcast spawners may exhibit courtship behavior. This allows the female to select a particular male. The trigger for egg and sperm release (spawning) causes the egg and sperm to be placed in a small area, enhancing the possibility of fertilization.

External fertilization in an aquatic environment protects the eggs from drying out. Broadcast spawning can result in a greater mixture of the genes within a group, leading to higher genetic diversity and a greater chance of species survival in a hostile environment. For sessile aquatic organisms like sponges, broadcast spawning is the only mechanism for fertilization and colonization of new environments. The presence of the fertilized eggs and developing young in the water provides opportunities for predation resulting in a loss of offspring. Therefore, millions of eggs must be produced by individuals, and the offspring produced through this method must mature rapidly. The survival rate of eggs produced through broadcast spawning is low.

Reading Question #3

Which of the following species is least likely to use external fertilization?

A. Sea anemones

B. Turtles

C. Cod fish

D. American bullfrog

Internal Fertilization

Internal fertilization occurs most often in land-based animals, although some aquatic animals also use this method. There are three ways that offspring are produced following internal fertilization. In oviparity, fertilized eggs are laid outside the parent's body and develop there, receiving nourishment from the yolk that is a part of the egg. This occurs in most bony fish, many reptiles, some cartilaginous fish, most amphibians, two mammals, and all birds. Reptiles and insects produce leathery eggs, while birds and turtles produce eggs with high concentrations of calcium carbonate in the shell, making them hard. Chicken eggs are an example of this second type.

In ovoviviparity, fertilized eggs are retained in the parent (usually the female), but the embryo obtains its nourishment from the egg's yolk and the young are fully developed when they are hatched. This occurs in some bony fish (like the guppy *Lebistes reticulatus*), some sharks, some lizards, some snakes (such as the garter snake *Thamnophis sirtalis*), some vipers, and some invertebrate animals (like the Madagascar hissing cockroach *Gromphadorhina portentosa*).

In viviparity the young develop within the female, receiving nourishment from the parent's blood through a placenta. The offspring develops in the female and is born alive. This occurs in most mammals, some cartilaginous fish, and a few reptiles.

Internal fertilization has the advantage of protecting the fertilized egg from dehydration on land. The embryo is isolated within the female, which limits predation on the young. Internal fertilization enhances the fertilization of eggs by a specific male. Fewer offspring are produced through this method, but their survival rate is higher than that for external fertilization.

Reading Question #4

The great white shark mother contains the fertilized egg and the yolk nourishes the embryo until it is mature enough to hatch. This is a description of:

A. Oviparity

B. Ovoviviparity

C. Viviparity

D. External fertilization

The Evolution of Reproduction

Once multicellular organisms evolved and developed specialized cells, some also developed tissues and organs with specialized functions. An early development in reproduction occurred in the Annelids. These organisms produce sperm and eggs from undifferentiated cells in their coelom and store them in that cavity. When the coelom becomes filled, the cells are released through an excretory opening or by the body splitting open. Reproductive organs evolved with the development of gonads that produce sperm and eggs. These cells went through meiosis, an adaptation of mitosis, which reduced the number of chromosomes in each reproductive cell by half, while increasing the number of cells through cell division.

Complete reproductive systems were developed in insects, with separate sexes. Sperm are made in testes and then travel through coiled tubes to the epididymis for storage. Eggs mature in the ovary. When they are released from the ovary, they travel to the uterine tubes for fertilization. Some insects have a specialized sac, called a spermatheca, which stores sperm for later use, sometimes up to a year. Fertilization can be timed with environmental or food conditions that are optimal for offspring survival.

Vertebrates have similar structures, with a few differences. Non-mammals, such as birds and reptiles, have a common body opening, called a cloaca, for the digestive, excretory and reproductive systems. Coupling between birds usually involves positioning the cloaca openings opposite each other for transfer of sperm. Mammals have separate openings for the systems in the female and a uterus for support of developing offspring. The uterus has two chambers in species that produce large numbers of offspring at a time, while species that produce one offspring, such as primates, have a single uterus.

Sperm transfer from the male to the female during reproduction ranges from releasing the sperm into the watery environment for external fertilization, to the joining of cloaca in birds, to the development of a penis for direct delivery into the female's vagina in mammals.

Reading Question #5

Which of the following statements correctly describes external and internal fertilization in sexual reproduction? Select all that apply.

A. In internal fertilization, the offspring is fertilized outside of the parent's body while in external fertilization, the offspring is fertilized inside of the parent's body.

B. In internal fertilization, the main advantage is that the embryo is protected from extrinsic factors such as wind and lack of humidity.

C. In external fertilization, there tends to be less offspring produced.

D. Three examples of external fertilization are oviparity, ovoviviparity, and vivparity.

References

Adapted from Clark, M.A., Douglas, M., and Choi, J. (2018). Biology 2e. OpenStax. Retrieved from https://openstax.org/books/biology-2e/pages/1-introduction

27. Chapter 27: Sexual reproduction

ANASTASIA CHOUVALOVA AND MASON TEDESCHI

Sexual reproduction

Sexual reproduction was likely an early evolutionary innovation after the appearance of eukaryotic cells. It appears to have been very successful because most eukaryotes are able to reproduce sexually and, in many animals, it is the only mode of reproduction. And yet, scientists also recognize some real disadvantages to sexual reproduction. On the surface, creating offspring that are genetic clones of the parent appears to be a better system. If the parent organism is successfully occupying a habitat, offspring with the same traits should be similarly successful. There is also the obvious benefit to an organism that can produce offspring whenever circumstances are favorable by asexual budding, fragmentation, or by producing eggs asexually. These methods of reproduction do not require a partner with which to reproduce. Indeed, some organisms that lead a solitary lifestyle have retained the ability to reproduce asexually. In addition, in asexual populations, every individual is capable of reproduction. In sexual populations, the males are not producing the offspring themselves, so hypothetically an asexual population could grow twice as fast.

However, multicellular organisms that exclusively depend on asexual reproduction are exceedingly rare. Why are meiosis and sexual reproductive strategies so common? These are important (and as yet unanswered) questions in biology, even though they have been the focus of much research beginning in the latter half of the 20th century. There are several possible explanations, one of which is that the variation that sexual reproduction creates among offspring is very important to the survival and reproduction of the population. Thus, on average, a sexually reproducing population will leave more descendants than an otherwise similar asexually reproducing population. The only source of variation in asexual organisms is mutation. Mutations that take place during the formation of germ cell lines are also a source of variation in sexually reproducing organisms. However, in contrast to mutation during asexual reproduction, the mutations during sexual reproduction can be continually reshuffled from one generation to the next when different parents combine their unique genomes and the genes are mixed into different combinations by crossovers during prophase I and random assortment at metaphase I.

Sexual reproduction requires the union of two specialized cells, called gametes, each of which contains one set of chromosomes. When gametes unite, they form a **zygote**, or fertilized egg that contains two sets of chromosomes. (Note: Cells that contain one set of chromosomes are called haploid; cells containing two sets of chromosomes are called diploid.) If the reproductive cycle is to continue for any sexually reproducing species, then the diploid cell must somehow reduce its number of chromosome sets to produce haploid gametes; otherwise, the number of chromosome sets will double with every future round of fertilization. Therefore, sexual reproduction requires a nuclear division that reduces the number of chromosome sets by half.

Most animals and plants and many unicellular organisms are diploid and therefore have two sets of chromosomes. In each somatic cell of the organism (all cells of a multicellular organism except the gametes or reproductive cells), the nucleus contains two copies of each chromosome, called **homologous chromosomes**. Homologous chromosomes are matched pairs containing the same genes in identical locations along their lengths. Diploid organisms inherit one copy of each homologous chromosome from each genetic contributor.

Meiosis is the *nuclear division* that forms haploid cells from diploid cells, and it employs many of the same cellular mechanisms as mitosis. However, as you have learned, **mitosis** produces daughter cells whose nuclei are genetically identical to the original parent nucleus. In mitosis, both the parent and the daughter nuclei are at the same "ploidy level"—diploid in the case of most multicellular animals. Plants use mitosis to grow as sporophytes, and to grow and produce eggs and sperm as gametophytes; so they use mitosis for both haploid and diploid cells (as well as for all other ploidies). In meiosis, the starting nucleus is always diploid and the daughter nuclei that result are haploid. To achieve this reduction in chromosome number, meiosis consists of one round of chromosome replication followed by two rounds of nuclear division. Because many events that occur during each of the division stages are analogous to the events of mitosis, the same stage names are assigned. However, because there are two rounds of division, the major process and the stages are designated with a "I" or a "II." Thus, meiosis I is the first round of meiotic division and consists of prophase I, prometaphase I, and so on. Likewise, Meiosis II (during which the second round of meiotic division takes place) includes prophase II, prometaphase II, and so on. We discussed meiosis (Figure 26.1) in great detail in BIOL 1403, so we will not spend as much time on it in BIOL 1404.

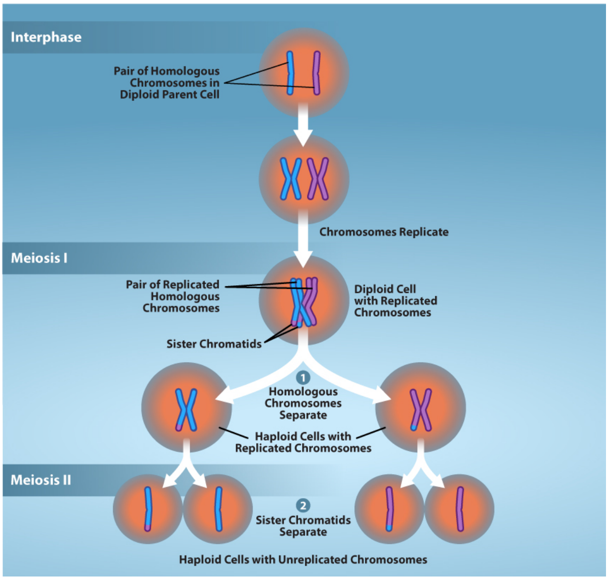


Figure 26.1 Overview of Meiosis. The production of gametes is a crucial process for sexually reproducing organisms. Meiosis is the mechanism used to reduce diploid cells to haploid gametes while introducing genetic diversity. Prior to meiosis, chromosomes are replicated in S-phase to ensure proper number of chromosomes in the resulting gametes. During meiosis, two successive rounds of division reduces the number of chromosomes (ploidy) of the cell by half. going from diploid cells to haploid gametes. Credit: Rao,

A., *Tag*, A, *Fletcher*, S., *and Ryan*, K. *Department of Biology, Texas A&M University.*

Evolution Connection

The Red Queen Hypothesis

Genetic variation is the outcome of sexual reproduction, but why are ongoing variations necessary, even under seemingly stable environmental conditions? Enter the Red Queen hypothesis, first proposed by Leigh Van Valen in 1973.[3] The concept was named in reference to the Red Queen's race in Lewis Carroll's book, *Through the Looking-Glass*.

All species **coevolve** (evolve together) with other organisms. For example, predators evolve with their prey, and parasites evolve with their hosts. Each tiny advantage gained by favorable variation gives a species a reproductive edge over close competitors, predators, parasites, or even prey. However, survival of any given genotype or phenotype in a population is dependent on the reproductive fitness of other genotypes or phenotypes within a given species. The only method that will allow a coevolving species to maintain its own share of the resources is to also *continually improve its* **fitness** (the capacity of the members to produce more reproductively viable offspring relative to others within a species). As one species gains an advantage, this increases selection on the other species; they must also develop an advantage or they will be outcompeted. No single species progresses too far ahead because genetic variation among the progeny of sexual reproduction provides all species with a mechanism to improve rapidly. Species that cannot keep up become extinct. The Red Queen's catchphrase was, "It takes all the running you can do to stay in the same place." This is an apt description of coevolution between competing species.

Life Cycles of Sexually Reproducing Organisms

Fertilization and meiosis alternate in sexual life cycles. What happens between these two events depends on the organism's "reproductive strategy." The process of meiosis reduces the chromosome number by half. Fertilization, the joining of two haploid gametes, restores the diploid condition. Some organisms have a multicellular diploid stage that is most obvious and only produce haploid reproductive cells. Animals, including humans, have this type of life cycle. Other organisms, such as fungi, have a multicellular haploid stage that is most obvious. Plants and some algae have alternation of generations, in which they have multicellular diploid and haploid life stages that are apparent to different degrees depending on the group.

Nearly all animals employ a diploid-dominant life-cycle strategy in which the only haploid cells produced by the organism are the gametes. Early in the development of the embryo, specialized diploid cells, called germ cells, are produced within the gonads (such as the testes and ovaries). Germ cells are capable of mitosis to perpetuate the germ cell line and meiosis to produce haploid gametes. Once the haploid gametes are formed, they lose the ability to divide again. There is no multicellular haploid life stage. Fertilization occurs with the fusion of two gametes, usually from different individuals, restoring the diploid state (Figure 26.2).

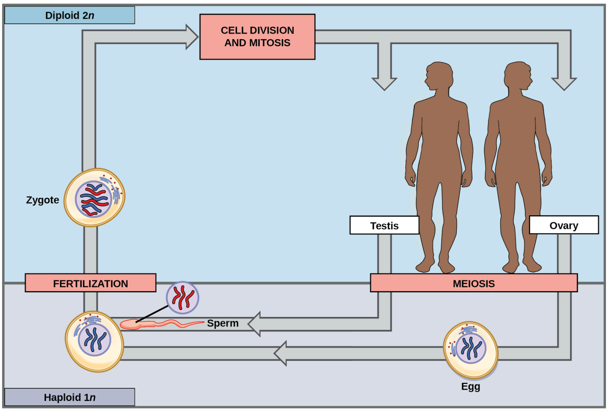


Figure 26.2 In animals, sexually reproducing adults form haploid gametes, called egg and sperm, from diploid germ cells. Fusion of the two gametes gives rise to a fertilized egg cell, or zygote. The zygote will undergo multiple rounds of mitosis to produce a multicellular offspring. The germ cells are generated early in the development of the zygote.

Most fungi and algae employ a life-cycle type in which the "body" of the organism—the ecologically important part of the life cycle—is haploid. The haploid cells that make up the tissues of the dominant multicellular stage are formed by mitosis. During sexual reproduction, specialized haploid cells from two individuals—designated the (+) and (−) mating types—join to form a diploid zygote. The zygote immediately undergoes meiosis to form four haploid cells called *spores*. Although these spores are haploid like the "parents," they contain a new genetic combination from two parents. The spores can remain dormant for various time periods. Eventually, when conditions are favorable, the spores form multicellular haploid structures through many rounds of mitosis (Figure 26.3).

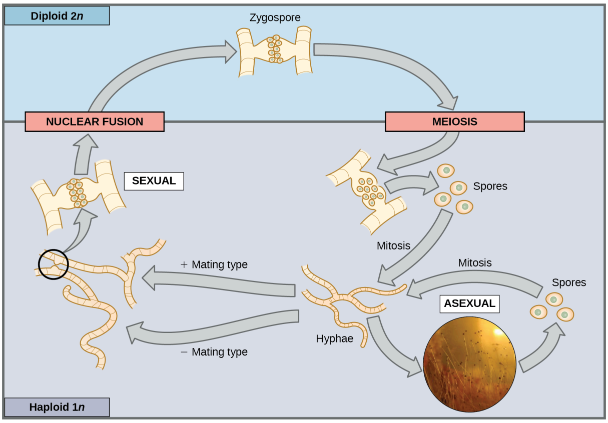


Figure 26.3 Fungi, such as black bread mold (Rhizopus nigricans), have a haploid multicellular stage that produces specialized haploid cells by mitosis that fuse to form a diploid zygote. The zygote undergoes meiosis to produce haploid spores. Each spore gives rise to a multicellular haploid organism by mitosis. Above, different mating hyphae types (denoted as + and −) join to form a zygospore through nuclear fusion. (credit "zygomycota" micrograph: modification of work by "Fanaberka" /Wikimedia Commons)

The third life-cycle type, employed by some algae and all plants, is a blend of the haploid-dominant and diploid-dominant extremes. Species with alternation of generations have both haploid and diploid multicellular organisms as part of their life cycle. The haploid multicellular plants are called gametophytes, because they produce gametes from specialized cells. Meiosis is not directly involved in the production of gametes in this case, because the organism that produces the gametes is already haploid. Fertilization between the gametes forms a diploid zygote. The zygote will undergo many rounds of mitosis and give rise to a diploid multicellular plant called a sporophyte. Specialized cells of the sporophyte will undergo meiosis and produce haploid spores. The spores will subsequently develop into the gametophytes (Figure 26.4).

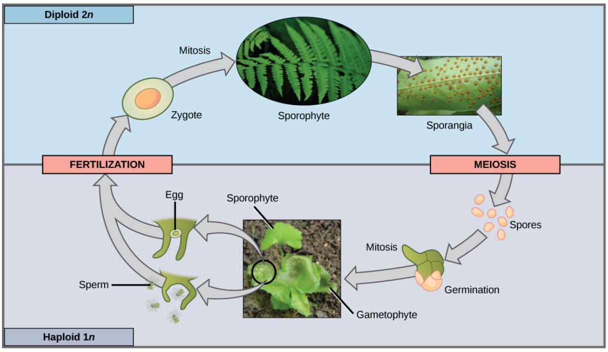


Figure 26.4 Plants have a life cycle that alternates between a multicellular haploid organism and a multicellular diploid organism. In some plants, such as ferns, both the haploid and diploid plant stages are free-living. The diploid plant is called a sporophyte because it produces haploid spores by meiosis. The spores develop into multicellular, haploid plants that are called gametophytes because they produce gametes. The gametes of two individuals will fuse to form a diploid zygote that becomes the sporophyte. (credit "fern": modification of work by

Cory Zanker; credit “sporangia”: modification of work by “Obsidian Soul”/Wikimedia Commons; credit “gametophyte and sporophyte”: modification of work by “Vlmastra”/ Wikimedia Commons)

Although all plants utilize some version of the alternation of generations, the relative size of the sporophyte and the gametophyte and the relationship between them vary greatly. In plants such as moss, the gametophyte organism is the free-living plant and the sporophyte is physically dependent on the gametophyte. In other plants, such as ferns, both the gametophyte and sporophyte plants are free-living; however, the sporophyte is much larger. In seed plants, such as magnolia trees and daisies, the gametophyte is composed of only a few cells and, in the case of the female gametophyte, is completely retained within the sporophyte.

Sexual reproduction takes many forms in multicellular organisms. The fact that nearly every multicellular organism on Earth employs sexual reproduction is strong evidence for the benefits of producing offspring with unique gene combinations, though there are other possible benefits as well.

Reading Question #1

Which of the following are benefits of sexual reproduction? Select all that apply.

A. Variation can lead to better adaptations and survival

B. Genetic diversity in the offspring

C. Less susceptible to being wiped out due to disease

D. Doesn’t require a partner

Gametogenesis

Gametogenesis, the production of sperm and eggs, takes place through the process of meiosis. During meiosis, two cell divisions separate the paired chromosomes in the nucleus and then separate the chromatids that were made during an earlier stage of the cell's life cycle. Meiosis produces haploid cells with half of each pair of chromosomes normally found in diploid cells. The production of sperm is called **spermatogenesis** and the production of eggs is called **oogenesis.**

Spermatogenesis

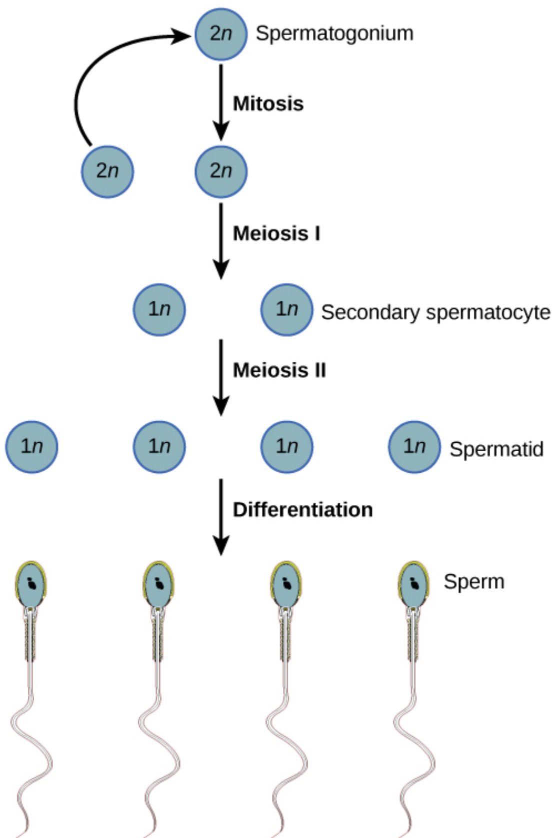


Figure 26.5. During spermatogenesis, four sperm result from each primary spermatocyte.

Meiosis starts with a cell called a primary spermatocyte. At the end of the first meiotic division, a haploid cell is produced called a secondary spermatocyte. This cell is haploid and must go through another meiotic cell division. The cell produced at the end of meiosis is called a spermatid and when it reaches the lumen of the tubule and grows a flagellum, it is called a sperm cell. Four sperm result from each primary spermatocyte that goes through meiosis.

Stem cells are deposited during gestation and are present at birth through the beginning of adolescence, but in an inactive state. During adolescence, gonadotropic hormones from the anterior pituitary cause the activation of these cells and the production of viable sperm. This continues into old age.

Link to Learning

Visit this site to see the process of spermatogenesis in more detail.

Oogenesis

Oogenesis, illustrated in Figure 26.6, occurs in the outermost layers of the ovaries. As with sperm production, oogenesis starts with a germ cell, called an oogonium (plural: oogonia), but this cell undergoes mitosis to increase in number, eventually resulting in up to about one to two million cells in the embryo.

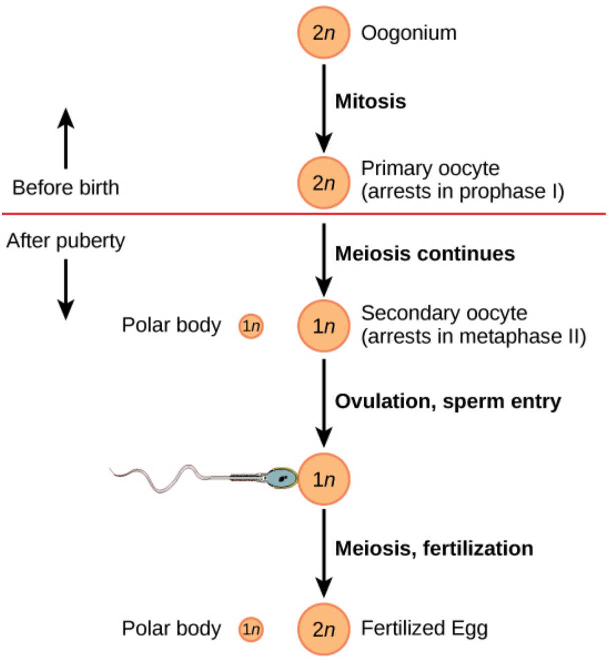


Figure 26.6 The process of oogenesis occurs in the ovary's outermost layer.

The cell starting meiosis is called a primary oocyte, as shown in Figure 26.6. This cell will start the first meiotic division and be arrested in its progress in the first prophase stage. At the time of birth, all future eggs are in the prophase stage. At adolescence, anterior pituitary hormones cause the development of a number of follicles in an ovary. This results in the primary oocyte finishing the first meiotic division. The cell divides unequally, with most of the cellular material and organelles going to one cell, called a secondary oocyte, and only one set of chromosomes and a small amount of cytoplasm going to the other cell. This second cell is called a polar body and usually dies. A secondary meiotic arrest occurs, this time at the metaphase II stage. At ovulation, this secondary oocyte will be released and travel toward the uterus through the oviduct. If the secondary oocyte is fertilized, the cell continues through the meiosis II, producing a second polar body and a fertilized egg containing all 46 chromosomes of a human being, half of them coming from the sperm.

Egg production begins before birth, is arrested during meiosis until puberty, and then individual cells continue through at each menstrual cycle. One egg is produced from each meiotic process, with the extra chromosomes and chromatids going into polar bodies that degenerate and are reabsorbed by the body.

Reading Question #2

Which of the following statements accurately describes a key difference between oogenesis and spermatogenesis?

A. Spermatogenesis produces polar bodies while oogenesis does not produce polar bodies.

B. In oogenesis, each meiosis round produces only one egg while in spermatogenesis, each meiosis round produces four sperm.

C. In oogenesis, each meiosis round produces four egg while in spermatogenesis, each meiosis round produces one sperm.

D. Spermatogenesis yields haploid cells while oogenesis yields diploid cells.

Hormonal Regulation of the Reproductive

System

Regulation of the reproductive system is a process that requires the action of hormones from the pituitary gland, theadrenal cortex, and the gonads. During puberty in both males and females, the hypothalamus produces gonadotropin-releasing hormone (GnRH), which stimulates the production and release of follicle-stimulating hormone (FSH) and luteinizing hormone (LH) from the anterior pituitary gland. These hormones regulate the gonads (testes in males and ovaries in females) and therefore are called gonadotropins. In both males and females, FSH stimulates gamete production and LH stimulates production of hormones by the gonads. An increase in gonad hormone levels inhibits GnRH production through a negative feedback loop.

Regulation of the Testicular Reproductive System

In the testes, FSH stimulates the maturation of sperm cells. FSH production is inhibited by the hormone inhibin, which is released by the testes. LH stimulates production of the sex hormones (androgens) by the interstitial cells of the testes and therefore is also called interstitial cell-stimulating hormone.

The most widely known androgen in males is testosterone. Testosterone promotes the production of sperm and a suite of secondary sex characteristics, such as the growth and development of the testes and penis, increased skeletal and muscular growth, enlargement of the larynx, increased growth and redistribution of body hair, and increased sexual drive. The adrenal cortex also produces small amounts of testosterone precursor, although the role of this additional hormone production is not fully understood. Testosterone secretion is regulated by both the hypothalamus and the anterior pituitary gland. The hypothalamus sends releasing hormones that stimulate the release of gonadotropins from the anterior pituitary gland.

Everyday Connection

The Dangers of Synthetic Hormones

Some athletes attempt to boost their performance by using artificial hormones that enhance muscle performance. Anabolic steroids, a form of testosterone, are one of the most widely known performance-enhancing drugs. Steroids are used in sports to help build muscle mass. Other hormones that are used to enhance athletic performance include erythropoietin, which triggers the production of red blood cells, and human growth hormone, which can help in building muscle mass. Most performance enhancing drugs are illegal for nonmedical purposes. They are also banned by national and international governing bodies including the International Olympic Committee, the U.S. Olympic Committee, the National Collegiate Athletic Association, the Major League Baseball, and the National Football League.

The side effects of synthetic hormones are often significant and nonreversible, and in some cases, fatal. Androgens can produce several complications such as liver dysfunctions and liver tumors, prostate gland enlargement, difficulty urinating, premature closure of epiphyseal cartilages, testicular atrophy, infertility, and immune system depression. The physiological strain caused by these substances is often greater than what the body can handle, leading to unpredictable and dangerous effects and linking their use to heart attacks, strokes, and impaired cardiac function.

Figure 26.7 Professional baseball player Jason Giambi publically admitted to, and apologized for, his use of anabolic steroids supplied by a trainer. (credit: Bryce Edwards)

Regulation of the Ovarian Reproductive System

In the ovaries, FSH stimulates development of egg cells, called ova, which develop in structures called follicles. Follicle cells produce the hormone inhibin, which inhibits FSH production. LH also plays a role in the development of ova, induction of ovulation, and stimulation of estradiol and progesterone production by the ovaries (as well as testosterone production by the testes), as illustrated in Figure 26.8. Estradiol and progesterone are steroid hormones that serve several functions in the human body. Estradiol causes the egg to mature and release during the menstrual cycle, and thickens the uterine lining prior to egg implantation. Estradiol also helps with bone health, nitric oxide production, and brain function.

(Low levels of estradiol have been connected to osteoporosis, mood swings, weight gain, and interrupted menstrual cycle. High levels of estradiol correlate with an increased risk of uterine and breast cancer, and cardiovascular disease.) During puberty, estradiol produces a suite of characteristics such as the increased development of breast tissue, redistribution of fat towards hips, legs, and breast, and the maturation of the uterus and vagina. Both estradiol and progesterone regulate the menstrual cycle.

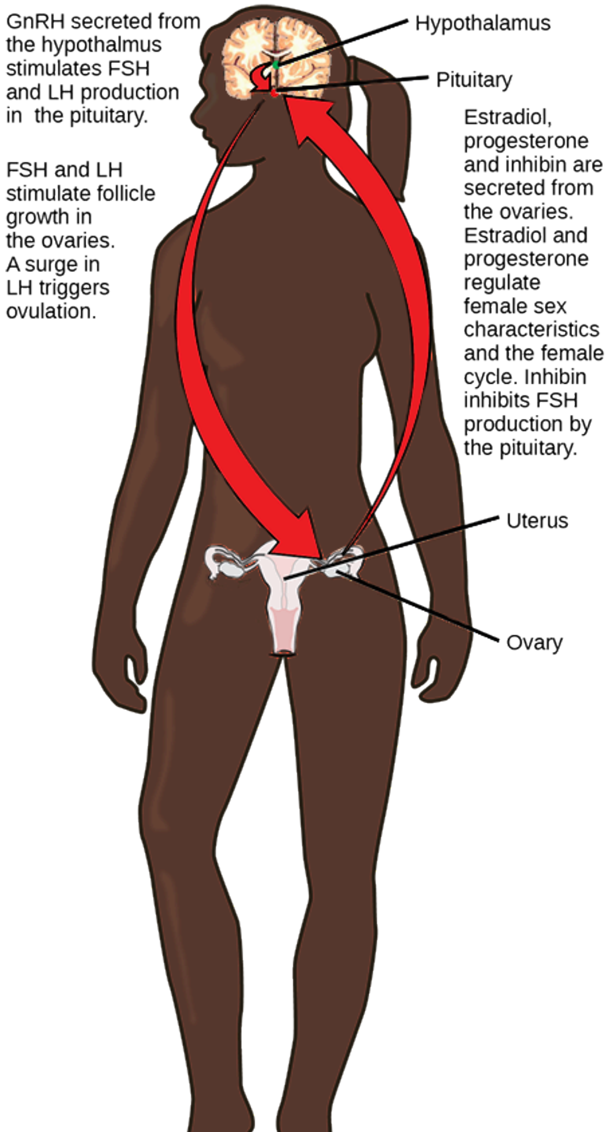


Figure 26.8 Hormonal regulation of the ovarian reproductive system involves hormones from the hypothalamus, pituitary, and ovaries.

In addition to producing FSH and LH, the anterior portion of the pituitary gland also produces the hormone prolactin (PRL). Prolactin stimulates the production of milk by the mammary glands following childbirth. Prolactin release inhibits the release of GnRH from the hypothalamus, resulting in a loss of FSH and LH release from the anterior pituitary. Prolactin levels are regulated by the hypothalamic hormones prolactin-releasing hormone (PRH) and prolactin-inhibiting hormone (PIH), which is now known to be dopamine. PRH stimulates the release of prolactin and PIH inhibits it.

The posterior pituitary releases the hormone oxytocin, which stimulates uterine contractions during childbirth. (Note: the posterior pituitary secretes only two hormones: antidiuretic hormone (ADH and oxytocin). The uterine smooth muscles are not very sensitive to oxytocin until late in pregnancy when the number of oxytocin receptors in the uterus peaks. Stretching of tissues in the uterus and cervix stimulates oxytocin release during childbirth. Contractions increase in intensity as blood levels of oxytocin rise via a positive feedback mechanism until the birth is complete. Oxytocin also stimulates the contraction of myoepithelial cells around the milk-producing mammary glands. As these cells contract, milk is forced from the secretory alveoli into milk ducts and is ejected from the breasts in milk ejection ("let-down") reflex. Oxytocin release is stimulated by the suckling of an infant, which triggers the synthesis of oxytocin in the hypothalamus and its release into circulation at the posterior pituitary.

Nearly all eukaryotes undergo sexual reproduction. The variation introduced into the reproductive cells by meiosis provides an important advantage that has made sexual reproduction evolutionarily successful. Meiosis and fertilization alternate in sexual life cycles. The process of meiosis produces unique reproductive cells called gametes, which have half the number of chromosomes as the parent cell. When two haploid gametes fuse, this restores the diploid condition in the new zygote. Thus, most sexually reproducing organisms alternate between haploid and diploid stages. However, the ways in which reproductive cells are produced and the timing between meiosis and fertilization vary greatly.

Reading Question #3

Match the function of the following hormones correctly.

A) Prolactin. B) Oxytocin. C) FSH. D) LH

1. Important during childbirth due to the stimulation of uterine contraction and also in breastfeeding.
2. Important in ovulation and stimulating ovarian hormone production.
3. Important after childbirth due to the stimulation of milk production
4. Important in stimulating egg cell development.

Menstruation

What Is the Menstrual Cycle?

The **menstrual cycle** refers to natural changes that occur in the female reproductive system each month during the reproductive years. The cycle is necessary for the production of eggs and the preparation of the uterus for pregnancy. It involves changes in both

the ovaries and the uterus and is controlled by pituitary and ovarian hormones. Day 1 of the cycle is the first day of the menstrual period, when bleeding from the uterus begins as the built-up endometrium lining the uterus is shed. The endometrium builds up again during the remainder of the cycle, only to be shed again during the beginning of the next cycle if pregnancy does not occur. In the ovaries, the menstrual cycle includes the development of a follicle, ovulation of a secondary oocyte, and the degeneration of the
follicle if pregnancy does not occur. Both uterine and ovarian changes during the menstrual cycle are generally divided into three phases, although the phases are not the same in the two organs.

Menarche and Menopause

The female reproductive years are delineated by the start and stop of the menstrual cycle. The first menstrual period usually occurs around 12 or 13 years of age, an event that is known as **menarche.** There is considerable variation among individuals in the age of menarche. It may occasionally occur as early as eight years of age or as late as 16 years of age and still be considered normal. The average age is generally later in the developing world, and earlier in the developed world. This variation is thought to be largely attributable to nutritional differences.

The cessation of menstrual cycles at the end of a woman's reproductive years is termed **menopause.** The average age of menopause is 52 years, but it may occur normally at any age between about 45 and 55 years of age. The age of menopause varies due to a variety of biological and environmental factors. It may occur earlier as a result of certain illnesses or medical treatments.

Variation in the Menstrual Cycle

The length of the menstrual cycle— as well as its phases — may vary considerably, not only among different individuals but also from month to month for a given person. The average length of time between the first day of one menstrual period and the first day of the next menstrual period is 28 days, but it may range from 21 days to 45 days. Cycles are considered regular when a woman's longest and shortest cycles differ by less than eight days. The menstrual period itself is usually about five days long, but it may vary in length from about two days to seven days.

Ovarian Cycle

The events of the menstrual cycle that take place in the ovaries make up the ovarian cycle. It consists of changes that occur in the follicles of one of the ovaries. The ovarian cycle is divided into the following three phases: the follicular phase, ovulation, and luteal phase. These phases are illustrated in Figure 26.9.

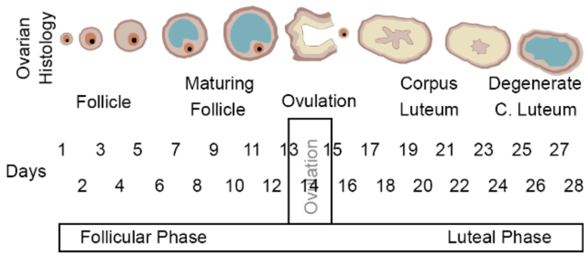


Figure 26.9 The diagram shows the maturation of follicles in the ovary, ovulation, and formation of corpus luteum durin g follicular and luteal phases of ovaries. The phases and days of the ovarian cycle are shown in this diagram. The ovarian cycle depicte d in the diagram represents a cycle in which fertilization does not occur so the corpus luteum dege nerates during the luteal phase.

Follicular Phase

The **follicular phase** is the first phase of the ovarian cycle. It generally lasts about 12 to 14 days for a 28-day menstrual cycle. During this phase, several ovarian follicles are stimulated to begin maturing, but usually only one — called the Graafian follicle— matures completely so it is ready to release an egg. The other maturing follicles stop growing and disintegrate. Follicular development occurs because of a rise in the blood level of follicle-stimulating hormone (FSH), which is secreted by the pituitary gland. The maturing follicle releases estrogen, the level of which rises throughout the follicular phase. You can see these and other changes in hormone levels that occur during the menstrual cycle in the chart in Figure 26.10.

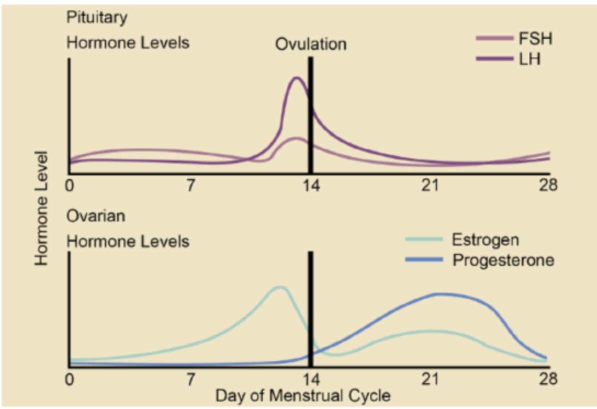


Figure 26.10. Pituitary and ovarian hormone levels. FSH in the pituitary andestrogen in the ovaries increase during the first half of themenstrual cycle. LH in the pituitary surges shortly before ovulation occurs due to the rise in estrogen in the ovaries. After ovulation, the level of progesterone and estrogen increases in ovaries due to the formation of the corpus luteum if pregnancy does not occur.

Ovulation

Ovulation is the second phase of the ovarian cycle. It usually occurs around day 14 of a 28-day menstrual cycle. During this phase, the Graafian follicle ruptures and releases its egg. Ovulation is stimulated by a sudden rise in the blood level of luteinizing hormone (LH) from the pituitary gland. This is called the LH surge. You can see the LH surge in the top hormone graph above. The LH surge generally starts around day 12 of the cycle and lasts for a day or two. The surge in LH is triggered by a continued rise in estrogen from the maturing follicle in the ovary. During the follicular phase, the rising estrogen level actually suppresses LH secretion by the pituitary. However, by the time the follicular phase is nearing its end, the level of estrogen reaches a threshold level above which this effect is reversed, and estrogen stimulates the release of a large amount of LH. The surge in LH matures the egg and weakens the wall of the follicle, causing the fully developed follicle to release its secondary oocyte.

Luteal Phase

The **luteal phase** is the third and final phase of the ovarian cycle. It typically lasts about 14 days in a 28-day menstrual cycle. At the beginning of the luteal phase, FSH and LH cause the Graafian follicle that ovulated the egg to transform into a structure called a corpus luteum. The corpus luteum secretes progesterone, which in turn suppresses FSH and LH production by the pituitary and stimulates the continued buildup of the endometrium in the uterus. How this phase ends depends on whether or not the egg has been fertilized.

- If fertilization has not occurred, the falling levels of FSH and LH during the luteal phase cause the corpus luteum to atrophy, so its production of progesterone declines. Without a high level of progesterone to maintain it, the endometrium starts to break down. By the end of the luteal phase, the endometrium can no longer be maintained, and the next menstrual cycle begins with the shedding of the endometrium (menses).

- If fertilization has occurred so a zygote forms and then divides to become a blastocyst, the outer layer of the blastocyst produces a hormone called human chorionic gonadotropin. This hormone is very similar to LH and preserves the corpus luteum. The corpus luteum can then continue to secrete progesterone to maintain the new pregnancy.

Uterine Cycle

The events of the menstrual cycle that take place in the uterus make up the uterine cycle. This cycle consists of changes that occur mainly in the endometrium, which is the layer of tissue that lines the uterus. The uterine cycle is divided into the following three phases: menstruation, proliferative phase, and secretory phase. These phases are illustrated in Figure 26.11.

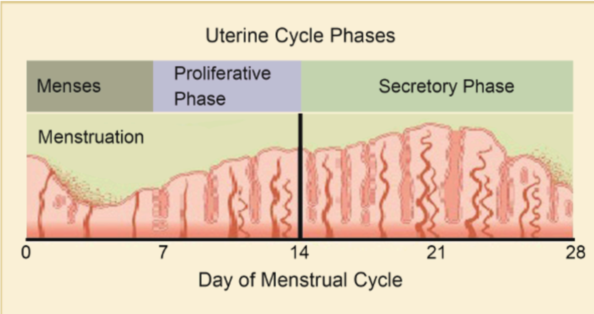


Figure 26.11. The uterine cycle begins with menstruation, which starts on day 1 of the cycle. The proliferative phase ranges from day 7 to 14. The secretory phase laster for the second half of the uterine cycle.

Menstruation

Menstruation (also called the menstrual period or menses) is the first phase of the uterine cycle. It occurs if fertilization has not taken place during the preceding menstrual cycle.
During menstruation, the endometrium of the uterus, which has built up during the preceding cycle, degenerates and is shed from the uterus. The average loss of blood during menstruation is about 35 mL. The flow of blood is often accompanied by uterine cramps, which may be severe in some people.

Proliferative Phase

The **proliferative phase** is the second phase of the uterine cycle. During this phase, estrogen secreted by cells of the maturing ovarian follicle causes the lining of the uterus to grow, or proliferate.Estrogen also stimulates thecervix of the uterus to secrete larger amounts of thinnermucus that can help sperm swim through the cervix and into the uterus, making fertilization more likely.

Secretory Phase

The **secretory phase** is the third and final phase of the uterine cycle. During this phase, progesterone produced by the corpus luteum in the ovary stimulates further changes in the endometrium so it is more receptive to implantation of a blastocyst. For example, progesterone increases blood flow to the uterus and promotes uterine secretions. It also decreases the contractility of smooth muscle tissue in the uterine wall.

Link to Society

Within the field of critical menstruation studies, we must pay attention to our depictions of menstruation and menstruators, and the knowledge we produce in the pursuit to de-stigmatize menstruation. Not all women menstruate, for example, trans women, postmenopausal women, pregnant women, and those experiencing amenorrhea, and not all who menstruate are women, for example, transmen. Experiences of menstruating later in life vary among menstruators as well. Some do not suffer from their periods in direct relation to their gender identity. Others do, as they disidentify with the body as a whole and/or with certain body parts such as the genitalia or the uterus, or with the bodily function of menstruation. This suffering is sometimes related to gender dysphoria. Testosterone treatments are a method adopted by some trans menstruators to get rid of unwanted bleeding. Preventing the menstrual period is not necessarily the main reason for using testosterone, but it can be one among several desired outcomes. Menstruators *are* of a variety of gender identities (far beyond those who identify as trans) and, hence, menstruation cannot be equated singularly with cis/womanhood.

Sexual reproduction in plants

Sexual reproduction takes place with slight variations in different groups of plants. Plants have two distinct stages in their lifecycle: the gametophyte stage and the sporophyte stage. The haploid gametophyte produces the male and female gametes by mitosis in distinct multicellular structures. Fusion of the male and females gametes forms the diploid zygote, which develops into the sporophyte. After reaching maturity, the diploid sporophyte produces spores by meiosis, which in turn divide by mitosis to produce the haploid gametophyte. The new gametophyte produces gametes, and the cycle continues. This is the alternation of generations, and is typical of plant reproduction (Figure 26.9).

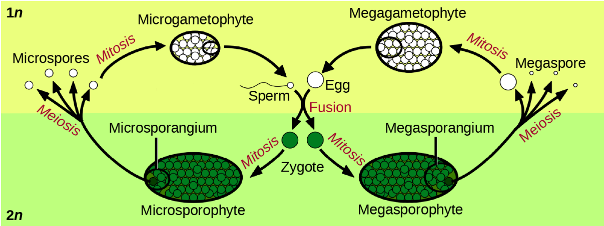


Figure 26.12. The alternation of generations in angiosperms is depicted in this diagram. (credit: modification of work by Peter Coxhead)

The life cycle of higher plants is dominated by the sporophyte stage, with the gametophyte borne on the sporophyte. In ferns, the gametophyte is free-living and very distinct in structure from the diploid sporophyte. In bryophytes, such as mosses, the haploid gametophyte is more developed than the sporophyte.

During the vegetative phase of growth, plants increase in size and produce a shoot system and a root system. As they enter the reproductive phase, some of the branches start to bear flowers. Many flowers are borne singly, whereas some are borne in clusters. The flower is borne on a stalk known as a receptacle. Flower shape, color, and size are unique to each species, and are often used by taxonomists to classify plants.

Sexual Reproduction in Angiosperms

The lifecycle of angiosperms follows the alternation of generations explained previously. The haploid gametophyte alternates with the diploid sporophyte during the sexual reproduction process of angiosperms. Flowers contain the plant's reproductive structures.

Flower Structure

A typical flower has four main parts—or whorls—known as the calyx, corolla, androecium, and gynoecium (Figure 26.13). The outermost whorl of the flower has green, leafy structures known as sepals. The sepals, collectively called the calyx, help to protect the unopened bud. The second whorl is comprised of petals—usually, brightly colored—collectively called the corolla. The number of sepals and petals varies depending on whether the plant is a monocot or dicot. In monocots, petals usually number three or multiples of three; in dicots, the number of petals is four or five, or multiples of four and five. Together, the calyx and corolla are known as the perianth. The third whorl contains the male reproductive structures and is known as the androecium. The androecium has stamens with anthers that contain the microsporangia. The innermost group of structures in the flower is the gynoecium, or the female reproductive component(s). The carpel is the individual unit of the gynoecium and has a stigma, style, and ovary. A flower may have one or multiple carpels.

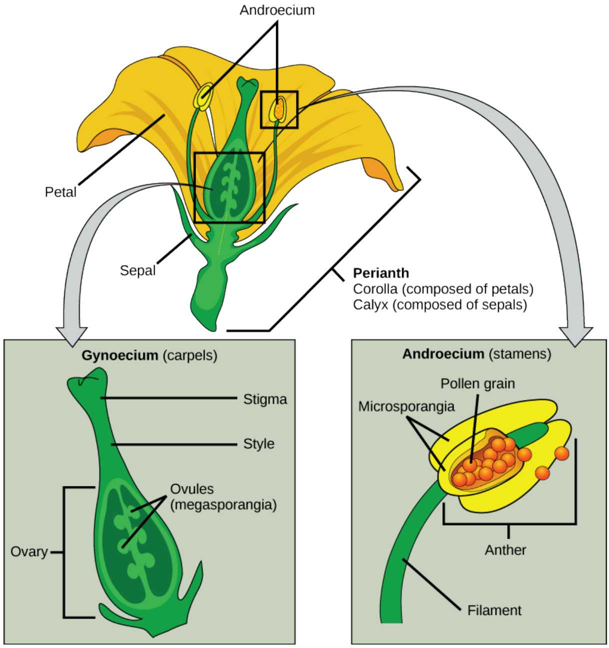


Figure 26.13. The four main parts of the flower are the calyx, corolla, androecium, and gynoecium. The androecium is the sum of all the male reproductive organs, and the gynoecium is the sum of the female reproductive organs. (credit: modification of work by Mariana Ruiz Villareal)

If all four whorls (the calyx, corolla, androecium, and gynoecium) are present, the flower is described as complete. If any of the four parts is missing, the flower is known as incomplete. Flowers that contain both an androecium and a gynoecium are called perfect, androgynous or hermaphrodites. There are two types of incomplete flowers: staminate flowers contain only an androecium, and carpellate flowers have only a gynoecium (Figure 26.14).

Figure 26.14

Reading Question #4

Which of the following statements is false about floral reproduction?

A. The process of producing spores necessitates meiosis.

B. Flowers have four main parts called the androecium, gynoecium, calyx, and corolla.

C. Hermaphrodite flowers do not exist.

d. The process of producing gametes necessitates mitosis.

Reading Question #5

Which of the following body systems is not directly involved with spermatogenesis?

A. Circulatory

B. Endocrine

C. Respiratory

D. Reproductive

Reading Question # 6

In what ways can testosterone affect spermatogenesis?

A. It can halt/stop it

B. It can increase it

C. It does not cause a change

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28. Chapter 28: Climate Change Introduction

ANASTASIA CHOUVALOVA

All biomes are *universally affected* by global conditions, such as **climate**, that ultimately shape each biome's environment. Scientists who study climate have noted a series of marked changes that have gradually become increasingly evident during the last sixty years. Global climate change is the term used to describe altered global weather patterns, especially a worldwide increase in temperature and resulting changes in the climate, due largely to rising levels of atmospheric carbon dioxide.

Climate and Weather

A common misconception about global climate change is that a specific weather event occurring in a particular region (for example, a very cool week in June in central Indiana) provides evidence of global climate change. However, a cold week in June is a weather-related event and not a climate-related one. These misconceptions often arise because of confusion over the terms ***climate*** and ***weather***.

Climate refers to the long-term, *predictable atmospheric conditions* of a specific area. The climate of a biome is characterized by having consistent seasonal temperature and rainfall ranges. Climate does not address the amount of rain that fell on one particular day in a biome or the colder-than-average temperatures that occurred on one day. In contrast, weather refers to the conditions of the atmosphere during a short period of time.

Weather forecasts are usually made for 48-hour cycles. Long-range weather forecasts are available but can be unreliable.

To better understand the difference between climate and weather, imagine that you are planning an outdoor event in northern Wisconsin. You would be thinking about *climate* when you plan the event in the summer rather than the winter because you have long-term knowledge that any given Saturday in the months of May to August would be a better choice for an outdoor event in Wisconsin than any given Saturday in January. However, you cannot determine the specific day that the event should be held on because it is difficult to accurately predict the weather on a specific day. Climate can be considered "average" weather that takes place over many years.

Reading Question #1

Which statement(s) correctly contrasts weather and climate? Select all that apply.

A. Weather is more predictable than climate.

B. Weather is less predictable than climate.

C. Climate encompasses the longer-term conditions of a specific area, while weather encompasses shorter-term conditions.

D. Climate encompasses the shorter-term conditions of a specific area, while weather encompasses longer-term conditions.

E. Weather encompasses changes in temperature, precipitation, wind, air pressure, and humidity while climate encompasses only temperature.

Global Climate Change

Climate change can be understood by approaching three areas of study:

- evidence of current and past global climate change
- drivers of global climate change
- documented results of climate change

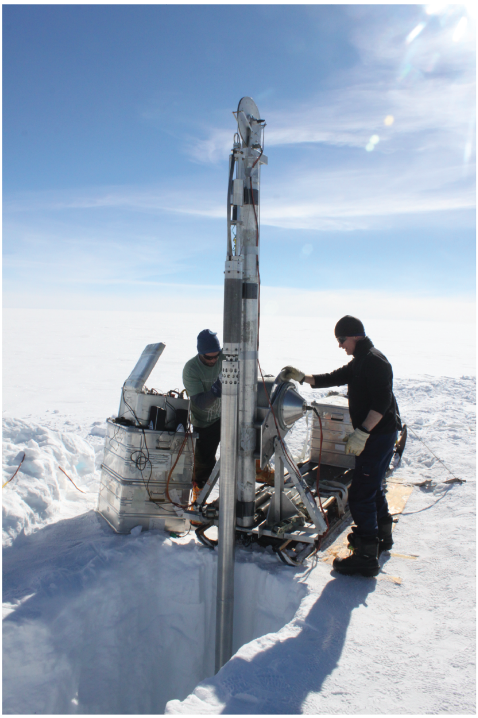
It is helpful to keep these three different aspects of climate change clearly separated when consuming media reports about global climate change. We should note that it is common for reports and discussions about global climate change to confuse the data showing that Earth's climate is changing with the factors that drive this climate change.

Evidence for Global Climate Change

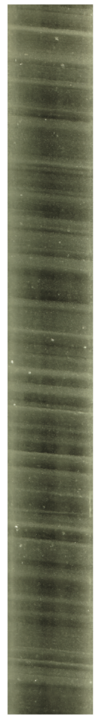
Since scientists cannot go back in time to directly measure climatic variables, such as average temperature and precipitation, they must instead indirectly measure temperature. To do this, scientists rely on *historical evidence of Earth's past climate.*

Antarctic ice cores are a key example of such evidence for climate change. These ice cores are samples of *polar ice*obtained by means of drills that reach thousands of meters into ice sheets or high mountain glaciers. Viewing the ice cores is like traveling backwards through time; the deeper the sample, the earlier the time period. Trapped within the ice are air bubbles and other biological evidence that can reveal temperature and carbon dioxide data. Antarctic ice cores have been collected and analyzed to indirectly estimate the temperature of the Earth over the past 400,000 years (Figure 27.1a). The data represented in Figure 27.2 is an example of such analyses. The 0 °C on this graph refers to the long-term average.

Temperatures that are greater than 0 °C exceed Earth's long-term average temperature. Conversely, temperatures that are less than 0 °C are less than Earth's average temperature. This figure shows that there have been periodic cycles of increasing and decreasing temperature.



(a)



(b)

Figure 27.1 a) Scientists drill for ice cores in polar regions. b) The ice contains air bubbles and biological substances that provide important information for researchers. (credit: a: Helle Astrid Kjær; b: National Ice Core Laboratory, USGS)

Before the late 1800s, the Earth has been as much as 9 °C cooler and about 3 °C warmer. Note that the graph in Figure 27.2b shows that the atmospheric concentration of carbon dioxide has also risen and fallen in periodic cycles. Also note the relationship between carbon dioxide concentration and temperature. Figure 44.27b shows that carbon dioxide levels in the atmosphere have historically cycled between 180 and 300 parts per million (ppm) by volume.

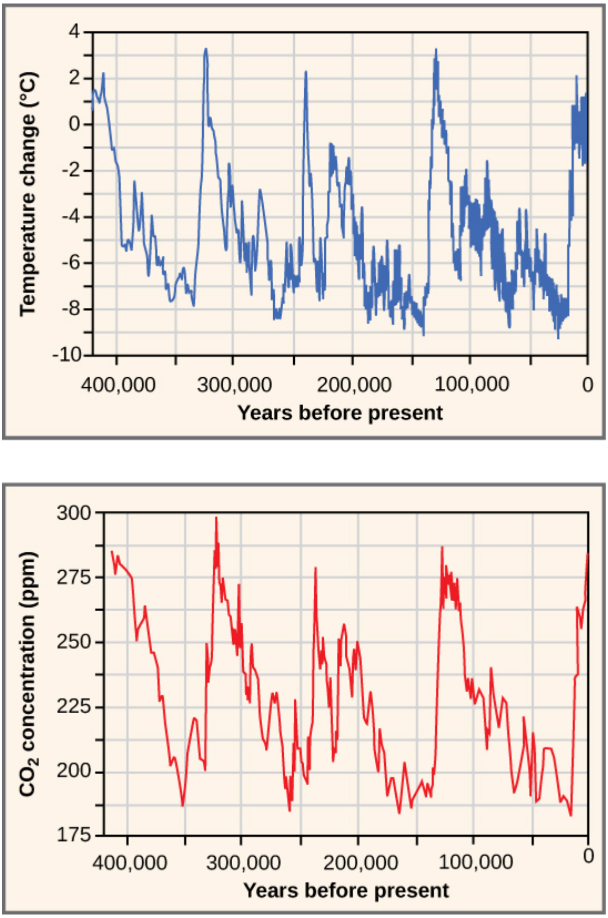


Figure 27.2 Ice at the Russian Vostok station in East Antarctica was laid down over the course of 420,000 years and reached a depth of over 3,000 m. a) A graph showing the changes in temperature in the past. b) A graph showing the changes in CO2 concentrations in the past. By measuring the amount of CO_2 trapped in the ice, scientists have determined past atmospheric CO_2 concentrations. Temperatures relative to modern day were determined from the amount of deuterium (a nonradioactive isotope of hydrogen)

present.

Reading Question #2

Take a close look at Figures 27.1a and 27.1b. *Approximately* how long is one “cycle” of 1) temperature and 2) CO2 changes? Hint: Take a look at the minima and minima, as if looking at a sine function.

A. 1) ~ 100, 000 years for temperature, 2) ~200, 000 years for CO2

B. 1) ~ 200, 000 years for temperature, 2) ~100, 000 years for CO2

C. 1) ~ 100, 000 years for temperature, 2) ~100, 000 years for CO2

D.1) ~ 200, 000 years for temperature, 2) ~200, 000 years for CO2

Figure 27.2a does not show the last 2,000 years with enough detail to compare the changes of Earth’s temperature during the last 400,000 years with the temperature change that has occurred in the more recent past. Two significant temperature anomalies, or *irregularities*, have occurred in the last 2,000 years. These are the *Medieval ClimateAnomaly* (or the Medieval Warm Period) and the ***Little Ice Age***. A third temperature anomaly aligns with the *Industrial Era*. The Medieval Climate Anomaly occurred between 900 and 1300 AD. During this time period, many climatescientists think that slightly warmer weather conditions prevailed in many parts of the world; the higher-than-average temperature changes varied between 0.10 °C and 0.20 °C above the norm. Although 0.10 °C does not seem large enough to produce any noticeable change, it did free seas of ice. Because of this warming, the Vikings were able to colonize Greenland.

The Little Ice Age was a cold period that occurred between 1550 AD and 1850 AD. During this time, a slight cooling of a little less than 1 °C was observed in North America, Europe, and possibly other areas of the Earth. This 1 °C change in global temperature is a seemingly small deviation in temperature (as was observed during the Medieval Climate Anomaly); however, it also resulted in noticeable climatic changes. Historical accounts reveal a time of exceptionally harsh winters with much snow and frost.

The *Industrial Revolution*, which began around 1750, was characterized by changes in much of human society. Advances in agriculture increased the food supply, which improved the standard of living for people in Europe and the United States. New technologies were invented that provided jobs and cheaper goods. These new technologies were powered using fossil fuels, especially coal. The Industrial Revolution starting in the early nineteenth century ushered in the beginning of the Industrial Era. When a fossil fuel is burned, carbon dioxide is released. With the beginning of the Industrial Era, atmospheric carbon dioxide began to rise (Figure 27.3).

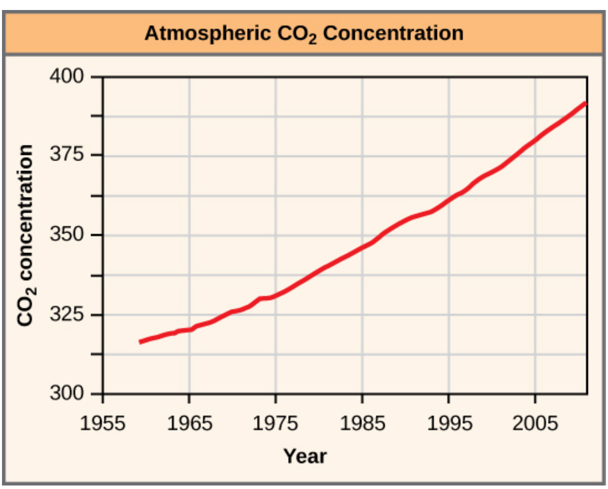


Figure 27.3

Current and Past Drivers of Global Climate Change

Because it is not possible to go back in time to directly observe and measure climate, scientists must use *indirect evidence* to determine the *drivers*, or factors, that may be responsible for climate change. The indirect evidence includes data collected using ice cores, *boreholes* (a narrow shaft bored into the ground), tree rings, glacier lengths, pollen remains, and ocean sediments. The data shows a correlation between the timing of temperature changes and drivers of climate change. Before the Industrial Era (pre-1780), there were three drivers of climate change that were not related to human activity or atmospheric gases. The first of these is the ***Milankovitch cycles.*** The Milankovitch cycles describe the effects of slight changes in the Earth's orbit on Earth's climate. The length of the Milankovitch cycles ranges between 19,000 and 100,000 years. In other words, one could expect to see some predictable changes in the Earth's climate associated with changes in the Earth's orbit at a minimum of every 19,000 years.

The *variation in the sun's intensity* is the second natural factor responsible for climate change. **Solar intensity** is the amount of solar power or energy the sun emits in a given amount of time. There is a direct relationship between solar intensity and temperature. As solar intensity increases (or decreases), the Earth's temperature correspondingly increases (or decreases). Changes in solar intensity have been proposed as one of several possible explanations for the Little Ice Age.

Finally, *volcanic eruptions* are a third natural driver of climate change. Volcanic eruptions can last a few days, but the solids and gases released during an eruption can influence the climate over a period of a few years, causing short-term climate changes. The gases and solids released by volcanic eruptions can include carbon dioxide, water vapor, sulfur dioxide, hydrogen sulfide, hydrogen, and carbon monoxide. Generally, volcanic eruptions cool the climate. This occurred in 1783 when volcanoes in Iceland erupted and caused the release of large volumes of sulfuric oxide. This led to haze-effect cooling, a global phenomenon that occurs when dust, ash, or other suspended particles block out sunlight and trigger lower global temperatures as a result; haze-effect cooling usually extends for one or more years before dissipating in intensity. In Europe and North America, haze-effect cooling produced some of the lowest average winter temperatures on record in 1783 and 1784.

Greenhouse gases are probably the most significant drivers of the climate. When heat energy from the sun strikes the Earth, gases known as greenhouse gases trap the heat in the atmosphere, in a similar manner as do the glass panes of a greenhouse keep heat from escaping. The greenhouse gases that affect Earth include carbon dioxide, methane, water vapor, nitrous oxide, and ozone. Approximately half of the radiation from the sun passes through these gases in the atmosphere and strikes the Earth. This radiation is converted into thermal (infrared) radiation on the Earth's surface, and then a portion of that energy is re-radiated back into the atmosphere. Greenhouse gases, however, reflect much of the thermal energy back to the Earth's surface. The more greenhouse gases there are in the atmosphere, the more thermal energy is reflected back to the Earth's surface, heating it up and the atmosphere immediately above it. Greenhouse gases absorb and emit radiation and are an important factor in the **greenhouse effect:** the warming of Earth due to carbon dioxide and other greenhouse gases in the atmosphere.

Direct evidence supports the relationship between atmospheric concentrations of carbon dioxide and temperature: as carbon dioxide rises, global temperature rises. Since 1950, the concentration of atmospheric carbon dioxide has increased from about 280 ppm to 382 ppm in 2006. In 2011, the atmospheric carbon dioxide concentration was 392 ppm. However, the planet would not be inhabitable by current life forms if water vapor did not produce its drastic greenhouse warming effect.

Scientists look at patterns in data and try to explain differences or deviations from these patterns. The atmospheric carbon dioxide data reveal a historical pattern of carbon dioxide increasing and decreasing, cycling between a low of 180 ppm and a high of 300 ppm. Scientists have concluded that it took around 50,000 years for the atmospheric carbon dioxide level to increase from its low minimum concentration to its higher maximum concentration. However, beginning only a few centuries ago, atmospheric carbon dioxide concentrations have increased beyond the historical maximum of 300 ppm. The current increases in atmospheric carbon dioxide have happened very quickly—in a matter of hundreds of years rather than thousands of years. What is the reason for this difference in the rate of change and the amount of increase in carbon dioxide? A key factor that must be recognized when comparing the historical data and the current data is the presence and industrial activities of modern human society; no other driver of climatechange has yielded changes in atmospheric carbon dioxide levels *at this rate or to this magnitude.*

Human activity releases carbon dioxide and methane, two of the most important greenhouse gases, into the atmosphere in several ways. The primary mechanism that releases carbon dioxide is the burning of fossil fuels, such as gasoline, coal, and natural gas (Figure 27.4). Deforestation, cement manufacture, animal agriculture, the clearing of land, and the burning of forests are other human activities that release carbon dioxide. Methane (CH_4) is produced when bacteria break down organic matter under anaerobic conditions. Anaerobic conditions can happen when organic matter is trapped underwater (such as in rice paddies) or in the intestines of herbivores. Methane can also be released from natural gas fields and the decomposition of animal and plant material that occurs in landfills. Another source of methane is the melting of *clathrates*. Clathrates are frozen chunks of ice and methane found at the bottom of the ocean. When water warms, these chunks of ice melt and methane is released. As the ocean's water temperature increases, the rate at which clathrates melt is increasing, releasing even more methane. This leads to increased levels of methane in the atmosphere, which further accelerates the rate of global warming.

This is an example of the positive feedback loop that is leading to the rapid rate of increase of global temperatures.

Figure 27.4. The burning of fossil fuels in industry and by vehicles releases carbon dioxide and other greenhouse gases into the atmosphere. (credit: "Pöllö"/Wikimedia Commons)

Greenhouse Gases in detail

Gardeners that live in moderate or cool environments use greenhouses because they trap heat and create an environment that is warmer than outside temperatures. This is great for plants that like heat, or are sensitive to cold temperatures, such as tomato and pepper plants. Greenhouses contain glass or plastic that allow visible light from the sun to pass. This light, which is a form of energy, is absorbed by plants, soil, and surfaces and heats them. Some of that heat energy is then radiated outwards in the form of infrared radiation, a different form of energy. Unlike with visible light, the glass of the greenhouse blocks the infrared radiation, thereby trapping the heat energy, causing the temperature within the greenhouse to increase.

The same phenomenon happens inside a car on a sunny day. Have you ever noticed how much hotter a car can get compared to the outside temperature? Light energy from the sun passes through the windows and is absorbed by the surfaces in the car such as seats and the dashboard. Those warm surfaces then radiate infrared radiation, which cannot pass through the glass. This trapped infrared energy causes the air temperatures in the car to increase. This process is commonly known as the **greenhouse effect**.

The greenhouse effect also happens with the entire Earth. Of course, our planet is not surrounded by glass windows. Instead, the Earth is wrapped with an atmosphere that contains **greenhouse gases** (GHGs). Much like the glass in a greenhouse, GHGs allow incoming visible light energy from the sun to pass, but they block infrared radiation that is radiated from the Earth towards space (Figure 27.5). In this way, they help trap heat energy that subsequently raises air temperature. Being a greenhouse gas is a physical property of certain types of gases; because of their molecular structure they absorb wavelengths of infrared radiation, but are transparent to visible light. Some notable greenhouse gases are water vapor (H_2O), carbon dioxide (CO_2), and methane (CH_4). GHGs act like a blanket, making Earth significantly warmer than it would otherwise be. Scientists estimate that average temperature on Earth would be -18° C without naturally-occurring GHGs.

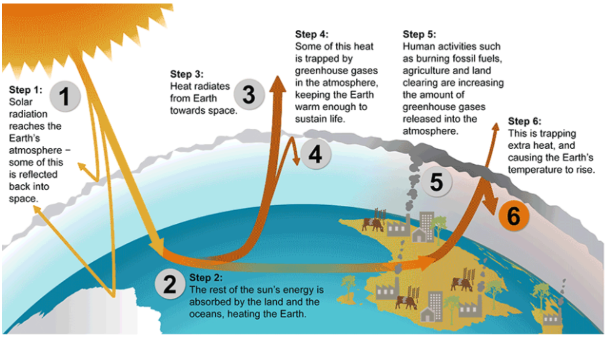


Figure 27.5. The enhanced greenhouse effect. Step 1: Some solar radiation reaches the Earth's surface, and some is reflected back into space. Step 2: The rest of the sun's energy is absorbed by the land and the oceans, heating the Earth. Step 3: Heat radiates from Earth towards space. Step 4: Some of the heat is trapped by greenhouse gases in the atmosphere, warming the Earth. Step 5: Human activities such as burning fossil fuels, agriculture, and land clearing have increased the concentrations of greenhouse gases in the atmosphere. Step 6: This

is trapping extra heat, causing the Earth's temperature to rise.

The most important GHGs directly emitted by humans include CO_2 and methane. **Carbon dioxide** (CO_2) is the primary greenhouse gas that is contributing to recent global climate change. CO_2 is a natural component of the carbon cycle, involved in such activities as photosynthesis, respiration, volcanic eruptions, and ocean-atmosphere exchange. Human activities, primarily the burning of fossil fuels and changes in land use, release very large amounts of CO_2 to the atmosphere, causing its concentration in the atmosphere to rise.

Although this concentration is far less than that of CO_2, **methane** (CH_4) is 28 times as potent a greenhouse gas. Methane is produced when bacteria break down organic matter under anaerobic conditions and can be released due to natural or anthropogenic processes. Anaerobic conditions can happen when organic matter is trapped underwater (such as in rice paddies) or in the intestines of herbivores. Anthropogenic causes now account for 60% of total methane release. Examples include agriculture, fossil fuel extraction and transport, mining, landfill use, and burning of forests. Specifically, raising cattle releases methane due to fermentation in their rumens produces methane that is expelled from their GI tract. Methane is more abundant in Earth's atmosphere now than at any time in at least the past 650,000 years, and CH_4 concentrations increased sharply during most of the 20th century. They are now more than two and-a-half times pre-industrial levels (1.9 ppm), but the rate of increase has slowed considerably in recent decades.

Water vapor is the most abundant greenhouse gas and also the most important in terms of its contribution to the natural greenhouse effect, despite having a short atmospheric lifetime. Some human activities can influence local water vapor levels. However, on a global scale, the concentration of water vapor is controlled by temperature, which influences overall rates of evaporation and precipitation. Therefore, the global concentration of water vapor is not substantially affected by direct human emissions.

Ground-level ozone (O_3), which also has a short atmospheric lifetime, is a potent greenhouse gas. Chemical reactions create ozone from emissions of nitrogen oxides and volatile organic compounds (VOCs) from automobiles, power plants, and other industrial and commercial sources in the presence of sunlight (as discussed in section 10.1). In addition to trapping heat, ozone is a pollutant that can cause respiratory health problems and damage crops and ecosystems.

Reading Question #3

Match the following four greenhouse gases (GHGs) to their respective descriptions.

A) CO2 B) Methane C) Ozone D) Water vapor

1. Derived from nitrogen oxides and causes respiratory health problems, such as asthma.
2. Many times more potent than CO2 and comes from agricultural practices.
3. Is the principal GHG.
4. Is the most abundant GHG and is not extremely related to anthropogenic causes.

Reading Question #4

It is important for you to understand the mechanism of greenhouse gases and how they are related to rising Earth temperatures. Which statement accurately describes this relationship?

A. Increasing amounts of GHGs cause more heat to be trapped within the Earth's atmosphere, causing temperatures to increase.

B. Decreasing amounts of GHGs cause more heat to be trapped within the Earth's atmosphere, causing temperatures to increase.

C. Increasing amounts of GHGs cause less heat to be trapped within the Earth's hydrosphere, causing temperatures to increase.

D. There is very weak evidence that GHGs are related to rising Earth temperatures.

Documented Results of Climate Change: Past and Present

Scientists have geological evidence of the consequences of long-ago climate change. Modern-day phenomena such as retreating glaciers and melting polar ice cause a continual rise in sea level. Meanwhile, changes in climate can negatively affect organisms.

Geological Climate Change

Global warming has been associated with at least one planet-wide extinction event during the geological past. The **Permian extinction** event occurred about 251 million years ago toward the end of the roughly 50-million-year-long geological time span known as the Permian period. This geologic time period was one of the three warmest periods in Earth's geologic history. Scientists estimate that approximately 70 percent of the terrestrial plant and animal species and 84 percent of marine species became extinct, vanishing forever near the end of the Permian period.

Organisms that had adapted to wet and warm climatic conditions, such as annual rainfall of 300–400 cm (118–157 in) and 20 °C–30 °C (68 °F–86 °F) in the tropical wet forest, may not have been able to survive the Permian climate change.

Link to learning

Take a look at this NASA video which discusses how global warming impacts plant growth. Interestingly, the increased temperatures in the 1980s-1990s led to increased plant productivity but this benefit has been counteracted by more frequent droughts. This reveals the complexity and mixed nature of the effects of global warming on plant growth.

Present Climate Change

A number of global events have occurred that may be attributed to climate change during our lifetimes. *Glacier National Park* in Montana is undergoing the retreat of many of its glaciers, a phenomenon known as glacier recession. In 1850, the area contained approximately 150 glaciers. By 2010, however, the park contained only about 24 glaciers greater than 25 acres in size. One of these glaciers is the *Grinnell Glacier* (Figure 27.5) at Mount Gould. Between 1966 and 2005, the size of Grinnell Glacier shrank by 40 percent. Similarly, the mass of the ice sheets in Greenland and the Antarctic is decreasing: Greenland lost 150–250 km^3 of ice per year between 2002 and 2006. In addition, the size and thickness of the Arctic sea ice is decreasing.

Figure 27.5. The effect of global warming can be seen in the continuing retreat of Grinnel Glacier. The mean annual temperature in the park has increased 1.33 °C since 1900. The loss of a glacier results in the loss of summer meltwaters, sharply reducing seasonal water supplies and severely affecting local ecosystems. (credit: modification of work by USGS)

This loss of ice is leading to increases in the global sea level. On average, the sea is rising at a rate of 1.8 mm per year. However, between 1993 and 2010 the rate of sea level increase ranged between 2.9 and 3.4 mm per year. A variety of factors affect the volume of water in the ocean, especially the temperature of the water (the density of water is related to its temperature: water volume expands as it warms, thus raising sea levels), as well as the *amount of water* found in rivers, lakes, glaciers, polar ice caps, and sea ice. As glaciers and polar ice caps melt, there is a significant contribution of liquid water that was previously frozen.

In addition to some abiotic conditions changing in response to climate change, many organisms are also being affected by the changes in temperature. Temperature and precipitation play key roles in determining the *geographic distribution* and *phenology* of plants and animals. (**Phenology** is the study of the effects of climatic conditions on the timing of periodic life cycle events, such as flowering in plants or migration in birds.) Researchers have shown that 385 plant species in Great Britain are flowering 4.5 days sooner than was recorded earlier during the previous 40 years. In addition, insect-pollinated species were more likely to flower earlier than wind-pollinated species. The impact of changes in flowering date would be mitigated if the insect pollinators emerged earlier. This mismatched timing of plants and pollinators could result in injurious ecosystem effects because, for continued survival, insect-pollinated plants must flower when their pollinators are present.

Scientific Consensus: Global Climate Change is Real

The **Intergovernmental Panel on Climate Change** (IPCC) was created in 1988 by the United Nations Environment Programme and the World Meteorological Organization. It is charged with the task of evaluating and synthesizing the scientific evidence surrounding global climate change. The IPCC uses this information to evaluate current impacts and future risks, in addition to providing policymakers with assessments. These assessments are released about once every every six years. The most recent report, the 5th Assessment, was released in 2013. Hundreds of leading scientists from around the world are chosen to author these reports. Over the history of the IPCC, these scientists have reviewed thousands of peer-reviewed, publicly available studies. The scientific consensus is clear: global climate change is real and humans are very likely the cause for this change.

Additionally, the major scientific agencies of the United States, including the National Aeronautics and Space Administration (NASA) and the National Oceanic and Atmospheric Administration (NOAA), also agree that climate change is occurring and that humans are driving it. In 2010, the US National Research Council concluded that "Climate change is occurring, is very likely caused by human activities, and poses significant risks for a broad range of human and natural systems". Many independent scientific organizations have released similar statements, both in the United States and abroad. This doesn't necessarily mean that every scientist sees eye to eye on each component of the climate change problem, but broad agreement exists that climate change is happening and is primarily caused by excess greenhouse gases from human activities. Critics of climate change, driven by ideology instead of evidence, try to suggest to the public that there is no scientific consensus on global climate change. Such an assertion is patently false.

Past and Present-day GHG Emissions Will Affect Climate Far into the Future

Many greenhouse gases stay in the atmosphere for long periods of time. As a result, even if emissions stopped increasing, atmospheric greenhouse gas concentrations would continue to remain elevated for hundreds of years. Moreover, if we stabilized concentrations and the composition of today's atmosphere remained steady (which would require a dramatic reduction in current greenhouse gas emissions), surface air temperatures would continue to warm. This is because the oceans, which store heat, take many decades to fully respond to higher greenhouse gas concentrations. The ocean's response to higher greenhouse gas concentrations and higher temperatures will continue to impact climate over the next several decades to hundreds of years.

Future Temperature Changes

Climate models project the following key temperature-related changes:

- Average global temperatures are expected to increase by 2°F to 11.5°F by 2100, depending on the level of future greenhouse gas emissions, and the outcomes from various climate models.
- By 2100, global average temperature is expected to warm at least twice as much as it has during the last 100 years.
- Ground-level air temperatures are expected to continue to warm more rapidly over land than oceans.
- Some parts of the world are projected to see larger temperature increases than the global average.

Future Precipitation and Storm Events

Patterns of precipitation and storm events, including both rain and snowfall are likely to change. However, some of these changes are less certain than the changes associated with temperature. Projections show that future precipitation and storm changes will vary by season and region. Some regions may have less precipitation, some may have more precipitation, and some may have little or no change. The amount of rain falling in heavy precipitation events is likely to increase in most regions, while storm tracks are projected to shift towards the poles. Climate models project the following precipitation and storm changes:

- Global average annual precipitation through the end of the

century is expected to increase, although changes in the amount and intensity of precipitation will vary by region.
- The intensity of precipitation events will likely increase on average. This will be particularly pronounced in tropical and high-latitude regions, which are also expected to experience overall increases in precipitation.
- The strength of the winds associated with tropical storms is likely to increase. The amount of precipitation falling in tropical storms is also likely to increase.
- Annual average precipitation is projected to increase in some areas and decrease in others.

Future Ice, Snowpack, and Permafrost

Arctic sea ice is already declining drastically. The area of snow cover in the Northern Hemisphere has decreased since 1970. Permafrost temperature has increased over the last century, making it more susceptible to thawing. Over the next century, it is expected that sea ice will continue to decline, glaciers will continue to shrink, snow cover will continue to decrease, and permafrost will continue to thaw.

For every 2°F of warming, models project about a 15% decrease in the extent of annually averaged sea ice and a 25% decrease in September Arctic sea ice.The coastal sections of the Greenland and Antarctic ice sheets are expected to continue to melt or slide into the ocean. If the rate of this ice melting increases in the 21st century, the ice sheets could add significantly to global sea level rise. Glaciers are expected to continue to decrease in size. The rate of melting is expected to continue to increase, which will contribute to sea level rise.

Future Sea Level Change

Warming temperatures contribute to sea level rise by expanding ocean water, melting mountain glaciers and ice caps, and causing portions of the Greenland and Antarctic ice sheets to melt or flow into the ocean. Since 1870, global sea level has risen by about 8 inches. Estimates of future sea level rise vary for different regions, but global sea level for the next century is expected to rise at a greater rate than during the past 50 years. The contribution of thermal expansion, ice caps, and small glaciers to sea level rise is relatively well-studied, but the impacts of climate change on ice sheets are less understood and represent an active area of research. Thus, it is more difficult to predict how much changes in ice sheets will contribute to sea level rise. Greenland and Antarctic ice sheets could contribute an additional 1 foot of sea level rise, depending on how the ice sheets respond.

Regional and local factors will influence future relative sea level rise for specific coastlines around the world. For example, relative sea level rise depends on land elevation changes that occur as a result of subsidence (sinking) or uplift (rising), in addition to things such as local currents, winds, salinity, water temperatures, and proximity to thinning ice sheets.

Future Ocean Acidification

Ocean acidification is the process of ocean waters decreasing in pH. Oceans become more acidic as carbon dioxide (CO_2) emissions in the atmosphere dissolve in the ocean. This change is measured on the pH scale, with lower values being more acidic. The pH level of the oceans has decreased by approximately 0.1 pH units since pre-industrial times, which is equivalent to a 25% increase in acidity. The pH level of the oceans is projected to decrease even more by the end of the century as CO_2 concentrations are expected to increase for the foreseeable future. Ocean acidification adversely affects many marine species, including plankton, mollusks, shellfish, and corals. As ocean acidification increases, the availability of calcium carbonate will decline. Calcium carbonate is a key building block for the shells and skeletons of many marine organisms. If atmospheric CO_2 concentrations double, coral calcification rates are projected to decline by more than 30%. If CO_2 concentrations continue to rise at their current rate, corals could become rare on tropical and subtropical reefs by 2050.

Mismatched Interactions

Climate change also affects phenology, the study of the effects of climatic conditions on the timing of periodic lifecycle events, such as flowering in plants or migration in birds. Researchers have shown that 385 plant species in Great Britain are flowering 4.5 days sooner than was recorded earlier during the previous 40 years. In addition, insect-pollinated species were more likely to flower earlier than wind-pollinated species. The impact of changes in flowering date would be mitigated if the insect pollinators emerged earlier. This mismatched timing of plants and pollinators could result in injurious ecosystem effects because, for continued survival, insect-pollinated plants must flower when their pollinators are present.

Likewise, migratory birds rely on daylength cues, which are not influenced by climate change. Their insect food sources, however, emerge earlier in the year in response to warmer temperatures. As a result, climate change decreases food availability for migratory bird species.

Spread of Disease

This rise in global temperatures will increase the range of disease-carrying insects and the viruses and pathogenic parasites they harbor. Thus, diseases will spread to new regions of the globe. This spread has already been documented with dengue fever, a disease the affects hundreds of millions per year, according to the World Health Organization. Colder temperatures typically limit the distribution of certain species, such as the mosquitoes that transmit malaria, because freezing temperatures destroy their eggs.

Not only will the range of some disease-causing insects expand, the increasing temperatures will also accelerate their lifecycles, which allows them to breed and multiply quicker, and perhaps evolve pesticide resistance faster. In addition to dengue fever, other diseases are expected to spread to new portions of the world as the global climate warms. These include malaria, yellow fever, West Nile virus, zika virus, and chikungunya.

Climate change does not only increase the spread of diseases in humans. Rising temperatures are associated with greater amphibian mortality due to chytridiomycosis (see Invasive Species). Similarly, warmer temperatures have exacerbated bark beetle infestations of coniferous trees, such as pine an spruce.

Climate Change Affects Everyone

Our lives are connected to the climate. Human societies have adapted to the relatively stable climate we have enjoyed since the last ice age which ended several thousand years ago. A warming climate will bring changes that can affect our water supplies, agriculture, power and transportation systems, the natural environment, and even our own health and safety.

Carbon dioxide can stay in the atmosphere for nearly a century, on average, so Earth will continue to warm in the coming decades. The warmer it gets, the greater the risk for more severe changes to the climate and Earth's system. Although it's difficult to predict the exact impacts of climate change, what's clear is that the climate we are accustomed to is no longer a reliable guide for what to expect in the future.

We can reduce the risks we will face from climate change. By making choices that reduce greenhouse gas pollution, and preparing for the changes that are already underway, we can reduce risks from climate change. Our decisions today will shape the world our children and grandchildren will live in.

You can take steps at home, on the road, and in your office to reduce greenhouse gas emissions and the risks associated with climate change. Many of these steps can save you money. Some, such as walking or biking to work, can even improve your health! You can also get involved on a local or state level to support energy efficiency, clean energy programs, or other climate programs.

Reading Question #5

Which of the following is not observed consequence of climate change?

A. Tropical storms will be stronger.

B. Plants will flower sooner.

C. Increases in global sea levels.

D. The pH of oceans will increase.

Summary

The Earth has gone through periodic cycles of increases and decreases in temperature. During the past 2,000 years, the Medieval Climate Anomaly was a warmer period, while the Little Ice Age was unusually cool. Both ofthese irregularities can be explained by natural causes of changes in climate, and, although the temperature changes were small, they had significant effects. Natural drivers of climate change include Milankovitch cycles, changes insolar activity, and volcanic eruptions. None of these factors, however, leads to rapid increases in global temperature or sustained increases in carbon dioxide.

The burning of fossil fuels is an important source of greenhouse gases, which play a major role in the greenhouse effect. Two hundred and fifty million years ago, global warming resulted in the Permian extinction: a large-scale extinction event that is documented in the fossil record. Currently, modern-day climate change is associated with the increased melting of glaciers and polar ice sheets, resulting in a gradual increase in sea level. Plants and animals can also be affected by global climate change when the timing of seasonal events, such as flowering or pollination, is affected by global warming.

References

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6.3.01%3A_The_Greenhouse_Effect_and_Climate_Change

29. Chapter 29 Biogeochemical Cycles

TAHMED

Biogeochemical Cycles

Learning Objectives

By the end of this section, you will be able to do the following:

- Discuss the biogeochemical cycles of water, carbon, nitrogen, phosphorus, and sulfur.
- Explain how human activities have impacted these cycles and the potential consequences for Earth.

Energy flows directionally through ecosystems, entering as sunlight (or inorganic molecules for chemoautotrophs) and leaving as heat during the many transfers between trophic levels. However, the matter that makes up living organisms is conserved and recycled. The six most common elements associated with organic molecules—carbon, nitrogen, hydrogen, oxygen, phosphorus, and sulfur—take a variety of chemical forms and may exist for long periods in the atmosphere, on land, in water, or beneath the Earth's surface. Geologic processes, such as weathering, erosion, water drainage, and the subduction of the continental plates, all play a role in this recycling of materials. Because geology and chemistry have major roles in the study of this process, the recycling of inorganic matter between living organisms and their environment is called a biogeochemical cycle.

Water contains hydrogen and oxygen, which is essential to all living processes. The hydrosphere is the area of the Earth where water movement and storage occurs. On or beneath the surface, water occurs in liquid or solid form in rivers, lakes, oceans, groundwater, polar ice caps, and glaciers. And it occurs as water vapor in the atmosphere. Carbon is found in all organic macromolecules and is an important constituent of fossil fuels. Nitrogen is a major component of our nucleic acids and proteins and is critical to human agriculture. Phosphorus, a major component of nucleic acid (along with nitrogen), is one of the main ingredients in artificial fertilizers used in agriculture and their associated environmental impacts on our surface water. Sulfur is critical to the 3-D folding of proteins, such as in disulfide binding.

The cycling of these elements is interconnected. For example, the movement of water is critical for the leaching of nitrogen and phosphate into rivers, lakes, and oceans. Furthermore, the ocean itself is a major reservoir for carbon. Thus, mineral nutrients are cycled, either rapidly or slowly, through the entire biosphere, from one living organism to another, and between the biotic and abiotic world.

Which of the following is true about the movement of energy and matter through ecosystems?

1. A) Energy is conserved and recycled, while matter flows directionally through trophic levels.
2. B) Energy flows directionally through trophic levels, while matter is conserved and recycled.
3. C) Both energy and matter are conserved and recycled in ecosystems.
4. D) Both energy and matter flow directionally through ecosystems.

Why is the cycling of water important to the cycling of other elements like nitrogen and phosphorus?

1. A) The movement of water is necessary for the leaching of minerals like nitrogen and phosphorus into rivers, lakes, and oceans.
2. B) Water is a major component of organic macromolecules and is necessary for the storage and movement of other elements.

3. C) Water is the only way that minerals can be cycled through ecosystems.
4. D) Water is not important to the cycling of other elements.

Link to Learning

Link to Learning

Head to this website to learn more about biogeochemical cycles.

The Water (Hydrologic) Cycle

Water is the basis of all living processes on Earth. When examining the stores of water on Earth, 97.5 percent of it is non-potable salt water (Figure 46.12). Of the remaining water, 99 percent is locked underground as water or as ice. Thus, less than 1 percent of fresh water is easily accessible from lakes and rivers. Many living things, such as plants, animals, and fungi, are dependent on that small amount of fresh surface water, a lack of which can have massive effects on ecosystem dynamics. To be successful, organisms must adapt to fluctuating water supplies. Humans, of course, have developed technologies to increase water availability, such as digging wells to harvest groundwater, storing rainwater, and using desalination to obtain drinkable water from the ocean.

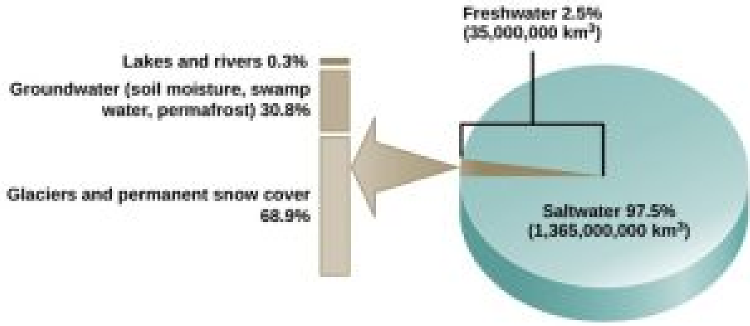

Figure 46.12 Only 2.5 percent of water on Earth is fresh water, and less than 1 percent of fresh water is easily accessible to living things.

Water cycling is extremely important to ecosystem dynamics. Water has a major influence on climate and, thus, on the environments of ecosystems. Most of the water on Earth is stored for long periods in the oceans, underground, and as ice. Figure 46.13

illustrates the average time that an individual water molecule may spend in the Earth's major water reservoirs. Residence time is a measure of the average time an individual water molecule stays in a particular reservoir.

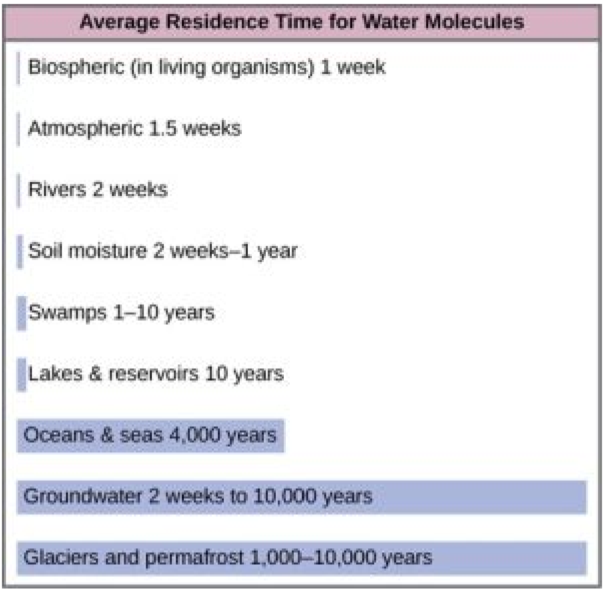

Figure 46.13 This graph shows the average residence time for water molecules in the Earth's water reservoirs.

There are various processes that occur during the cycling of water, shown in Figure 46.14. These processes include the following:

- evaporation/sublimation
- condensation/precipitation
- subsurface water flow
- surface runoff/snowmelt
- streamflow

The water cycle is driven by the sun's energy as it warms the oceans and other surface waters. This leads to the evaporation (water to water vapor) of liquid surface water and the sublimation (ice to water vapor) of frozen water, which deposits large amounts of water vapor into the atmosphere. Over time, this water vapor condenses into clouds as liquid or frozen droplets and is eventually followed by precipitation (rain or snow), which returns water to the Earth's surface. Rain eventually permeates into the ground, where it may evaporate again if it is near the surface, flow beneath the surface, or be stored for long periods. More easily observed is surface runoff: the flow of fresh water either from rain or melting ice. Runoff can then make its way through streams and lakes to the oceans or flow directly to the oceans themselves.

What drives the water cycle?

1. a) Wind's energy
2. b) The sun's energy
3. c) Earth's rotation
4. d) Gravity

How does precipitation return water to the Earth's surface?

1. a) By sublimation
2. b) By evaporation
3. c) By condensation
4. d) By infiltration

Link to Learning

Link to Learning

Head to this website to learn more about the world's fresh water supply.

Rain and surface runoff are major ways in which minerals, including carbon, nitrogen, phosphorus, and sulfur, are cycled from land to water. The environmental effects of runoff will be discussed later as these cycles are described.

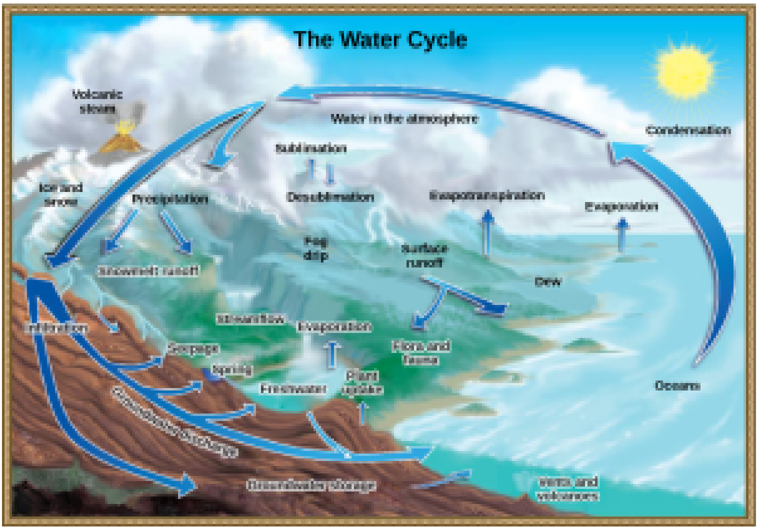

Figure 46.14 Water from the land and oceans enters the atmosphere by evaporation or sublimation, where it condenses into clouds and falls as rain or snow. Precipitated water may enter freshwater bodies or infiltrate the soil. The cycle is complete when surface or groundwater reenters the ocean. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

The Carbon Cycle

Carbon is the second most abundant element in living organisms. Carbon is present in all organic molecules, and its role in the structure of macromolecules is of primary importance to living organisms.

The carbon cycle is most easily studied as two interconnected sub-cycles: one dealing with rapid carbon exchange among living organisms and the other dealing with the long-term cycling of carbon through geologic processes. The entire carbon cycle is shown in Figure 46.15.

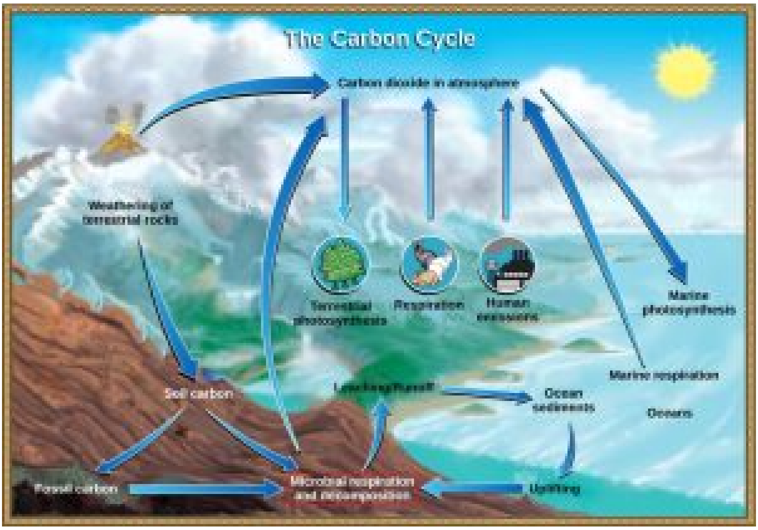

Figure 46.15 Carbon dioxide gas exists in the atmosphere and is dissolved in water. Photosynthesis converts carbon dioxide gas to organic carbon, and respiration cycles the organic carbon back into carbon dioxide gas. Long-term storage of organic carbon occurs when matter from living organisms is buried deep underground and becomes fossilized. Volcanic activity and, more recently, human emissions, bring this stored carbon back into the carbon cycle. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

Link to Learning

Link to Learning

Click this link to read information about the United States Carbon Cycle Science Program.

The Biological Carbon Cycle

Living organisms are connected in many ways, even between ecosystems. A good example of this connection is the exchange of carbon between autotrophs and heterotrophs within and between ecosystems by way of atmospheric carbon dioxide. Carbon dioxide is the basic building block that most autotrophs use to build multicarbon, high energy compounds, such as glucose. The energy harnessed from the sun is used by these organisms to form the covalent bonds that link carbon atoms together. These chemical bonds thereby store this energy for later use in the process of respiration. Most terrestrial autotrophs obtain their carbon dioxide directly from the atmosphere, while marine autotrophs acquire it in the dissolved form (carbonic acid, H2CO3−). However carbon dioxide is acquired, a by-product of the process is oxygen. The photosynthetic organisms are responsible for depositing approximately 21 percent oxygen content of the atmosphere that we observe today.

Heterotrophs and autotrophs are partners in biological carbon exchange (especially the primary consumers, largely herbivores). Heterotrophs acquire the high-energy carbon compounds from the autotrophs by consuming them, and breaking them down by respiration to obtain cellular energy, such as ATP. The most efficient type of respiration, aerobic respiration, requires oxygen obtained from the atmosphere or dissolved in water. Thus, there is a constant exchange of oxygen and carbon dioxide between the autotrophs (which need the carbon) and the heterotrophs (which need the oxygen). Gas exchange through the atmosphere and water is one way that the carbon cycle connects all living organisms on Earth.

The Biogeochemical Carbon Cycle

The movement of carbon through the land, water, and air is complex, and in many cases, it occurs much more slowly geologically than as seen between living organisms. Carbon is stored for long periods in what are known as carbon reservoirs, which include the atmosphere, bodies of liquid water (mostly oceans), ocean sediment, soil, land sediments (including fossil fuels), and the Earth's interior.

As stated, the atmosphere is a major reservoir of carbon in the form of carbon dioxide and is essential to the process of photosynthesis. The level of carbon dioxide in the atmosphere is greatly influenced by the reservoir of carbon in the oceans. The exchange of carbon between the atmosphere and water reservoirs influences how much carbon is found in each location, and each one affects the other reciprocally. Carbon dioxide (CO2) from the atmosphere dissolves in water and combines with water molecules to form carbonic acid, and then it ionizes to carbonate and bicarbonate ions (Figure 46.16)

Step 1: CO_2 (atmospheric) $\rightleftharpoons$ CO_2 (dissolved)
Step 2: CO_2 (dissolved) + H_2O $\rightleftharpoons$ H_2CO_3 (carbonic acid)
Step 3: H_2CO_3 $\rightleftharpoons$ + H^+ + HCO_3^- (bicarbonate ion)
Step 4: HCO_3^- $\rightleftharpoons$ H^+ + CO_3^{2-} (carbonate ion)

Figure 46.16 Carbon dioxide reacts with water to form bicarbonate and carbonate ions.

The equilibrium coefficients are such that more than 90 percent of the carbon in the ocean is found as bicarbonate ions. Some of these ions combine with seawater calcium to form calcium carbonate (CaCO3), a major component of marine organism shells. These organisms eventually form sediments on the ocean floor. Over geologic time, the calcium carbonate forms limestone, which comprises the largest carbon reservoir on Earth.

On land, carbon is stored in soil as a result of the decomposition of living organisms (by decomposers) or from weathering of terrestrial rock and minerals. This carbon can be leached into the water reservoirs by surface runoff. Deeper underground, on land and at sea, are fossil fuels: the anaerobically decomposed remains of plants that take millions of years to form. Fossil fuels are considered a nonrenewable resource because their use far exceeds their rate of formation. A nonrenewable resource, such as fossil fuel, is either regenerated very slowly or not at all. Another way for carbon to enter the atmosphere is from land (including land beneath the surface of the ocean) by the eruption of volcanoes and other geothermal systems. Carbon sediments from the ocean floor are taken deep within the Earth by the process of subduction: the movement of one tectonic plate beneath another. Carbon is released as carbon dioxide when a volcano erupts or from volcanic hydrothermal vents.

Humans contribute to atmospheric carbon by the burning of fossil fuels and other materials. Since the Industrial Revolution, humans have significantly increased the release of carbon and carbon compounds, which has in turn affected the climate and overall environment.

Animal husbandry by humans also increases atmospheric carbon. The large numbers of land animals raised to feed the Earth's growing population results in increased carbon dioxide levels in the atmosphere due to farming practices and respiration and methane production. This is another example of how human activity indirectly affects biogeochemical cycles in a significant way. Although much of the debate about the future effects of increasing atmospheric carbon on climate change focuses on fossils fuels, scientists take natural processes, such as volcanoes and respiration, into account as they model and predict the future impact of this increase.

The Nitrogen Cycle

Getting nitrogen into the living world is difficult. Plants and phytoplankton are not equipped to incorporate nitrogen from the atmosphere (which exists as tightly bonded, triple covalent N2) even though this molecule comprises approximately 78 percent of the atmosphere. Nitrogen enters the living world via free-living and symbiotic bacteria, which incorporate nitrogen into their macromolecules through nitrogen fixation (conversion of N2). Cyanobacteria live in most aquatic ecosystems where sunlight is present; they play a key role in nitrogen fixation. Cyanobacteria are able to use inorganic sources of nitrogen to "fix" nitrogen. *Rhizobium* bacteria live symbiotically in the root nodules of legumes (such as peas, beans, and peanuts) and provide them with the organic nitrogen they need. (For example, gardeners often grow peas both for their produce and to naturally add nitrogen to the soil. This practice goes back to ancient times, even if the science has only been recently understood.) Free-living bacteria, such as *Azotobacter*, are also important nitrogen fixers.

Organic nitrogen is especially important to the study of ecosystem dynamics since many ecosystem processes, such as primary production and decomposition, are limited by the available supply of nitrogen. As shown in Figure 46.17, the nitrogen that enters living systems by nitrogen fixation is successively converted from organic nitrogen back into nitrogen gas by bacteria. This process occurs in three steps in terrestrial systems: ammonification, nitrification, and denitrification. First, the ammonification process converts nitrogenous waste from living animals or from the remains of dead animals into ammonium (NH_4^+) by certain bacteria and fungi. Second, the ammonium is converted to nitrites (NO_2^-) by nitrifying bacteria, such as *Nitrosomonas*, through nitrification. Subsequently, nitrites are converted to nitrates (NO_3^-) by similar organisms. Third, the process of denitrification occurs, whereby bacteria, such as *Pseudomonas* and *Clostridium*, convert the nitrates into nitrogen gas, allowing it to reenter the atmosphere.

Visual Connection

Visual Connection

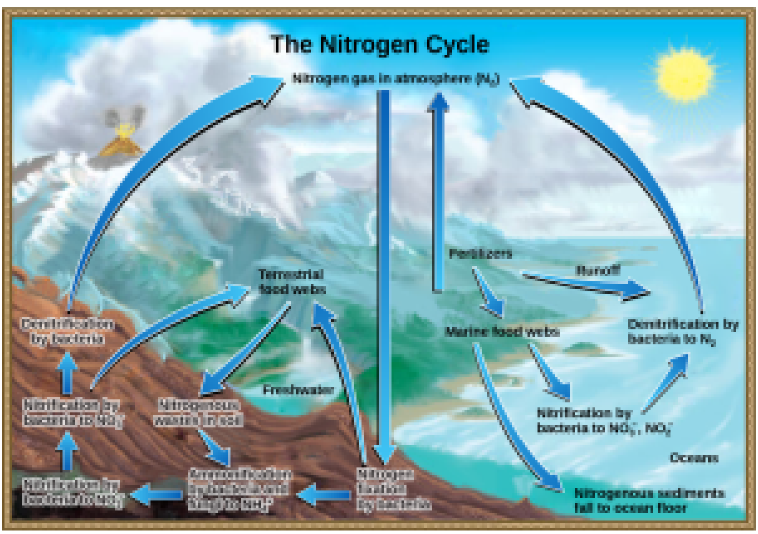

Figure 46.17 Nitrogen enters the living world from the atmosphere via nitrogen-fixing bacteria. This nitrogen and nitrogenous waste from animals is then processed back into gaseous nitrogen by soil bacteria, which also supply terrestrial food webs with the organic

nitrogen they need. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

Which of the following statements about the nitrogen cycle is false?

1. Ammonification converts organic nitrogenous matter from living organisms into ammonium ($NH4+$).
2. Denitrification by bacteria converts nitrates ($NO3-$) to nitrogen gas ($N2$).
3. Nitrification by bacteria converts nitrates ($NO3-$) to nitrites ($NO2-$).
4. Nitrogen fixing bacteria convert nitrogen gas ($N2$) into organic compounds.

Human activity can release nitrogen into the environment by two primary means: the combustion of fossil fuels, which releases different nitrogen oxides, and by the use of artificial fertilizers in agriculture, which are then washed into lakes, streams, and rivers by surface runoff. Atmospheric nitrogen is associated with several effects on Earth's ecosystems including the production of acid rain (as nitric acid, $HNO3$) and greenhouse gas (as nitrous oxide, $N2O$) potentially causing climate change. A major effect from fertilizer runoff is saltwater and freshwater eutrophication, a process whereby nutrient runoff causes the excess growth of microorganisms, depleting dissolved oxygen levels and killing ecosystem fauna.

A similar process occurs in the marine nitrogen cycle, where the ammonification, nitrification, and denitrification processes are performed by marine bacteria. Some of this nitrogen falls to the ocean floor as sediment, which can then be moved to land in geologic time by uplift of the Earth's surface and thereby incorporated into terrestrial rock. Although the movement of nitrogen from rock directly into living systems has been traditionally seen as insignificant compared with nitrogen fixed from the atmosphere, a recent study showed that this process may indeed be significant and should be included in any study of the global nitrogen cycle.3

The Phosphorus Cycle

Phosphorus is an essential nutrient for living processes; it is a major component of nucleic acid and phospholipids, and, as calcium phosphate, makes up the supportive components of our bones. Phosphorus is often the limiting nutrient (necessary for growth) in aquatic ecosystems (Figure 46.18).

Phosphorus occurs in nature as the phosphate ion (PO43−). In addition to phosphate runoff as a result of human activity, natural surface runoff occurs when it is leached from phosphate-containing rock by weathering, thus sending phosphates into rivers, lakes, and the ocean. This rock has its origins in the ocean. Phosphate-containing ocean sediments form primarily from the bodies of ocean organisms and from their excretions. However, in remote regions, volcanic ash, aerosols, and mineral dust may also be significant phosphate sources. This sediment then is moved to land over geologic time by the uplifting of areas of the Earth's surface.

Phosphorus is also reciprocally exchanged between phosphate dissolved in the ocean and marine ecosystems. The movement of phosphate from the ocean to the land and through the soil is extremely slow, with the average phosphate ion having an oceanic residence time between 20,000 and 100,000 years.

What is the primary source of phosphate-containing ocean sediments?

1. A) Volcanic ash and aerosols
2. B) Mineral dust
3. C) Bodies of ocean organisms and their excretions
4. D) Human activities

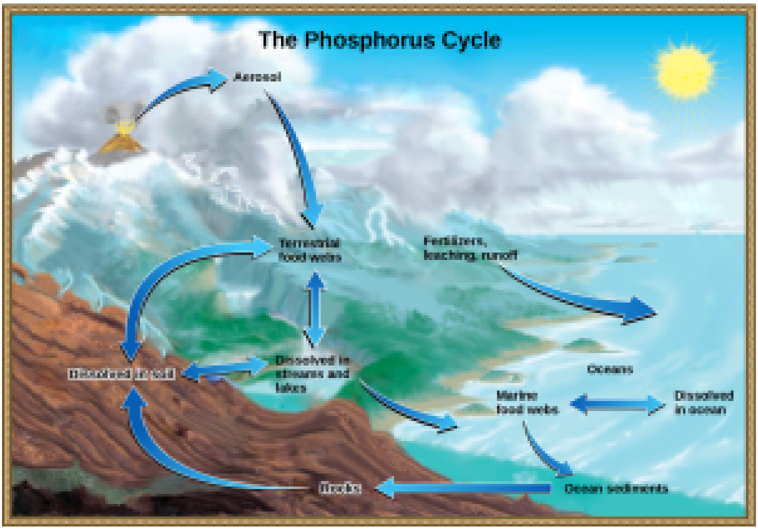

Figure 46.18 In nature, phosphorus exists as the phosphate ion (PO_4^{3-}). Weathering of rocks and volcanic activity releases phosphate into the soil, water, and air, where it becomes available to terrestrial food webs. Phosphate enters the oceans via surface runoff, groundwater flow, and river flow. Phosphate dissolved in ocean water cycles into marine food webs. Some phosphate from the marine food webs falls to the ocean floor, where it forms sediment. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

As discussed in Chapter 44, excess phosphorus and nitrogen that enters these ecosystems from fertilizer runoff and from sewage causes excessive growth of microorganisms and depletes the dissolved oxygen, which leads to the death of many ecosystem fauna, such as shellfish and finfish. This process is responsible for dead zones in lakes and at the mouths of many major rivers (Figure 46.19).

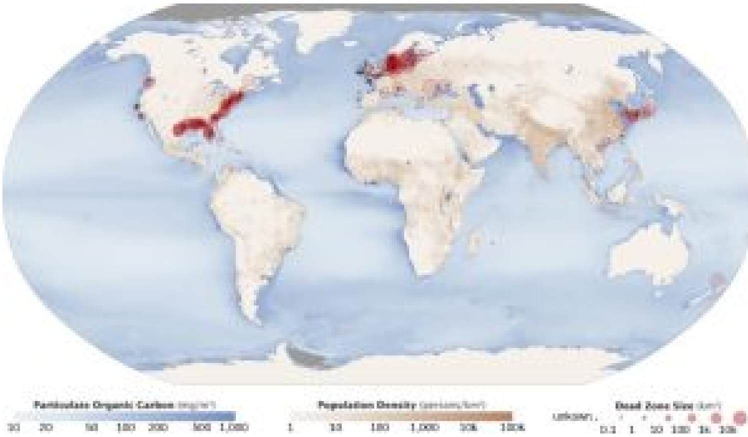

Figure 46.19 Dead zones occur when phosphorus and nitrogen from fertilizers cause excessive growth of microorganisms, which depletes oxygen and kills fauna. Worldwide, large dead zones are found in coastal areas of high population density. (credit: NASA Earth Observatory)

As discussed earlier, a dead zone is an area within a freshwater or marine ecosystem where large areas are depleted of their normal flora and fauna; these zones can be caused by eutrophication, oil spills, dumping of toxic chemicals, and other human activities. The number of dead zones has been increasing for several years, and more than 400 of these zones were present as of 2008. One of the worst dead zones is off the coast of the United States in the Gulf of Mexico, where fertilizer runoff from the Mississippi River basin has created a dead zone of over 8463 square miles. Phosphate and nitrate runoff from fertilizers also negatively affect several lake and bay ecosystems including the Chesapeake Bay in the eastern United States.

Everyday Connection

Everyday Connection

Chesapeake Bay

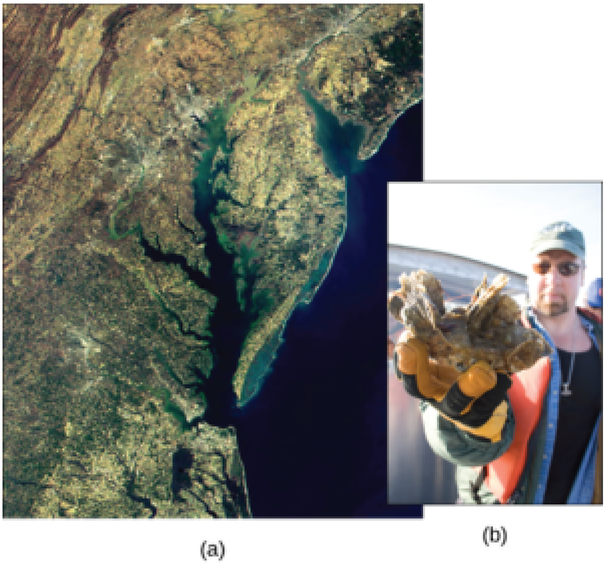

Figure 46.20 This (a) satellite image shows the Chesapeake Bay, an ecosystem affected by phosphate and nitrate runoff. A (b) member of the Army Corps of Engineers holds a clump of oysters being used as a part of the oyster restoration effort in the bay. (credit a: modification of work by NASA/MODIS; credit b: modification of work by U.S. Army)

The Chesapeake Bay has long been valued as one of the most scenic areas on Earth; it is now in distress and is recognized as a declining ecosystem. In the 1970s, the Chesapeake Bay was one of the first ecosystems to have identified dead zones, which continue to kill many fish and bottom-dwelling species, such as clams, oysters, and worms. Several species have declined in the Chesapeake Bay due to surface water runoff containing excess nutrients from artificial fertilizer used on land. The source of the fertilizers (with high nitrogen and phosphate content) is not limited to agricultural practices. There are many nearby urban areas and more than 150 rivers and streams empty into the bay that are carrying fertilizer runoff from lawns and gardens. Thus, the decline of the Chesapeake Bay is a complex issue and requires the cooperation of industry, agriculture, and everyday homeowners.

Of particular interest to conservationists is the oyster population; it is estimated that more than 200,000 acres of oyster reefs existed in the bay in the 1700s, but that number has now declined to only 36,000 acres. Oyster harvesting was once a major industry for Chesapeake Bay, but it declined 88 percent between 1982 and 2007. This decline was due not only to fertilizer runoff and dead zones but also to overharvesting. Oysters require a certain minimum population density because they must be in close proximity to reproduce. Human activity has altered the oyster population and locations, greatly disrupting the ecosystem.

The restoration of the oyster population in the Chesapeake Bay has been ongoing for several years with mixed success. Not only do many people find oysters good to eat, but they also clean up the bay. Oysters are filter feeders, and as they eat, they clean the water around them. In the 1700s, it was estimated that it took only a few days for the oyster population to filter the entire volume of the bay. Today, with changed water conditions, it is estimated that the present population would take nearly a year to do the same job.

Restoration efforts have been ongoing for several years by nonprofit organizations, such as the Chesapeake Bay Foundation. The restoration goal is to find a way to increase population density so the oysters can reproduce more efficiently. Many disease-resistant varieties (developed at the Virginia Institute of Marine Science for the College of William and Mary) are now available and have been used in the construction of experimental oyster reefs. Efforts to clean and restore the bay by Virginia and Delaware have been hampered because much of the pollution entering the bay comes from other states, which stresses the need for interstate cooperation to gain successful restoration.

The new, hearty oyster strains have also spawned a new and economically viable industry—oyster aquaculture—which not only supplies oysters for food and profit, but also has the added benefit of cleaning the bay.

The Sulfur Cycle

Sulfur is an essential element for the macromolecules of living things. As a part of the amino acid cysteine, it is involved in the formation of disulfide bonds within proteins, which help to determine their 3-D folding patterns, and hence their functions. As shown in Figure 46.21, sulfur cycles between the oceans, land, and atmosphere. Atmospheric sulfur is found in the form of sulfur dioxide (SO2) and enters the atmosphere in three ways: from the decomposition of organic molecules, from volcanic activity and geothermal vents, and from the burning of fossil fuels by humans.

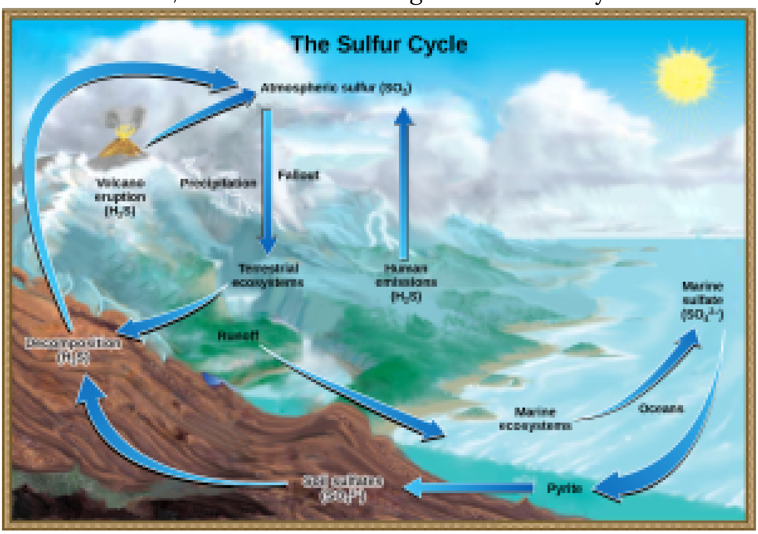

Figure 46.21 Sulfur dioxide from the atmosphere becomes available to terrestrial and marine ecosystems when it is dissolved in precipitation as weak sulfurous acid or when it falls directly to the Earth as fallout. Weathering of rocks also makes sulfates available to terrestrial ecosystems. Decomposition of living organisms returns sulfates to the ocean, soil, and atmosphere. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

On land, sulfur is deposited in four major ways: precipitation, direct fallout from the atmosphere, rock weathering, and geothermal vents (Figure 46.21). Atmospheric sulfur is found in the form of sulfur dioxide (SO2), and as rain falls through the atmosphere, sulfur is dissolved in the form of weak sulfurous acid (H2SO3). Sulfur can also fall directly from the atmosphere in a process called fallout. Also, the weathering of sulfur-containing rocks releases sulfur into the soil. These rocks originate from ocean sediments that are moved to land by the geologic uplifting of ocean sediments. Terrestrial ecosystems can then make use of these soil sulfates ($SO4-$

), and upon the death and decomposition of these organisms, release the sulfur back into the atmosphere as hydrogen sulfide ($H2S$) gas.

Figure 46.22 At this sulfur vent in Lassen Volcanic National Park in northeastern California, the yellowish sulfur deposits are visible near the mouth of the vent.

Sulfur enters the ocean via runoff from land, from atmospheric fallout, and from underwater geothermal vents. Some ecosystems (Figure 46.9) rely on chemoautotrophs using sulfur as a biological energy source. This sulfur then supports marine ecosystems in the form of sulfates.

Human activities have played a major role in altering the balance of the global sulfur cycle. The burning of large quantities of fossil fuels, especially from coal, releases larger amounts of hydrogen sulfide gas into the atmosphere. Acid rain is caused by rainwater falling to the ground through this sulfur dioxide gas, turning it into weak sulfuric acid. Acid rain damages the natural environment by lowering the pH of lakes, which kills many of the resident fauna;

it also affects the man-made environment through the chemical degradation of buildings. For example, many marble monuments, such as the Lincoln Memorial in Washington, DC, have suffered significant damage from acid rain over the years.

Source Text:

Clark, Mary Ann, Jung Choi, and Matthew Douglas. *Biology 2e*. Rice University, 2018.

Additional reading:

- Scott L. Morford, Benjamin Z. Houlton, and Randy A. Dahlgren, "Increased Forest Ecosystem Carbon and Nitrogen Storage from Nitrogen Rich Bedrock," N*ature* 477, no. 7362 (2011): 78–81.

30. Chapter 30: Biomes

ANASTASIA CHOUVALOVA

Introduction to Biomes

A **biome** is a large, distinctive complex of plant communities created and maintained by **climate**. How many biomes are there?

A study published in 1999 concluded that there are 150 different "ecoregions" in North America alone. It is rational to lump these into **8 biomes**:

- tundra
- taiga
- temperate deciduous forest
- scrub forest (called chaparral in California)
- grassland
- desert
- tropical rain forest
- temperate rain forest

Figure 29.1 shows the distribution of these 8 biomes around the world. A number of climatic factors interact in the creation and maintenance of a biome. Where precipitation is moderately abundant — 40 inches (about 1 m) or more per year — and distributed fairly evenly throughout the year, the major determinant is **temperature**. It is not simply a matter of average temperature, but includes such limiting factors as whether it ever freezes or length of the growing season. If there is ample rainfall, we find 4 characteristic biomes as we proceed from the tropics (high temperatures) to the extreme latitudes (low temperatures). In order, they are:

- tropical rain forest or jungle
- temperate deciduous forest
- taiga
- tundra

The Earth's biomes are categorized into two major groups: *terrestrial* and *aquatic*. Terrestrial biomes are based on land, while aquatic biomes include both ocean and freshwater biomes. The eight major terrestrial biomes on Earth are each distinguished by characteristic temperatures and amount of precipitation. Comparing the annual totals of precipitation and fluctuations in precipitation from one biome to another provides clues as to the importance of abiotic factors in the distribution of biomes. Temperature variation on a daily and seasonal basis is also important for predicting the geographic distribution of the biome and the vegetation type in the biome. The distribution of these biomes shows that the same biome can occur in geographically distinct areas with similar climates (Figure 29.1).

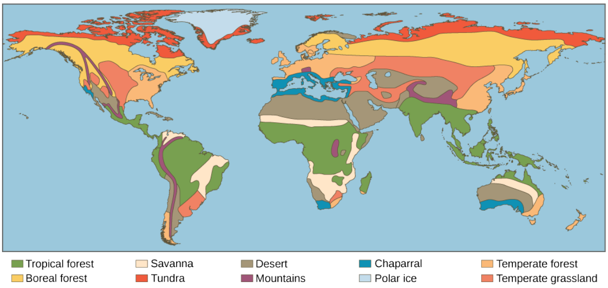

Figure 29.1 Each of the world's major biomes is distinguished by characteristic temperatures and amounts of precipitation. Polar ice and mountains are also shown.

Reading Question #1

Examine Figure 29.1. Which statement below accurately describes the distribution of tropical forests vs. boreal forests? Select all that apply.

A. Generally, boreal forests are at higher latitudes than tropical forests.

B. Generally, boreal forests are at lower latitudes than tropical forests.

C. Generally, boreal forests are likely to be colder than tropical forests.

D. Generally, boreal forests are likely to be hotter than tropical forests.

1. Tropical Wet Forest

Tropical wet forests are also referred to as tropical rainforests. This biome is found in equatorial regions (Figure 29.1). The vegetation is characterized by plants with broad leaves that fall and are replaced throughout the year. Unlike the trees of deciduous forests, the trees in this biome do not have a seasonal loss of leaves associated with variations in temperature and sunlight; these forests are "evergreen" year-round.

The temperature and sunlight profiles of tropical wet forests are very stable in comparison to that of other terrestrial biomes, with the temperatures ranging from 20 °C to 34 °C (68 °F to 93 °F). When one compares the annual temperature variation of tropical wet forests with that of other forest biomes, the lack of seasonal temperature variation in the tropical wet forest becomes apparent. This lack of seasonality leads to year-round plant growth, rather than the seasonal (spring, summer, and fall) growth seen in other more temperate biomes. In contrast to other ecosystems, tropical ecosystems do not have long days and short days during the yearly cycle. Instead, a constant daily amount of sunlight (11–12 hrs per day) provides more solar radiation, thereby, a longer period of time for plant growth.

The annual rainfall in tropical wet forests ranges from 125 cm to 660 cm (50–200 in) with some monthly variation. While sunlight and temperature remain fairly consistent, annual rainfall is highly variable. Tropical wet forests typically have wet months in which there can be more than 30 cm (11–12 in) of precipitation, as well as dry months in which there are fewer than 10 cm (3.5 in) of rainfall. However, the driest month of a tropical wet forest still exceeds the *annual* rainfall of some other biomes, such as deserts.

Tropical wet forests have high net primary productivity because the annual temperatures and precipitation values in these areas are ideal for plant growth. Therefore, the extensive biomass present in the tropical wet forest leads to plant communities with very high species diversities (Figure 29.2). Tropical wet forests have more species of trees than any other biome; on average between 100 and 300 species of trees are present in a single hectare (2.5 acres) of South American Amazonian rain forest. One way to visualize this is to compare the distinctive horizontal layers within the tropical wet forest biome. On the forest floor is a sparse layer of plants and decaying plant matter. Above that is an understory of short shrubby foliage. A layer of trees rises above this understory and is topped by a closed upper canopy—the uppermost overhead layer of branches and leaves. Some additional trees emerge through this closed upper canopy. These layers provide diverse and complex habitats for the variety of plants, fungi, animals, and other organisms within the tropical wet forests.

For example, epiphytes are plants that grow on other plants, which typically are not harmed. Epiphytes are found throughout tropical wet forest biomes. Many species of animals use the variety of plants and the complex structure of the tropical wet forests for food and shelter. Some organisms live several meters above ground and have adapted to this arboreal lifestyle.

Figure 29.2. Tropical wet forests, such as these forests along the Madre de Dios river, Peru, near the Amazon River, have high species diversity. (credit: Roosevelt Garcia)

2. Savannas

Savannas are grasslands with scattered trees, and they are located in Africa, South America, and northern Australia (Figure 29.1). Savannas are usually hot, tropical areas with temperatures averaging from 24 °C to 29 °C (75 °F to 84 °F) and an annual rainfall of 10–40 cm (3.9–15.7 in). Savannas have an extensive dry season; for this reason, forest trees do not grow as well as they do in the tropical wet forest (or other forest biomes). As a result, within the grasses and *forbs* (herbaceous flowering plants) that dominate the savanna, there are relatively few trees (Figure 29.3). Since fire is an important source of disturbance in this biome, plants have evolved well-developed root systems that allow them to quickly resprout after a fire.

Figure 29.3 Savannas, like this one in Taita Hills Wildlife Sanctuary in Kenya, are dominated by grasses. (credit: Christopher T. Cooper)

3. Subtropical Deserts

Subtropical deserts exist between 15° and 30° north and south latitude and are centered on the Tropics of Cancer and Capricorn (Figure 29.1). This biome is very dry; in some years, evaporation exceeds precipitation. Subtropical hot deserts can have daytime soil surface temperatures above 60 °C (140 °F) and nighttime temperatures approaching 0 °C (32 °F). This is largely due to the lack of atmospheric water. In cold deserts, temperatures can be as high as 25 °C and can drop below -30 °C (-22 °F). Subtropical deserts are characterized by low annual precipitation of fewer than 30 cm (12 in) with little monthly variation and lack of predictability in rainfall. In some cases, the annual rainfall can be as low as 2 cm (0.8 in) in subtropical deserts located in central Australia ("the Outback") and northern Africa.

The vegetation and low animal diversity of this biome is closely related to low and unpredictable precipitation. Very dry deserts lack perennial vegetation that lives from one year to the next; instead, many plants are annuals that grow quickly and reproduce when rainfall does occur, and then die. Many other plants in these areas are characterized by having a number of adaptations that conserve water, such as deep roots, reduced foliage, and water-storing stems (Figure 29.4). Seed plants in the desert produce seeds that can be in dormancy for extended periods between rains. Adaptations in desert animals include nocturnal behavior and burrowing.

4. Chaparral

The chaparral is also called the scrub forest and is found in California, along the Mediterranean Sea, and along the southern coast of Australia (Figure 29.1). The annual rainfall in this biome ranges from 65 cm to 75 cm (25.6–29.5 in), and the majority of the rain falls in the winter. Summers are very dry and many chaparral plants are dormant during the summertime. The chaparral vegetation, shown in Figure 29.4, is dominated by shrubs adapted to periodic fires, with some plants producing seeds that only germinate after a hot fire. The ashes left behind after a fire are rich in nutrients like nitrogen that fertilize the soil and promote plant regrowth.

Figure 29.4 The chaparral is a shrub-dominated biome. (credit: Miguel Vieira)

5. Temperate Grasslands

Temperate grasslands are found throughout central North America, where they are also known as *prairies*; they are also in Eurasia, where they are known as *steppes* (Figure 29.1). Temperate grasslands have pronounced annual fluctuations in temperature with hot summers and cold winters. The annual temperature variation produces specific growing seasons for plants. Plant growth is possible when temperatures are warm enough to sustain plant growth and when ample water is available, which occurs in the spring, summer, and fall. During much of the winter, temperatures are low, and water, which is stored in the form of ice, is not available for plant growth.

Annual precipitation ranges from 25 cm to 75 cm (9.8–29.5 in). Because of relatively lower annual precipitation in temperate grasslands, there are few trees except for those found growing along rivers or streams. The dominant vegetation tends to consist of grasses dense enough to sustain populations of grazing animals Figure 44.17. The vegetation is very dense and the soils are fertile because the subsurface of the soil is packed with the roots and *rhizomes* (underground stems) of these grasses. The roots and rhizomes act to anchor plants into the ground and replenish the organic material (humus) in the soil when they die and decay.

Figure 29.5 The American bison (Bison bison), more commonly called the buffalo, is a grazing mammal that once populated American prairies in huge numbers. (credit: Jack Dykinga, USDA Agricultural Research Service)

Fires, mainly caused by lightning, are a *natural disturbance* in temperate grasslands. When fire is suppressed in temperate grasslands, the vegetation eventually converts to scrub and sometimes dense forests with drought-tolerant tree species. Often, the restoration or management of temperate grasslands requires the use of controlled burns to suppress the growth of trees and maintain the grasses.

6. Temperate Forests

Temperate forests are the most common biome in eastern North America, Western Europe, Eastern Asia, Chile, and New Zealand (Figure 29.1). This biome is found throughout mid-latitude regions. Temperatures range between -30 °C and 30 °C (-22 °F to 86 °F) and drop to below freezing periodically during cold winters. These temperatures mean that temperate forests have defined growing seasons during the spring, summer, and early fall. Precipitation is relatively constant throughout the year and ranges between 75 cm and 150 cm (29.5–59 in).

Because of the moderate annual rainfall and temperatures, deciduous trees are the dominant plant in this biome (Figure 29.6). Deciduous trees lose their leaves each fall and remain leafless in the winter. Thus, no photosynthesis occurs in the deciduous trees during the dormant winter period. Each spring, new leaves appear as the temperature increases. Because of the dormant period, the net primary productivity of temperate forests is less than that of tropical wet forests. In addition, temperate forests show less diversity of tree species than tropical wet forest biomes.

Figure 29.6 The dominant plant in the temperate forest biome is deciduous trees. (credit: Oliver Herold)

The trees of the temperate forests leaf out and shade much of the ground; however, this biome is more open than tropical wet forests because most trees in the temperate forests do not grow as tall as the trees in tropical wet forests. The soils of the temperate forests are rich in inorganic and organic nutrients. This is due to the thick layer of leaf litter on forest floors, which does not develop in tropical rainforests. As this leaf litter decays, nutrients are returned to the soil. The leaf litter also protects soil from erosion, insulates the ground, and provides habitats for invertebrates (such as the pill bug or roly-poly, *Armadillidium vulgare*) and their predators, such as the red-backed salamander (*Plethodon cinereus*).

7. Boreal Forests

The boreal forest, also known as taiga or coniferous forest, is found south of the Arctic Circle and across most of Canada, Alaska, Russia, and northern Europe (Figure 29.1). This biome has cold, dry winters and short, cool, wet summers. The annual precipitation is from 40 cm to 100 cm (15.7–39 in) and usually takes the form of snow. Little evaporation occurs because of the cold temperatures.

The long and cold winters in the boreal forest have led to the predominance of cold-tolerant cone-bearing (coniferous) plants. These are evergreen coniferous trees like pines, spruce, and fir, which retain their needle-shaped leaves year-round. Evergreen trees can photosynthesize earlier in the spring than deciduous trees because less energy from the sun is required to warm a needle-like leaf than a broad leaf. This benefits evergreen trees, which grow faster than deciduous trees in the boreal forest. In addition, soils in boreal forest regions tend to be acidic with little available nitrogen. Leaves are a nitrogen-rich structure and deciduous trees must produce a new set of these nitrogen-rich structures each year. Therefore, coniferous trees that retain nitrogen-rich needles may have a competitive advantage over the broad-leafed deciduous trees.

The net primary productivity of boreal forests is lower than that of temperate forests and tropical wet forests. The above-ground biomass of boreal forests is high because these slow-growing tree species are long-lived and accumulate a large standing biomass over time. Plant species diversity is less than that seen in temperate forests and tropical wet forests. Boreal forests lack the pronounced elements of the layered forest structure seen in tropical wet forests. The structure of a boreal forest is often only a tree layer and a ground layer (Figure 29.7). When conifer needles are dropped, they decompose more slowly than broad leaves; therefore, fewer nutrients are returned to the soil to fuel plant growth.

Figure 29.7 Low-lying plants and conifer trees are characteristic flora in the boreal forest, also known as the taiga. (credit: L.B. Brubaker)

8. Arctic Tundra

The Arctic tundra lies north of the subarctic boreal forest and is located throughout the Arctic regions of the northern hemisphere (Figure 29.1). The average winter temperature is −34 °C (−29.2 °F) and the average summer temperature is from 3 °C to 12 °C (37 °F–52 °F). Plants in the arctic tundra have a very short growing season of approximately 10–12 weeks.

However, during this time, there are almost 24 hours of daylight and plant growth is rapid. The annual precipitation of the Arctic tundra is very low with little annual variation in precipitation. And, as in the boreal forests, there is little evaporation due to the cold temperatures.

Plants in the Arctic tundra are generally low to the ground (Figure 29.8). There is little species diversity, low net primary productivity, and low above-ground biomass. The soils of the Arctic tundra may remain in a perennially frozen state referred to as permafrost. The permafrost makes it impossible for roots to penetrate deep into the soil and slows the decay of organic matter, which inhibits the release of nutrients from organic matter. During the growing season, the ground of the Arctic tundra can be completely covered with plants or lichens.

Figure 29.8 Low-growing plants such as shrub willow dominate the tundra landscape, shown here in the Arctic National Wildlife Refuge. (credit: USFWS Arctic National Wildlife Refuge)

Link to Learning

For an overview of biomes, watch this Assignment Discovery: Biomes video. To explore further, select one of the biomes on the extended playlist: desert, savanna, temperate forest, temperate grassland, tropic, tundra.

Reading Question #2

Match the following biomes to their descriptions.

A) Subtropical desert. B) Savannah. C) Chaparral. D) Temperate Grassland

1. This biome is mainly comprised of shrub plants and most precipitation falls in the cold season.
2. Precipitation is extremely low in this biome and plants have been forced to develop many adaptations to this condition
3. Precipitation is fairly low in this biome yet vegetation is dense.
4. This biome is characterized by a prolonged dry season, resulting in low tree abundance.

Reading Question #3

Match the following biomes to their descriptions.

A) Boreal forest. B) Temperate forest. C) Tropical wet forest. D) Arctic tundra

1. Plants in this biome grow at a fast rate but have a

short growing season.

2. This biome is dominated by deciduous trees and has consistent precipitation throughout the year.
3. Most precipitation falls as snow in this biome and most plants are coniferous.
4. This biome features highly stable temperature and sunlight conditions and has high precipitation levels throughout the year, allowing for high plant biodiversity.

Now that we have covered all eight terrestrial biomes in detail, let's move onto the second major type of biome – aquatic biomes.

Aquatic biomes

Abiotic Factors Influencing Aquatic Biomes

Like terrestrial biomes, aquatic biomes are influenced by a series of abiotic factors. The aquatic medium—water— has different physical and chemical properties than air, however. Even if the water in a pond or other body of water is perfectly clear (there are no suspended particles), water, on its own, absorbs light. As one descends into a deep body of water, there will eventually be a depth which the sunlight cannot reach. While there are some abiotic and biotic factors in a terrestrial ecosystem that might obscure light (like fog, dust, or insect swarms), usually these are not permanent features of the environment. The importance of light in aquatic biomes is central to the communities of organisms found in both freshwater and marine ecosystems. In freshwater systems, stratification due to differences in density is perhaps the most critical abiotic factor and is related to the energy aspects of light. The thermal properties of water (rates of heating and cooling and the ability to store much larger amounts of energy than the air) are significant to the function of marine systems and have major impacts on global climate and weather patterns. Marine systems are also influenced by large-scale physical water movements, such as currents; these are less important in most freshwater lakes.

The ocean is categorized by several areas or zones (Figure 29.9). All of the ocean's open water is referred to as the pelagic realm (or zone). The benthic realm (or zone) extends along the ocean bottom from the shoreline to the deepest parts of the ocean floor. Within the pelagic realm is the photic zone, which is the portion of the ocean that light can penetrate (approximately 200 m or 650 ft). At depths greater than 200 m, light cannot penetrate; thus, this is referred to as the aphotic zone. The majority of the ocean is aphotic and lacks sufficient light for photosynthesis. The deepest part of the ocean, the Challenger Deep (in the Mariana Trench, located in the western Pacific Ocean), is about 11,000 m (about 6.8 mi) deep. To give some perspective on the depth of this trench, the ocean is, on average, 4267 m or 14,000 ft deep. These realms and zones are relevant to freshwater lakes as well.

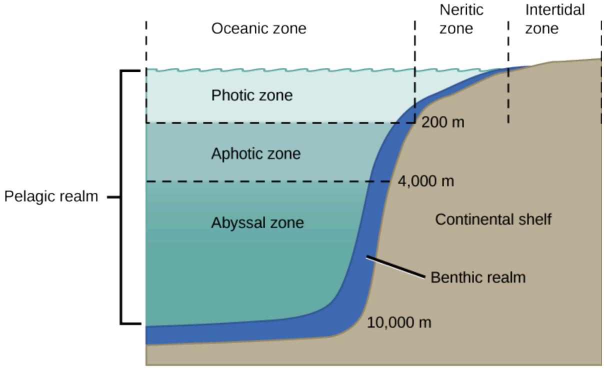

Figure 29.9 The ocean is divided into different zones based on water depth and distance from the shoreline.

Reading Question #4

Examine Figure 29.9 closely. In which zone(s) would you be least likely to find photosynthetic organisms? (Hint: There are two correct answers)

A. Aphotic zone

B. Photic zone

C. Pelagic zone

D. Abyssal zone

Marine Biomes

The ocean is the largest marine biome. It is a continuous body of salt water that is relatively uniform in chemical composition; in fact, it is a weak solution of mineral salts and decayed biological matter. Within the ocean, coral reefs are a second kind of marine biome. Estuaries, coastal areas where salt water and fresh water mix, form a third unique marine biome.

Ocean

The physical diversity of the ocean is a significant influence on plants, animals, and other organisms. The ocean is categorized into different zones based on how far light reaches into the water. Each zone has a distinct group of species adapted to the biotic and abiotic conditions particular to that zone.

The intertidal zone, which is the zone between high and low tide, is the oceanic region that is closest to land (Figure 29.9). Generally, most people think of this portion of the ocean as a sandy beach. In some cases, the intertidal zone is indeed a sandy beach, but it can also be rocky or muddy. The intertidal zone is an extremely variable environment because of action of tidal ebb and flow. Organisms are exposed to air and sunlight at low tide and are underwater most of the time, especially during high tide. Therefore, living things that thrive in the intertidal zone are adapted to being dry for long periods of time. The shore of the intertidal zone may also be repeatedly struck by waves, and the organisms found there are adapted to withstand damage from their pounding action (Figure 44.22). The exoskeletons of shoreline crustaceans (such as the shore crab, *Carcinus maenas*) are tough and protect them from desiccation (drying out) and wave damage. Another consequence of the pounding waves is that few algae and plants establish themselves in the constantly moving rocks, sand, or mud.

Figure 29.10 Some common sea creatures in the intertidal zone include mussel shells, starfish, and sea urchins. This photo was taken in Kachemak Bay, Alaska. (credit: NOAA)

The neritic zone (Figure 29.9) extends from the intertidal zone to depths of about 200 m (or 650 ft) at the edge of the *continental shelf* (the underwater landmass that extends from a continent). Since light can penetrate this depth, photosynthesis can still occur in the neritic zone. The water here contains silt and is well-oxygenated, low in pressure, and stable in temperature. Phytoplankton and floating *Sargassum* (a type of free-floating marine seaweed) provide a habitat for some sea life found in the neritic zone. Zooplankton, protists, small fishes, and shrimp are found in the neritic zone and are the base of the food chain for most of the world's fisheries.

Beyond the neritic zone is the open ocean area known as the **pelagic** or **open oceanic zone** (Figure 29.9). Within the oceanic zone there is *thermal stratification* where warm and cold waters mix because of ocean currents. Abundant plankton serve as the base of the food chain for larger animals such as whales and dolphins. Nutrients are scarce and this is a relatively less productive part of the marine biome. When photosynthetic organisms and the protists and animals that feed on them die, their bodies fall to the bottom of the ocean, where they remain. Unlike freshwater lakes, most of the open ocean lacks a process for bringing the organic nutrients back up to the surface. (Exceptions include major oceanic upwellings within the Humboldt Current along the western coast of South America.) The majority of organisms in the aphotic zone include sea cucumbers (phylum Echinodermata) and other organisms that survive on the nutrients contained in the dead bodies of organisms in the photic zone.

Beneath the pelagic zone is the benthic realm, the deep-water region beyond the continental shelf (Figure 29.9). The bottom of the benthic realm is composed of sand, silt, and dead organisms. Temperature decreases, remaining above freezing, as water depth increases. This is a nutrient-rich portion of the ocean because of the dead organisms that fall from the upper layers of the ocean. Because of this high level of nutrients, a diversity of fungi, sponges, sea anemones, marine worms, sea stars, fishes, and bacteria exist.

The deepest part of the ocean is the abyssal zone, which is at depths of 4000 m or greater. The abyssal zone (Figure 29.9) is very cold and has very high pressure, very low or no oxygen content, and high nutrient content as the dead and decomposing material that drifts down from the layers above. There are a variety of invertebrates and fishes found in this zone, but the abyssal zone does not have plants because of the lack of light. Hydrothermal vents are found primarily in the abyssal zone; chemosynthetic bacteria utilize the hydrogen sulfide and other minerals emitted from the vents. These chemosynthetic bacteria use the hydrogen sulfide as an energy source and serve as the base of the food chain found in the abyssal zone.

Coral Reefs

Coral reefs are *ocean ridges* formed by marine invertebrates, comprising mostly cnidarians and molluscs, living in warm shallow waters within the photic zone of the ocean. They are found within 30° north and south of the equator. The Great Barrier Reef is perhaps the best-known and largest reef system in the world—visible from the International Space Station! This massive and ancient reef is located several miles off the northeastern coast of Australia. Other coral reef systems are fringing islands, which are directly adjacent to land, or atolls, which are circular reef systems surrounding a former landmass that is now underwater. The coral organisms (members of phylum Cnidaria) are colonies of saltwater polyps that secrete a calcium carbonate skeleton. These calcium-rich skeletons slowly accumulate, forming the underwater reef (Figure 29.11). Corals found in shallower waters (at a depth of approximately 60 m or about 200 ft) have a mutualistic relationship with photosynthetic unicellular algae. The relationship provides corals with the majority of the nutrition and the energy they require. The waters in which these corals live are nutritionally poor and, without this mutualism, it would not be possible for large corals to grow. Some corals living in deeper and colder water do not have a mutualistic relationship with algae; these corals attain energy and nutrients using stinging cells called cnidocytes on their tentacles to capture prey.

It is estimated that more than 4,000 fish species inhabit coral reefs. These fishes can feed on coral, the cryptofauna(invertebrates found within the calcium carbonate substrate of the coral reefs), or the seaweed and algae that are associated with the coral. In addition, some fish species inhabit the boundaries of a coral reef; these species include predators, herbivores, and planktivores, which consume planktonic organisms such as bacteria, archaea, algae, and protists floating in the pelagic zone.

Figure 29.11 Coral reefs are formed by the calcium carbonate skeletons of coral organisms, which are marine invertebrates in the phylum Cnidaria. (credit: Terry Hughes)

Evolution Connection

Global Decline of Coral Reefs

It takes many thousands of years to build a coral reef. The animals that create coral reefs have evolved over millions of years, continuing to slowly deposit the calcium carbonate that forms their characteristic ocean homes. Bathed in warm tropical waters, the coral animals and their symbiotic algal partners evolved to survive at the upper limit of ocean water temperature.

Together, climate change and human activity pose dual threats to the long-term survival of the world's coral reefs. As global warming due to fossil fuel emissions raises ocean temperatures, coral reefs are suffering. The excessive warmth causes the reefs to lose their symbiotic, food-producing algae, resulting in a phenomenon known as bleaching. When bleaching occurs, the reefs lose much of their characteristic color as the algae and the coral animals die if loss of the symbiotic zooxanthellae is prolonged.

Rising levels of atmospheric carbon dioxide further threaten the corals in other ways; as CO_2 dissolves in ocean waters, it lowers the pH and increases ocean acidity. As acidity increases, it interferes with the calcification that normally occurs when coral animals build their calcium carbonate shelters.

When a coral reef begins to die, species diversity plummets as animals lose food and shelter. Coral reefs are also economically important tourist destinations, so the decline of coral reefs poses a serious threat to coastal economies.

Human population growth has damaged corals in other ways, too. As human coastal populations increase, the runoff of sediment and agricultural chemicals has increased, as well, causing some of the once-clear tropical waters to become cloudy. At the same time, overfishing of popular fish species has allowed the predator species that eat corals to go unchecked.

Although a rise in global temperatures of 1–2 °C (a conservative scientific projection) in the coming decades may not seem large, it is very significant to this biome. When change occurs rapidly, species can become extinct before evolution can offer new adaptations. Many scientists believe that global warming, with its rapid (in terms of evolutionary time) and inexorable increases in temperature, is tipping the balance beyond the point at which many of the world's coral reefs can recover.

Estuaries: Where the Ocean Meets Fresh Water

Estuaries are biomes that occur where a source of fresh water, such as a river, meets the ocean. Therefore, both fresh water and salt water are found in the same vicinity; mixing results in a diluted (*brackish*) saltwater. Estuaries form protected areas where many of the young offspring of crustaceans, molluscs, and fish begin their lives, which also creates important breeding grounds for other animals. Salinity is a very important factor that influences the organisms and the adaptations of the organisms found in estuaries. The salinity of estuaries varies considerably and is based on the rate of flow of its freshwater sources, which may depend on the seasonal rainfall. Once or twice a day, high tides bring salt water into the estuary. Low tides occurring at the same frequency reverse the current of salt water.

The short-term and rapid variation in salinity due to the mixing of fresh water and salt water is a difficult physiological challenge for the plants and animals that inhabit estuaries. Many estuarine plant species are halophytes: plants that can tolerate salty conditions. Halophytic plants are adapted to deal with the salinity resulting from saltwater on their roots or from sea spray. In some halophytes, filters in the roots remove the salt from the water that the plant absorbs. Other plants are able to pump oxygen into their roots. Animals, such as mussels and clams (phylum Mollusca), have developed behavioral adaptations that expend a lot of energy to function in this rapidly changing environment. When these animals are exposed to low salinity, they stop feeding, close their shells, and switch from aerobic respiration (in which they use gills to remove oxygen from the water) to anaerobic respiration (a process that does not require oxygen and takes place in the cytoplasm of the animal's cells). When high tide returns to the estuary, the salinity and oxygen content of the water increases, and these animals open their shells, begin feeding, and return to aerobic respiration.

Freshwater Biomes

Freshwater biomes include lakes and ponds (standing water) as well as rivers and streams (flowing water). They also include wetlands, which will be discussed later. Humans rely on freshwater biomes to provide ecosystem benefits, which are aquatic resources for drinking water, crop irrigation, sanitation, and industry. Lakes and ponds are connected with abiotic and biotic factors influencing their terrestrial biomes.

Lakes and Ponds

Lakes and ponds can range in area from a few square meters to thousands of square kilometers. Temperature is an important abiotic factor affecting living things found in lakes and ponds. In the summer, as we have seen, thermal stratification of lakes and ponds occurs when the upper layer of water is warmed by the sun and does not mix with deeper, cooler water. Light can penetrate within the photic zone of the lake or pond. Phytoplankton (algae and cyanobacteria) are found here and carry out photosynthesis, providing the base of the food web of lakes and ponds. Zooplankton, such as rotifers and larvae and adult crustaceans, consume these phytoplankton. At the bottom of lakes and ponds, bacteria in the aphotic zone break down dead organisms that sink to the bottom.

Nitrogen and phosphorus are important limiting nutrients in lakes and ponds. Because of this, they are the determining factors in the amount of phytoplankton growth that takes place in lakes and ponds. When there is a large input of nitrogen and phosphorus (from sewage and runoff from fertilized lawns and farms, for example), the growth of algae skyrockets, resulting in a large accumulation of algae called an algal bloom. Algal blooms (Figure 29.12) can become so extensive that they reduce light penetration in water. They may also release toxic byproducts into the water, contaminating any drinking water taken from that source. In addition, the lake or pond becomes aphotic, and photosynthetic plants cannot survive. When the algae die and decompose, severe oxygen depletion of the water occurs. Fishes and other organisms that require oxygen are then more likely to die, resulting in a dead zone. Lake Erie and the Gulf of Mexico represent freshwater and marine habitats where phosphorus control and storm water runoff pose significant environmental challenges.

Figure 29.12 The uncontrolled growth of algae in this lake has resulted in an algal bloom. (credit: Jeremy Nettleton)

Rivers and Streams

Rivers and streams are continuously moving bodies of water that carry large amounts of water from the source, or *headwater*, to a lake or ocean. The largest rivers include the Nile River in Africa, the Amazon River in South America, and the Mississippi River in North America.

Abiotic features of rivers and streams vary along the length of the river or stream. Streams begin at a point of origin referred to as source water. The source water is usually cold, low in nutrients, and clear. The channel (the width of the river or stream) is narrower than at any other place along the length of the river or stream. Because of this, the current is often faster here than at any other point of the river or stream.

The fast-moving water results in minimal silt accumulation at the bottom of the river or stream; therefore, the water is usually clear and free of debris. Photosynthesis here is mostly attributed to algae that are growing on rocks; the swift current inhibits the growth of phytoplankton. An additional input of energy can come from leaves and other organic material that fall downstream into the river or stream, as well as from trees and other plants that border the water. When the leaves decompose, the organic material and nutrients in the leaves are returned to the water. Plants and animals have adapted to this fast-moving water. For instance, some species of mayfly (phylum Arthropoda) have flattened bodies and legs with modified claws to help them cling to the underside of submerged rocks. This body form reduces drag and allows these species to benefit from the high oxygen concentrations in fast-moving currents without being dislodged. Freshwater trout species (phylum Chordata) are an important predator in these fast-moving rivers and streams.

As the river or stream flows away from the source, the width of the channel gradually widens and the current slows. This slow-moving water, caused by the gradient decrease and the volume increase as tributaries unite, has more sedimentation. Phytoplankton can also be suspended in slow-moving water. Therefore, the water will not be as clear as it is near the source. The water is also warmer. Worms (phylum Annelida) and insects (phylum Arthropoda) can be found burrowing into the mud. The higher order predator vertebrates (phylum Chordata) include waterfowl, frogs, and fishes. These predators must find food in these slow moving, sometimes murky, waters and, unlike the trout in the waters at the source, these vertebrates may not be able to use vision as their primary sense to find food. Instead, they are more likely to use taste or chemical cues to find prey.

Wetlands

Wetlands are environments in which the soil is either permanently or periodically saturated with water. Wetlands are different from lakes because wetlands are shallow bodies of water whereas lakes vary in depth. Emergent vegetationconsists of wetland plants that are rooted in the soil but have portions of leaves, stems, and flowers extending above the water's surface. There are several types of wetlands including marshes, swamps, bogs, mudflats, and salt marshes (Figure 29.13). The three shared characteristics among these types—what makes them wetlands—are their hydrology, hydrophytic vegetation, and hydric soils.

Figure 29.13 Located in southern Florida, Everglades National Park is vast array of wetland environments, including sawgrass marshes, cypress swamps, and estuarine mangrove forests. Here, a great egret walks among cypress trees. (credit: NPS)

Freshwater marshes and swamps are characterized by slow and steady water flow. Bogs, however, develop in depressions where water flow is low or nonexistent. Bogs usually occur in areas where there is a clay bottom with poor percolation of water. (Percolation is the movement of water through the pores in the soil or rocks.) The water found in a bog is stagnant and oxygen-depleted because the oxygen used during the decomposition of organic matter is not readily replaced. As the oxygen in the water is depleted, decomposition slows. This leads to a buildup of acids and a lower water pH. The lower pH creates challenges for plants because it limits the available nitrogen. As a result, some bog plants (such as sundews, pitcher plants, and Venus flytraps) capture insects in order to extract the nitrogen from their bodies. Bogs have low net primary productivity because the water found in bogs has low levels of nitrogen and oxygen.

Reading Question #5

A researcher has previously obtained two samples of water, described in the following statements, and is trying to trace them back to their sources because he forgot where he found them! (Note: this is why keeping a good lab notebook is critical). He needs your help to figure out where he obtained the two samples from.

Sample A contains no oxygen and has low pH while Sample B contains a mixture of fresh and salt water.

A. Sample A comes from a river and Sample B comes from a lake.

B. Sample A comes from a lake and Sample B comes from a river.

C. Sample A comes from an bog and Sample B comes from an estuary.

D. Sample A comes from an estuary and Sample B comes from a bog.

E. Options A and C are equally likely.

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31. Chapter 31: Climate diagrams

ANASTASIA CHOUVALOVA

In this textbook chapter, we will start by discussing the usefulness of graphs in biology. Then, you will see a variety of climate diagrams (also called climatograms) and answer the corresponding questions. Lastly, we will learn about how weather data is collected over time to eventually produce these climatograms.

Types of Data

There are different types of data that can be collected in an experiment. Typically, we try to design experiments that collect objective, quantitative data.

Objective data is fact-based, measurable, and observable. This means that if two people made the same measurement with the same tool, they would get the same answer. The measurement is determined by the object that is being measured. The length of a worm measured with a ruler is an objective measurement. The observation that a chemical reaction in a test tube changed color is an objective measurement. Both of these are observable facts.

Subjective data is based on opinions, points of view, or emotional judgment. Subjective data might give two different answers when collected by two different people. The measurement is determined by the subject who is doing the measuring. Surveying people about which of two chemicals smells worse is a subjective measurement. Grading the quality of a presentation is a subjective measurement. Rating your relative happiness on a scale of 1-5 is a subjective measurement. All of these depend on the person who is making the observation – someone else might make these measurements differently.

Quantitative measurements gather numerical data. For example, measuring a worm as being 5cm in length is a quantitative measurement.

Qualitative measurements describe a quality, rather than a numerical value. Saying that one worm is longer than another worm is a qualitative measurement.

After you have collected data in an experiment, you need to figure out the best way to present that data in a meaningful way. Depending on the type of data, and the story that you are trying to tell using that data, you may present your data in different ways.

Reading Question #1

Classify the following two statements as examples of quantitative or qualitative data.

Statement 1: Sample A is more opaque than Sample B.

Statement 2: Sample A is three times more contaminated than Sample B.

A. Both statements are quantitative data.

B. Both statements are qualitative data.

C. Statement 1 is quantitative and Statement 2 is qualitative.

D. Statement 1 is qualitative and Statement 2 is quantitative.

Data Tables

The easiest way to organize data is by putting it into a data table (for an example, see Figure 30.1). In most data tables, the independent variable (the variable that you are testing or changing on purpose) will be in the column to the left and the dependent variable(s) will be across the top of the table.

Height of seedlings for germinated seeds					
Water Type	**Trial**	**Trial average of seedling height /mm ±0.5mm**	**Trial Standard Deviation**	**Overall average height /mm ±0.5mm**	**Overall standard deviation**
De-ionized	1	13.0	13.4	**23.4**	**13.6**
	2	11.8	13.9		
Smoked	1	57.8	24.5	**59.5**	**12.4**
	2	61.1	22.3		

Figure 30.1

Reading Question #2

Examine Figure 30.1. What is the independent and dependent variable?

A. The independent variable is the water type (i.e., de-ionized and smoked) and the dependent variable is the seedling height.

B. The independent variable is the seedling height and the dependent variable is the water type (i.e., de-ionized and smoked).

C. The independent variable is the trial and the dependent variable is the water type (i.e., de-ionized and smoked).

D. The independent variable is the water type (i.e., de-ionized and smoked) and the dependent variable is the standard deviation.

Be sure to:

- Label each row and column so that the table can be interpreted
- Include the units that are being used
- Add a descriptive caption for the table

Graphing

Graphs are used to display data because it is easier to see trends in the data when it is displayed visually compared to when it is displayed numerically in a table. Complicated data can often be displayed and interpreted more easily in a graph format than in a data table.

In a graph, the X-axis runs horizontally (side to side) and the Y-axis runs vertically (up and down). Typically, the independent variable will be shown on the X axis and the dependent variable will be shown on the Y axis (just like you learned in math class!).

1. Line Graph

Line graphs (Figure 30.2) are the best type of graph to use when you are displaying a change in something over a continuous range. For example, you could use a line graph to display a change in temperature over time. Time is a continuous variable because it can have any value between two given measurements. It is measured along a continuum. Between 1 minute and 2 minutes are an infinite number of values, such as 1.1 minute or 1.93456 minutes.

Changes in several different samples can be shown on the same graph by using lines that differ in color, symbol, etc.

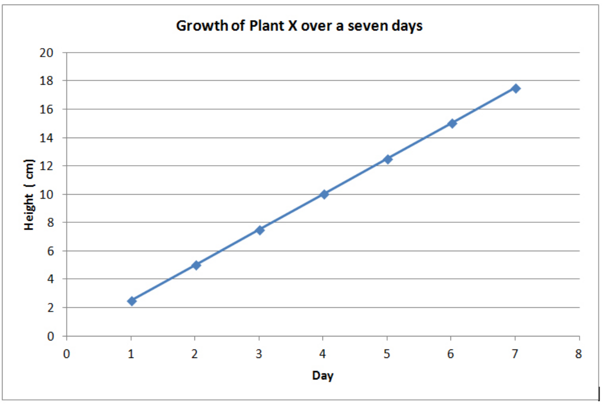

Figure 30.2 A line graph showing the change in height of Plant X over a period of seven days. (Credit: Western Sydney University)

2. Bar Graph

Bar graphs (Figure 30.3) are used to compare measurements between different groups. Bar graphs should be used when your data is not continuous, but rather is divided into different categories. If you counted the number of birds of different species, each species of bird would be its own category. There is no value between "robin" and "eagle", so this data is not continuous.

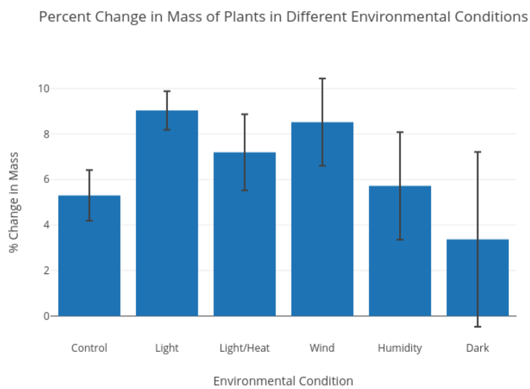

Figure 30.3 A bar graph showing the % change in mass of plants placed in various environmental conditions. (Credit: [Chart-Studio, Plotly](#))

3. Scatter Plot

Scatter plots (Figure 30.4) are used to evaluate the relationship between two different continuous variables. These graphs compare changes in two different variables at once. For example, you could look at the relationship between height and weight. Both height and weight are continuous variables. You could not use a scatter plot to look at the relationship between number of children in a family and weight of each child because the number of children in a family is not a continuous variable: you can't have 2.3 children in a family.

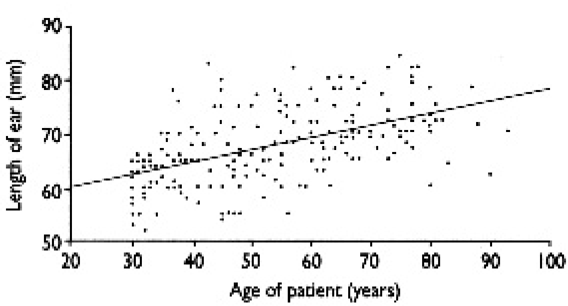

Figure 30.4 A scatter plot showing the relationship of ear length and age. (Credit: [Heathcoate, 1995](#))

How to make a graph

1. Identify your independent and dependent variables.
2. Choose the correct type of graph by determining whether each variable is continuous or not.
3. Determine the values that are going to go on the X and Y axis. If the values are continuous, they need to be evenly spaced based on the value.
4. Label the X and Y axis, including units.
5. Graph your data.
6. Add a descriptive caption to your graph. Note that data tables are titled above the figure and graphs are captioned below the figure.

Descriptive captions

All figures that present data should stand alone – this means that you should be able to interpret the information contained in the figure without referring to anything else (such as the methods section of the paper). This means that all figures should have a descriptive caption that gives information about the independent and dependent variable. Another way to state this is that the caption should describe what you are testing and what you are measuring. A good starting point to developing a caption is "the effect of [the independent variable] on the [dependent variable]."

Here are some examples of good caption for figures:

- The effect of exercise on heart rate
- Growth rates of E. coli at different temperatures
- The relationship between heat shock time and transformation efficiency

Here are a few less effective captions:

- Heart rate and exercise
- Graph of E. coli temperature growth
- Table for experiment 1

Reading Question #3

For your undergraduate research project, you have gathered data about the beak length of five bird species. What graph is most suited to visualize this information? (Hint: What type of data are we dealing with? Continuous, categorical, etc.?)

A. A line graph

B. A bar graph

C. A scatter plot

D. Either a bar graph or scatter plot would be suitable.

Climatograms

We can use climate to describe the long-term conditions of biomes. Several abiotic factors (e.g., temperature, precipitation, wind, humidity) interact to produce a biome's unique climate which in turn, determines which flora and fauna are able to survive within that biome and establish a niche.

For simplicity, climate is primarily classified by both average annual precipitation and average annual temperature ranges. Climatograms (for an example, see Figure 30.5) are a type of graph that show annual temperature ranges and precipitation totals for an average year for a given location. They often utilize a double-Y axis which plots both the average annual temperature and precipitation. A bar graph is often used to plot precipitation and is labeled on the left y-axis, while a line graph is used to show temperature and is labeled on the right y-axis. The x-axis contains the months of the year.

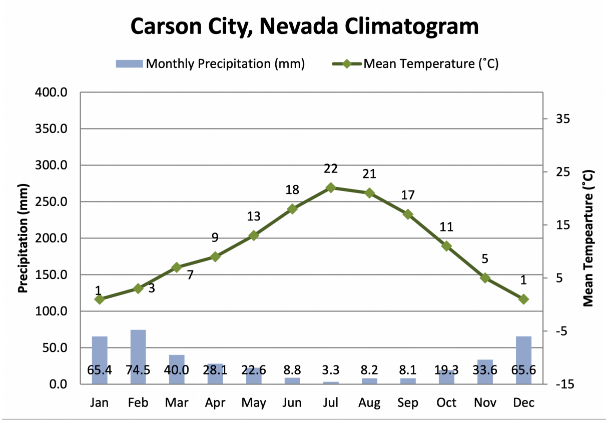

Figure 30.5 Climatogram for Carson City, Nevada. (Credit: Precipitation data from NASA's TRMM Satellite, Average Monthly Precipitation Climatology, 1998-2010 retrieved from https://mynasadata.larc.nasa.gov/live-access-server/, temperature data from http://www.weather.com)

Reading Question #4 (0.5 points)

Take a look at Figure 30.5. Which of the following statements is false about the climate in Carson City, Nevada?

A. Most precipitation falls from December to February.

B. July is the month of highest temperature and lowest precipitation.

C. The temperature range is 21°C.

D. The precipitation consistently exceeds 100.00 mm.

Let's look at another climatogram of El Paso, Texas.

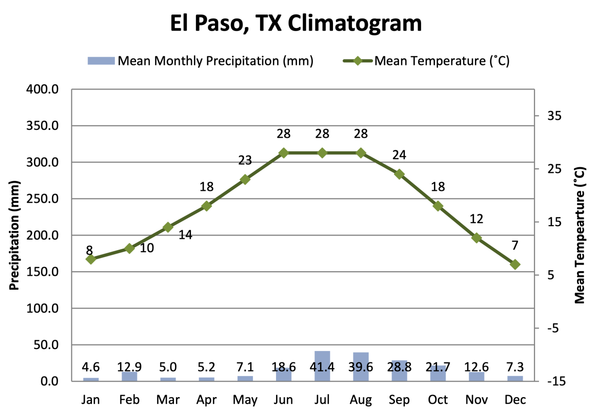

Figure 30.6 Climatogram for El Paso, Texas. (Credit: Precipitation data from NASA's TRMM Satellite, Average Monthly Precipitation Climatology, 1998-2010 retrieved from https://mynasadata.larc.nasa.gov/live-access-server/, temperature data from http://www.weather.com)

Reading Question #5 (0.5 points)

Examine Figure 30.6. Which of the following statements accurately describes the climate trend? Select all that apply.

A. Summer is the driest and hottest season.

B. Summer is the wettest and hottest season.

C. Winter tends to be dry and above-freezing temperatures.

D. Winter tends to be wet and below-freezing temperatures.

Collecting weather data

Weather forecasts are better than they ever have been. According to the World Meteorological Organization (WMO), a 5-day weather forecast today is as reliable as a 2-day forecast was 20 years ago! This is because forecasters now use advanced technologies to gather weather data, along with the world's most powerful computers. Together, the data and computers produce complex models that more accurately represent the conditions of the atmosphere. These models can be programmed to predict how the atmosphere and the weather will change. Despite these advances, weather forecasts are still often incorrect. Weather is extremely difficult to predict because it is a complex and chaotic system.

To make a weather forecast, the conditions of the atmosphere must be known for that location and for the surrounding area. Temperature, air pressure, and other characteristics of the atmosphere must be measured and the data collected.

Thermometers

Thermometers measure temperature. In an old-style mercury thermometer, mercury is placed in a long, very narrow tube with a bulb. Because mercury is temperature sensitive, it expands when temperatures are high and contracts when they are low. A scale on the outside of the thermometer matches up with the air temperature.Some modern thermometers use a coiled strip composed of two kinds of metal, each of which conducts heat differently. As the temperature rises and falls, the coil unfolds or curls up tighter. Other modern thermometers measure infrared radiation or electrical resistance. Modern thermometers usually produce digital data that can be fed directly into a computer.

Barometers

Meteorologists use **barometers** to measure air pressure. A barometer may contain water, air, or mercury, but like thermometers, barometers are now mostly digital. A change in barometric pressure indicates that a change in weather is coming. If air pressure rises, a high pressure cell is on the way and clear skies can be expected. If pressure falls, a low pressure cell is coming and will likely bring storm clouds. Barometric pressure data over a larger area can be used to identify pressure systems, fronts, and other weather systems.

Weather Stations

Weather stations contain some type of thermometer and barometer. Other instruments measure different characteristics of the atmosphere such as wind speed, wind direction, humidity, and amount of precipitation. These instruments are placed in various locations so that they can check the atmospheric characteristics of that location. According to the WMO, weather information is collected from 15 satellites, 100 stationary buoys, 600 drifting buoys, 3,000 aircraft, 7,300 ships, and some 10,000 land-based stations. The official weather stations used by the National Weather Service is called the Automated Surface Observing System (ASOS).

Radiosondes

Radiosondes is a balloon that measures atmospheric characteristics, such as temperature, pressure, and humidity as they move through the air. Radiosondes in flight can be tracked to obtain wind speed and direction. Radiosondes use a radio to communicate the data they collect to a computer. Radiosondes are launched from about 800 sites around the globe twice daily to provide a profile of the atmosphere. Radiosondes can be dropped from a balloon or airplane to make measurements as they fall. This is done to monitor storms, for example, since they are dangerous places for airplanes to fly.

Radar

Radar stands for Radio Detection and Ranging. A transmitter sends out radio waves that bounce off the nearest object and then return to a receiver. Weather radar can sense many characteristics of precipitation: its location, motion, intensity, and the likelihood of future precipitation. Doppler radar can also track how fast the precipitation falls. Radar can outline the structure of a storm and can be used to estimate its possible effects.

Satellites

Weather satellites have been increasingly important sources of weather data since the first one was launched in 1952 and are the best way to monitor large scale systems, such as storms. Satellites are able to record long-term changes, such as the amount of ice cover over the Arctic Ocean in September each year.

They also observe all energy from all wavelengths in the electromagnetic spectrum.The flagship of the National Weather Service is the Geostationary Operational Environmental Satellites (GOES). These satellites are the ones you see on the nightly news where it looks like the clouds are moving, but not the planet. That is because these satellites are "geo-fixed" on a particular location over Earth rotating around the planet as fast as Earth's rotation at a distance of over 23,000 miles above the planet. There are basically three different types of GOES: visible, infrared, and water vapor. Visible light images record storms, clouds, fires, and smog. Infrared images record clouds, water and land temperatures, and features of the ocean, such as ocean currents. The final type of GOES imagery is water vapor. This type of imagery looks at the moisture content in the upper-half of the atmosphere. This is important for determining if clouds can grow to great heights like cumulonimbus thunderstorms.

The other type of satellite commonly used in weather forecasting is called a Polar Orbiting Environmental Satellites (POES). These types of satellites fly much lower to the earth, only about 530 miles, and orbit the planet pole-to-pole. You've probably seen these satellites at night when you see one crossing the sky. Look for their direction and odds are they are moving northward or southward toward each pole.

Just like the weather satellites on the news, you've seen these images often when you are looking at natural disasters like hurricanes or volcanic eruptions, wars like have occurred in Afghanistan, Iraq, or recently in Syria. Even the Malaysian flight that "disappeared" in the Indian Ocean for weeks was ultimately discovered using polar orbiting satellites. Common types of these satellites include: Landsat, MODIS, and the Tropical Rainfall Measuring Mission (TRMM).

Numerical Weather Prediction

The most accurate weather forecasts are made by advanced computers, with analysis and interpretation added by experienced meteorologists. These computers have up-to-date mathematical models that can use much more data and make many more calculations than would ever be possible by scientists working with just maps and calculators. Meteorologists can use these results to give much more accurate weather forecasts and climate predictions.

In Numerical Weather Prediction (NWP), atmospheric data from many sources are plugged into supercomputers running complex mathematical models. The models then calculate what will happen over time at various altitudes for a grid of evenly spaced locations. The grid points are usually between 10 and 200 kilometers apart. Using the results calculated by the model, the program projects weather further into the future. It then uses these results to project the weather still further into the future, as far as the meteorologists want to go. Once a forecast is made, it is broadcast by satellites to more than 1,000 sites around the world.

NWP produces the most accurate weather forecasts, but as anyone knows, even the best forecasts are not always right. Weather prediction is extremely valuable for reducing property damage and even fatalities. If the proposed track of a hurricane can be predicted, people can try to secure their property and then evacuate.

Weather maps

Weather maps, also called **synoptic maps**, simply and graphically depict meteorological conditions in the atmosphere from a spatial perspective. Weather maps may display only one feature of the atmosphere or multiple features. They can depict information from computer models or from human observations.

On a weather map, important meteorological conditions are plotted for each weather station. Metorologists use many different symbols as a quick and easy way to display information on the map.

Reading Question #5

Match the following instruments to their function.

A) Thermometer B) Barometer C) Radiosondes D) Radar E) Satellites

1. Can be used to track storms and wind parameters using radio waves.
2. Can be used to track storms using all wavelengths.
3. Used to measure air pressure and predict various weather systems.
4. Can be used to track various properties of precipitation using radio waves

5. Has historically used toxic metals that change volume in response to temperature changes.

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32. Chapter 32: Migration

ANASTASIA CHOUVALOVA

Migration can be defined as the long-range seasonal movement of organisms, often due to seasonal changes in temperature. It is an evolved, adapted response to variation in resource availability, and it is a common phenomenon found in all major groups of animals. Birds fly south for the winter to get to warmer climates with sufficient food, and salmon migrate to their spawning grounds. The popular 2005 documentary *March of the Penguins* followed the 62-mile migration of emperor penguins through Antarctica to bring food back to their breeding site and to their young. Wildebeests (Figure 31.1) migrate over 1800 miles each year in search of new grasslands.One of the negative impacts of climate change is the forced changes upon animals' migration patterns.

Figure 31.1 Wildebeests migrate in a clockwise fashion over 1800 miles each year in search of rain-ripened grass. (credit: Eric Inafuku)

Although migration is thought of as innate behavior, only some migrating species always migrate (obligate migration). Animals that exhibit facultative migration can choose to migrate or not. Additionally, in some animals, only a portion of the population migrates, whereas the rest does not migrate (incomplete migration). For example, owls that live in the tundra may migrate in years when their food source, small rodents, is relatively scarce, but not migrate during the years when rodents are plentiful.

KQED: Flyways: The Migratory Routes of Birds

For thousands of years and countless generations, migratory birds have flown the same long-distance paths between their breeding and feeding grounds. Understanding the routes these birds take, called **flyways**, helps conservation efforts and gives scientists better knowledge of global changes, both natural and man-made.

Link to Learning

View this video which discusses flyways and how biologists track the migratory patterns of birds.

Migration in humans

Early Hominin Migrations

Human species were migratory from the beginning, moving as small populations of gatherers and hunters within eastern and southern Africa. By following game and the availability of seasonal vegetation from place to place, these small groups of nomads learned about their landscape, interacted with each other, and met their subsistence needs. Their daily needs came through interaction with a changing environment. With the emergence of *Homo erectus* around 1.89 million years BP (before the present), hominins expanded their territories and began to exhibit increasing control over their environment and an ability to adapt, evidenced by the development of new subsistence systems, including cultivation, pastoralism, and agriculture, and an upsurge in migration within Africa and, eventually, into Asia and Europe. This expansion into new geographical regions was a hallmark of the later human species.

There are several theories on possible migratory sequences within and beyond the African continent. One possibility is that by 1.75 million years ago, *Homo ergaster* had begun migrating out of Africa, moving northward into Eurasia. Another theory argues that an earlier hominin species, either australopithecine or an early as-yet-unknown species of the genus *Homo*, migrated out of Africa around 2 million years ago, eventually evolving into the population of Dmanisi hominins who were settled in eastern Europe by 1.85 million years ago, possibly representing another link between *H. erectus* and *H. ergaster*. Although settlement dates are currently being retested and reexamined for precision (Matsu'ura et al. 2020), it is known that between 1.3 and 1.6 million years ago, *H. erectus* settled on Java, an island that is now part of Indonesia. They likely traveled there by a land route, as seas were lower during the Pleistocene Ice Age (approximately 2.588 million–11,700 years ago), allowing for more passage through interior coastal routes. (For more on early human migrations, see The Genus Homo *Homo* and the Emergence of Us.)

Regardless of the specific time frame and migration pattern, it is well established that there was gene flow between various hominin populations, which indicates that there were migration and exchange. With the migration of these early hominin populations, cultural practices and improvements in toolmaking spread as well.

Wherever humans traveled, they carried with them their traditions, intermingling and reproducing both physically and culturally.

Reading Question #1

Which of the following were influences of the migration of early hominins? Select all that apply.

A. Gene flow between different hominin populations

B. Enhanced skills such as toolmaking

C. Reduced resistance to disease

D. Species' expansion from Eurasia to Africa

Controversies Surrounding the Peopling of the Americas

Current evidence points to the emergence of the genus *Homo* in Africa. From these beginnings, human populations began moving toward the global north, east, and south in migratory waves. Motivations for these migrations included animal movements, overcrowding and resource scarcity, and, likely, curiosity and adventure. The movement into the Western Hemisphere, into North and South America, occurred significantly later than migrations into Europe and Asia; how much later is a question of enormous controversy today. How did the first peoples make their way to the Americas? When did they first arrive, and how did they migrate within these vast continents? The available evidence is inconclusive, leaving us with one of the biggest enigmas in human evolution.

While there is some debate on whether earlier human species migrated into the Americas, the evidence we have today points to members of the species *Homo sapiens* being the earliest humans to do so. At this point, there is no evidence of any earlier hominin species in either North or South America. The Western Hemisphere was wholly settled by migrants coming from other continents.

There are many theories regarding the first human migration into the Western Hemisphere. Because of changing global climate conditions and the retreat of glaciers toward the end of the Pleistocene epoch, new lands opened to migrating animals and the humans who were likely hunting them (Wooller et al. 2018). As always, because of limited and ambiguous artifact and fossil findings, the primary pieces of evidence are open to multiple interpretations. Upon examining the range of theories, two primary arguments are apparent. Both of these arguments are backed by supporting evidence, and both rely on migratory patterns of *H. sapiens* in the Americas that have been definitively established. While both migration theories are valid, the question that remains open to argument is which came first, coastal or interior migration?

- The *interior route*, also called the Bering Strait theory, is the best-known and most accepted theory for the first human migration into the Americas. The foundation of this theory is the Beringia "land bridge," which connected northeast Siberia and what is now Alaska when sea levels were lower due to glacial ice formation on the continents. This theory proposes that the earliest human habitants of the Americas crossed this marshy land on foot, most likely beginning around 15,000 years ago based on artifacts and dating sequences. The Beringia land bridge was alternately exposed and submerged multiple times over the earth's history. According to the interior route theory, the earliest humans crossed this marshy land in pursuit of migratory herds of mammals and then proceeded to filter southward, splitting into multiple groups, some of which penetrated into the interior of North America as they continued to move east and south.

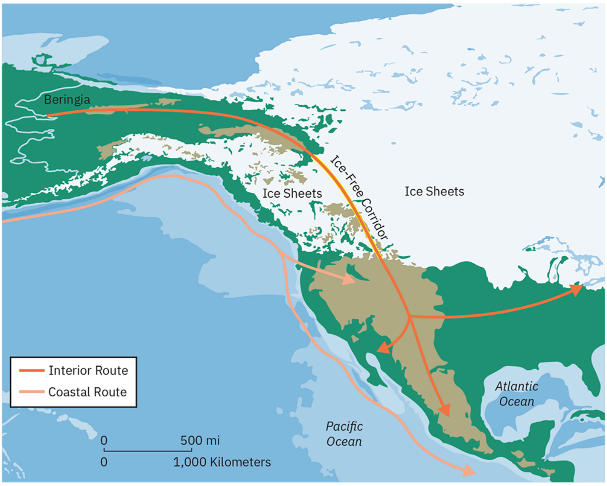

Figure 31.2 The interior route theory argues that a northeastern Siberian population of hunters first entered the Americas on foot from Beringia following migrating herds, while the coastal route theory argues that the earliest migrants followed fish and sea animals by boat along the Pacific coast of the Western Hemisphere. Although the precise date for the earliest migrations is debated, it is estimated to be between 15,000 and 18,000 years ago. (credit: Copyright Rice University, OpenStax, under CC BY 4.0 license)

- The *coastal route* is also based on the migration of a northeastern Siberian population into the Western Hemisphere, but by boat rather than on foot. This theory, sometimes called the kelp highway hypothesis, proposes that the earliest migratory populations followed the continental coastline southward, subsisting on kelp, fish, shellfish, birds, and sea mammals. Research by archaeologist Jon Erlandson (Erlandson et al. 2007; Ocean Wise 2017) suggests that migrants may have followed these food sources all along the continental shelf, a shallow sea area near the shore. Some believe that they eventually reached as far south as Chile, in South America, before breaking into groups and penetrating the interior lands.

Each theory presents its own probabilities and problems in relation to dating sequences and artifacts, and there were possibly multiple early routes for the peopling the Americas. Scientific research does agree on some known facts, however. Genetic sequencing shows continuity between the earliest Americans and populations in northeastern Siberia that indicates the earliest inhabitants of the Americas arrived no more than 25,000 years ago, making the Americas the most recent continental habitation (outside of Antarctica). Humans were already inhabiting Australia by the time other humans first arrived in the Americas.

Archaeological sites in the Americas present fascinating evidence of early human migrations, with the dating sequences continually being retested and revised. Based on some of the early archaeological evidence, scientists had believed that the first American inhabitants were part of what is known as the Clovis culture, identified with a leaf-shaped projectile point used in hunting. As excavations have continued, though, there is growing indication of an extensive pre-Clovis culture, evidenced by a pre-Clovis technology based on gathering, hunting, and fishing, with dates extending back further than 13,200 years before present. Pre-Clovis projectile points are smaller, less standardized, and less worked (flaked), indicating a less advanced tool production. Many pre-Clovis sites are located below the Clovis period occupation. As archaeologists have continued excavations, the dates for earliest occupation continue to be pushed backward.

Figure 31.3 Clovis points from the Virginia Aquarium and Marine Science Center. Clovis points are long, leaf-shaped points that are bifacial, or flaked on both sides. (credit: "Virginia Aquarium & Marine Science Center Arrowheads Clovis Point Stone Tools" by C Watts/ flickr, CC BY 2.0)

Why so much debate about the settling of the Americas? There are various reasons for the difficulties in establishing settlement dates. The Bering land bridge was periodically exposed and submerged under water during periods of glacial growth and retreat. Using core samples obtained by drilling down into the shallow sea floor, archaeologists have found evidence of large mammals and even fluted points (hunting tools) in and around the Aleutian Islands, through which the land bridge would have crossed. Establishing and cross-checking dates, though, has been difficult because most evidence is now submerged. This is a challenge also for the coastal route theory, as coastlines have receded since the end of the Pleistocene, and encampments would have likely been small, possibly temporary sites. Many sites are likely now submerged offshore (Gruhn 2020).

Among the best-known pre-Clovis sites are the following:

- *Monte Verde Site*, Chile. This is one of the most studied pre-Clovis sites. An extensive array of artifacts has been found at Monte Verde, including hearths, wooden and stone tools, animal bones, and even human footprints. The dates assigned to these artifacts, as early as 16,000 BP, put this site within the range of pre-Clovis dates seen in North America.
- *Debra L. Friedkin Site*, Texas. This pre-Clovis site has a dating sequence of 13,500 to 15,500 BP. A wide range of pre-Clovis tools have been found here, including partially flaked tools, blades, and scrapers.
- *Cactus Hill Site*, Virginia. A well-document Clovis site has been identified at Cactus Hill, but below this level of artifacts, there is evidence of pre-Clovis projectile points. Although controversial, these points have possible dating sequences of 18,000–22,000 BP.

Figure 31.4 A pre-Clovis archaeological site in Sussex County, Virginia, in the United States (credit: "Nottoway Archaeological Site Entrance" by Nyttend/Wikimedia Commons, Public Domain)

Based on this new evidence, scientists now agree that the Americas were first settled by a pre-Clovis population. How they arrived, when they arrived, what movements they made, and in what order they made them are major archaeological questions today. What we can conclude is that human populations continued to migrate after peopling the Americas.

Temperature and habitat

Temperature affects the physiology of organisms as well as the density and state of water. Temperature exerts an important influence on living things because few living things can survive at temperatures below 0 °C (32 °F) due to metabolic constraints. It is also rare for living things to survive at temperatures exceeding 45 °C (113 °F); this is a reflection of evolutionary response to typical temperatures near the Earth's surface. Enzymes are most efficient within a narrow and specific range of temperatures; enzyme degradation can occur at higher temperatures. Therefore, organisms either must maintain an internal temperature or they must inhabit an environment that will keep the body within a temperature range that supports metabolism. Some animals have adapted to enable their bodies to survive significant temperature fluctuations, such as seen in hibernation or reptilian torpor. Similarly, some Archaea bacteria have evolved to tolerate extremely hot temperatures such as those found in the geysers within Yellowstone National Park. Such bacteria are examples of *extremophiles*: organisms that thrive in extreme environments.

The temperature (of both water and air) can limit the distribution of living things. Animals faced with temperature fluctuations may respond with adaptations, such as migration, in order to survive. Migration, the regular movement from one place to another, is an adaptation found in many animals, including many that inhabit seasonally cold climates. Migration solves problems related to temperature, locating food, and finding a mate. For example, the Arctic Tern (*Sterna paradisaea*) makes a 40,000 km (24,000 mi) round-trip flight each year between its feeding grounds in the southern hemisphere and its breeding grounds in the Arctic Ocean. Monarch butterflies (*Danaus plexippus*) live in the eastern and western United States in the warmer months, where they build up enormous populations, and migrate to areas around Michoacan, Mexico as well as areas along the Pacific Coast, and the southern United States in the wintertime. Some species of mammals also make migratory forays. Reindeer (*Rangifer tarandus*) travel about 5,000 km (3,100 mi) each year to find food. Amphibians and reptiles are more limited in their distribution because they generally lack migratory ability. Not all animals that could migrate do so: migration carries risk and comes at a high-energy cost.

Some animals *hibernate* or *estivate* to survive hostile temperatures. Hibernation enables animals to survive cold conditions, and estivation allows animals to survive the hostile conditions of a hot, dry climate. Animals that hibernate or estivate enter a state known as *torpor*: a condition in which their metabolic rate is significantly lowered. This enables the animal to wait until its environment better supports its survival. Some amphibians, such as the wood frog (*Rana sylvatica*), have an antifreeze-like chemical in their cells, which retains the cells' integrity and prevents them from freezing and bursting.

Reading Question #2

Is the following statement true or false?

Q: Some species have narrow distribution because they are able to easily migrate.

Climate change and effects on migration behaviors

Climate change, and specifically the *anthropogenic* (meaning, caused by humans) warming trend presentlyescalating, is recognized as a major extinction threat, particularly when combined with other threats such as habitat loss and the expansion of disease organisms. Scientists disagree about the likely magnitude of the effects, with extinction rate estimates ranging from 15 percent to 40 percent of species destined for extinction by 2050. Scientists do agree, however, that climate change will alter regional climates, including rainfall and snowfall patterns, making habitats less hospitable to the species living in them, in particular, the endemic species. The warming trendwill shift colder climates toward the north and south poles, forcing species to move with their adapted climate norms while facing habitat gaps along the way. The shifting ranges will impose new competitive regimes on species as they find themselves in contact with other species not present in their historic range. One such unexpected species contact is between polar bears and grizzly bears. Previously, these two distinct species had separate ranges. Now, their ranges are overlapping and there are documented cases of these two species mating and producing viable offspring, which may or may not be viable crossing back to either parental species. Changing climates also throw off species' delicate timed adaptations to seasonal food resources and breeding times. Many contemporary mismatches to shifts in resource availability and timing have already been documented.

*Figure 31.3 Since 2008, grizzly bears (*Ursus arctos horribilis*) have been spotted farther north than their historic range, a possible consequence of climate change. As a result, grizzly bear habitat now overlaps polar bear (*Ursus marit imus*) habitat. The two species of bears, which are capable of mating and producing viable offspring, are considered separate "ecological" species because historically they lived in different habitats and never met. However, in 2006 a hunter shot a wild grizzly-polar bear hybrid known as a grolar bear, the first wild*

hybrid ever found.

Range shifts are already being observed: for example, some European bird species ranges have moved 91 km northward. The same study suggested that the optimal shift based on warming trends was double that distance, suggesting that the populations are *not* moving quickly enough. Range shifts have also been observed in plants, butterflies, other insects, freshwater fishes, reptiles, and mammals.

Climate gradients will also move up mountains, eventually crowding species higher in altitude and eliminating the habitat for those species adapted to the highest elevations. Some climates will completely disappear. The accelerating rate of warming in the arctic significantly reduces snowfall and the formation of sea ice. Without the ice, species like polar bears cannot successfully hunt seals, which are their only reliable source of food. Sea ice coverage has been decreasing since observations began in the mid-twentieth century, and the rate of decline observed in recent years is far greater than previously predicted.

Reading Question #3

Grolar bears are a novel observation and are hybrids of polar and grizzly bears. To what can this observation be attributed?

A. They have become less aggressive towards each other and less competitive.

B. The habitats of these two species have started to overlap more.

C. They have become more aggressive towards each other and more competitive.

D. The habitats of these two species have started to become more separate.

Species adapting to climate change

The same way the musicians of an orchestra rely on a conductor to remain synchronised, migratory species rely on environmental cues, such as day length and temperature, to decide when they need to start moving from one area to the next. But because different species rely on different environmental cues to time their life cycles (e.g. breeding), not all species will adjust to climate change at the same rate. There is consequently a high likelihood that climate change will disrupt these synchronous movements that the animal kingdom has developed over thousands of years (Renner and Zohner, 2018). This disruption of timed aspects of a species' life cycle, such as migration and breeding, is called **phenological mismatch** or trophic asynchrony. Researchers have already seen signs of phenological mismatch: some migratory birds that overwinter in the tropics have started to migrate to their European breeding grounds at earlier dates than before (Both et al., 2006; Vickery et al., 2014). If these trends hold, they may soon start breeding before peak food availability, which could lead to lower fitness of offspring.

We can already see evidence of how climate change is disrupting migrations and mutualistic relationships that were developed over thousands of years.

Resident species are also vulnerable to phenological mismatch. While these species might not be known for large-scale movements around the globe, they may still have to adjust their ranges to keep track of their climatic niches. Considering the improbability of different species will adapt at the same pace, there is thus a danger that important mutualistic relationships might be pulled apart these during range adaptations. This is of concern for species with specialized feeding niches, as seen in some pollinators. For example, studies from South Africa have shown how necessary range adjustments under climate change threaten both sunbirds—which show low adaptability (Simmons et al., 2004)—and their host plants, if specialized pollinator niches are left vacant (Huntley and Barnard, 2012). Extinctions arising from this decoupling of mutualistic relationships are referred to as coextinction (Koh et al., 2004), while a series of linked coextinctions is called an extinction cascade.

Reading Question #4 and 5

Researchers have observed that bear and fish interactions have drastically been reduced in British Columbia, Canada. What is the most likely reason for this?

A. Loss-of-function mutations resulting in the reduced hunting ability of bears

B. Gain-of-function mutations resulting in the increased evasion ability of fish

C. Phenomenological mismatch resulting in the less disparate habitats of bears and fish

D. Phenomenological mismatch resulting in the more disparate habitats of bears and fish

What is phenological mismatch or trophic asynchrony?

A) The synchronous movement of migratory species

B) The disruption of timed aspects of a species' life cycle due to climate change

C) The reliance of different species on different environmental cues

D) The timing of breeding and migration in migratory birds

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33. Chapter 33 Adaptation and Extinction

TAHMED

Learning Objectives

- Identify the early and predicted effects of climate change on biodiversity.
- Impact of Global Climate Change on Biodiversity
- The Role of Plants in Carbon Storage and Greenhouse Gas Emissions
- Adaptations to Climate Change in C3, C4, and CAM Plants

Effects of climate change on biodiversity

Global climate change is a consequence of human population needs for energy and the use of fossil fuels to meet those needs (Figure 47.10). Environmental issues, such as toxic pollution, have specific targeted effects on species, but they are not generally seen as threats at the magnitude of the others.

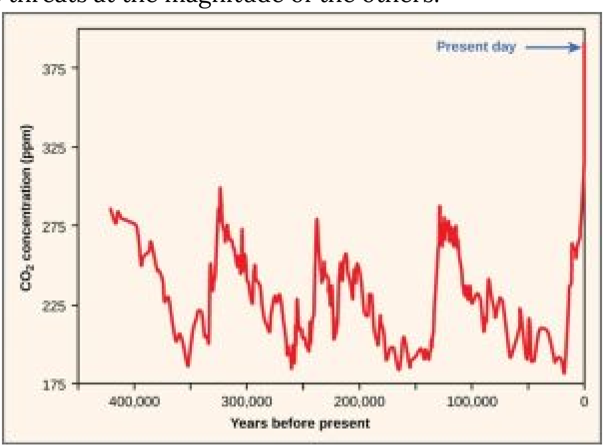

Figure 47.10 Atmospheric carbon dioxide levels fluctuate in a

cyclical manner. However, the burning of fossil fuels in recent history has caused a dramatic increase in the levels of carbon dioxide in the Earth's atmosphere, which have now reached levels never before seen in human history. Scientists predict that the addition of this "greenhouse gas" to the atmosphere is resulting in climate change that will significantly impact biodiversity in the coming century.

Climate Change

Climate change, and specifically the *anthropogenic* (meaning, caused by humans) warming trend presently escalating, is recognized as a major extinction threat, particularly when combined with other threats such as habitat loss and the expansion of disease organisms. Scientists disagree about the likely magnitude of the effects, with extinction rate estimates ranging from 15 percent to 40 percent of species destined for extinction by 2050. Scientists do agree, however, that climate change will alter regional climates, including rainfall and snowfall patterns, making habitats less hospitable to the species living in them, in particular, the endemic species. The warming trend will shift colder climates toward the north and south poles, forcing species to move with their adapted climate norms while facing habitat gaps along the way. The shifting ranges will impose new competitive regimes on species as they find themselves in contact with other species not present in their historic range. One such unexpected species contact is between polar bears and grizzly bears. Previously, these two distinct species had separate ranges. Now, their ranges are overlapping and there are documented cases of these two species mating and producing viable offspring, which may or may not be viable crossing back to either parental species. Changing climates also throw off species' delicate timed adaptations to seasonal food resources and breeding times. Many contemporary mismatches to shifts in resource availability and timing have already been documented.

Range shifts are already being observed: for example, some European bird species ranges have moved 91 km northward. The same study suggested that the optimal shift based on warming trends was double that distance, suggesting that the populations are *not* moving quickly enough. Range shifts have also been observed in plants, butterflies, other insects, freshwater fishes, reptiles, and mammals.

Climate gradients will also move up mountains, eventually crowding species higher in altitude and eliminating the habitat for those species adapted to the highest elevations. Some climates will completely disappear. The accelerating rate of warming in the arctic significantly reduces snowfall and the formation of sea ice. Without the ice, species like polar bears cannot successfully hunt seals, which are their only reliable source of food. Sea ice coverage has been decreasing since observations began in the mid-twentieth century, and the rate of decline observed in recent years is far greater than previously predicted.

Finally, global warming will raise ocean levels due to meltwater from glaciers and the greater volume of warmer water. Shorelines will be inundated, reducing island size, which will have an effect on some species, and a number of islands will disappear entirely. Additionally, the gradual melting and subsequent refreezing of the poles, glaciers, and higher elevation mountains—a cycle that has provided freshwater to environments for centuries—will also be jeopardized. This could result in an overabundance of salt water and a shortage of fresh water.

Global climate change is resulting in increases in daily, seasonal, and annual mean temperatures, and increases in the intensity, frequency, and duration of abnormally low and high temperatures. Temperature and other environmental variations have a direct impact on plant growth and are major determining factors in plant distribution. Since humans rely on plants—directly and indirectly—a crucial food source, knowing how well they're able to withstand and/or acclimate to the new environmental order is crucial.

What effect will climate change have on the ranges of animal species?

1. a) Species will not be affected

2. b) Species will move with their adapted climate norms
3. c) Species will not move with their adapted climate norms
4. d) None of the above

Impact of Global Climate Change on Biodiversity

Current Rates and Causes of Extinction

In the fossil record, an individual vertebrate (amphibian, bird, fish, mammal, or reptile) species lasts on average at least one million years before it becomes extinct. Thus, in an average year, no more than one out of one million species should go extinct. The current observed extinction rate since 1,600, for vertebrates, is 2.6 per 10,000 species per year. That is at least 260 times the background rate of extinction. At this rate, it would take less than 15,000 years to equal the extinction event that killed the dinosaurs over several million years. Further, because we know that the primary cause of modern extinctions is the loss, degradation, and fragmentation of habitat, and because we know the response to habitat loss is not linear, we expect that background rate to continue to increase and probably become an order of magnitude greater than it is currently.

The reason for this increased and increasing rate of extinction is not difficult to fathom. Humans have been strongly implicated in global extinctions for tens of thousands of years, but the current mass extinction is due to the fact that in the last 50 years we have used more of Earth's resources than we have for the entire history of humanity before that point. We are losing topsoil at least ten times faster than it can be replaced, about 10 % of the Earth's agricultural land has become unfit for agriculture in the past 40 years while the population continues to expand, 80 % of the world's fish stocks for which assessment information is available are reported as fully exploited or overexploited, we are using more than 20 % of the world's renewable fresh water just for irrigation, and about 40 % of the world's rainforests have been lost in the past 50 years. The human population has increased from 3.0 to 6.9 billion during those same 50 years and we are expecting another two billion over the next 40 years.

However, the current rate of extinction might pale compared to what anthropogenic climate change threatens. If we do not do something about climate change then all the money and the effort that has gone into saving species from extinction will likely be lost. This is particularly true because the current threat from habitat destruction and fragmentation interacts with climate change in a nonlinear way so that the negative impacts are greater than expected by looking at the threats independently.

Current and Future Rates of Global Climate Change

Over the past century the Earth has warmed approximately 0.74 oC, averaged over all land and ocean surfaces (IPCC 2007a). This warming of the Earth has clear effects on the species that live there. By the 1990s data started being published showing that 1,700 species had shifted their ranges an average of 6.1 km per decade toward the poles and that the timing of spring activities (e.g., breeding, migration, egg laying, flowering of plants) were occurring several days earlier each decade over the past 50 years. There is now a vast amount of data showing changes in the biology of plants and animals which are in accordance with expectations under a warming climate. Predictions for the next century are for increases in average global temperature of anywhere from 1.1 oC to 6.4 oC due mostly to unprecedented increases in the atmospheric concentrations of the three most important greenhouse gases, carbon dioxide, methane, and nitrous oxide. However, growth in emissions continues to far exceed expectations and it is possible that predicted increases in temperature are conservative. Further, temperatures are expected to increase for at least several centuries beyond this one, because of the half-life of CO_2 in the atmosphere, loss of polar ice which reflects rather than absorbs the sun's energy (Albedo effect), release of energy from the ocean into the atmosphere, and interactions between atmospheric warming and release of CO_2 from sources such as melting permafrost.

Another major impact of climate change includes effects on rainfall patterns and water storage. Rainfall is expected to become more variable with longer droughts and more flooding. Drought areas have more than doubled over the past 40 years . In many parts of the world more precipitation will fall as rain instead of snow, snows at higher elevations will melt earlier, and this will cause deleterious changes in river flow. These changes are already causing a looming water crisis in the western USA. Similarly, the Tibetan plateau and the Himalayas are sources for the five major rivers of Asia, all of which are vitally important to already threatened biodiversity and to 1.4 billion people. Changes in temperature and precipitation are expected to drastically alter snow melt patterns over the next 40 years, so that the Indus, Brahmaputra, and Mekong basins are likely to experience severe negative effects owing to the dependence on irrigated agricul- ture and meltwater in these areas.

In terms of temperature, sea levels, and other climatic factors, we are headed towards conditions that have not existed for millions or probably tens of millions of years. Even the most rapid changes in the Earth's climate that led to those conditions in the past took at least 100,000 years to occur, not a couple of centuries or less.

Climate Change and Biodiversity

There are three possible fates for populations and species making up the current biodiversity of Earth, in a rapidly changing environment: (1) Plants and animals can migrate in order to leave unfavorable environmental conditions in one area and take up residence in an area with environmental conditions that are more conducive to survival and reproduction. The evidence that plants and animals have migrated long distances during past warming and cooling periods over the past 250,000 years is irrefutable. We already see such movement in extant species and can expect to see much more in the future. (2) Adapt to changing conditions through selection on genetic diversity present or arising in the population during the period of climatic change. (3) Go extinct when some combination of the first two are not sufficient to keep the population or species extant. Over hundreds of millions of years, the Earth has experienced innumerable cooling and heating periods of different magnitudes and rates. Periods of rapid change are usually accompanied by increases in extinction rates.

Projections of species extinction rates during the current period of global climate change are controversial because of uncertainty concerning how much the climate will change and how fast, because of methodological challenges especially concerning species ability to migrate through a human-dominated habitat matrix, and because of imperfect data from past extinctions. However, much is known and reasonable estimates can be made by looking at past extinctions under global climate change. An analysis of the fossil record over the past 520 million years provides a consistent relationship between global temperatures and biodiversity levels. During warm phases, extinction rates have been relatively high in both terrestrial and marine environments. Extinction rates may increase approximately 10 % for every 1 oC increase in temperature. The end-Permian event that caused the extinction of approximately 95 % of all species on Earth was accompanied by a 6 oC increase in global temperatures over a few million years. An increase in temperature of approximately 5 oC over several million years caused a great loss of plant biodiversity in Greenland.

The biodiversity currently extant on Earth faces a much more difficult situation than does biodiversity during past periods of rapid climate change. There are two major reasons for this: (1) Species habitats are smaller than in the past. Smaller habitats support smaller populations which harbor less genetic diversity and have less evolutionary potential. This evolutionary potential is critical for species' ability to adapt to the changing environmental conditions. (2) Species habitats are more fragmented than in the past. The fragmentation prevents individ- uals from being able to shift their distribution in response to climate-related impacts as easily as in the past. Recall, these are the two fates available to species other than going extinct: adapt to climate change or migrate in response to climate change in order to track environmental conditions favorable to survival. The current rate of climate change is probably unprecedented and would present extreme challenges to the biota of the planet under normal circumstances. How- ever, the combination of the magnitude of change, the extreme fragmentation of habitats, and the fact that there are 6.9 billion people using a very large proportion of the Earth's resources means that neither evolution nor migration will be sufficient to allow many species to cope with current rates of global climate change. They will go extinct and their value to humans and their beauty lost.

Many of the extinction may not be due directly to global climate change alone. The interactions between climate change and other factors will likely be extremely important. Habitat destruction and conversion continues in Southeast Asia and the Amazon, both places where I have done research and both areas rich in biodiversity. The continued fragmentation and loss of these forested areas alone is cause for grave concern. However, when you factor in that destruction of forests in these areas further limits movement of species trying to track a changing environment and that this continues to fuel further climate change by dumping more CO2 into the atmosphere, it starts to appear catastrophic. Warmer temperatures will cause novel diseases to spread into naïve populations and will act as a general stress causing species to be susceptible to diseases their immune systems once were able to fight. The interaction between global climate change and diseases is already manifest in the widespread extinction of amphibians. Increases in the frequency of drought and the introduction of novel diseases form an almost perfect combina- tion for driving populations extinct, as these are the two biggest causes for population collapse among vertebrates. Temperature stress, and other forms of environmental stress incurred through climate change, will interact with declining population size and loss of genetic diversity in a way that makes populations more vulnerable than either factor independently.

Table 2 Several million species of plant and animals face extinction due to global climate change, perhaps as early as 2050. Species most affected would be poor dispersers or those for which anthropogenic habitat fragmentation prevents dispersal and those with very narrow thermal toler- ances and/or low genetic variation that prevent(s) evolution of new tolerances. The table below is based on the results of Thomas et al. (2007), who predicted extinction under different warming and movement scenarios. Migration rates are certainly somewhere between the extreme of no move- ment and the ability to track moving habitats perfectly, and current data suggests that warming trends will be close to the warmest predictions of Thomas et al. (2007). Consequently, ::'33 % of known species may be doomed to extinction by 2050

Warming level	No movement (%)	Perfect movement (%)
Low	34 extinction	11 extinction
Medium	45 extinction	19 extinction
High	58 extinction	33 extinction

Exactly how bad will it get? The prediction from a team of experts is that if temperatures increase by >3.5 oC, 40–70 % of plant and animal species will face extinction (Rosenzweig et al. 2008). One prominent study suggests that about 25 % of known plant and animal species will be committed to extinction by 2050 under current warming predictions (Table 2) (Thomas et al. 2004). A recent study suggests that 20 % of lizards may be extinct by 2080 as a direct result of increasing global temperatures (Sinervo et al. 2010). Exact predictions are of course impossible, but the combination of extremely rapid climate change, reduced population sizes, and fragmented habitats suggest that a very large proportion of Earth's biodiversity (>50 % of plants and animals) suffers a very high risk of extinction, particularly if definitive measures are not taken rapidly to ameliorate climate change. This level of species extinctions will be associated with an even larger percentage loss of populations and genetic diversity. This represents a very large proportion of the biodiversity and biological resources that humans need now more than ever.

Future Direction

In order to stave off huge losses in biodiversity and to save vast amounts of human suff
a high quality of life in a way that does not endanger the planet. The following are some u
climate change:

- Limit land-use change and make intelligent choices in land-use changes that balan
but also in boreal and temperate forests. Zero-loss of old-growth forests must be the imm
enforce laws that protect forests from illegal logging and pillaging from corporations at th

- Aggressive climate change mitigation, including immediate implementation of existin immediate legislation to increase fuel efficiency for motor vehicles.
- Place a global cap on greenhouse gas emissions and sell permits up to that cap in a

global auction. Use the profits to finance the other mitigation measures discussed. Includ
associated with production of goods, governments must regulate rather than subsidize co
for lack of enforcement or collusion with corporations.

- Stabilize and eventually reduce human population size through intense family plannin
- Make human-dominated landscapes more hospitable to biodiversity. Reclamation of
- Education of people, especially in the rural tropics, concerning biodiversity and the v short-term profiteering and financial markets toward science, engineering, innovatio
- Create space and opportunities for ecosystems to self-adapt and reorganize because

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The Role of Plants in Carbon Storage and Greenhouse Gas Emissions

When it comes to the global carbon cycle, plants are the ultimate carbon-capturing champions. While artificial carbon capture technologies are being developed to address climate change, photosynthesis can be thought of as a “technology” that has been perfected and deployed for over 2 billion years. The rate of atmospheric carbon uptake by plants via photosynthesis dwarfs all other forms of carbon capture. Land plants pull an estimated 120 petagrams of carbon from the atmosphere each year-over 15% of the total atmospheric carbon pool.

Plants, in addition to being the primary conduits for CO_2 removal from the atmosphere, can sequester carbon. As mentioned above, the global terrestrial plant carbon pool stores approximately 560 petagrams of carbon. It is easier to estimate aboveground plant carbon pools than it is to estimate carbon in soils. Plants, and more specifically the reflectance of the chlorophyll in leaves, can be measured from satellites in space. This technique is called remote sensing and is a powerful tool for assessing the amount of plant biomass on the land surface. Changes in reflectance over time are correlated with changes in leaf area, which in turn is directly related to rates of plant growth. Thus, satellite imagery repeated over time can be used to estimate how much plant growth is occurring on land. Below ground plant parts, namely roots, are much harder to estimate than above ground plant parts, as roots are hidden from view. Roots can extend deep into soils. Roots can be large, like the structural roots of trees, or small and ephemeral, like the main absorptive roots of grasses and herbs. Although measuring root biomass is difficult, it is important for understanding the carbon cycle. In some ecosystems there is as much root carbon below ground as is stored in plant biomass above ground. Roots are also important because they are the main conduits for soil organic matter formation.

Roots are generally assumed to be a greater contributor to soil carbon stocks than aboveground plant tissues because roots are already buried below ground and can be more easily captured and sequestered in the soil than aboveground tissues. Thus, roots play a key role as transmitters of carbon into soils.

What is the main point of the text?

1. a) Plants are the ultimate carbon-capturing champions
2. b) Artificial carbon capture technologies are more efficient

than photosynthesis
3. c) The rate of atmospheric carbon uptake by plants is decreasing
4. d) None of the above

What percentage of the total atmospheric carbon pool is pulled by land plants each year?

1. a) 5%
2. b) 10%
3. c) 15%
4. d) 20%

Forests as carbon sinks and sources

Overall, trees store more carbon than any other plant type. Forests cover about 30% of the total land area on Earth and account for approximately 80% of the terrestrial plant biomass. This means that forests store an estimated 350 petagrams of carbon in their tissues, most of which is in wood. Forests are vulnerable to natural and human-caused disturbance events such as fire, logging, pests, and weather-related disturbances. Some estimates suggest that 60% of the world's forests are in some stage of recovery from the last disturbance event. Forest disturbance often leads to the emissions of greenhouse gases. Deforestation is a big contributor to global greenhouse gas emissions, especially in the tropics. At a global scale, tropical deforestation accounts for about 10% of all greenhouse gas emissions annually. Some of the greenhouse gas emissions from deforestation result from disturbance to soils. Tree cutting and removal can break up soil aggregates, exposing previously trapped carbon to microbial decomposition and providing fuel to microbes that produce CO2, methane, and nitrous oxide. Greenhouse gases are also released during the decomposition of the plant litter produced from deforestation.

Forest fire and biomass burning is another large source of green house gas emissions. Fires consume biomass and produce CO2, meth ane, and nitrous oxide, among other gases. Globally, 2 to 3 petagrams of carbon are emitted to the atmosphere annually from fires. Over 80% of this comes from tropical regions, with approximately 1 petagram of carbon per year coming from savannas (wooded grasslands). Climate change is increasing the frequency and severity of drought in some regions, and this can in turn increase the occurrence of fires.

Emission Reduction via Agricultural Management

Management of agricultural lands has historically been a major contributor to climate change, amounting to approximately 25% of global greenhouse gas emissions. When plants and animals are harvested from working lands, the associated carbon and nutrients are harvested as well. Fertilizer can replace some of the nutrients harvested, and plant growth can bring new carbon into ecosystems, but rarely do we replace all the carbon and nutrients that are lost. Fertilization, irrigation, and biomass burning, as well as practices that disturb soils such as plowing and tillage, can increase emissions of all three of the major greenhouse gases. Human land use over the last 12,000 years has resulted in the loss of an estimated 116 petagrams of SOC in the top 2 meters of soil, globally. Deforestation, primarily in the tropics, results in the loss of approximately 1.7 petagrams organic carbon per year from ecosystems. In order to slow climate change, and bend the curve, greenhouse gas emissions from working lands must be reduced. There are several possible approaches for reducing emissions that can yield significant greenhouse gas savings, including improved fertilizer, tillage, water, and residue management, as well as matching crops to appropriate soils and climates, and incorporating fallow periods. Improved grazing land and livestock management, together with better manure management, are additional practices that are known to reduce emissions. Taken together at a global scale, these practices have been estimated to have the potential to save over 3 petagrams in CO2 equivalents (CO2e) per year. Below, we detail two examples of approaches that can reduce emissions and offer valuable co-benefits.

Nitrogen fertilizer

Nitrogen fertilizer comes in organic and inorganic forms and is widely used in agriculture to enhance plant growth. Inorganic nitrogen fertilizer can be a large source of greenhouse gas emissions, from production to field application. The manufacturing of inorganic nitrogen fertilizer is a carbon-intensive activity. A lot of energy is required to convert dinitrogen gas to ammonia during fertilizer production. In 2004, the fertilizer industry used approximately 1% of the world's energy, with 90% of that used to produce ammonia. Producing the 119 million metric tons (MMT) of nitrogen fertilizer applied to soils globally in 2018 resulted in at least 492 MMT of CO2 emissions (values calculated using Statista 2014). This is assuming that natural gas was used in the manufacturing process; if coal was used, the energy cost was higher. To compound the problem, nitrogen is often applied to fields in excess of plant requirements. This extra nitrogen fertilizer stimulates microorganisms in the soils that make nitrous oxide gas, and nitrous oxide emissions increase exponentially with the amount of nitrogen fertilizer added.

At the field scale, there are several approaches that can lower green house gas emissions from fertilizer use. Careful monitoring of plant re quirements could significantly lower the amount of nitrogen fertilizer needed for agriculture. There are important co-benefits from this rela tively simple action. Less fertilizer applied means that less fertilizer will need to be produced, lowering the carbon footprint of fertilizer manu facturing. Lower fertilizer application rates will also lower nitrous oxide emissions. More efficient fertilization application could save the farmer money, helping to support a more financially sustainable agricultural industry. And finally, less fertilizer use can help reduce nitrogen runoff and pollution of waterways. Some additional ways to lower greenhouse gas emissions associated with fertilizer use include the following:

► Use low-carbon or no-carbon fuels in fertilizer manufacturing.

► Capture biosolids and wastewaters and convert them to nitrogen amendments: this also helps remove nitrogen pollution from waterways.

► Use organic nitrogen and slow-release fertilizer. If the fertilizer is released slowly, it can result in lower emissions and have a lower overall carbon footprint.

► Use buried or drip irrigation. Supplying only the amount of water the plant needs can minimize overwatering that can stimulate nitrous oxide emissions.

► Use nitrogen-fixing cover crops. Nitrogen-fixing plants are species.

that can pull nitrogen from the atmosphere and supply it to soils. Nitrogen-fixing plants in the legume (pea) family are often used as cover crops during fallow periods (see below). Nitrogen-fixing cover crops can also stimulate nitrous oxide emissions but do not result in the energy costs associated with inorganic nitrogen fertil izer production.

The total greenhouse gas savings from these improved practices have not yet been estimated at a global scale, but models suggest the results will be very promising.

Environmental Impact on Photosynthesis

All plants ingest atmospheric carbon dioxide and convert it into sugars and starches through the process of photosynthesis but they do it in different ways. The specific photosynthesis method (or pathway) used by each plant class is a variation of a set of chemical reactions called the Calvin Cycle. These reactions impact the number and type of carbon molecules a plant creates, the places where those molecules are stored, and, most importantly for the study of climate change, a plant's ability to withstand low carbon atmospheres, higher temperatures, and reduced water and nitrogen.

These processes of photosynthesis—designated by botanists as C3, C4, and CAM,—are directly relevant to global climate change studies because C3 and C4 plants respond differently to changes in atmospheric carbon dioxide concentration and changes in temperature and water availability.

Humans are currently dependent on plant species that do not thrive in hotter, dryer, and more erratic conditions. As the planet continues to warm up, researchers have begun exploring ways in which plants can be adapted to the changing environment. Modifying the photosynthesis processes may be one way to do that.

C3 Plants

The vast majority of land plants we rely on for human food and energy use the C3 pathway, which is the oldest of the pathways for carbon fixation, and it is found in plants of all taxonomies. Almost all extant nonhuman primates across all body sizes, including prosimians, new and old world monkeys, and all the apes—even those who live in regions with C4 and CAM plants—depend on C3 plants for sustenance.

- **Species**: Grain cereals such as rice, wheat, soybeans, rye, and barley; vegetables such as cassava, potatoes, spinach, tomatoes, and yams; trees such as apple, peach, and eucalyptus
- **Enzyme**: Ribulose bisphosphate (RuBP or Rubisco) carboxylase oxygenase (Rubisco)
- **Process**: Convert CO_2 into a 3-carbon compound 3-phosphoglyceric acid (or PGA)
- **Where Carbon Is Fixed**: All leaf mesophyll cells
- **Biomass Rates**: -22% to -35%, with a mean of -26.5%

While the C3 pathway is the most common, it is also inefficient. Rubisco reacts not only with CO_2 but also O_2, leading to photorespiration, a process that wastes assimilated carbon. Under current atmospheric conditions, potential photosynthesis in C3 plants is suppressed by oxygen as much as 40%. The extent of that suppression increases under stress conditions such as drought, high light, and high temperatures. As global temperatures rise, C3 plants will struggle to survive—and since we're reliant on them, so will we.

C4 Plants

Only about 3% of all land plant species use the C4 pathway, but they dominate nearly all grasslands in the tropics, subtropics, and warm temperate zones. C4 plants also include highly productive crops such as maize, sorghum, and sugar cane. While these crops lead the field for bioenergy, they aren't entirely suitable for human consumption. Maize is the exception, however, it's not truly digestible unless ground into a powder. Maize and other crop plants are also used as animal feed, converting the energy to meat—another inefficient use of plants.

- **Species:** Common in forage grasses of lower latitudes, maize, sorghum, sugarcane, fonio, tef, and papyrus
- **Enzyme:** Phosphoenolpyruvate (PEP) carboxylase
- **Process:** Convert CO2 into 4-carbon intermediate
- **Where Carbon Is Fixed:** The mesophyll cells (MC) and the bundle sheath cells (BSC). C4s have a ring of BSCs surrounding each vein and an outer ring of MCs surrounding the bundle sheath, known as the Kranz anatomy.
- **Biomass Rates:** -9 to -16%, with a mean of -12.5%.

C4 photosynthesis is a biochemical modification of the C3 photosynthesis process in which the C3 style cycle only occurs in the interior cells within the leaf. Surrounding the leaves are mesophyll cells that contain a much more active enzyme called phosphoenolpyruvate (PEP) carboxylase. As a result, C4 plants thrive on long growing seasons with lots of access to sunlight. Some are even saline-tolerant, allowing researchers to consider whether areas that have experienced salinization resulting from past irrigation efforts can be restored by planting salt-tolerant C4 species.

CAM Plants

CAM photosynthesis was named in honor of the plant family in which *Crassulacean*, the stonecrop family or the orpine family, was first documented. This type of photosynthesis is an adaptation to low water availability and occurs in orchids and succulent plant species from arid regions.

In plants employing full CAM photosynthesis, the stomata in the leaves are closed during daylight hours to lessen evapotranspiration and open at night in order to take in carbon dioxide. Some C4 plants also function at least partially in C3 or C4 mode. In fact, there's even a plant called *Agave Angustifolia* that switches back and forth between modes as the local system dictates.

- **Species:** Cactuses and other succulents, Clusia, tequila agave, pineapple.
- **Enzyme:** Phosphoenolpyruvate (PEP) carboxylase
- **Process:** Four phases that are tied to available sunlight, CAM plants collect CO2 during the day and then fix CO2 at night as a 4 carbon intermediate.
- **Where Carbon Is Fixed:** Vacuoles
- **Biomass Rates:** Rates can fall into either C3 or C4 ranges.

CAM plants exhibit the highest water-use efficiencies in plants which enable them to do well in water-limited environments, such as semi-arid deserts. With the exceptions of pineapple and a few agave species, such as the tequila agave, CAM plants are relatively unexploited in terms of human use for food and energy resources.

Evolution and Possible Engineering

Global food insecurity is already an extremely acute problem, rendering the continued reliance on inefficient food and energy sources a dangerous course, especially when we don't know how plant cycles will be affected as our atmosphere becomes more carbon-rich. The reduction in atmospheric CO2 and the drying of the Earth's climate are thought to have promoted C4 and CAM evolution, which raises the alarming possibility that elevated CO2 may reverse the conditions that favored these alternatives to C3 photosynthesis.

Evidence from our ancestors shows that hominids can adapt their diet to climate change. *Ardipithecus ramidus* and *Ar anamensis* were both reliant on C3 plants but when a climate change altered eastern Africa from wooded regions to savannah about four million years ago, the species that survived—*Australopithecus afarensis* and *Kenyanthropus platyops*—were mixed C3/C4 consumers. By 2.5 million years ago, two new species had evolved: *Paranthropus*, whose focus shifted to C4/CAM food sources, and early *Homo sapiens* that consumed both C3 and C4 plant varieties.

C3 to C4 Adaptation

The evolutionary process that changed C3 plants into C4 species has occurred not once but at least 66 times in the past 35 million years. This evolutionary step led to enhanced photosynthetic performance and increased water- and nitrogen-use efficiency.

As a result, C4 plants have twice as the photosynthetic capacity as C3 plants and can cope with higher temperatures, less water, and available nitrogen. It's for these reasons, biochemists are currently trying to find ways to move C4 and CAM traits (process efficiency, tolerance of high temperatures, higher yields, and resistance to drought and salinity) into C3 plants as a way to offset environmental changes faced by global warming.

At least some C3 modifications are believed possible because comparative studies have shown these plants already possess some rudimentary genes similar in function to those of C4 plants. While hybrids of C3 and C4 have been pursued more than five decades, due to chromosome mismatching and hybrid sterility success has remained out of reach.

What is the benefit of C4 plants compared to C3 plants?

a) C4 plants are more resistant to cold temperatures

b) C4 plants require less water and nitrogen than C3 plants

c) C4 plants have less photosynthetic capacity than C3 plants

d) C4 plants are more susceptible to diseases than C3 plants

The Future of Photosynthesis

The potential to enhance food and energy security has led to marked increases in research on photosynthesis. Photosynthesis provides our food and fiber supply, as well as most of our sources of energy. Even the bank of hydrocarbons that reside in the Earth's crust was originally created by photosynthesis.

As fossil fuels are depleted—or should humans limit the use of fossil fuel to forestall global warming—the world will face the challenge of replacing that energy supply with renewable resources. Expecting the evolution of humans to keep up with the rate of climate change over the next 50 years is not practical. Scientists are hoping that with the use of enhanced genomics, plants will be another story.

What is the potential benefit of enhancing photosynthesis?

1. a) Enhancing photosynthesis can help in reducing the atmospheric CO2 levels.
2. b) Enhancing photosynthesis can provide more water to plants.
3. c) Enhancing photosynthesis can enhance food and energy security.
4. d) Enhancing photosynthesis can increase the pollution levels.

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34. Chapter 34: Feedback loops

ANASTASIA CHOUVALOVA

Human activity releases carbon dioxide and methane, two of the most important greenhouse gases, into the atmosphere in several ways. The primary mechanism that releases carbon dioxide is the burning of fossil fuels, such as gasoline, coal, and natural gas. Deforestation, cement manufacture, animal agriculture, the clearing of land, and the burning of forests are other human activities that release carbon dioxide. Methane (CH4) is produced when bacteria break down organic matter under anaerobic conditions. Anaerobic conditions can happen when organic matter is trapped underwater (such as in rice paddies) or in the intestines of herbivores. Methane can also be released from natural gas fields and the decomposition of animal and plant material that occurs in landfills. Another source of methane is the melting of clathrates. Clathrates are frozen chunks of ice and methane found at the bottom of the ocean. When water warms, these chunks of ice melt and methane is released. As the ocean's water temperature increases, the rate at which clathrates melt is increasing, releasing even more methane. This leads to increased levels of methane in the atmosphere, which further accelerates the rate of global warming. This is an example of the *positive feedback loop* that is leading to the rapid rate of increase of global temperatures.

Reading Question #1

What is a positive feedback loop?

A. An event in which the product of a reaction slows down that reaction, leading to greater proximity to a balance or set point.

B. An event in which the product of a reaction amplifies that reaction, leading to further deviation from a balance or set point.

C. An event in which the substrate of a reaction stabilizes that reaction.

D. An event in which the product of a reaction stabilizes that reaction.

In class, we will discuss other feedback loops related to climate change with a focus on permafrost and algal blooms. Below you will find introductions to these concepts, although you have briefly read about them in previous chapters in Unit 4.

Permafrost

An important component of the **cryosphere** (i.e., an Earth system containing frozen water) is permafrost, or frozen ground. The majority of permafrost is found in the Arctic (Figure 33.1), though the small area of land in Antarctica that is not covered by ice sheets also has permafrost. Regions containing permafrost are often categorized by the quantity of total area of the region that is frozen. Continuous permafrost, as its name implies is nearly entirely frozen with 90-100% of the land area of the region containing permafrost.

Discontinuous permafrost, as the name implies, is not a single, solid sheet of frozen land (less than 90% of the total area is frozen), and can be sporadic (10-50% frozen area) or isolated (less than 10% frozen area).

Permafrost currently covers 24% of the exposed land in the high latitudes of Northern and Southern Hemispheres. Climate change scientists are carefully watching the impact of global warming on the seasonally and permanently frozen soil of the Arctic and subarctic.

Figurer 33.1 (Credit: National Snow and Ice Data Center)

As with other components of the cryosphere, permafrost is particularly sensitive to warming. One mechanism for tracking changes in permafrost extent is to measure the depth of the active layer, or the unfrozen soil that overlays permafrost. The Circumpolar Active Layer Monitoring (CALM) program tracks soil temperature and active layer depth in over 200 permafrost sites in both hemispheres.

The fate of permafrost in the future is dire. You may not think much about if you live outside the Arctic regions where permafrost is common. Scientists predict that 40 percent of the world's permafrost could thaw if temperatures rise 2^{o}C (3.6^{o}F) due to global warming. Thawing of the permfrost could allow carbon that has been stored for thousands of years to be released into the atmosphere fueling additional warming. This would increase the respiratory activity of soil organisms, further increasing the release of CO2 in Arctic ecosystems. This represents a concerning feedback loop by which warming caused by atmospheric greenhouse gases leads to thawing of permafrost, which releases more greenhouse gases into the atmosphere, exacerbating warming trends and thawing of permafrost.

In addition, thawing results in land subsidence and mass movement because of the destabilized soil profile – this will lead to sinkholes, mudslides, and collapse of infrastructure. Buildings and infrastruce-like roads, landing strips, and pipeleines, upon which residents depend have been constructed to account for the expansion and contraction that takes place in the active layer of permafrost. Rising temperature due to climate change threatens structures built under a different permafrost freeze-thaw regime.

The Arctic has experienced a signicant rise in air temperature over the last few decades and the permafrost that undelies much of the surface is undergoing substantial changes. Continuous permafrost on Alaska's North Slope has warmed 2.2^{o}-3.9^{o} C (4^{o} – 7^{o} F) over the last century making it more susceptible to erosion and mass movement. Some places in Alaska have subsided by 4.6 meters (15ft) due to thawing of the permanently frozen subsurface. Accompanied by rising sea level, Alaskan coastal communities near the Arctic Ocean and Bering Sea are being threatened.

Link to Learning

View this video to learn more about permafrost.

Reading Question #2

Which of the following are projected consequences of melting permafrost? Select all that apply.

A. Buildings built on permafrost may be compromised.

B. Reduced release of greenhouse gases into the atmosphere

C. Stabilization of carbon in the lithosphere

D. Northern communities may be more vulnerable to landslides and moving land masses.

Introduction to eutrophication

Eutrophication occurs when excess nutrients are introduced into a body of water. This process increases the rate of supply of organic matter in an ecosystem and stimulates aquatic plant growth. At normal levels, these nutrients feed the growth of organisms called cyanobacteria or algae. But with too many nutrients, cyanobacteria grow out of control. Excess algae block the sunlight needed by bottom-dwelling plants and lead to a decrease in oxygen in the water and consequently leads to negative outcomes.

Eutrophication occurs naturally but anthropogenic activities such as industrial effluent and runoff of fertilizers rich in nitrogen and phosphorus contribute heavily to eutrophication events. When supplied with an excess of nutrients, the algae can grow out of control. This event is known as an "algal bloom," and disrupts the balance of the ecosystem. As described above, the increased growth blocks the availability of sunlight to benthic organisms and other plants and organisms in the photic zone. The overgrowth of algae eventually begins to die off and is broken down by microbes that consume oxygen during the decomposition process. This creates a hypoxic environment and decreases oxygen availability in the water to other organisms.

Some of the negative effects of this excessive algae production, or algal blooms, are:

- The production of dangerous toxins that can kill animals and people
- The creation of "dead zones" (low oxygen *hypoxic zones*, or no oxygen *anoxic zones*) in the ocean
- An increase in treatment costs for cleaning water
- Harm to industries and communities that rely on the affected watershed

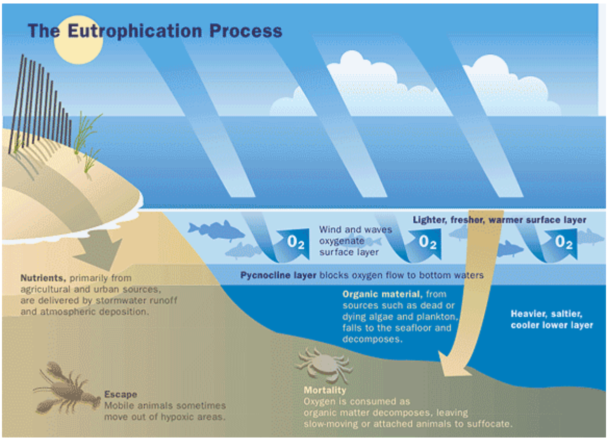


Figure 33.6 The Eutrophication Process and how it leads to hypoxia. Source: https://www.wri.org/our-work/project/eutrophication-and-hypoxia/about-eutrophication

Link to Learning

This link directs you to a video made by Khan Academy that explains the process of eutrophication and how dead zones are formed.

Reading Question #3

What is the main anthropogenic cause for eutrophication?

A. Agricultural runoff

B. Depositing too many algae organisms into water bodies

C. Humans feeding the algae organisms too much

D. Increased levels of minerals in the water

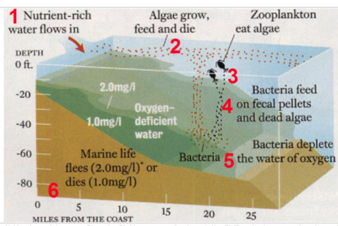
Sources of Eutrophication

Point source

A point source pollution is one that is directly identifiable and can be traced back to a singular distinguishable source. Factories and sewage treatment plants are the most common types of point sources that cause eutrophication. Some factories discharge their waste, called effluent, directly into a water body from sewage pipes. Unregulated discharge of effluent can cause severe damage to human health and the environment. The consequences of unregulated discharge include water pollution, unsafe drinking water, and restricted recreational activities. The sewage dump can deposit nutrients in streams that can be carried out to sea and cause eutrophication events. Symptoms caused by exposure to algal toxins in drinking water can include nausea, vomiting, and throat irritation. When water is consumed in sufficient quantities, the toxins can affect the liver and nervous system. This can also indirectly affect the economy because of the loss of working days due to such health problems.

Non-point source

Non-point source pollution is pollution where the origin is less specified and more diffuse. Non-point source pollution is difficult to remedy as the source cannot be pinpointed. Agricultural runoff is the largest non-point source cause of pollution leading to eutrophication in the Delta. More than 200 million pounds of pesticides are applied to California farms every year which are washed into the delta. Water runoff over landscapes with excess fertilizer can pick up nutrients and carry them out to bodies of water. Urban runoff is also considered a non-point source of pollution affecting eutrophication.



Nutrient-based Hypoxia Formation:1) Nutrient-rich water flows in, 2) Algae grow, feed, and die, 3) Zooplankton eat the algae, 4) Bacteria feed on fecal pellets and dead algae, 5) Bacteria deplete the water of oxygen, 6) Marine life flees or dies

Figure 33.7 Source: Gulf of Mexico Hypoxia https://gulfhypoxia.net/about-hypoxia/

As plant and animal biomass increase, species diversity decreases and the affected area will become overpopulated by phytoplankton feeding off the increased algae. This will also change the dominant biota in the region.

Turbidity is the clouding of water due to sediment. It can be caused by excessive phytoplankton, algae growth, urban runoff, or sediments from erosion. These suspended particles, in addition to making the water look dirty, also help promote the toxins in water as heavy metals and toxic organic compounds can attach easily to the suspended sediment. These suspended particles also absorb heat from the sun, making turbid waters warmer. This also reduces the oxygen content in the water, as more oxygen is dissolved in colder waters. The suspended particles also scatter light, decreasing the photosynthetic activity of plants and algae, which results in a positive feedback loop for decreasing oxygen even more. Some biological impacts include: fish eggs and larvae will be covered and suffocated, and gills will become clogged and damaged. Thus, turbidity is a plausible and extremely harmful effect of eutrophication.

Reading Question #4

Researchers visiting a a lake in northern Texas have noticed an algal bloom and have determined that a nearby farm had inappropriate overuse of a fertilizer. Which of the following statements is true? Select all that apply.

A. This is a non-anthropogenic cause of pollution.

B. This is an anthropogenic cause of pollution.

C. This is a point source of pollution.

D. This is a non-point source of pollution.

Hypoxia

Eutrophication can lead to hypoxia in the water column. Hypoxia event occurs when there is low oxygen level in the water. This incident is a consequence of eutrophication due to an excess of nutrient input (nitrogen and phosphorus) in the water that stimulates the growth of phytoplankton and consequently affects fishes and other organisms. Human activities have increased the rate of eutrophication through point source and non-point discharge of nutrients such as nitrogen and phosphorus.

Algal blooms

Ever been told to only eat shellfish during the months that have the letter "R", (September-April)? Well this rule is actually pretty important for keeping the health of people safe and to allow for many species of shellfish to repopulate. But why are the other months of the year not safe for people to eat shellfish? In short its because of the algae that grow during this time of year and as ocean temperatures rise. During these specific months of warmer weather, billions upon billions of these microorganisms start to take over our oceans and can have many consequences for us.

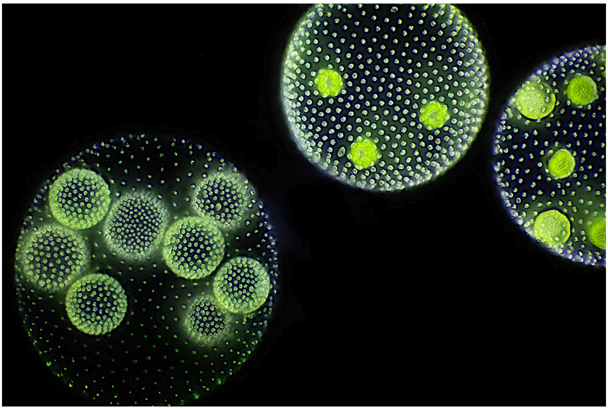


Figure 33.3 "Multicellular Green Algae" by Frank Fox [CC by 2.0]

Before going into what red tide is or how the populations of these microorganisms seem to be increasing significantly as oceans warm up, lets take a closer look at algae. Most species of algae are single-celled organisms but some species can be multi-cellular as seen in the photo above. Algae are autotrophs, meaning they use photosynthesis as their means of producing energy for themselves. Though similar to plants in the way they are both producers, algae have no stems or leaves and are more closely related to other groups of protists. Habitats for algae include any bodies of water including fresh and salt water, or have extreme external environment factors. There are few cases where they have been found on land such as rocks, trees, hot springs, etc… Species of algae have been well documented to be able to survive many harsh environments and have been on earth far longer than most living organisms to this day. They contributed to the Earth being able to house life by producing oxygen through photosynthesis. Overall Algae species are very tough and can survive in a wide range of environments, which can be seen as both a positive and negative situation.

The red tide occurs when the algae from algal blooms becomes so numerous that it discolors the water. It is also sometime referred to as a Harmful Algal Bloom or "HAB". This is where the name "red tide"comes from. Some key factors involved in red tides forming are warm ocean surface temperatures, low salinity, high nutrient content, calm seas, and rain followed by sunny days during the summer months. Some effects of the red tide are that it could deplete the oxygen in the water and/or release toxins into the water. The toxins in the water could have negative effects on the health of humans and animals exposed to them. There are three types of algae that can release these harmful toxins, they are *Alexandrium fundyense*, *Alexandrium catenella* and *Karenia brevis*.

Figure 33.4 "Red Tides in Isahaya Bay, Japan / Algal Bloom in Pelee Island, Ontario" by Marufish and Tom Archer [CC by 2.0]

What is important to recognize about "Red tides" and Algal blooms is that it isn't always obvious that algae growth is there. They are not always a red color. The photos above show two examples of Algal blooms from two very different parts of the world, yet both species are considered "Red Tide" and harmful to some shellfish and animals that eat the shellfish. Algae alone is not an issue and even during the time of the year where there seems to be an excess amount of growth, this is a natural occurrence. What becomes a problem or what classifies as a "Red Tide" are the algae that release toxins in the air and water when they grow. Very few algae species can produce this toxin but when a large enough group forms on shores it can have a negative effect on both the marine environment and humans. The toxins produced can often affect the respiratory and nervous systems of all life forms. Thus when smaller marine animals feed on the algae, the trophic level above them can become poisoned as well. Paralytic Shellfish Poisoning is typically found along the Pacific and Atlantic coasts of the United States and Canada. It can cause paralysis and in extreme cases death. Some of the toxins that cause Paralytic Shellfish Poisoning can be 1,000 times more potent than cyanide. Diarrhetic Shellfish Poisoning is another example of a harmful effect from eating contaminated shellfish. It is caused by Okadaic acid, which is produced by several species of dinoflagellates, and is usually non-deadly to humans. Small amounts of the okadaic acid usually do not have any harmful effects and only become an issue when large amounts are consumed. Amnesic Shellfish Poisoning is the third common poisoning that humans will get from eating contaminated shellfish. It can be life threatening and cause both gastrointestinal and neurological disorders. These disorders are caused by domoic acid. After an incident in Canada in 1987 where 4 people died from Amnesic Shellfish Poisoning, the levels of domoic acid in shellfish are now being monitored.

Figure 33.5 "Toxic Algae Bloom in Lake Erie" by NASA Earth Observatory Under Public Domain [CC by 2.0].

Algal Blooms can have serious effects on corals. Red algae, brown algae, and green algae are a few examples of macro-algae that can have a very negative effect on corals. They do this by outcompeting, overgrowing and eventually replacing sea-grasses and coral reef habitats. According to some research that is being done, harmful tropical algal blooms are increasing in frequency and intensity. This can have a significant impact on coral reefs.

Notable Red Tides:

1844: First recorded case off the Florida Gulf Coast.

1972: Red tides killed 3 children and hospitalized 20 adults in Papua New Guinea.

2005: The Canadian red tide was discovered to have come further south than it has in years prior by the ship (R/V) Oceanus, closing shellfish beds in Maine and Massachusetts. Authorities were also alerted as far south as Montauk to check their beds. The experts who discovered the reproductive cysts in the seabed warned of a possible spread to Long Island in the future. This halted the area's fishing and shellfish industry.

2013: In January, a red tide occurred on the West Coast Sea of Sabah in the Malaysian Borneo. There were two fatalities reported after they consumed a shellfish that had been contaminated with the red tide toxin.

2015: In September, a red tide bloom occurred in the Gulf of Mexico, affecting Padre Island National Seashore along North Padre Island and South Padre Island in Texas.

Scientists have been able to help control the spread of the effects of harmful algal blooms by developing new technology to help track them better. Tracking these harmful algal blooms could help prevent people from eating contaminated shellfish and knowing which areas will be most effected by them. Some examples of the technology that can help with monitoring them are better and more advanced satellite imagery. Also the development of an antidote to the toxins produced is another way to reduce the harmful effects. Even though they are a natural occurrence, what is alarming some scientists is that they may start to last longer and occur more often during the year as ocean temperatures and CO_2 levels rise.

Reading Question #5

What is a large concern with red tides? Select all that apply.

A. Neurological consequences.

B. Algae releasing toxins into the water.

C. Algae extinction.

D. Jeopardization of coral reef ecosystems.

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35. Chapter 35: Climate Change Adaptation

TAHMED

Learning Objectives:

Differentiate between actions to mitigate vs adapt to climate change impacts

The climate crisis is increasingly distressing. Fortunately, there are many things we can do to ensure our future is as prosperous as possible. These actions fall into one of two broad categories: climate change adaptation and climate change mitigation. These terms go hand-in-hand while navigating through the climate crisis, but they mean very different things.

Climate change mitigation

Climate change mitigation means avoiding and reducing emissions of heat-trapping greenhouse gases into the atmosphere to prevent the planet from warming to more extreme temperatures. **Climate change adaptation** means altering our behavior, systems, and—in some cases—ways of life to protect our families, our economies, and the environment in which we live from the impacts of climate change. The more we reduce emissions right now, the easier it will be to adapt to the changes we can no longer avoid.

Mitigation actions will take decades to affect rising temperatures, so we must adapt now to the change that is already upon us—and will continue to affect us in the foreseeable future.

What is the definition of climate change mitigation?

1. a) Altering our behavior to protect our families from the impacts of climate change
2. b) Reducing emissions of greenhouse gases to prevent extreme warming
3. c) Adapting to the changes that are already upon us
4. d) None of the above

The mitigation piece of the puzzle is easy to explain, but difficult to accomplish. We must transition from powering our world with fossil fuels to using clean, renewable energy. And we need to stop deforestation and restore our natural habitats until we reach net-zero carbon emissions—meaning that the release of greenhouse gases into the atmosphere is balanced with the capture and storage of those gases in places like tree roots. Much like investing in a retirement fund, the sooner we act to mitigate the impacts of climate change, the better off we'll be in the future. So far, the world has been slow to act, but momentum is shifting.

What is the goal of mitigation in the context of climate change?

1. a) To use fossil fuels more efficiently
2. b) To transition from fossil fuels to clean, renewable energy
3. c) To increase the rate of deforestation
4. d) None of the above

Why is it important to act now to mitigate the impacts of climate change?

1. a) Because it will be easier to accomplish mitigation later
2. b) Because the world has been slow to act
3. c) Because the impacts of climate change will become more severe over time
4. d) Both b and c

Climate change adaptation

If you grew up in Florida and suddenly relocated to North Dakota, you wouldn't survive for long if you didn't make a few adjustments to your lifestyle. To start, you would need warmer clothes and to learn how to drive in icy conditions. In other words, you would have to adapt to a new climate. In a warming world, however, you don't have to move somewhere far away to experience a different climate—a new climate is coming to you. Climate change affects where we can grow food, how much water we have, and where we can build our homes. And we'll face new challenges: firefighters will need to battle longer and more intense forest fire seasons; our public health officials may need to manage diseases that are not currently a problem; and city planners will need to encourage development away from areas we like to live, such as on coastlines and river fronts.

Climate change affects

a) where we can grow food,
b) how much water we have
c) where we can build our home
d) all of the above

Adaptation solutions vary from place to place, are difficult to predict, and involve many trade-offs. The first step to adapting to climate change is understanding local risks and developing plans to manage them. The next step is taking action—putting systems in place to respond to impacts we are experiencing today as we prepare for an uncertain tomorrow. These actions can include diversifying crops that can tolerate warmer and drier or wetter conditions; ensuring infrastructure can withstand more extreme weather; helping communities reduce their risk from sea level rise and increased floods; and making sure we manage our food, water, and other natural resources wisely in the context of a changing climate.

Which of the following actions can be taken to adapt to climate change?

1. a) Cutting down more trees to make space for new crops
2. b) Ensuring infrastructure cannot withstand extreme weather
3. c) Diversifying crops to tolerate extreme weather conditions
4. d) Wasting water and other natural resources

Researchers are working to better understand how a changing climate impacts wildlife and finding ways to help them adapt. Protecting wildlife—stopping poaching, curbing overfishing, and conserving habitats—is more important than ever with the added pressures of climate change.

We're in this together

Climate change adaptation and mitigation are both equally important and time-sensitive and we need to do both. You can help mitigate climate change by reducing emissions in your own life, letting your representatives know you support climate-smart policies, and supporting businesses and organizations embracing renewable energy. Help your community adapt by learning how your area is vulnerable to climate change and advocating for smart policies that reduce risk. You can also support local initiatives that help people prepare for and recover from extreme weather events or simply reduce your use of water in times of drought. Climate change is a serious problem, but our planet can continue to thrive if we all work together to both avoid the worst impacts and adapt to our changing world.

Source Text

https://www.worldwildlife.org/stories/what-s-the-difference-between-climate-change-mitigation-and-adaptation