Welcome to AP Biology! This summer you are asked to complete the work for ECOLOGY as an independent study. When you return to school in the fall you will perform a couple of ecology based labs followed by a test on the ecology unit. This will all happen the first week back from summer vacation so please complete this work over the summer.

**SUMMER WORK:** You are to read Chapters 50 -54 from the on-line text (feel free to print off and highlight) and use the guided notes for each chapter as you read. There is a power point presentation for each chapter that you should also use as you study. Answer questions as you read.

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I am looking forward to working with each of you next school year! Enjoy your summer! ☺
Chapter 50: An Introduction to Ecology and the Biosphere

Overview: The Scope of Ecology

- **Ecology** is the scientific study of the interactions between organisms and their environment.

**Concept 50.1 Ecology is the study of interactions between organisms and the environment**

- Ecologists ask questions about factors affecting the distribution and abundance of organisms.
- Ecologists might study how interactions between organisms and the environment affect the number of species living in an area, the cycling of nutrients, or the growth of populations.

*Ecology and evolutionary biology are closely related sciences.*

- Ecology has a long history as a descriptive science.
- Modern ecology is also a rigorous experimental science.
- Ecology and evolutionary biology are closely related sciences.
- Events that occur over ecological time (minutes to years) translate into effects over evolutionary time (decades to millennia).
  - For example, hawks feeding on field mice kill certain individuals (over ecological time), reducing population size (an ecological effect), altering the gene pool (an evolutionary effect), and selecting for mice with fur color that camouflages them in their environment (over evolutionary time).

*Ecological research ranges from the adaptations of individual organisms to the dynamics of the biosphere.*

- The environment of any organism includes the following components:
  - **Abiotic components:** nonliving chemical and physical factors such as temperature, light, water, and nutrients.
  - **Biotic components:** all living organisms in the individual’s environment.
- Ecology can be divided into a number of areas of study.
- **Organismal ecology** is concerned with the behavioral, physiological, and morphological ways individuals interact with the environment.
- A **population** is a group of individuals of the same species living in a particular geographic area. **Population ecology** examines factors that affect population size and composition.
- A **community** consists of all the organisms of all the species that inhabit a particular area. **Community ecology** examines the interactions between species and considers how factors such as predation, competition, disease, and disturbance affect community structure and organization.
- An **ecosystem** consists of all the abiotic factors in addition to the entire community of species that exist in a certain area. **Ecosystem ecology** studies energy flow and cycling of chemicals among the various abiotic and biotic components.

- A **landscape** or **seascape** consists of several different ecosystems linked by exchanges of energy, materials, and organisms. **Landscape ecology** deals with arrays of ecosystems and their arrangement in a geographic region.
  - Each landscape or seascape consists of a mosaic of different types of patches, an environmental characteristic ecologists refer to as **patchiness**. **Landscape ecological research** focuses on the factors controlling exchanges of energy, materials, and organisms among ecosystem patches.

- The **biosphere** is the global ecosystem, the sum of all of the planet’s ecosystems. The biosphere includes the entire portion of Earth inhabited by life, ranging from the atmosphere to a height of several kilometers to the oceans and water bearing rocks to a depth of several kilometers.

**Ecology provides a scientific context for evaluating environmental issues.**

- It is important to clarify the difference between **ecology**, the scientific study of the distribution and abundance of organisms, and **environmentalism**, advocacy for the protection or preservation of the natural environment.

- To address environmental problems, we need to understand the interactions of organisms and the environment.
  - The science of ecology provides that understanding.

- In 1962, Rachel Carson’s book *Silent Spring* warned that the use of pesticides such as DDT was causing population declines in many nontarget organisms.

- Today, acid precipitation, land misuse, toxic wastes, habitat destruction, and the growing list of endangered or extinct species are just a few of the problems that threaten the Earth.

- Many influential ecologists feel a responsibility to educate legislators and the general public about decisions that affect the environment.
  - It is important to communicate the scientific complexity of environmental issues.

- Our ecological information is always incomplete. The **precautionary principle** (essentially “an ounce of prevention is worth a pound of cure”) can guide decision making on environmental issues.

**Concept 50.2 Interactions between organisms and the environment limit the distribution of species**

- Ecologists have long recognized distinct global and regional patterns in the distribution of organisms.

- **Biogeography** is the study of past and present distributions of individual species in the context of evolutionary theory.

- Ecologists ask a series of questions to determine what limits the geographical distribution of any species.

**Species dispersal contributes to the distribution of organisms.**
• The movement of individuals away from centers of high population density or from their area of origin is called **dispersal**.

• The dispersal of organisms is crucial to understanding geographic isolation in evolution and the broad patterns of geographic distribution of species.

• One way to determine if dispersal is a key factor limiting distribution is to observe the results when humans have accidentally or intentionally transplanted a species to areas where it was previously absent.
  ○ For the transplant to be considered successful, the organisms must not only survive in the new area, but also reproduce there.

• If the transplant is successful, then the *potential* range of the species is larger than its *actual* range.

• Species introduced to new geographic locations may disrupt the communities and ecosystems to which they are introduced.
  ○ Consequently, ecologists rarely conduct transplant experiments today.
  ○ Instead, they study the outcome when a species has been transplanted accidentally or for another purpose.

**Behavior and habitat selection contribute to the distribution of organisms.**

• Sometimes organisms do not occupy all of their potential range but select particular habitats.

• Does behavior play a role in limiting distribution in such cases?

• Habitat selection is one of the least-understood ecological processes, but it appears to play an important role in limiting the distribution of many species.

**Biotic factors affect the distribution of organisms.**

• Do biotic factors limit the distribution of species?
  ○ Negative interactions with other organisms in the form of predation, parasitism, disease, or competition may limit the ability of organisms to survive and reproduce.
    ▪ Predator-removal experiments can provide information about how predators limit distribution of prey species.
  ○ Absence of other species may also limit distribution of a species.
    ▪ For example, the absence of a specific pollinator or prey species may limit distribution of an organism.

**Abiotic factors affect the distribution of organisms.**

• The global distribution of organisms broadly reflects the influence of abiotic factors such as temperature, water, and sunlight.

• The environment is characterized by *spatial* and *temporal* heterogeneity.

• Environmental temperature is an important factor in the distribution of organisms because of its effect on biological processes.
  ○ Very few organisms can maintain an active metabolism at very high or very low temperatures.
  ○ Some organisms have extraordinary adaptations to allow them to live outside the temperature range habitable for most other living things.
The variation in water availability among habitats is an important factor in species distribution.
- Most aquatic organisms are restricted to either freshwater or marine environments.
- Terrestrial organisms face a nearly constant threat of desiccation and have adaptations to allow them to obtain and conserve water.

Sunlight provides the energy that drives nearly all ecosystems.
- Intensity of light is not the most important factor limiting plant growth in most terrestrial environments, although shading by a forest canopy makes competition for light in the understory intense.
- In aquatic environments, light intensity limits distribution of photosynthetic organisms.
  - Every meter of water depth selectively absorbs 45% of red light and 2% of blue light passing through it.
  - As a result, most photosynthesis in aquatic environments occurs near the surface.
- Photoperiod, the relative length of daytime and nighttime, is a reliable indicator of seasonal events and is an important cue for the development or behavior of many organisms.

Wind amplifies the effects of temperature by increasing heat loss due to evaporation and convection. It also increases water loss by increasing the rate of evaporative cooling in animals and transpiration in plants.

The physical structure, pH, and mineral composition of soils and rocks limit distribution of plants and, thus, of the animals that feed upon them, contributing to the patchiness of terrestrial ecosystems.

In streams and rivers, substrate composition can affect water chemistry, affecting distribution of organisms.

In marine environments, the structure of substrates in the intertidal areas or seafloor limits the organisms that can attach to or burrow in those habitats.

Four abiotic factors are the major components of climate.

- Climate is the prevailing weather conditions in an area.
  - Four abiotic factors—temperature, water, sunlight, and wind—are the major components of climate.
  - Climatic factors, especially temperature and water, have a major influence on the distribution of organisms.
- Climate patterns can be described on two scales. Macroclimate patterns are on global, regional, or local levels, and microclimate patterns are very fine patterns such as the conditions experienced by a community of organisms under a fallen log.
- Climate determines the makeup of biomes, the major types of ecosystems.
  - Annual means for temperature and rainfall are reasonably well correlated with the biomes found in different regions.
- Global climate patterns are determined by sunlight and Earth’s movement in space.
  - The sun’s warming effect on the atmosphere, land, and water establishes the temperature variations, cycles of air movement, and evaporation of water that are responsible for latitudinal variations in climate.
• Bodies of water and topographic features such as mountain ranges create regional climatic variations, while smaller features of the landscape affect local climates.

• Ocean currents influence climate along the coast by heating or cooling overlying air masses, which may pass over land.
  ° Coastal regions are generally moister than inland areas at the same latitude.
  ° In general, oceans and large lakes moderate the climate of nearby terrestrial environments.
    ▪ In certain regions, cool, dry ocean breezes are warmed when they move over land, absorbing moisture and creating a hot, rainless climate slightly inland.
    ▪ This Mediterranean climate pattern occurs inland from the Mediterranean Sea.
  ° Ocean currents also influence climate in coastal areas.

• Mountains have a significant effect on the amount of sunlight reaching an area, as well as on local temperature and rainfall.
  ° In the Northern Hemisphere, south-facing slopes receive more sunlight than north-facing slopes, and are therefore warmer and drier.
  ° These environmental differences affect species distribution.

• At any given latitude, air temperature declines 6°C with every 1,000-m increase in elevation.
  ° This temperature change is equivalent to that caused by an 880-km increase in latitude.

• As moist, warm air approaches a mountain, it rises and cools, releasing moisture on the windward side of the peak.
  ° On the leeward side of the mountain, cool, dry air descends, absorbing moisture and producing a rain shadow.
  ° Deserts commonly occur on the leeward side of mountain ranges.

• The changing angle of the sun over the course of a year affects local environments.
  ° Belts of wet and dry air on either side of the equator shift with the changing angle of the sun, producing marked wet and dry seasons around 20° latitude.
  ° Seasonal changes in wind patterns produce variations in ocean currents, occasionally causing the upwelling of nutrient-rich, cold water from deep ocean layers.

• Lakes are also sensitive to seasonal temperature changes.
  ° During the summer and winter, many temperate lakes are thermally stratified or layered vertically according to temperature.
  ° These lakes undergo a semiannual mixing, or turnover, of their waters in spring and fall. Turnover brings oxygenated water to the bottom and nutrient-rich water to the surface.

• Many features in the environment influence microclimates.
  ° Forest trees moderate the microclimate beneath them.
    ▪ Cleared areas experience greater temperature extremes than the forest interior.
  ° A log or large stone shelters organisms, buffering them from temperature and moisture fluctuations.
  ° Every environment on Earth is characterized by a mosaic of small-scale differences in abiotic factors that influence the local distribution of organisms.
- Long-term climate changes profoundly affect the biosphere.
- One way to predict possible effects of current climate changes is to consider the changes that have occurred in temperate regions since the end of the last Ice Age.
- Until about 16,000 years ago, continental glaciers covered much of North America and Eurasia.
- As the climate warmed and the glaciers melted, tree distribution expanded northward.
  - A detailed record of these migrations is captured in fossil pollen in lake and pond sediments.
- If researchers can determine the climatic limits of current geographic distributions for individual species, they can predict how that species distribution will change with global warming.
  - A major question for tree species is whether seed dispersal is rapid enough to sustain the migration of the species as climate changes.
  - Consider the American beech, *Fagus grandifolia*.
    - Climate models predict that the northern and southern limit of the beech’s range will move 700–900 km north over the next century.
      - The beech will have to migrate 7–9 km per year to maintain its distribution.
    - However, since the Ice Age, the beech has migrated into its present range at a rate of only 0.2 km per year.
    - Without human assistance, the beech will become extinct.

**Concept 50.3 Abiotic and biotic factors influence the structure and dynamics of aquatic biomes**

- Varying combinations of biotic and abiotic factors determine the nature of the Earth’s **biomes**, major types of ecological associations that occupy broad geographic regions of land or water.

**Aquatic biomes occupy the largest part of the biosphere.**

- Ecologists distinguish between freshwater and marine biomes on the basis of physical and chemical differences.
  - Marine biomes generally have salt concentrations that average 3%, while freshwater biomes have salt concentrations of less than 1%.
- Marine biomes cover approximately 75% of the earth’s surface and have an enormous effect on the biosphere.
  - The evaporation of water from the oceans provides most of the planet’s rainfall.
  - Ocean temperatures have a major effect on world climate and wind patterns.
  - Photosynthesis by marine algae and photosynthetic bacteria produce a substantial proportion of the world’s oxygen. Respiration by these organisms consumes huge amounts of atmospheric carbon dioxide.
- Freshwater biomes are closely linked to the soils and biotic components of the terrestrial biomes through which they pass.
  - The pattern and speed of water flow and the surrounding climate are also important.
Most aquatic biomes are physically and chemically stratified.

Light is absorbed by the water and by photosynthetic organisms, so light intensity decreases rapidly with depth.
  - There is sufficient light for photosynthesis in the upper **photic zone**.
  - Very little light penetrates to the lower **aphotic zone**.

The substrate at the bottom of an aquatic biome is the **benthic zone**.
  - This zone is made up of sand and sediments and is occupied by communities of organisms called **benthos**.
  - A major food source for benthos is dead organic material or **detritus**, which rains down from the productive surface waters of the photic zone.

Sunlight warms surface waters, while deeper waters remain cold.
  - As a result, water temperature in lakes is stratified, especially in summer and winter.
  - In the ocean and most lakes, a narrow stratum of rapid temperature change called a **thermocline** separates the more uniformly warm upper layer from more uniformly cold deeper waters.

In aquatic biomes, community distribution is determined by depth of the water, distance from shore, and open water versus bottom.

In marine communities, phytoplankton, zooplankton, and many fish species live in the relatively shallow photic zone.

The aphotic zone contains little life, except for microorganisms and relatively sparse populations of luminescent fishes and invertebrates.

The major aquatic biomes include lakes, wetlands, streams, rivers, estuaries, intertidal biomes, oceanic pelagic biomes, coral reefs, and marine benthic biomes.

Freshwater lakes vary greatly in oxygen and nutrient content.
  - **Oligotrophic** lakes are deep, nutrient poor, oxygen rich, and contain little life.
  - **Eutrophic** lakes are shallow, nutrient rich, and oxygen poor.

In lakes, the **littoral zone** is the shallow, well-lit water close to shore.
  - The **limnetic zone** is the open surface water.

**Wetlands** are areas covered with sufficient water to support aquatic plants.
  - They can be saturated or periodically flooded.
  - Wetlands include marshes, bogs, and swamps.
  - They are among the most productive biomes on Earth and are home to a diverse community of invertebrates and birds.
  - Because of the high organic production and decomposition in wetlands, their water and soil are low in dissolved oxygen.
  - Wetlands have a high capacity to filter dissolved nutrients and chemical pollutants.
  - Humans have destroyed many wetlands, but some are now protected.

**Streams** and **rivers** are bodies of water moving continuously in one direction.
  - Headwaters are cold, clear, turbulent, and swift.
    - They carry little sediment and relatively few mineral nutrients.
  - As water travels downstream, it picks up O₂ and nutrients on the way.
Nutrient content is largely determined by the terrain and vegetation of the area. Many streams and rivers have been polluted by humans, degrading water quality and killing aquatic organisms. Damming and flood control impairs the natural functioning of streams and rivers and threatens migratory species such as salmon.

- **Estuaries** are areas of transition between river and sea.
  - The salinity of these areas can vary greatly.
  - Estuaries have complex flow patterns, with networks of tidal channels, islands, levees, and mudflats.
  - They support an abundance of fish and invertebrate species and are crucial feeding areas for many species of waterfowl.

- **An intertidal zone** is a marine biome that is periodically submerged and exposed by the tides.
  - The upper intertidal zone experiences longer exposure to air and greater variation in salinity and temperature than do the lower intertidal areas.
  - Many organisms live only at a particular stratum in the intertidal.

- **The oceanic pelagic biome** is the open blue water, mixed by wind-driven oceanic currents.
  - The surface waters of temperate oceans turn over during fall through spring.
  - The open ocean has high oxygen levels and low nutrient levels.
  - This biome covers 70% of the Earth’s surface and has an average depth of 4,000 meters.

- **Coral reefs** are limited to the photic zone of stable tropic marine environments with high water clarity. They are found at temperatures between 18°C and 30°C.
  - They are formed by the calcium carbonate skeletons of coral animals.
  - Mutualistic dinoflagellate algae live within the tissues of the corals.
  - Coral reefs are home to a very diverse assortment of vertebrates and invertebrates.
  - Collecting of coral skeletons and overfishing for food and the aquarium trade have reduced populations of corals and reef fishes.
  - Global warming and pollution contribute to large-scale coral mortality.

- **The marine benthic zone** consists of the seafloor below the surface waters of the coastal or neritic zone and the offshore pelagic zone.
  - Most of the ocean’s benthic zone receives no sunlight.
  - Organisms in the very deep abyssal zone are adapted to continuous cold (about 3°C) and extremely high pressure.
  - Unique assemblages of organisms are associated with deep-sea hydrothermal vents of volcanic origin on mid-ocean ridges.
    - The primary producers in these communities are chemoautotrophic prokaryotes that obtain energy by oxidizing H₂S formed by a reaction of volcanically heated water with dissolved sulfate (SO₄²⁻).

**Concept 50.4 Climate largely determines the distribution and structure of terrestrial biomes**
Because there are latitudinal patterns of climate over the Earth’s surface, there are also latitudinal patterns of biome distribution.

A **climograph** denotes the annual mean temperature and precipitation of a region.
- Temperature and rainfall are well correlated with different terrestrial biomes, and each biome has a characteristic climograph.

Most terrestrial biomes are named for major physical or climatic features or for their predominant vegetation.

Vertical stratification is an important feature of terrestrial biomes.
- The **canopy** of the tropical rain forest is the top layer, covering the low-tree stratum, shrub understory, ground layer, litter layer, and root layer.
- Grasslands have a canopy formed by grass, a litter layer, and a root layer.
- Stratification of vegetation provides many different habitats for animals.

Terrestrial biomes usually grade into each other without sharp boundaries. The area of intergradation, called the **ecotone**, may be narrow or wide.

The species composition of any biome differs from location to location.

Biomes are dynamic, and natural disturbance rather than stability tends to be the rule.
- Hurricanes create openings for new species in tropical and temperate forests.
- In northern coniferous forests, snowfall may break branches and small trees, producing gaps that allow deciduous species to grow.
- As a result, biomes exhibit patchiness, with several different communities represented in any particular area.

In many biomes, the dominant plants depend on periodic disturbance.
- For example, natural wildfires are an integral component of grasslands, savannas, chaparral, and many coniferous forests.

Human activity has radically altered the natural patterns of periodic physical disturbance.
- Fires are now controlled for the sake of agricultural land use.

Humans have altered much of the Earth’s surface, replacing original biomes with urban or agricultural ones.

The major terrestrial biomes include tropical forest, desert, savanna, chaparral, temperate grassland, coniferous forest, temperate broadleaf forest, and tundra.

**Tropical forests** are found close to the equator.
- **Tropical rain forests** receive constant high amounts of rainfall (200 to 400 cm annually).
- In tropical dry forests, precipitation is highly seasonal.
- In both, air temperatures range between 25°C and 29°C year round.
- Tropical forests are stratified, and competition for light is intense.
- Animal diversity is higher in tropical forests than in any other terrestrial biome.

**Deserts** occur in a band near 30° north and south latitudes and in the interior of continents.
- Deserts have low and highly variable rainfall, generally less than 30 cm per year.
- Temperature varies greatly seasonally and daily.
- Desert vegetation is usually sparse and includes succulents such as cacti and deeply rooted shrubs.
- Many desert animals are nocturnal, so they can avoid the heat.
- Desert organisms display adaptations to allow them to resist or survive desiccation.

- **Savanna** is found in equatorial and subequatorial regions.
  - Rainfall is seasonal, averaging 30–50 cm per year.
  - The savanna is warm year-round, averaging 24–29°C with some seasonal variation.
  - Savanna vegetation is grassland with scattered trees.
  - Large herbivorous mammals are common inhabitants.
    - The dominant herbivores are insects, especially termites.
  - Fire is important in maintaining savanna biomes.

- **Chaparrals** have highly seasonal precipitation with mild, wet winters and dry, hot summers.
  - Annual precipitation ranges from 30 to 50 cm.
  - Chaparral is dominated by shrubs and small trees, with a high diversity of grasses and herbs.
  - Plant and animal diversity is high.
  - Adaptations to fire and drought are common.

- **Temperate grasslands** exhibit seasonal drought, occasional fires, and seasonal variation in temperature.
  - Large grazers and burrowing mammals are native to temperate grasslands.
  - Deep fertile soils make temperate grasslands ideal for agriculture, especially for growing grain.
  - Most grassland in North America and Eurasia has been converted to farmland.

- **Coniferous forest**, or taiga, is the largest terrestrial biome on Earth.
  - Coniferous forests have long, cold winters and short, wet summers.
  - The conifers that inhabit these forests are adapted for snow and periodic drought.
  - Coniferous forests are home to many birds and mammals.
  - These forests are being logged at a very high rate and old-growth stands of conifers may soon disappear.

- **Temperate broadleaf forests** have very cold winters, hot summers, and considerable precipitation.
  - A mature temperate broadleaf forest has distinct vertical layers, including a closed canopy, one or two strata of understory trees, a shrub layer, and an herbaceous layer.
  - The dominant deciduous trees in Northern Hemisphere broadleaf forests drop their leaves and become dormant in winter.
  - In the Northern Hemisphere, many mammals in this biome hibernate in the winter, while many bird species migrate to warmer climates.
  - Humans have logged many temperate broadleaf forests around the world.

- **Tundra** covers large areas of the Arctic, up to 20% of the Earth’s land surface.
  - *Alpine tundra* is found on high mountaintops at all latitudes, including the tropics.
- The plant communities in alpine and Arctic tundra are very similar.
  - The Arctic tundra winter is long and cold, while the summer is short and mild. The growing season is very short.
  - Tundra vegetation is mostly herbaceous, consisting of a mixture of lichens, mosses, grasses, forbs, and dwarf shrubs and trees.
  - A permanently frozen layer of permafrost prevents water infiltration and restricts root growth.
  - Large grazing musk oxen are resident in Arctic tundra, while caribou and reindeer are migratory.
  - Migratory birds use Arctic tundra extensively during the summer as nesting grounds.
  - Arctic tundra is sparsely settled by humans but has recently become the focus of significant mineral and oil extraction.
Chapter 51: Behavioral Ecology

Overview: Studying Behavior

- Humans have studied animal behavior for as long as we have lived on Earth.
- As hunter and hunted, knowledge of animal behavior was essential to human behavior.
- The modern scientific discipline of behavioral ecology studies how behavior develops, evolves, and contributes to survival and reproductive success.

Concept 51.1 Behavioral ecologists distinguish between proximate and ultimate causes of behavior

- Scientific questions that can be posed about any behavior can be divided into two classes: those that focus on the immediate stimulus and mechanism for the behavior and those that explore how the behavior contributes to survival and reproduction.
- What is behavior?
  - Behavioral traits are an important part of an animal’s phenotype.
  - Many behaviors result from an animal’s muscular activity, such as a predator chasing a prey.
    - In some behaviors, muscular activity is less obvious, as in bird song.
  - Some nonmuscular activities are also behaviors, as when an animal secretes a pheromone to attract a member of the opposite sex.
  - Learning is also a behavioral process.
- Put simply, behavior is everything an animal does and how it does it.
- Proximate questions are mechanistic, concerned with the environmental stimuli that trigger a behavior, as well as the genetic, physiological, and anatomical mechanisms underlying a behavioral act.
  - Proximate questions are referred to as “how?” questions.
- Ultimate questions address the evolutionary significance of a behavior and why natural selection favors this behavior.
  - Ultimate questions are referred to as “why?” questions.
- Red-crowned cranes breed in spring and early summer.
  - A proximate question about the timing of breeding by this species might ask, “How does day length influence breeding by red-crowned cranes?”
    - A reasonable hypothesis for the proximate cause of this behavior is that breeding is triggered by the effect of increased day length on the crane’s production of and response to particular hormones.
  - An ultimate hypothesis might be that red-crowned cranes reproduce in spring and early summer because that is when breeding is most productive.
    - At that time of year, parent birds can find an ample supply of food for rapidly growing offspring, providing an advantage in reproductive success compared to birds that breed in other seasons.
• These two levels of causation are related.
  ° Proximate mechanisms produce behaviors that evolved because they increase fitness in some way.
  ° For example, increased day length has little adaptive significance for red-crowned cranes, but because it corresponds to seasonal conditions that increase reproductive success, such as the availability of food for feeding young birds, breeding when days are long is a proximate mechanism that has evolved in cranes.

Classical ethology presaged an evolutionary approach to behavioral biology.
• In the mid-20th century, a number of pioneering behavioral biologists developed the discipline of ethology, the scientific study of animal behavior.
• In 1963, Niko Tinbergen suggested four questions that must be answered to fully understand any behavior.
  1. What is the mechanistic basis of the behavior, including chemical, anatomical, and physiological mechanisms?
  2. How does development of the animal, from zygote to mature individual, influence the behavior?
  3. What is the evolutionary history of the behavior?
  4. How does the behavior contribute to survival and reproduction (fitness)?
• Tinbergen’s list includes both proximate and ultimate questions.
  ° The first two, which concern mechanism and development, are proximate questions, while the second two are ultimate, or evolutionary, questions.
• A fixed action pattern (FAP) is a sequence of unlearned behavioral acts that is essentially unchangeable and, once initiated, is usually carried to completion.
• A FAP is triggered by an external sensory stimulus called a sign stimulus.
  ° In the red-spined stickleback, the male attacks other males that invade his nesting territory.
  ° The stimulus for the attack is the red underside of the intruder.
  ° A male stickleback will attack any model that has some red visible on it.
• A proximate explanation for this aggressive behavior is that the red belly of the intruding male acts as a sign stimulus that releases aggression in a male stickleback.
• An ultimate explanation is that by chasing away other male sticklebacks, a male decreases the chance that eggs laid in his nesting territory will be fertilized by another male.
• Imprinting is a type of behavior that includes learning and innate components and is generally irreversible.
  ° Imprinting has a sensitive period, a limited phase in an animal’s behavior that is the only time that certain behaviors can be learned.
• An example of imprinting is young geese following their mother.
  ° In species that provide parental care, parent-offspring bonding is a critical time in the life cycle.
    ▪ During the period of bonding, the young imprint on their parent and learn the basic behavior of the species, while the parent learns to recognize its offspring.
° Among gulls, the sensitive period for parental bonding on young lasts one or two days.
  ▪ If bonding does not occur, the parent will not initiate care of the infant, leading to certain death of the offspring and decreasing the parent’s reproductive success.
• How do young gulls know on whom—or what—to imprint?
  ° The tendency to respond is innate in birds.
  ° The world provides the *imprinting stimulus*, and young gulls respond to and identify with the first object they encounter that has certain key characteristics.
    ▪ In greylag geese, the key stimulus is movement of the object away from the young.
• A proximate explanation for young geese following and imprinting on their mother is that during an early, critical developmental stage, the young geese observe their mother moving away from them and calling.
• An ultimate explanation is that, on average, geese that follow and imprint on their mother receive more care and learn necessary skills, and thus have a greater chance of surviving, than those that do not follow.
• Early study of imprinting and fixed action patterns helped make the distinction between proximate and ultimate causes of behavior.
  ° They also helped to establish a strong tradition of experimental approaches in behavioral ecology.

**Concept 51.2 Many behaviors have a strong genetic component**

*B*Behavior results from both genes and environmental factors.*

• Behavioral traits, like other aspects of a phenotype, are the result of complex interactions between genetic and environmental factors.
• In biology, the nature-versus-nurture issue is not about whether genes or environment influence behavior, but about how both are involved.
  ° All behaviors are affected by both genes and environment.
• Behavior can be viewed in terms of the norm of reaction.
  ° We can measure the behavioral phenotypes for a particular genotype that develop in a range of environments.
  ° In some cases, the behavior is variable, depending on environmental experience.
  ° In other cases, nearly all individuals in the population exhibit identical behavior, despite internal and external environmental differences during development and throughout life.
    ▪ Behavior that is *developmentally fixed* is called **innate behavior**.
    ▪ Such behaviors are under strong genetic influence.
  ° The range of environmental differences among individuals does not appear to alter innate behavior.

*Many animal movements are under substantial genetic influence.*

• A *kinesis* is a simple change in activity or turning rate in response to a stimulus.
For example, sowbugs are more active in dry areas and less active in humid areas. This increases the chance that they will leave a dry area and encounter a moist area.

- A **taxis** is an automatic, oriented movement toward or away from a stimulus.
  - For example, many stream fishes exhibit positive rheotaxis, automatically swimming or orienting themselves in an upstream direction (toward the current).
  - This keeps them from being swept away and keeps them facing in the direction in which food is coming.

- Ornithologists have found that many features of migratory behavior in birds are genetically programmed.
  - **Migration** is the regular movement of animals over relatively long distances.

- One of the best-studied migratory birds is the blackcap (*Sylvia atricapilla*), a small warbler that ranges from the Cape Verde Islands off the coast of West Africa to northern Europe.

- Migratory behaviors of blackcaps vary greatly among populations.
  - During the migration season, captive migratory blackcaps hop restlessly about their cages all night or rapidly flap their wings while sitting on a perch.

- Peter Berthold studied the genetic basis of this behavior, known as “migratory restlessness,” in several populations of blackcaps.

- In one study, the researchers crossed migratory blackcaps with nonmigratory ones and subjected their offspring to environments simulating one location or the other.
  - Forty percent of offspring raised in both conditions showed migratory restlessness, leading Berthold to conclude that migration is under genetic control and follows a polygenic inheritance pattern.

Animal communication is an essential component of interactions between individuals.

- Much of the social interaction between animals involves transmitting information through specialized behaviors called signals.
  - In behavioral ecology, a **signal** is a behavior that causes a change in another animal’s behavior.

- The transmission, reception, and response to signals constitute animal communication.

- Some features of animal communication are under strong genetic control, although the environment makes a significant contribution to all communication systems.

- Many signals are efficient in energy costs.
  - For example, a territorial fish erects its fins when aggressively approaching an intruder.
  - It takes less energy to erect fins that to attack an invading fish.

- Animals communicate using visual, auditory, chemical, tactile, and electrical signals.

- The type of signal is closely related to an animal’s lifestyle and environment.
  - For example, nocturnal species use olfactory and auditory signals.
  - Birds are diurnal and have a poor olfactory sense.
    - They communicate primarily by visual and auditory signals.
Human senses are more attentive to the colors and songs of birds than the rich olfactory signals of many other animals because of our own senses.

Many animals secrete chemical substances called pheromones.
- These chemicals are especially common in mammals and insects and often relate to reproductive behaviors.
- In honeybees, pheromones produced by the queens and her daughters (workers) maintain the hive’s very complex social order.
  - Male drones are attracted to the queen’s pheromone when they are outside the hive.
- Pheromones can also function in nonreproductive behavior.
  - When a minnow is injured, an alarm substance is released from glands in the fish’s skin, inducing a fright response among other fish in the area.
    - They become more vigilant and group in tightly packed schools.
- Pheromones are effective at very low concentrations.

The songs of most birds are at least partly learned.

In contrast, in many species of insect, mating rituals include characteristic songs that are under direct genetic control.

In *Drosophila*, males produce a song by wing vibration.
- A variety of evidence suggests that song structure in *Drosophila* is controlled genetically and is under strong selective pressure.
  - Females can recognize the songs of males of their own species.
  - Males raised in isolation produce a characteristic song with no exposure to other singing males.
  - The male song shows little variation among individuals.

Some insect species are morphologically identical and can be identified only through courtship songs or behaviors.
- For example, morphologically identical green lacewings were once thought to belong to a single species.
- However, studies of their courtship songs revealed the presence of at least 15 different species, each with a different song.
- Hybrid offspring sing songs that contain elements of the songs of both parental species, leading researchers to conclude that the songs are genetically controlled.

**Prairie vole mating and parental behaviors are under strong genetic influence.**

Mating and parental behavior by male prairie voles (*Microtus ochrogaster*) are under strong genetic control.

Prairie voles and a few other vole species are monogamous, a social trait found in only 3% of mammalian species.
- Male prairie voles help their mates care for young, a relatively uncommon trait among male mammals.
- Male prairie voles form a strong pair-bond with a single female after they mate, engaging in grooming and huddling behaviors.
- Mated males are intensely aggressive to strange males or females, while remaining nonaggressive to their mate and pups.
Research by Thomas Insel at Emory University suggests that arginine-vasopressin (AVP), a nine-amino-acid neurotransmitter released in mating, mediates both pair-bond formation and aggression in male prairie voles.

In the CNS, AVP binds to a receptor called the V₁a receptor.
- The researcher found significant differences in the distribution of V₁a receptors between the brains of monogamous prairie voles and related promiscuous montane voles.

Insel inserted the prairie vole V₁a receptor gene into laboratory mice.
- The mice developed the same distribution of V₁a receptors as the prairie voles and also showed many of the mating behaviors of the voles.

Thus, a single gene appears to mediate much of the complex mating and parental behavior of the prairie vole.

Concept 51.3 Environment, interacting with an animal’s genetic makeup, influences the development of behaviors

- Environmental factors modify many behaviors.
- Diet plays an important role in mate selection by Drosophila mojavensis, which mates and lays its eggs in rotting cactus tissues.
- Two populations of this fruit fly species use different species of cactus for their eggs.
- Flies from each population were raised on artificial media in the lab.
  - Females would mate only with males from their own population.
  - The food eaten by male flies as larvae strongly influenced mate selection by female flies.
    - The proximate cause in the female mate choices was in the exoskeletons of the flies, assessed by the sense of taste in female flies.
    - When males from the other population were “perfumed” with hydrocarbons extracted from males of the same population, they were accepted by female flies.
- The California mouse (Peromyscus californicus) is monogamous.
  - Like male prairie voles, male California mice are highly aggressive to other mice and provide considerable parental care.
    - Unlike prairie voles, even unmated California mice are aggressive.
- Researchers placed newborn California mice in the nests of white-footed mice (and vice versa).
  - White-footed mice are not monogamous and provide little parental care.
- This cross-fostering changed the behavior of both species.
  - Cross-fostered California mice provided less parental care and were less aggressive toward intruders when they grew up and reared their own young.
    - Their brains had reduced levels of AVP, compared with California mice raised by their own parents.
  - White-footed mice reared by California mice were more aggressive as parents than those raised by their own parents.
One of the most powerful ways that environmental conditions can influence behavior is through **learning**, the modification of behavior based on specific experiences.

- Learned behaviors can be very simple, such as imprinting, or highly complex.

- **Habituation** involves a loss of responsiveness to unimportant stimuli or stimuli that do not provide appropriate feedback.
  - For example, some animals stop responding to warning signals if signals are not followed by a predator attack (the “cry wolf” effect).
  - In terms of ultimate causation, habituation may increase fitness by allowing an animal’s nervous system to focus on meaningful stimuli, rather than wasting time on irrelevant stimuli.

*The fitness of an organism may be enhanced by the capacity for spatial learning.*

- Every natural environment shows spatial variation.

- As a consequence, it may be advantageous for animals to modify their behavior based on experience with the spatial structure of their environment, including the locations of nest sites, hazards, food, and prospective mates.
  - The fitness of an animal may be enhanced by the capacity for **spatial learning**.

- Niko Tinbergen found that digger wasps found their nest entrances by using **landmarks**, or location indicators, in their environment.
  - Landmarks must be stable within the time frame of the activity.
  - Because some environments are more stable than others, animals may use different kinds of information for spatial learning in different environments.
    - Sticklebacks from a river learned a maze by learning a pattern of movements.
    - Sticklebacks from a more stable pond environment used a combination of movements and landmarks to learn the maze.
      - The degree of environmental variability influences the spatial learning strategies of animals.
  - Some animals form **cognitive maps**, internal codes of spatial relationships of objects in their environment.
    - It is difficult to distinguish experimentally between the use of landmarks and the development of a true cognitive map.
      - Researchers have obtained good evidence that corvids (a bird family including ravens, crows, and jays) use cognitive maps.
      - Many corvids store food in caches and retrieve it later.
      - Pinyon jays may store nuts in as many as a thousand widely dispersed caches, keeping track of location and food quality (based on time since the food was stored).
      - Birds can learn that caches are halfway between two landmarks.

*Many animals can learn to associate one stimulus with another.*

- **Associative learning** is the ability of animals to learn to associate one stimulus with another.
  - For example, a mouse may have an unpleasant experience with a colorful, poisonous caterpillar and learn to avoid all caterpillars with that coloration.

- **Classical conditioning** is a type of associative learning.
Researchers trained *Drosophila melanogaster* to avoid air carrying a particular scent by coupling exposure to the odor with an electrical shock.

*Drosophila* has a surprising capacity for learning.

- Associative learning may play an important role in helping animals to avoid predators.
  - Zebra fish, an Asian minnow, and pike, an American predatory fish, do not occur together in the wild.
  - Researchers exposed zebra fish in an experimental group to an influx of 20 mL of water containing an alarm substance and then, 5 minutes later, to 20 mL of water with pike odor.
  - Zebra fish had no innate negative reaction to pike odor, but learned to associate pike odor with the alarm substance.
  - The zebra fish were *conditioned* to associate pike odor with the alarm substance.

- **Operant conditioning** is also called trial-and-error learning.

- An animal learns to associate one of its own behaviors with a reward or a punishment.
  - An example is the mouse eating the poisonous caterpillar and learning to avoid such caterpillars in the future.

The study of cognition connects behavior with nervous system function.

- The term *cognition* is variously defined.
  - In a narrow sense, it is synonymous with consciousness or awareness.
  - In a broad sense, animal *cognition* is the ability of an animal’s nervous system to perceive, store, process, and use information gathered by sensory receptors.

- The study of animal cognition, called **cognitive ethology**, examines the connection between an animal’s nervous system and its behavior.

- One area of research investigates how an animal’s brain represents physical objects in the environment.

- Cognitive ethnologists have discovered that many animals, including insects, categorize objects in their environment as “same” or “different.”

- Primates, dolphins, and corvids (crow, ravens, and jays) are capable of novel problem-solving behavior.
  - Individual animals may show great individual variation in the way they attempt to solve a problem.

- Many animals solve problems by observing the behavior of other individuals.
  - Chimpanzees learn to solve problems by copying the behavior of other chimpanzees.

Varying degrees of genetic and environmental factors contribute to the learning of complex behavior.

- Considerable research on the development of songs by birds has revealed varying degrees of genetic and environmental influence on the learning of complex behavior.

- In some species, learning plays only a small part in the development of song.
• For instance, New World flycatchers that are reared away from adults of their own species will sing the song characteristic of their own species without ever having heard it.

• Some songbirds have a sensitive period for developing their songs.
  ° Individual white-crowned sparrows reared in silence perform abnormal songs, but if recordings of the proper songs are played early in the life of the bird, normal songs develop.
  ° Although the young bird does not sing during the sensitive period, it memorizes the song of its own species by listening to other white-crowned sparrows sing.
  ° During the sensitive period, white-crowned sparrows fledging seem to be stimulated more by songs of their own species than songs of other species, chirping more in response.
  ° The young birds learn the songs, but the learning appears to be bounded by genetically controlled preferences.

• The sensitive period in a white-crowned sparrow’s learning of his song is followed by a second learning phase, when the juvenile bird sings some tentative notes that researchers call a subsong.
  ° The juvenile bird hears its own song and compares it with the song that it memorized in the sensitive period.
  ° Once they match, the bird sings that song for the rest of his life.

• Canaries may learn new song “syllables” each year, adding to their song during a yearly plastic song stage.

**Concept 51.4 Behavioral traits can evolve by natural selection**

• Because of the influence of genes on behavior, natural selection can result in the evolution of behavioral traits in populations.

**Behavior varies in natural populations.**

• Behavioral differences between closely related species are common.
  ° Males of different *Drosophila* species sing different courtship songs.
  ° Species of voles differ in paternal care.

• Although less obvious, significant differences in behavior can be found within animal species.

• When behavioral variation within a species corresponds to variation in environmental conditions, it may be evidence of past evolution.

• One of the best-known examples of genetically based variation in behavior within a species is prey selection by the garter snake *Thamnophis elegans*.
  ° Coastal garter snakes feed on salamanders, frogs, and toads, but mainly on slugs.
  ° Inland snakes eat frogs, leeches, and fish, but not slugs.

• Stevan Arnold investigated this variation.
  ° He offered slugs to snakes from both populations, but only coastal snakes readily accepted the slugs.
He tested newborn snakes born in the laboratory and found that 73% of young snakes from coastal mothers attacked slugs they were offered.
- Only 35% of naïve snakes from inland mothers attacked the slugs.

Arnold proposed that when inland snakes colonized coastal environments 10,000 years ago, a small fraction of the population had the ability to recognize slugs by chemoreception.
- These snakes took advantage of the abundant food source that slugs represented and had higher fitness than snakes that ignored slugs.
- The capacity to recognize slugs as prey increased in frequency in coastal populations.

The funnel web spider *Agelenopsis aperta* lives in riparian zones and the surrounding arid environment in the western United States.
- The spider’s web is a silken sheet ending in a hidden funnel, where the spider sits and watches for food while foraging.
- When prey strikes the web, the spider runs out across the web to make its capture.

Riechert and her colleagues found a striking contrast in the behavior of spiders in riparian forests and those in arid habitats.
- In arid, food-poor habitats, *A. aperta* is more aggressive to potential prey and to other spiders in defense of its web, and it returns to foraging more quickly following disturbance.

Hedrick and Riechert reared spiders in the lab and found that the differences in aggressiveness between desert and riparian spiders are genetic.
- Highly productive riparian sites are rich in prey for spiders, but the density of bird predators is also high.
- The timid behavior of *A. aperta* in riparian habitats was selected for by predation risk.

*Experiments provide evidence for behavioral evolution.*

Researchers are carrying out experiments on organisms with short life spans, looking for evidence of evolution in laboratory populations.

Marla Sokolowski studied a polymorphism in a gene for foraging in *Drosophila melanogaster*.

- The gene is called *for*, and it has two alleles.
  - One allele, *for*<sup>R</sup>, results in a “rover” phenotype in which the fly larva moves more than usual.
  - The other allele, *for*<sup>S</sup>, results in a “sitter” phenotype in which the fly larva moves less than usual.

Sokolowski reared *Drosophila* at high and low population densities for 74 generations.
- The *for*<sup>S</sup> allele increased in low-density populations, while *for*<sup>R</sup> increased in high-density populations.
- At low densities, short-distance foraging yielded sufficient food.
- At high densities, long-distance foraging helped the larvae to move beyond areas of food depletion.
Peter Berthold and his colleagues captured 20 male and 20 female blackcaps wintering in Britain and transported them to southwest Germany.

- The birds were caged in glass-covered funnel cages lined with carbon paper.
- As the birds moved around the funnels, the marks they made on the paper showed the direction they were trying to migrate.
  - The migratory orientation of wintering adult birds captured in Britain was similar to their laboratory-reared offspring.
  - Young birds originally from Germany had a very different migratory orientation.
  - This study indicates a genetic basis for migratory orientation of the young birds.
- Has the behavior evolved over time?
  - Berthold’s study suggests that the change in migratory behavior of the blackcaps is recent and rapid, having taken place over the past 50 years.
  - Before 1960, there were no westward-migrating blackcaps in Germany.
  - By the 1990s, westward migrants made up 7–11% of the blackcap populations of Germany.
  - Berthold suggested that westward migrants benefited from their new behavior, due to the milder winter climate and greater abundance of bird feeders in Britain.

**Concept 51.5 Natural selection favors behaviors that increase survival and reproductive success**

- The genetic components of behavior evolve through natural selection favoring traits that enhance survival and reproductive success in a population.
- Two of the most direct ways that behavior can affect fitness are through influences on foraging and mate choice.
- Foraging includes not only eating, but also any mechanisms that an animal uses to recognize, search for, and capture food items.
- **Optimal foraging theory** views foraging behavior as a compromise between the benefits of nutrition and the costs of obtaining food, such as the energy expenditure and risk of predation while foraging.
  - Natural selection should favor foraging behavior that minimizes the costs of foraging and maximizes the benefits.
- Behavioral ecologists apply cost-benefit analysis to study the proximate and ultimate causes of diverse foraging strategies.
- Reta Zach of the University of British Columbia carried out a cost-benefit analysis of feeding behavior in crows.
  - Crows search the tide pools of Mandarte Island, B.C., for snails called whelks.
  - A crow flies up and drops the whelk onto the rocks to break its shell.
  - If the drop is successful, the crow eats the snail’s soft body.
  - If it is not successful, the crow flies higher and tries again.
Zach predicted—and found—that crows would, on average, fly to a height that would provide the most food relative to the total amount of energy required to break the whelk shells.

- Bluegill sunfish feed on small crustaceans called *Daphnia*, selecting larger individuals that supply the most energy per unit time.
  - Smaller individuals will be selected if larger prey are too far away.

- Optimal foraging theory predicts that the proportion of small to large prey captured will vary with prey density.
  - At high densities, it is efficient for bluegill sunfish to feed only on large crustaceans.
  - At low densities, bluegill sunfish should exhibit little size selectivity because all prey are needed to meet energy requirements.

- In experiments, young bluegill sunfish forage efficiently but not as close to optimum as older individuals.
  - Perhaps younger fish do not judge size and distance as accurately because their vision is not yet completely developed.
  - Learning may also improve the foraging efficiency of bluegill sunfish as they age.

- Risk of predation is one of the most significant potential costs to a forager.

- Mule deer are preyed on by mountain lions throughout their range.
  - Researchers studied mule deer populations in Idaho to determine if they forage in a way that reduces their risk of falling prey to mountain lions.
  - The researchers found that food available to mule deer was fairly uniform across the potential foraging area.
    - Risk of predation varied greatly, however.
    - Mountain lions killed most mule deer at forest edges.
      * Few were killed in open areas and forest interiors.

- How does mule deer feeding behavior respond to the differences in feeding risk?
  - Mule deer feed predominantly in open areas, avoiding forest edges and forest interiors.
  - When deer are at the forest edge, they spend significantly more time scanning their surroundings than when they are in other areas.

- Mating behavior, which includes seeking and attracting mates, choosing among potential mates, and competing for mates, is the product of a form of natural selection called sexual selection.

- The mating relationship between males and females varies a great deal from species to species.
  - In many species, mating is promiscuous, with no strong pair-bond or lasting relationships.
  - In species where the mates remain together for a longer period, the relationship may be monogamous (one male mating with one female) or polygamous (one individual mating with several partners).
  - Polygamous relationships may involve a single male and many females (*polygyny*) or a single female and many males (*polyandry*).
Among monogamous species, males and females are often so much alike morphologically that they are impossible to distinguish based on external characteristics.

- Polygynous species are generally dimorphic, with males being larger and more showy.
- In polyandrous species, females are ornamented and larger than males.

The needs of young are an important factor constraining the evolution of mating systems.

Parental investment refers to the time and resources expended for the raising of offspring.

Most newly hatched birds cannot care for themselves and require a large, continuous food supply that a single parent cannot provide.

- In such cases, a male will have more successful offspring if he helps his partner to rear their chicks than if he goes off to seek more mates.
- This is why most birds are monogamous.

Birds with young that can feed and care for themselves from birth, such as pheasant and quail, have less need for parents to stay together.

- Males of these species can maximize their reproductive success by seeking other mates.

In mammals, the lactating female is often the only food source for the young, and males play no role in caring for them in most mammal species.

- In some mammal species, males protect many females and their young.

Certainty of paternity can influence mating systems and parental care.

- If the male is unsure if offspring are his, parental investment is likely to be lower.
- Females can be sure that they contributed to an offspring when they give birth or lay eggs.
  - Males do not have that assurance because the acts of mating and birth are separated over time.
- Males in many species with internal fertilization engage in behaviors that appear to increase their certainty of paternity, including guarding females, removing sperm from the female’s reproductive tract before copulation, and introducing large numbers of sperm to displace the sperm of other males.
- Certainty of paternity is much higher when egg laying and mating occur together, in external fertilization.
- Parental care in aquatic invertebrates, fishes, and amphibians, when it occurs, is as likely to be by males as females.
  - Male parental care occurs in only 7% of fish and amphibian families with internal fertilization and in 69% of families with external fertilization.
- The expression *certainty of paternity* does not imply conscious awareness of paternity by the father.

Sexual selection is a form of natural selection.

- Sexual dimorphism within a species results from sexual selection, a form of natural selection in which differences in reproductive success among individuals are a consequence of differences in mating success.
Sexual selection can take the form of *intersexual selection*, in which members of one sex choose mates on the basis of particular characteristics of the other sex—such as courtship songs, or *intrasexual selection*, which involves competition among members of one sex for mates.

- Mate preferences by females may play a central role in the evolution of male behavior and anatomy through intersexual selection.
- Witte and Sawka experimented to see whether imprinting by young zebra finches on their parents influenced their choice of mates when they matured.
  - They taped a red feather to the heads of both parents, male parent only, or female parent only, before the young chicks opened their eyes.
  - Control zebra finches were reared by unadorned parents.
- When the chicks matured, they were given a choice of ornamented or unornamented mate finches.
  - Males showed no preference, but females reared by ornamented fathers preferred ornamented mates.
- These results suggest that females imprint on their fathers and that mate choice by female zebra finches has played a key role in evolution of ornamentation in male zebra finches.
- Courtship behaviors of stalk-eyed flies are fascinating.
  - Males have elongated eyestalks, which they display to females during courtship.
    - Females prefer to mate with males with relatively long eyestalks.
    - How is this preference adaptive for females?
      - Researchers have correlated certain genetic disorders in male flies with an inability to develop long eyestalks.
      - Males with long eyestalks may be demonstrating their genetic quality to females.
- In general, ornaments such as long eyestalks and brightly colored feathers correlate with a male’s health and vitality.
  - A female that chooses a healthy male increases the chance that her offspring will be healthy.
- Males compete with each other by (often ritualized) *agonistic behaviors* that determine which competitors gain access to resources.
  - The outcome of such contests may be determined by strength or size.
- In some species, more than one mating behavior can result in successful reproduction.
  - In such cases, intrasexual selection has led to the evolution of alternative male mating behavior and morphology.
- Alternative male mating behaviors have been documented in the marine intertidal isopod *Paracerceis sculpta*, which lives in sponges in the Gulf of California.
- This species includes three genetically distinct male types—alpha, beta, and gamma.
  - Large alpha males defend harems of females within intertidal sponges, largely against other alpha males.
  - Beta males mimic female morphology and behavior and gain access to guarded harems.
  - Tiny gamma males invade and live within large harems.
• The mating success of each type of isopod depends on the relative density of males and females in the sponges.
  ° The alpha males sire the majority of young when defending a single female.
  ° If more than one female is present, beta males father 60% of the offspring.
  ° The reproductive rate of gamma males increases linearly with harem size.
• Overall, all three types of males have approximately equal mating success, and variation among males in this species is sustained by natural selection.

**Game theory can model behavioral strategies.**
• Game theory evaluates alternative strategies in situations where the outcome depends on each individual’s strategies and the strategies of other individuals.
• Barry Sinervo and Curt Lively used game theory to account for the existence of three different male phenotypes in populations of side-blotched lizards (*Uta stansburiana*).
• Males have three genetically controlled colors: orange throats, blue throats, and yellow throats.
  ° Orange-throat males are the most aggressive and defend large territories with many females.
  ° Blue-throat males are also aggressive but defend smaller territories with fewer females.
  ° Yellow-throat males are nonterritorial and use sneaky tactics to mimic females and sneak copulations.
  ° Frequency of the three types of males varies from year to year.
  ° Modeling showed that the relative success of different males varies with the abundance of other types of males.
    ▪ When blue-throat males are abundant, they can defend their few females from the sneaky yellow-throat males.
    ▪ However, they cannot defend their territories against the aggressive orange-throat males.
    ▪ Orange-throat males take over large territories but cannot defend large numbers of females against the sneaky yellow-throat males.
    ▪ Yellow-throat males then increase in numbers but are defeated by the blue-throat males.
    ▪ The cycle continues.

**Concept 51.6 The concept of inclusive fitness can account for most altruistic social behavior**
• Most social behaviors are selfish, meaning that they benefit the individual at the expense of others, especially competitors.
• Behavior that maximizes an individual’s survival and reproductive success is favored by selection, regardless of its effect on other individuals.
• How do we account for behaviors that help others?
  ° **Altruism** is defined as behavior that appears to decrease individual fitness but increases the fitness of others.
• Belding’s ground squirrel lives in some mountainous regions of the western United States.
  ° The squirrel is vulnerable to predators such as coyotes and hawks.
  ° If a squirrel sees a predator approach, it often gives a high-pitched alarm call, which alerts unaware individuals.
    ▪ The alerted squirrels then retreat to their burrows.
  ° This conspicuous alarm behavior calls attention to the caller, who has a greater risk of being killed.
• In honeybees, workers are sterile but labor on behalf of a single fertile queen.
  ° Workers will sacrifice themselves to sting intruders in defense of the hive.
• Naked mole rats are highly social rodents that live in underground chambers and tunnels in Africa.
  ° These rodents are hairless and nearly blind and live in colonies of 75–250 individuals.
  ° Each colony has only one reproducing female, the queen, who mates with one to three males, called kings.
  ° The rest of the colony consists of nonreproductive females and males who forage for underground roots and tubers and care for the kings, queen, and young rats.
• How can a naked mole rat (or a honeybee or a ground squirrel) enhance its fitness by helping other members of the population?
  ° How is altruistic behavior maintained by evolution?
  ° If related individuals help each other, they are, in effect, helping keep their own genes in the population.
• Inclusive fitness is defined as the effect an individual has on proliferating its own genes by reproducing and by helping relatives raise offspring.
• William Hamilton proposed a quantitative measure for predicting when natural selection should favor altruistic acts.
  ° Hamilton’s rule states the conditions under which altruistic acts will be favored by natural selection.
• The three key variables are as follows:
  1. The benefit to the recipient is \( B \).
  2. The cost to the altruist is \( C \).
  3. The coefficient of relatedness is \( r \), which equals the probability that a particular gene present in one individual will also be inherited from a common parent or ancestor in a second individual.
• The rule is as follows:
  ° \( rB > C \)
  ° The more closely related two individuals are, the greater the value of altruism.
• Kin selection is the mechanism of inclusive fitness, where individuals help relatives raise young.
• Some animals behave altruistically toward others who are not close relatives.
  ° Such behavior can be adaptive if the aided individual can be counted on to return the favor in the future.
This exchange of aid is called reciprocal altruism and is commonly used to explain altruism between unrelated humans.

Reciprocal altruism is limited to species with stable social groups in which individuals have many opportunities to exchange aid and where there would be negative social consequences for those who “cheat” and refuse to return favors to those who have helped them in the past.

However, because cheating may provide a large benefit to cheaters, behavioral ecologists have questioned how reciprocal altruism could arise.

To answer this question, behavioral ecologists have turned to game theory.

- Axelrod and Hamilton found that reciprocal altruism can evolve and persist in a population where individuals adopt a behavioral strategy called tit for tat.
  - In this strategy, an individual treats another individual the same way it was treated the last time they met.
  - Individuals are always altruistic, or cooperative, on the first encounter, and will remain so as long as their altruism is reciprocated.
    - When it is not, they will retaliate immediately but will return to cooperative behavior as soon as the other individual becomes cooperative.

Animals learn by observing others.

- Social learning is learning through observing others.
  - Social learning forms the roots of culture, which can be defined as a system of information transfer through social learning or teaching.
    - Cultural transfer of information has the potential to alter behavioral phenotypes and influence the fitness of individuals.

Social learning is not restricted to humans.

In many species, mate choice is strongly influenced by social learning.

- Mate choice copying, a behavior in which individuals in a population copy the mate choices of others, has been extensively studied in the guppy Poecilia reticulata.

- Female guppies prefer to mate with males having a high percentage of orange coloration.

- However, if a female sees another female engaging in courtship with a male with relatively little orange, she will choose a male with little orange herself.
  - Below a certain threshold of difference in mate color, mate choice copying by female guppies can mask genetically controlled female preference for orange males.

- What is the advantage for females?
  - A female that mates with males that are attractive to other females may increase the probability that her male offspring will also be attractive and have high reproductive success.

- In their studies of vervet monkeys in Amboseli National Park, Kenya, Dorothy Cheny and Richard Seyfarth found that performance of a behavior can improve through learning.

- Vervet monkeys (Cercopithecus aethiops) produce a complex set of alarm calls.
Distinct alarm calls warn of leopards, eagles, or snakes, all of which prey on the small vervets.

Vervets react to each alarm differently, depending on the threat.

Infant vervets give alarm calls but in an undiscriminating way.

- For example, they call “eagle” for any bird.
- With age, they improve their accuracy.
- Vervets learn how to give the right call by observing other members of the group and by receiving social confirmation for accurate calls.

Sociobiology places social behavior in an evolutionary context.

- Human culture is related to evolutionary theory in the discipline of sociobiology, whose main premise is that certain behavioral characteristics exist because they are expressions of genes that have been perpetuated by natural selection.

- In his seminal 1975 book *Sociobiology: The New Synthesis*, E. O. Wilson speculated about the evolutionary basis of certain kinds of social behavior in nonhuman animals, but he also included human culture, sparking a heated debate.

- The spectrum of possible human social behaviors may be influenced by our genetic makeup, but that is very different from saying that genes are rigid determinants of behavior.

- This distinction is at the core of the debate about evolutionary perspectives on human behavior.
  
  - Evolutionary explanations of human behavior do not reduce us to robots stamped out of rigid genetic molds.
  
  - Just as individuals vary extensively in anatomy, so we should expect variation in behavior.

- Because of our capacity for learning, human behavior is probably more plastic than that of any other animal.

- Over our recent evolutionary history, we have built up a diversity of structured societies with governments, laws, religions, and cultural values that define acceptable and unacceptable behavior, even when unacceptable behavior might enhance an individual’s Darwinian fitness.

  - In human behavior, as in other animals, genes and environmental factors build on each other.

- What is unique about our species?
  
  - Perhaps it is our social and cultural institutions that provide us with the only uniquely human feature.
Chapter 52: Population Ecology

Overview: Earth’s Fluctuating Populations

- To understand human population growth, we must consider the general principles of population ecology.
- Population ecology is the study of populations in relation to the environment, including environmental influences on population density and distribution, age structure, and population size.

Concept 52.1 Dynamic biological processes influence population density, dispersion, and demography

- A population is a group of individuals of a single species that live in the same general area.
- Members of a population rely on the same resources, are influenced by similar environmental factors, and have a high likelihood of interacting with and breeding with one another.
- Populations can evolve through natural selection acting on heritable variations among individuals and changing the frequencies of various traits over time.

Two important characteristics of any population are density and the spacing of individuals.

- Every population has a specific size and specific geographical boundaries.
  - The density of a population is measured as the number of individuals per unit area or volume.
  - The dispersion of a population is the pattern of spacing among individuals within the geographic boundaries.
- Measuring density of populations is a difficult task.
  - We can count individuals, but we usually estimate population numbers.
  - It is almost always impractical to count all individuals in a population.
  - Instead, ecologists use a variety of sampling techniques to estimate densities and total population sizes.
    - For example, they might count the number of individuals in a series of randomly located plots, calculate the average density in the samples, and extrapolate to estimate the population size in the entire area.
  - Such estimates are accurate when there are many sample plots and a homogeneous habitat.
  - A sampling technique that researchers commonly use to estimate wildlife populations is the mark-recapture method.
    - Individuals are trapped and captured, marked with a tag, recorded, and then released.
    - After a period of time has elapsed, traps are set again, and individuals are captured and identified.
    - The second capture yields both marked and unmarked individuals.
From these data, researchers estimate the total number of individuals in the population.

The mark-recapture method assumes that each marked individual has the same probability of being trapped as each unmarked individual.

This may not be a safe assumption, as trapped individuals may be more or less likely to be trapped a second time.

- Density results from dynamic interplay between processes that add individuals to a population and those that remove individuals from it.
  - Additions to a population occur through birth (including all forms of reproduction) and immigration (the influx of new individuals from other areas).
  - The factors that remove individuals from a population are death (mortality) and emigration (the movement of individuals out of a population).
  - Immigration and emigration may represent biologically significant exchanges between populations.
- Within a population’s geographic range, local densities may vary substantially.
  - Variations in local density are important population characteristics, providing insight into the environmental and social interactions of individuals within a population.
    - Some habitat patches are more suitable that others.
    - Social interactions between members of a population may maintain patterns of spacing.
- Dispersion is clumped when individuals aggregate in patches.
  - Plants and fungi are often clumped where soil conditions favor germination and growth.
  - Animals may clump in favorable microenvironments (such as isopods under a fallen log) or to facilitate mating interactions.
  - Group living may increase the effectiveness of certain predators, such as a wolf pack.
- Dispersion is uniform when individuals are evenly spaced.
  - For example, some plants secrete chemicals that inhibit the germination and growth of nearby competitors.
  - Animals often exhibit uniform dispersion as a result of territoriality, the defense of a bounded space against encroachment by others.
- In random dispersion, the position of each individual is independent of the others, and spacing is unpredictable.
  - Random dispersion occurs in the absence of strong attraction or repulsion among individuals in a population, or when key physical or chemical factors are relatively homogeneously distributed.
  - For example, plants may grow where windblown seeds land.
  - Random patterns are not common in nature.

Demography is the study of factors that affect population density and dispersion patterns.

- Demography is the study of the vital statistics of populations and how they change over time.
• Of particular interest are birth rates and how they vary among individuals (specifically females), and death rates.

• A **life table** is an age-specific summary of the survival pattern of a population.

• The best way to construct a life table is to follow the fate of a **cohort**, a group of individuals of the same age, from birth throughout their lifetimes until all are dead.

• To build a life table, we need to determine the number of individuals that die in each age group and calculate the proportion of the cohort surviving from one age to the next.

• A graphic way of representing the data in a life table is a **survivorship curve**.
  - This is a plot of the numbers or proportion of individuals in a cohort of 1,000 individuals still alive at each age.
  - There are several patterns of survivorship exhibited by natural populations.
  - A Type I curve is relatively flat at the start, reflecting a low death rate in early and middle life, and drops steeply as death rates increase among older age groups.
    - Humans and many other large mammals exhibit Type I survivorship curves.
  - The Type II curve is intermediate, with constant mortality over an organism’s life span.
    - Many species of rodent, various invertebrates, and some annual plants show Type II survivorship curves.
  - A Type III curve drops slowly at the start, reflecting very high death rates early in life, then flattens out as death rates decline for the few individuals that survive to a critical age.
    - Type III survivorship curves are associated with organisms that produce large numbers of offspring but provide little or no parental care.
    - Examples are many fishes, long-lived plants, and marine invertebrates.

• Many species fall somewhere between these basic types of survivorship curves or show more complex curves.
  - Some invertebrates, such as crabs, show a “stair-stepped” curve, with increased mortality during molts.

• Reproductive rates are key to population size in populations without immigration or emigration.
  - Demographers who study sexually reproducing populations usually ignore males and focus on females because only females give birth to offspring.
  - A **reproductive table** is an age-specific summary of the reproductive rates in a population.
    - The best way to construct a reproductive table is to measure the reproductive output of a cohort from birth until death.
    - For sexual species, the table tallies the number of female offspring produced by each age group.
    - Reproductive output for sexual species is the product of the proportion of females of a given age that are breeding and the number of female offspring of those breeding females.
  - Reproductive tables vary greatly from species to species.
    - Squirrels have a litter of two to six young once a year for less than a decade, while mussels may release hundreds of thousands of eggs in a spawning cycle.
**Concept 52.2 Life history traits are products of natural selection**

- Natural selection favors traits that improve an organism’s chances of survival and reproductive success.
- In every species, there are trade-offs between survival and traits such as frequency of reproduction, number of offspring produced, and investment in parental care.
- The traits that affect an organism’s schedule of reproduction and survival make up its **life history**.

**Life histories are highly diverse, but they exhibit patterns in their variability.**

- Life histories entail three basic variables: when reproduction begins, how often the organism reproduces, and how many offspring are produced during each reproductive episode.
- Life history traits are evolutionary outcomes reflected in the development, physiology, and behavior of an organism.
- Some organisms, such as the agave plant, exhibit what is known as **big-bang reproduction**, in which an individual produces a large number of offspring and then dies.
  - This is known as **semelparity**.
- By contrast, some organisms produce only a few offspring during **repeated reproductive** episodes.
  - This is known as **iteroparity**.
- What factors contribute to the evolution of semelparity versus iteroparity?
- In other words, how much does an individual gain in reproductive success through one pattern versus the other?
  - The critical factor is survival rate of the offspring.
  - When the survival of offspring is low, as in highly variable or unpredictable environments, big-bang reproduction (semelparity) is favored.
  - Repeated reproduction (iteroparity) is favored in dependable environments where competition for resources is intense.
    - In such environments, a few, well-provisioned offspring have a better chance of surviving to reproductive age.

**Limited resources mandate trade-offs between investment in reproduction and survival.**

- Organisms have finite resources, and limited resources mean trade-offs.
- Life histories represent an evolutionary resolution of several conflicting demands.
  - Sometimes we see trade-offs between survival and reproduction when resources are limited.
  - For example, red deer females have a higher mortality rate in winters following summers in which they reproduce.
- Selective pressures also influence the trade-off between number and size of offspring.
Plants and animals whose young are subject to high mortality rates often produce large numbers of relatively small offspring.

- Plants that colonize disturbed environments usually produce many small seeds, only a few of which reach suitable habitat.
- Smaller seed size may increase the chance of seedling establishment by enabling seeds to be carried longer distances to a broader range of habitats.

In other organisms, extra investment on the part of the parent greatly increases the offspring’s chances of survival.

- Oak, walnut, and coconut trees all have large seeds with a large store of energy and nutrients to help the seedlings become established.
- In animals, parental care does not always end after incubation or gestation.
- Primates provide an extended period of parental care.

Concept 52.3 The exponential model describes population growth in an idealized, unlimited environment

- All populations have a tremendous capacity for growth.
- However, unlimited population increase does not occur indefinitely for any species, either in the laboratory or in nature.
- The study of population growth in an idealized, unlimited environment reveals the capacity of species for increase and the conditions in which that capacity may be expressed.
- Imagine a hypothetical population living in an ideal, unlimited environment.
- For simplicity’s sake, we will ignore immigration and emigration and define a change in population size during a fixed time interval based on the following verbal equation.

\[
\text{Change in population size} = \frac{\text{Births during}}{\text{time interval}} - \frac{\text{Deaths during}}{\text{time interval}}
\]

- Using mathematical notation, we can express this relationship more concisely:
  - If \( N \) represents population size, and \( t \) represents time, then \( \Delta N \) is the change is population size and \( \Delta t \) is the time interval.
  - We can rewrite the verbal equation as:
    \[
    \frac{\Delta N}{\Delta t} = B - D
    \]
    where \( B \) is the number of births and \( D \) is the number of deaths.

- We can convert this simple model into one in which births and deaths are expressed as the average number of births and deaths per individual during the specified time period.
- The per capita birth rate is the number of offspring produced per unit time by an average member of the population.
  - If there are 34 births per year in a population of 1,000 individuals, the annual per capita birth rate is 34/1000, or 0.034.
- If we know the annual per capita birth rate (expressed as \( b \)), we can use the formula \( B = bN \) to calculate the expected number of births per year in a population of any size.
• Similarly, the per capita death rate (symbolized by $m$ for mortality) allows us to calculate the expected number of deaths per unit time for a population of any size.

• Now we will revise the population growth equation, using per capita birth and death rates:
  \[ \frac{\Delta N}{\Delta t} = bN - mN \]

• Population ecologists are most interested in the differences between the per capita birth rate and the per capita death rate.
  - This difference is the per capita rate of increase or $r$, which equals $b - m$.

• The value of $r$ indicates whether a population is growing ($r > 0$) or declining ($r < 0$).

• If $r = 0$, then there is zero population growth (ZPG).
  - Births and deaths still occur, but they balance exactly.

• Using the per capita rate of increase, we rewrite the equation for change in population size as:
  \[ \frac{\Delta N}{\Delta t} = rN \]

• Ecologist use differential calculus to express population growth as growth rate at a particular instant in time:
  \[ \frac{dN}{dt} = rN \]

• Population growth under ideal conditions is called exponential population growth.
  - Under these conditions, we may assume the maximum growth rate for the population ($r_{max}$), called the intrinsic rate of increase.
  - The equation for exponential population growth is:
    \[ \frac{dN}{dt} = r_{max}N \]

• The size of a population that is growing exponentially increases at a constant rate, resulting in a J-shaped growth curve when the population size is plotted over time.
  - Although the intrinsic rate of increase is constant, the population accumulates more new individuals per unit of time when it is large.
  - As a result, the curve gets steeper over time.

• A population with a high intrinsic rate of increase grows faster than one with a lower rate of increase.

• J-shaped curves are characteristic of populations that are introduced into a new or unfilled environment or whose numbers have been drastically reduced by a catastrophic event and are rebounding.

**Concept 52.4 The logistic growth model includes the concept of carrying capacity**

• Typically, resources are limited.

• As population density increases, each individual has access to an increasingly smaller share of available resources.

• Ultimately, there is a limit to the number of individuals that can occupy a habitat.
  - Ecologists define carrying capacity ($K$) as the maximum stable population size that a particular environment can support.
Carrying capacity is not fixed but varies over space and time with the abundance of limiting resources.

- Energy limitation often determines carrying capacity, although other factors, such as shelters, refuges from predators, soil nutrients, water, and suitable nesting sites can be limiting.
- If individuals cannot obtain sufficient resources to reproduce, the per capita birth rate \( b \) will decline.
- If they cannot find and consume enough energy to maintain themselves, the per capita death rate \( m \) may increase.
  - A decrease in \( b \) or an increase in \( m \) results in a lower per capita rate of increase \( r \).
- We can modify our mathematical model to incorporate changes in growth rate as the population size nears the carrying capacity.
- In the **logistic population growth** model, the per capita rate of increase declines as carrying capacity is reached.
  - Mathematically, we start with the equation for exponential growth, adding an expression that reduces the rate of increase as \( N \) increases.
  - If the maximum sustainable population size (carrying capacity) is \( K \), then \( K - N \) is the number of additional individuals the environment can accommodate and \( (K - N)/K \) is the fraction of \( K \) that is still available for population growth.
  - By multiplying the intrinsic rate of increase \( r_{\text{max}} \) by \( (K - N)/K \), we modify the growth rate of the population as \( N \) increases.
    - \( \frac{dN}{dt} = r_{\text{max}} N \left(\frac{K - N}{K}\right) \)
    - When \( N \) is small compared to \( K \), the term \( (K - N)/K \) is large and the per capita rate of increase is close to the intrinsic rate of increase.
    - When \( N \) is large and approaches \( K \), resources are limiting.
      - In this case, the term \( (K - N)/K \) is small and so is the rate of population growth.
  - Population growth is greatest when the population is approximately half of the carrying capacity.
    - At this population size, there are many reproducing individuals, and the per capita rate of increase remains relatively high.
  - The logistic model of population growth produces a sigmoid (S-shaped) growth curve when \( N \) is plotted over time.
    - New individuals are added to the population most rapidly at intermediate population sizes, when there is not only a breeding population of substantial size, but also lots of available space and other resources in the population.
    - Population growth rate slows dramatically as \( N \) approaches \( K \).
  - How well does the logistic model fit the growth of real populations?
    - The growth of laboratory populations of some organisms fits an S-shaped curve fairly well.
    - These populations are grown in a constant environment without predators or competitors.
  - Some of the assumptions built into the logistic model do not apply to all populations.
The logistic model assumes that populations adjust instantaneously and approach the carrying capacity smoothly.
- In most natural populations, there is a lag time before the negative effects of increasing population are realized.
- Populations may overshoot their carrying capacity before settling down to a relatively stable density.

Some populations fluctuate greatly, making it difficult to define the carrying capacity.

The logistic model assumes that regardless of population density, an individual added to the population has the same negative effect on population growth rate.
- Some populations show an *Allee effect*, in which individuals may have a more difficult time surviving or reproducing if the population is too small.
- Animals may not be able to find mates in the breeding season at small population sizes.
- A plant may be protected in a clump of individuals but vulnerable to excessive wind if it stands alone.

The logistic population growth model provides a basis from which we can consider how real populations grow and can construct more complex models.
- The model is useful in conservation biology for estimating how rapidly a particular population might increase in numbers after it has been reduced to a small size, or for estimating sustainable harvest rates for fish or wildlife populations.

The logistic model predicts different per capita growth rates for populations of low or high density relative to carrying capacity of the environment.
- At high densities, each individual has few resources available, and the population grows slowly.
- At low densities, per capita resources are abundant, and the population can grow rapidly.

Different life history features are favored under each condition.
- At high population density, selection favors adaptations that enable organisms to survive and reproduce with few resources.
  - Competitive ability and efficient use of resources should be favored in populations that are at or near their carrying capacity.
  - These are traits associated with iteroparity.
- At low population density, adaptations that promote rapid reproduction, such as the production of numerous, small offspring, should be favored.
  - These are traits associated with semelparity.
- Ecologists have attempted to connect these differences in favored traits at different population densities with the logistic model of population growth.
  - Selection for life history traits that are sensitive to population density is known as *K-selection*, or density-dependent selection.
    - *K*-selection tends to maximize population size and operates in populations living at a density near *K*.
  - Selection for life history traits that maximize reproductive success at low densities is known as *r-selection*, or density-independent selection.
r-selection tends to maximize \( r \), the rate of increase, and occurs in environments in which population densities fluctuate well below \( K \), or when individuals face little competition.

- Laboratory experiments suggest that different populations of the same species may show a different balance of \( K \)-selected and \( r \)-selected traits, depending on conditions.
- Many ecologists claim that the concepts of \( r \)- and \( K \)-selection oversimplify the variation seen in natural populations.

**Concept 52.5 Populations are regulated by a complex interaction of biotic and abiotic influences**

- Why do all populations eventually stop growing?
- What environmental factors stop a population from growing?
- Why do some populations show radical fluctuations in size over time, while others remain relatively stable?
- These questions have practical applications at the core of management programs for agricultural pests or endangered species.
- The first step to answering these questions is to examine the effects of increased population density on rates of birth, death, immigration, and emigration.
- **Density-dependent** factors have an increased effect on a population as population density increases.
  - This is a type of negative feedback.
- **Density-independent** factors are unrelated to population density.

**Negative feedback prevents unlimited population growth.**

- A variety of factors can cause negative feedback on population growth.
- Resource limitation in crowded populations can reduce population growth by reducing reproductive output.
  - Intraspecific competition for food can lead to declining birth rates.
- In animal populations, territoriality may limit density.
  - In this case, territory space becomes the resource for which individuals compete.
  - The presence of nonbreeding individuals in a population is an indication that territoriality is restricting population growth.
- Population density can also influence the health and thus the survival of organisms.
  - As crowding increases, the transmission rate of a disease may increase.
  - Tuberculosis, caused by bacteria that spread through the air when an infected person coughs or sneezes, affects a higher percentage of people living in high-density cities than in rural areas.
- Predation may be an important cause of density-dependent mortality for a prey species if a predator encounters and captures more food as the population density of the prey increases.
As a prey population builds up, predators may feed preferentially on that species, consuming a higher percentage of individuals.

- The accumulation of toxic wastes can contribute to density-dependent regulation of population size.
  - In wine, as yeast population increases, they accumulate alcohol during fermentation.
  - However, yeast can only withstand an alcohol percentage of approximately 13% before they begin to die.

- For some animal species, intrinsic factors appear to regulate population size.
  - White-footed mice individuals become more aggressive as population size increases, even when food and shelter are provided in abundance.
  - Eventually the population ceases to grow.
  - These behavioral changes may be due to hormonal changes, which delay sexual maturation and depress the immune system.

- All populations for which we have data show some fluctuation in numbers.
- The study of population dynamics focuses on the complex interactions between biotic and abiotic factors that cause variation in population size.
- Populations of large mammals, such as deer and moose, were once thought to remain relatively stable over time.
  - A long-term population study of a moose population on Isle Royale has challenged that view.
  - The population has had two major increases and collapses over the past 40 years.

- Large mammal populations do show much more stability than other populations.
  - Dungeness crab populations fluctuated hugely over a 40-year period.
  - One key factor causing these fluctuations is cannibalism.
    - Large numbers of juveniles are eaten by older juveniles and older crabs.
  - In addition, successful settlement of crabs is dependent on water temperatures and ocean currents.
    - Small changes in these variables cause large fluctuations in crab population numbers.

- Immigration and emigration can also influence populations.
  - This is particularly true when a group of populations is linked together to form a metapopulation.

- Some populations undergo regular boom-and-bust cycles, fluctuating in density with regularity.
  - For example, voles and lemmings tend to have 3- to 4-year cycles.
  - Ruffed grouse and ptarmigan have 9- to 11-year cycles.

- A striking example of population cycles is the 10-year cycles of lynx and snowshoe hare in northern Canada and Alaska.
- Three main hypotheses have been proposed to explain the lynx/hare cycles.
  1. The cycles may be caused by food shortage during winter.
  2. The cycles may be due to predator-prey interactions.
3. The cycles may be affected by a combination of food resource limitation and excessive predation.

- If hare cycles are due to winter food shortage, they should stop if extra food is added to a field population.
- Researchers conducted such an experiment over 20 years.
- They found that hare populations increased, but that populations of lynx and hares continued to cycle.
- The first hypothesis can be discarded.
- Field ecologists have placed radio collars on hares, to find them as they die and determine the cause of death.
- 90% of dead hares were killed by predators; none appear to have died of starvation.
- These data support the second or third hypothesis.
- Ecologists tested these hypotheses by excluding predators from one area and by both excluding predators and adding food to another area.
- The results support the hypothesis that the hare cycle is driven largely by predation but that food availability also plays an important role, especially in winter.
- Perhaps better-fed hares are more likely to escape from predators.
- Many different predators contribute to these cycles, not only lynx.
- Long-term experimental studies continue to be conducted to help unravel the complex causes of these population cycles.

**Concept 52.6 Human population growth has slowed after centuries of exponential increase**

- The concepts of population dynamics can be applied to the specific case of the human population.
- It is unlikely that any other population of large animals has ever sustained so much population growth for so long.
- The human population increased relatively slowly until about 1650 when approximately 500 million people inhabited Earth.
- The Plague took a large number of lives.
- Since then, human population numbers have doubled three times.
- The global population now numbers more than 6 billion people, and is increasing by about 73 million each year, or 201,000 people each day.
- Population ecologists predict a population of 7.3–8.4 billion people on Earth by the year 2025.
- Although the global population is still growing, the rate of growth began to slow approximately 40 years ago.
  - The rate of increase in the global population peaked at 2.19% in 1962.
  - By 2003, it had declined to 1.16%. 
• Current models project a decline in overall growth rate to just over 0.4% by 2050.
• Human population growth has departed from true exponential growth, which assumes a constant rate.
• The declines are the result of fundamental changes in population dynamics due to diseases and voluntary population control.
• To maintain population stability, a regional human population can exist in one of 2 configurations:
  Zero population growth = High birth rates − High death rates.
  Zero population growth = Low birth rates − Low death rates.
• The movement from the first toward the second state is called the **demographic transition**.
• After 1950, mortality rates declined rapidly in most developing countries.
  ° Birth rates have declined in a more variable manner.
• In the developed nations, populations are near equilibrium, with reproductive rates near the replacement level.
• In many developed nations, the reproductive rates are in fact **below** replacement level.
• These populations will eventually decline if there is no immigration and no change in birth rate.
• Most population growth is concentrated in developing countries, where 80% of the world’s people live.
• A unique feature of human population growth is the ability to control it with family planning and voluntary contraception.
  ° Reduced family size is the key to the demographic transition.
  ° Delayed marriage and reproduction help to decrease population growth rates and move a society toward zero population growth.
• However, there is disagreement among world leaders as to how much support should be provided for global family planning efforts.
• One important demographic variable is a country’s **age structure**.
• Age structure is shown as a pyramid showing the percentage of the population at each age.
  ° Age structure differs greatly from nation to nation.
  ° Age structure diagrams can predict a population’s growth trends and can point to future social conditions.
• **Infant mortality**, the number of infant deaths per 1,000 live births, and **life expectancy at birth**, the predicted average length of life at birth, also vary widely among different human populations.
  ° These differences reflect the quality of life faced by children at birth.

**Estimating Earth’s carrying capacity for humans is a complex problem.**
• Predictions of future human population vary from 7.3 to 10.3 billion people by the year 2050.
  ° Will Earth be overpopulated by this time?
Is it already overpopulated?

What is the carrying capacity of Earth for humans?

- This question is difficult to answer.
- Estimates of the answer have ranged from less than 1 billion to more than 1 trillion.

Carrying capacity is difficult to estimate, and scientists have used different methods to obtain their answers.

- Some use curves like those produced by the logistic equation to predict the future maximum human population size.
- Others generalize from existing “maximum” population density and multiply by the area of habitable land.
- Other estimates are based on a single limiting factor, usually food.

- Humans have multiple constraints. We need food, water, fuel, building materials, and other amenities.

- The concept of an ecological footprint summarizes the aggregate land and water area appropriated by each nation to produce all the resources it consumes and to absorb all the waste it generates.

- Six types of ecologically productive areas are distinguished in calculating the ecological footprint:
  1. Arable land (suitable for crops)
  2. Pasture
  3. Forest
  4. Ocean
  5. Built-up land
  6. Fossil energy land (land required for vegetation to absorb the carbon dioxide absorbed by burning fossil fuels)

- Countries vary greatly in their individual footprint size and in their available ecological capacity (the actual resource base of each country).

- The overall analysis of human impact via ecological footprints suggests that the world is at or slightly above its carrying capacity.

- We can only speculate about Earth’s ultimate carrying capacity for humans, or about the factors that will eventually limit our growth.
  - Perhaps food will be the main factor.
  - Malnutrition and famine result mainly from unequal distribution, rather than inadequate production, of food.
  - So far, technological improvements in agriculture have allowed food supplies to keep up with global population growth.
    - Environments can support a larger number of herbivores than carnivores.
  - Perhaps we will eventually be limited by suitable space.
  - Humans may run out of nonrenewable resources, such as certain metals or fossil fuels.
  - The demands of many populations have already far exceeded the local and regional supplies of water.
• More than one billion people lack access to sufficient water for basic sanitation.
  ◦ It is possible that the human population will eventually be limited by the capacity of the environment to absorb its wastes.
• Some optimists suggest that there is no practical limit to human population growth, due to our ability to develop technology.
• Exactly what the world’s carrying capacity is, and when and how we will approach it, are topics of great concern and debate.
• Unlike other organisms, we can decide whether zero population growth will be attained through social changes based on human choices or increased mortality due to resource limitation, war, or environmental degradation.
Chapter 53: Community Ecology

Overview: What Is a Community?

- A community is defined as an assemblage of species living close enough together for potential interaction.
- Communities differ in their species richness, the number of species they contain, and the relative abundance of different species.

Concept 53.1 A community’s interactions include competition, predation, herbivory, symbiosis, and disease

- There are a number of possible interspecific interactions that link the species of a community.
- Interspecific interactions can be symbolized by the positive (+) or negative (−) effects of the interaction on the individual populations.
  - 0 indicates that a population is not affected by the interaction.
  - The effect of an interaction between two species may change as circumstances change.
- **Interspecific competition** can occur when species compete for a specific limiting resource.
  - When two species compete for a resource, the result is detrimental to one or both species (−/−)
- Strong competition can lead to the local elimination of one of the two competing species, a process called **competitive exclusion**.
  - The competitive exclusion principle states that two species with similar needs for the same limiting resources cannot coexist in the same place.
- The ecological niche is the sum total of a species’ use of abiotic and biotic resources in the environment.
  - In the analogy stated by ecologist Eugene Odum, an organism’s habitat is its “address,” and the niche is the organism’s “profession.”
  - For example, the niche of a tropical tree lizard includes the temperature range it tolerates, the size of branches it perches on, the time of day when it is active, and the kind of insects it eats.
  - The competitive exclusion principle can be restated to say that two species cannot coexist in a community if their niches are identical.
  - However, ecologically similar species can coexist in a community if their niches differ in one or more significant ways.
- A species’ fundamental niche is the niche potentially occupied by that species.
  - The fundamental niche may differ from the realized niche, the niche a species actually occupies in a particular environment.
- When competition between two species with identical niches does not lead to the local extinction of either species, it is generally because evolution by natural selection results in modification of the resources used by one of the species.
Resource partitioning is the differentiation of niches that enables two similar species to coexist in a community.

Character displacement is the tendency for characteristics to be more divergent in sympatric populations of two species than in allopatric populations of the same two species.

Predation is a +/- interaction between species in which one species, the predator, kills and eats the other, the prey.

The term predation elicits images such as a lion attacking and eating an antelope.

- This interaction also includes interactions such as seed predation, in which seed-eating weevils eat plant seeds.

Natural selection favors adaptations of predators and prey.

- Predators have many feeding adaptations, including acute senses and weaponry such as claws, fangs, stingers, or poison to help catch and subdue prey.
- Predators that pursue prey are generally fast and agile; those who lie in ambush are often camouflaged.

Prey animals have evolved adaptations that help them avoid being eaten.

- Behavioral defenses include fleeing, hiding, and self-defense.
- Alarm calls may summon many individuals of the prey species to mob the predator.
- Adaptive coloration has evolved repeatedly in animals.
  - Camouflage or cryptic coloration makes prey difficult to spot against the background.
- Some animals have mechanical or chemical defenses.
  - Chemical defenses include odors and toxins.
  - Animals with effecting chemical defenses often exhibit bright warning aposematic coloration.
    * Predators are cautious in approaching potential prey with bright coloration.

One prey species may gain protection by mimicking the appearance of another prey species.

- In Batesian mimicry a harmless, palatable species mimics a harmful, unpalatable model.
- In Müllerian mimicry, two or more unpalatable species resemble each other.
  - Each species gains an additional advantage because predators are more likely to encounter an unpalatable prey and learn to avoid prey with that appearance.

Predators may also use mimicry.

- Some snapping turtles have tongues resembling wiggling worms to lure small fish.

Herbivory is a +/- interaction in which an herbivore eats parts of a plant or alga.

- Herbivores include large mammals and small invertebrates.
- Herbivores have specialized adaptations.
  - Many herbivorous insects have chemical sensors on their feet to recognize appropriate food plants.
  - Mammalian herbivores have specialized dentition and digestive systems to process vegetation.

Plants may produce chemical toxins, which may act in combination with spines and thorns to prevent herbivory.
Parasitism is a +/- symbiotic interaction in which a parasite derives its nourishment from a host, which is harmed in the process.

- Endoparasites live within the body of the host; ectoparasites live and feed on the external surface of the host.
- Parasitoidism is a special type of parasitism in which an insect (usually a wasp) lays eggs on or in living hosts.
  - The larvae feed on the body of the host, eventually killing it.
  - Many parasites have complex life cycles involving a number of hosts.
  - Some parasites change the behavior of their hosts in ways that increase the probability of the parasite being transferred from one host to another.
  - Parasites can have significant direct and indirect effects on the survival, reproduction, and density of their host populations.

Pathogens are disease-causing agents that have deleterious effects on their hosts (+/-)

- Pathogens are typically bacteria, viruses, or protists.
- Fungi and prions can also be pathogenic.

Parasites are generally large, multicellular organisms, while most pathogens are microscopic.

- Many pathogens are lethal.

Mutualism is an interspecific symbiosis in which two species benefit from their interaction (+/+).

- Examples of mutualism include nitrogen fixation by bacteria in the root nodules of legumes; digestion of cellulose by microorganisms in the guts of ruminant mammals; and the exchange of nutrients in mycorrhizae, the association of fungi and plant roots.

Mutualistic interactions may result in the evolution of related adaptations in both species.

Commensalism is an interaction that benefits one species but neither harms nor helps the other (+/0).

- Commensal interactions are difficult to document in nature because any close association between species likely affects both species, if only slightly.
- For example, “hitchhiking” species, such as the barnacles that attach to whales, are sometimes considered commensal.
  - The hitchhiking barnacles gain access to a substrate and seem to have little effect on the whale.
  - However, the barnacles may slightly reduce the host’s efficiency of movement.
  - Conversely, they may provide some camouflage.

Coevolution refers to reciprocal evolutionary adaptations of two interacting species.

- A change in one species acts as a selective force on another species, whose adaptation in turn acts as a selective force on the first species.
- The linkage of adaptations requires that genetic change in one of the interacting populations of the two species be tied to genetic change in the other population.
  - An example is the gene-for-gene recognition between a plant species and a species of virulent pathogen.
  - In contrast, the aposematic coloration of various tree frog species and the aversion reactions of various predators are not examples of coevolution.
    - These are adaptations to other organisms in the community rather than coupled genetic changes in two interacting species.
Concept 53.2 Dominant and keystone species exert strong controls on community structure

*Species diversity is a fundamental aspect of community structure.*

- A small number of species in the community exert strong control on that community’s structure, especially on the composition, relative abundance, and diversity of species.
- The *species diversity* of a community is the variety of different kinds of organisms that make up the community.
- Species diversity has two components.
  - *Species richness* is the total number of different species in the community.
  - The *relative abundance* of the different species is the proportion each species represents of the total individuals in the community.
  - Species diversity is dependent on both species richness and relative abundance.
- Measuring species diversity may be difficult, but is essential for understanding community structure and for conserving biodiversity.

*Trophic structure is a key factor in community dynamics.*

- The *trophic structure* of a community is determined by the feeding relationships between organisms.
- The transfer of food energy up the trophic levels from its source in autotrophs (usually photosynthetic organisms) through herbivores (primary consumers) and carnivores (secondary and tertiary consumers) and eventually to decomposers is called a *food chain*.
- In the 1920s, Oxford University biologist Charles Elton recognized that food chains are not isolated units but are linked together into *food webs*.
  - A food web uses arrows to link species according to who eats whom in a community.
- How are food chains linked into food webs?
  - A given species may weave into the web at more than one trophic level.
- Food webs can be simplified in two ways.
  - We can group species in a given community into broad functional groups.
    - For example, phytoplankton can be grouped as primary producers in an aquatic food web.
  - A second way to simplify a food web is to isolate a portion of the web that interacts little with the rest of the community.
- Each food chain within a food web is usually only a few links long.
  - Charles Elton pointed out that the length of most food chains is only four or five links.
- Why are food chains relatively short?
  - The *energetic hypothesis* suggests that the length of a food chain is limited by the inefficiency of energy transfer along the chain.
    - Only about 10% of the energy stored in the organic matter of each trophic level is converted to organic matter at the next trophic level.
    - The energetic hypothesis predicts that food chains should be relatively longer in habitats with higher photosynthetic productivity.
The dynamic stability hypothesis suggests that long food chains are less stable than short chains.

- Population fluctuations at lower trophic levels are magnified at higher levels, making top predators vulnerable to extinction.
  - In a variable environment, top predators must be able to recover from environmental shocks that can reduce the food supply all the way up the food chain.
- The dynamic stability hypothesis predicts that food chains should be shorter in unpredictable environments.

- Most of the available data supports the energetic hypothesis.
- Another factor that may limit the length of food chains is that, with the exception of parasites, animals tend to be larger at successive trophic levels.
- Certain species have an especially large impact on community structure because they are highly abundant or because they play a pivotal role in community dynamics.
  - The exaggerated impact of these species may occur through their trophic interactions or through their influences on the physical environment.

**Dominant species** are those species in a community that are most abundant or have the highest **biomass** (the sum weight of all individuals in a population).

- There is no single explanation for why a species becomes dominant in a community.
  - One hypothesis suggests that dominant species are competitively successful at exploiting limiting resources.
  - Another hypothesis suggests that dominant species are most successful at avoiding predation or disease.
    - This could explain why invasive species can achieve such high biomass in their new environments, in the absence of their natural predators and pathogens.
- One way to investigate the impact of a dominant species is to remove it from the community.

**Keystone species** are not necessarily abundant in a community.

- They influence community structure by their key ecological niches.
- If keystone species are removed, community structure is greatly affected.
  - Ecologist Robert Paine of the University of Washington first developed the concept of keystone species.
  - Paine removed the sea star *Pisaster ochraceous* from rocky intertidal communities.
    - *Pisaster* is a predator on mussels such as *Mytilus californianus*, a superior competitor for space in the intertidal areas.
    - After Paine removed *Pisaster*, the mussels were able to monopolize space and exclude other invertebrates and algae from attachment sites.
    - When sea stars were present, 15 to 20 species of invertebrates and algae occurred in the intertidal zone.
    - After experimental removal of *Pisaster*, species diversity declined to fewer than 5 species.
    - *Pisaster* thus acts as a keystone species, exerting an influence on community structure that is disproportionate to its abundance.
  - Some organisms exert their influence by causing physical changes in the environment that affect community structure.
An example of such a species is the beaver, which transforms landscapes by felling trees and building dams.

- Such species are called ecosystem “engineers” or “foundation species.”
- These influential species act as facilitators, with positive effects on the survival and reproduction of other species.

The structure of a community may be controlled from the bottom up by nutrients or from the top down by predators.

- Simplified models based on relationships between adjacent trophic levels are useful for discussing how communities might be organized.
  - Consider three possible relationships between plants ($V$ for vegetation) and herbivores ($H$).
    - $V \rightarrow H$, $V \leftarrow H$, $V \leftrightarrow H$
  - Arrows indicate that a change in biomass at one trophic level causes a change in biomass at in the other trophic level.

- We can define two models of community organization.
  - The bottom-up model postulates $V \rightarrow H$ linkages, in which the presence or absence of mineral nutrients ($N$) controls plant ($V$) numbers, which control herbivore ($H$) numbers, which control predator ($P$) numbers.
    - A simplified bottom-up model is $N \rightarrow V \rightarrow H \rightarrow P$.
  - The top-down model postulates that it is mainly predation that controls community organization.
    - Predators limit herbivores, which limit plants, which limit nutrient levels through the uptake of nutrients during growth and reproduction.
    - A simplified top-down model is thus $N \leftarrow V \leftarrow H \leftarrow P$.
    - The top-down control of community structure is also called the trophic cascade model.
    - The effect of any manipulation thus moves down the trophic structure as a series of $+/−$ effects.

- Many intermediate models are between extreme bottom-up and top-down models.
  - For example, all interactions between trophic levels may be reciprocal ($\leftrightarrow$).
  - The direction of interaction may alternate over time.
  - Communities vary in their relative degree of bottom-up and top-down control.

- Simplified models are valuable as a starting point for the analysis of communities.
  - Pollution has degraded freshwater lakes in many countries.
  - Because many freshwater lakes seem to be structured according to the top-down model, ecologists have a potential means of improving water quality.
    - This strategy is called biomanipulation.
    - In lakes with three trophic levels, removing fish may improve water quality by increasing zooplankton and thus decreasing algal populations.
    - In lakes with four trophic levels, adding top predators will have the same effect.

**Concept 53.3 Disturbance influences species diversity and composition**
- **Stability** is the tendency of a community to reach and maintain a relatively constant composition of species despite disturbance.
  - Many communities seem to be characterized by change rather than stability.

- The **nonequilibrium model** proposes that communities constantly change following a disturbance.

- A **disturbance** is an event that changes a community by removing organisms or altering resource availability.
  - Storms, fires, floods, droughts, frosts, human activities, or overgrazing can be disturbances.

- A disturbance can have a beneficial effect on a community.
  - Disturbances can create opportunities for species that have not previously occupied habitat in a community.
  - Small-scale disturbances can enhance environmental patchiness and thus maintain species diversity in a community.

- The **intermediate disturbance hypothesis** suggest that moderate levels of disturbance can create conditions that foster greater species diversity than low or high levels of disturbance.

- Frequent small-scale disturbances may prevent a large-scale disturbance.

- Increasing evidence suggests that some amount of nonequilibrium resulting from disturbance is the norm for communities.

**Humans are the most widespread agents of disturbance.**

- Human activities cause more disturbances than natural events do.
  - Agricultural development has disrupted the vast grasslands of the North American prairie.
  - Logging and clearing for urban development have reduced large tracts of forest to small patches of disconnected woodlots throughout North America and Europe.
  - Tropical rain forests are disappearing due to clear-cutting.

- Human-caused disturbances usually reduce species diversity in communities.

**Ecological succession is the sequence of community changes after a disturbance.**

- **Ecological succession** is the transition in species composition in disturbed areas over ecological time.

- **Primary succession** begins in a lifeless area where soil has not yet formed, such as a volcanic island or the moraine left behind as a glacier retreats.
  - Initially, only autotrophic prokaryotes may be present.
  - Next, mosses and lichens colonize and cause the development of soil.
  - Once soil is present, grasses, shrubs, and trees sprout from seeds blown or carried in from nearby areas.

- **Secondary succession** occurs where an existing community has been removed by a disturbance such as a clear-cut or fire, while the soil is left intact.
  - Herbaceous species grow first, from wind-blown or animal-borne seeds.
  - Woody shrubs replace the herbaceous species, and they in turn are replaced by forest trees.

- Early arrivals and later-arriving species are linked in one of three key processes.
1. Early arrivals may *facilitate* the appearance of later species by changing the environment.
   - For example, early herbaceous species may increase soil fertility.

2. Early species may *inhibit* establishment of later species.

3. Early species may *tolerate* later species but neither hinder nor help their colonization.

**Concept 53.4 Biogeographic factors affect community biodiversity**

- Two key factors correlated with a community’s biodiversity (species diversity) are its geographic location and its size.

- In the 1850s, both Charles Darwin and Alfred Wallace pointed out that plant and animal life were more abundant and varied in the tropics.
  - They also noted that small or remote islands have fewer species than large islands or those near continents.

- Such observations suggest that biogeographic patterns in biodiversity conform to a set of basic principles.

*Species richness generally declines along an equatorial-polar gradient.*

- Tropical habitats support much larger numbers of species of organisms than do temperate and polar regions.

- What causes these gradients?
  - The two key factors are probably evolutionary history and climate.

- Over the course of evolutionary time, species diversity may increase in a community as more speciation events occur.
  - Tropical communities are generally older than temperate or polar communities.
  - The growing season in the tropics is about five times longer than that in a tundra community.
    - Biological time thus runs five times faster in the tropics.
  - Repeated glaciation events have eliminated many temperate and polar communities.

- Climate is likely the primary cause of latitudinal gradients in biodiversity.
  - Solar energy input and water availability can be combined as a measure of evapotranspiration, the evaporation of water from soil plus the transpiration of water from plants.
    - *Actual evapotranspiration*, determined by the amount of solar radiation, temperature, and water availability, is much higher in hot areas with abundant rainfall than in areas with low temperatures or precipitation.
    - *Potential evapotranspiration*, a measure of energy availability, is determined by the amount of solar radiation and temperature.
    - The species richness of plants and animals correlates with both measures of evapotranspiration.

*Species richness is related to a community’s geographic size.*

- The *species-area curve* quantifies what may seem obvious: the larger the geographic area of a community, the greater the number of species.
  - Larger areas offer a greater diversity of habitats and microhabitats than smaller areas.
In conservation biology, developing species-area curves for the key taxa in a community allows ecologists to predict how loss of habitat is likely to affect biodiversity.

**Species richness on islands depends on island size and distance from the mainland.**

- Because of their size and isolation, islands provide excellent opportunities for studying some of the biogeographic factors that affect the species diversity of communities.
- “Islands” include oceanic islands as well as habitat islands on land, such as lakes, mountain peaks, or natural woodland fragments.
- An island is thus any patch surrounded by an environment unsuitable for the “island” species.
- Robert MacArthur and E. O. Wilson developed a general hypothesis of island biogeography to identify the key determinants of species diversity on an island with a given set of physical characteristics.
- Imagine a newly formed oceanic island that receives colonizing species from a distant mainland.
- Two factors will determine the number of species that eventually inhabit the island:
  1. The rate at which new species immigrate to the island.
  2. The rate at which species become extinct on the island.
- Two physical features of the island affect immigration and extinction rates:
  1. Its size.
  2. Its distance from the mainland.
- Small islands have lower immigration rates because potential colonizers are less likely to happen upon them.
- Small islands have higher extinction rates because they have fewer resources and less diverse habitats for colonizing species to partition.
- Islands closer to the mainland will have a higher immigration rate than islands that are farther away.
- Arriving colonists of a particular species will reduce the chance that the species will go extinct.
- At any given time, an island’s immigration and extinction rates are also affected by the number of species already present.
  - As the number of species increases, any individual reaching the island is less likely to represent a new species.
  - As more species are present, extinction rates increase because of the greater likelihood of competitive exclusion.
- The hypothesis of island biogeography predicts that a dynamic equilibrium will eventually be reached where the rate of species immigration equals the rate of species extinction.
  - The number of species at this equilibrium point is correlated with the island’s size and distance from the mainland.
- Studies of plants and animals on many island chains, including the Galapagos, support these predictions.
- The island equilibrium model has been attacked as an oversimplification.
  - Over longer periods, abiotic disturbances such as storms, adaptive evolutionary changes, and speciation may alter species composition and community structure on islands.
**Concept 53.5 Contrasting views of community structure are the subject of continuing debate**

- **The integrated hypothesis** of community structure depicts a community as an assemblage of closely linked species locked into association by mandatory biotic interactions.
  - The community functions as an integrated unit, as a superorganism.

- **The individualistic hypothesis** of community structure depicts a community as a chance assemblage of species found in the same area because they happen to have similar abiotic requirements for rainfall, temperature, or soil type.

- These two very different hypotheses suggest different priorities in studying biological communities.
  - The integrated hypothesis emphasizes assemblages of species as the essential units for understanding the interactions and distributions of species.
  - The individualistic hypothesis emphasizes single species.

- The hypotheses make contrasting predictions about how plant species should be distributed along an environmental gradient.
  - The integrated hypothesis predicts that species should be clustered into discrete communities with noticeable boundaries because the presence or absence of a particular species is largely governed by the presence or absence of other species.
  - The individualistic hypothesis predicts that communities should generally lack discrete geographic boundaries because each species has an independent, individualistic, distribution along the environmental gradient.

- In most cases where there are broad regions characterized by gradients of environmental variation, the composition of plant communities does seem to change continuously, with each species more or less independently distributed.

*The debate continues with the rivet and redundancy models.*

- The individualistic hypothesis is generally accepted by plant ecologists.
- Further debate arises when these ideas are applied to animals.
- American ecologists Anne and Paul Ehrlich proposed the **rivet model** of communities.
  - This hypothesis is a reincarnation of the interactive model and suggests that most animal species are associated with particular other species in the community.
    - Reducing or increasing the abundance of one species in a community will affect many other species.
- Australian ecologist Brian Walker’s **redundancy model** proposes that most animal species in a community are not closely associated with one another.
  - Species operate independently, and an increase or decrease in one species in a community has little effect on other species.
  - In this sense, species in a community are redundant.
  - If a predator disappears, another predatory species will take its place as a consumer of specific prey.
- The rivet and redundancy models represent extremes; most communities have some features of each model.
We still do not have enough information to answer the fundamental questions raised by these models: Are communities loose associations of species or highly integrated units?

To fully assess these models, we need to study how species interact in communities and how tight these interactions are.
Chapter 54: Ecosystems

Overview: Ecosystems, Energy, and Matter

- An ecosystem consists of all the organisms living in a community as well as all the abiotic factors with which they interact.
- The dynamics of an ecosystem involve two processes that cannot be fully described by population or community processes and phenomena: energy flow and chemical cycling.
- Energy enters most ecosystems in the form of sunlight. It is converted to chemical energy by autotrophs, passed to heterotrophs in the organic compounds of food, and dissipated as heat.
- Chemical elements are cycled among abiotic and biotic components of the ecosystem.
- Energy, unlike matter, cannot be recycled. An ecosystem must be powered by a continuous influx of energy from an external source, usually the sun.
- Energy flows through ecosystems, while matter cycles within them.

Concept 54.1 Ecosystem ecology emphasizes energy flow and chemical cycling

- Ecosystem ecologists view ecosystems as transformers of energy and processors of matter.
- We can follow the transformation of energy by grouping the species in a community into trophic levels of feeding relationships.

Ecosystems obey physical laws.

- The law of conservation of energy states that energy cannot be created or destroyed but only transformed. Plants and other photosynthetic organisms convert solar energy to chemical energy, but the total amount of energy does not change.
- The total amount of energy stored in organic molecules plus the amounts reflected and dissipated as heat must equal the total solar energy intercepted by the plant.
- The second law of thermodynamics states that some energy is lost as heat in any conversion process. We can measure the efficiency of ecological energy conversions.
- Chemical elements are continually recycled. A carbon or nitrogen atom moves from one trophic level to another and eventually to the decomposers and back again.

Trophic relationships determine the routes of energy flow and chemical cycling in ecosystems.

- Autotrophs, the primary producers of the ecosystem, ultimately support all other organisms.
Most autotrophs are photosynthetic plants, algae or bacteria that use light energy to synthesize sugars and other organic compounds.

Chemosynthetic prokaryotes are the primary producers in deep-sea hydrothermal vents.

Heterotrophs are at trophic levels above the primary producers and depend on their photosynthetic output.

Herbivores that eat primary producers are called **primary consumers**.

Carnivores that eat herbivores are called **secondary consumers**.

Carnivores that eat secondary producers are called **tertiary consumers**.

Another important group of heterotrophs is the **detritivores**, or **decomposers**.

They get energy from **detritus**, nonliving organic material such as the remains of dead organisms, feces, fallen leaves, and wood.

Detritivores play an important role in material cycling.

**Decomposition connects all trophic levels.**

The organisms that feed as detritivores form a major link between the primary producers and the consumers in an ecosystem.

Detritivores play an important role in making chemical elements available to producers.

Detritivores decompose organic material and transfer chemical elements in inorganic forms to abiotic reservoirs such as soil, water, and air.

Producers then recycle these elements into organic compounds.

An ecosystem’s main decomposers are fungi and prokaryotes.

**Concept 54.2 Physical and chemical factors limit primary production in ecosystems**

The amount of light energy converted to chemical energy by an ecosystem’s autotrophs in a given time period is an ecosystem’s **primary production**.

An ecosystem’s energy budget depends on primary production.

Most primary producers use light energy to synthesize organic molecules, which can be broken down to produce ATP.

The amount of photosynthetic production sets the spending limit of the entire ecosystem.

A global energy budget can be analyzed.

Every day, Earth is bombarded by approximately $10^{23}$ joules of solar radiation.

- The intensity of solar energy striking Earth varies with latitude, with the tropics receiving the greatest input.
- Most of this radiation is scattered, absorbed, or reflected by the atmosphere.
- Much of the solar radiation that reaches Earth’s surface lands on bare ground or bodies of water that either absorb or reflect the energy.
- Only a small fraction actually strikes algae, photosynthetic prokaryotes, or plants, and only some of this is of wavelengths suitable for photosynthesis.
Of the visible light that reaches photosynthetic organisms, only about 1% is converted to chemical energy.

Although this is a small amount, primary producers produce about 170 billion tons of organic material per year.

- Total primary production in an ecosystem is known as **gross primary production (GPP)**.
  - This is the amount of light energy that is converted into chemical energy per unit time.

- Plants use some of these molecules as fuel in their own cellular respiration.

- **Net primary production (NPP)** is equal to gross primary production minus the energy used by the primary producers for respiration (R):

\[ \text{NPP} = \text{GPP} - \text{R} \]

- To ecologists, net primary production is the key measurement, because it represents the storage of chemical energy that is available to consumers in the ecosystem.

- Primary production can be expressed as energy per unit area per unit time, or as biomass of vegetation added to the ecosystem per unit area per unit time.
  - This should not be confused with the total biomass of photosynthetic autotrophs present in a given time, which is called the **standing crop**.
  - Primary production is the amount of new biomass added in a given period of time.
  - Although a forest has a large standing cross biomass, its primary production may actually be less than that of some grasslands, which do not accumulate vegetation because animals consume the plants rapidly.

- Different ecosystems differ greatly in their production as well as in their contribution to the total production of the Earth.
  - Tropical rain forests are among the most productive terrestrial ecosystems.
  - Estuaries and coral reefs also are very productive, but they cover only a small area compared to that covered by tropical rain forests.
  - The open ocean has a relatively low production per unit area but contributes more net primary production than any other single ecosystem because of its very large size.

- Overall, terrestrial ecosystems contribute two-thirds of global net primary production, and marine ecosystems contribute approximately one-third.

**In aquatic ecosystems, light and nutrients limit primary production.**

- Light is a key variable controlling primary production in oceans, since solar radiation can only penetrate to a certain depth known as the photic zone.
  - The first meter of water absorbs more than half of the solar radiation.

- If light were the main variable limiting primary production in the ocean, we would expect production to increase along a gradient from the poles toward the equator, which receives the greatest intensity of light.
  - There is no such gradient.
  - There are parts of the ocean in the tropics and subtropics that exhibit low primary production, while some high-latitude ocean regions are relatively productive.

- More than light, nutrients limit primary production in aquatic ecosystems.
A **limiting nutrient** is an element that must be added for production to increase in a particular area.

- The nutrient most often limiting marine production is either nitrogen or phosphorus.
  - In the open ocean, nitrogen and phosphorous levels are very low in the photic zone but are higher in deeper water where light does not penetrate.
- Nitrogen is the nutrient that limits phytoplankton growth in many parts of the ocean.
  - This knowledge can be used to prevent algal blooms by limiting pollution that fertilizes phytoplankton.
- Some areas of the ocean have low phytoplankton density despite their relatively high nitrogen concentrations.
  - For example, the Sargasso Sea has a very low density of phytoplankton.
  - Nutrient-enrichment experiments showed that iron availability limits primary production in this area.
- Marine ecologists carried out large-scale field experiments in the Pacific Ocean, spreading low concentrations of dissolved iron over 72 km² of ocean.
  - A massive phytoplankton bloom occurred, with a 27-fold increase in chlorophyll concentration in water samples from test sites.
- Why are iron concentrations naturally low in certain oceanic areas?
  - Windblown dust from the land delivers iron to the ocean, and relatively little dust reaches the central Pacific and Atlantic Oceans.
- The iron factor in marine ecosystems is related to the nitrogen factor.
- When iron is limiting, adding iron stimulates the growth of cyanobacteria that fix nitrogen.
- Phytoplankton proliferate, once released from nitrogen limitation.
  - Iron → cyanobacteria → nitrogen fixation → phytoplankton production
- In areas of upwelling, nutrient-rich deep waters circulate to the ocean surface.
  - These areas have exceptionally high primary production, supporting the hypothesis that nutrient availability determines marine primary production.
  - Areas of upwelling are prime fishing locations.
- Nutrient limitation is also common in freshwater lakes.
- Sewage and fertilizer pollution can add nutrients to lakes.
- Additional nutrients shifted many lakes from phytoplankton communities dominated by diatoms and green algae to communities dominated by cyanobacteria.
  - This process is called **eutrophication** and has a wide range of ecological impacts, including the loss of most fish species.
- David Schindler of the University of Alberta conducted a series of whole lake experiments that identified phosphorus as the nutrient that limited cyanobacteria growth.
  - His research led to the use of phosphate-free detergents and other water quality reforms.

*In terrestrial ecosystems, temperature and moisture are the key factors limiting primary production.*
• Tropical rain forests, with their warm, wet conditions, are the most productive of all terrestrial ecosystems.
• By contrast, low-productivity ecosystems are generally dry (deserts) or dry and cold (arctic tundra).
• Between these extremes lie temperate forest and grassland ecosystems with moderate climates and intermediate productivity.
• These contrasts in climate can be represented by a measure called **actual evapotranspiration**, which is the amount of water annually transpired by plants and evaporated from a landscape.
  - Actual evapotranspiration increases with precipitation and with the amount of solar energy available to drive evaporation and transpiration.
• On a more local scale, mineral nutrients in the soil can play a key role in limiting primary production in terrestrial ecosystems.
• Primary production removes soil nutrients.
• A single nutrient deficiency may cause plant growth to slow and cease.
• Nitrogen and phosphorus are the soil nutrients that most commonly limit terrestrial production.
• Scientific studies relating nutrients to terrestrial primary production have practical applications in agriculture.
  - Farmers can maximize crop yields with the right balance of nutrients for the local soil and type of crop.

**Concept 54.3 Energy transfer between trophic levels is usually less than 20% efficient**
• The amount of chemical energy in consumers’ food that is converted to their own new biomass during a given time period is called the **secondary production** of an ecosystem.
• We can measure the efficiency of animals as energy transformers using the following equation:
  - production efficiency = net secondary production / assimilation of primary production
• Net secondary production is the energy stored in biomass represented by growth and reproduction.
• Assimilation consists of the total energy taken in and used for growth, reproduction, and respiration.
• **Production efficiency** is thus the fraction of food energy that is not used for respiration.
  - This differs among organisms.
    - Birds and mammals generally have low production efficiencies of between 1% and 3% because they use so much energy to maintain a constant body temperature.
    - Fishes have production efficiencies of around 10%.
- Insects are even more efficient, with production efficiencies averaging 40%.

- **Trophic efficiency** is the percentage of production transferred from one trophic level to the next.
  - Trophic efficiencies must always be less than production efficiencies because they take into account not only the energy lost through respiration and contained in feces, but also the energy in organic material at lower trophic levels that is not consumed.
  - Trophic efficiencies usually range from 5% to 20%.
  - In other words, 80–95% of the energy available at one trophic level is not transferred to the next.

- This loss is multiplied over the length of a food chain.
  - If 10% of energy is transferred from primary producers to primary consumers, and 10% of that energy is transferred to secondary consumers, then only 1% of net primary production is available to secondary consumers.

- **Pyramids of net production** represent the multiplicative loss of energy in a food chain.
  - The size of each block in the pyramid is proportional to the new production of each trophic level, expressed in energy units.

- **Biomass pyramids** represent the ecological consequences of low trophic efficiencies.
  - Most biomass pyramids narrow sharply from primary producers to top-level carnivores because energy transfers are so inefficient.
  - In some aquatic ecosystems, the pyramid is inverted and primary consumers outweigh producers.
  - Such inverted biomass pyramids occur because the producers—phytoplankton—grow, reproduce, and are consumed by zooplankton so rapidly that they never develop a large standing crop.
  - They have a short **turnover time**, which means they have a small standing crop biomass compared to their production.
    - turnover time = standing crop biomass (mg/m²) / production (mg/m²/day)
  - Because the phytoplankton replace their biomass at such a rapid rate, they can support a biomass of zooplankton much greater than their own biomass.

- Because of the progressive loss of energy along a food chain, any ecosystem cannot support a large biomass of top-level carnivores.
  - With some exceptions, predators are usually larger than the prey they eat.
  - Top-level predators tend to be fairly large animals.
  - As a result, the limited biomass at the top of an ecological pyramid is concentrated in a small number of large individuals.

- In a **pyramid of numbers**, the size of each block is proportional to the number of individuals present in each trophic level.

- The dynamics of energy through ecosystems have important implications for the human population.
  - Eating meat is an inefficient way of tapping photosynthetic production.
  - Worldwide agriculture could feed many more people if humans all fed as primary consumers, eating only plant material.

*Herbivores consume a small percentage of vegetation: the green world hypothesis.*
• According to the green world hypothesis, herbivores consume relatively little plant biomass because they are held in check by a variety of factors, including predators, parasites, and disease.

• How green is our world?
  ○ 83 \times 10^{10} metric tons of carbon are stored in the plant biomass of terrestrial ecosystems.
  ○ Herbivores annually consume less than 17% of the total net primary production.

• The green world hypothesis proposes several factors that keep herbivores in check:
  ○ Plants have defenses against herbivores.
  ○ Nutrients, not energy supply, usually limit herbivores.
    ▪ Animals need certain nutrients that plants tend to supply in relatively small amounts.
    ▪ The growth and reproduction of many herbivores are limited by availability of essential nutrients.
  ○ Abiotic factors limit herbivores.
    ▪ Temperature and moisture may restrict carrying capacities for herbivores below the level that would strip vegetation.
  ○ Intraspecific competition can limit herbivore numbers.
    ▪ Territorial behavior and competitive behaviors may reduce herbivore population density.
  ○ Interspecific interactions check herbivore densities.
    ▪ Parasites, predators, and disease limit the growth of herbivore populations.
    ▪ This applies the top-down model of community structure.

Concept 54.4 Biological and geochemical processes move nutrients between organic and inorganic parts of the ecosystem

• Chemical elements are available to ecosystems only in limited amounts.
  ○ Life on Earth depends on the recycling of essential chemical elements.

• Nutrient circuits involve both biotic and abiotic components of ecosystems and are called biogeochemical cycles.

• There are two general categories of biogeochemical cycles: global and regional.
  ○ Gaseous forms of carbon, oxygen, sulfur, and nitrogen occur in the atmosphere, and cycles of these elements are global.
  ○ Elements that are less mobile in the environment, such as phosphorus, potassium, calcium, and trace elements generally cycle on a more localized scale in the short term.
    ▪ Soil is the main abiotic reservoir for these elements.

• We will consider a general model of chemical cycling that includes the main reservoirs of elements and the processes that transfer elements between reservoirs.
  ○ Each reservoir is defined by two characteristics: whether it contains organic or inorganic materials and whether or not the materials are directly available for use by organisms.
- **Reservoir a.** The nutrients in living organisms and in detritus are available to other organisms when consumers feed and when detritivores consume nonliving organic material.

- **Reservoir b.** Some materials move to the fossilized organic reservoir as dead organisms and are buried by sedimentation over millions of years. Nutrients in fossilized deposits cannot be assimilated directly.

- **Reservoir c.** Inorganic elements and compounds that are dissolved in water or present in soil or air are available for use by organisms.

- **Reservoir d.** Inorganic elements present in rocks are not directly available for use by organisms. These nutrients may gradually become available through erosion and weathering.

- Describing biogeochemical cycles in general terms is much simpler than trying to trace elements through these cycles.
  - Ecologists study chemical cycling by adding tiny amounts of radioactive isotopes to the elements they are tracing.

**There are a number of important biogeochemical cycles.**

- We will consider the cycling of water, carbon, nitrogen, and phosphorus.

**The water cycle**

- **Biological importance**
  - Water is essential to all organisms and its availability influences rates of ecosystem processes.

- **Biologically available forms**
  - Liquid water is the primary form in which water is used.

- **Reservoirs**
  - The oceans contain 97% of the water in the biosphere.
  - 2% is bound as ice, and 1% is in lakes, rivers, and groundwater.
  - A negligible amount is in the atmosphere.

- **Key processes**
  - The main processes driving the water cycle are evaporation of liquid water by solar energy, condensation of water vapor into clouds, and precipitation.
  - Transpiration by terrestrial plants moves significant amounts of water.
  - Surface and groundwater flow returns water to the oceans.

**The carbon cycle**

- **Biological importance**
  - Organic molecules have a carbon framework.

- **Biologically available forms**
  - Autotrophs convert carbon dioxide to organic molecules that are used by heterotrophs.

- **Reservoirs**
- The major reservoirs of carbon include fossil fuels, soils, aquatic sediments, the oceans, plant and animal biomass, and the atmosphere (CO₂).

- **Key processes**
  - Photosynthesis by plants and phytoplankton fixes atmospheric CO₂.
  - CO₂ is added to the atmosphere by cellular respiration of producers and consumers.
  - Volcanoes and the burning of fossil fuels add CO₂ to the atmosphere.

*The nitrogen cycle*

- **Biological importance**
  - Nitrogen is a component of amino acids, proteins, and nucleic acids.
  - It may be a limiting plant nutrient.

- **Biologically available forms**
  - Plants and algae can use ammonium (NH₄⁺) or nitrate (NO₃⁻).
  - Various bacteria can also use NH₄⁺, NO₃⁻, or NO₂.
  - Animals can use only organic forms of nitrogen.

- **Reservoirs**
  - The major reservoir of nitrogen is the atmosphere, which is 80% nitrogen gas (N₂).
  - Nitrogen is also bound in soils and the sediments of lakes, rivers, and oceans.
  - Some nitrogen is dissolved in surface water and groundwater.
  - Nitrogen is stored in living biomass.

- **Key processes**
  - Nitrogen enters ecosystems primarily through bacterial nitrogen fixation.
    - Some nitrogen is fixed by lightning and industrial fertilizer production.
  - *Ammonification* by bacteria decomposes organic nitrogen.
  - In *nitrification*, bacteria convert NH₄⁺ to NO₃⁻.
  - In *denitrification*, bacteria use NO₃⁻ for metabolism instead of O₂, releasing N₂.

*The phosphorus cycle*

- **Biological importance**
  - Phosphorus is a component of nucleic acids, phospholipids, and ATP and other energy-storing molecules.
  - It is a mineral constituent of bones and teeth.

- **Biologically available forms**
  - The only biologically important inorganic form of phosphorus is phosphate (PO₄³⁻), which plants absorb and use to synthesize organic compounds.

- **Reservoirs**
  - The major reservoir of phosphorus is sedimentary rocks of marine origin.
  - There are also large quantities of phosphorus in soils, dissolved in the oceans, and in organisms.

- **Key processes**
Weathering of rocks gradually adds phosphate to soil.

- Some phosphate leaches into groundwater and surface water and moves to the sea.
- Phosphate may be taken up by producers and incorporated into organic material.
- It is returned to soil or water through decomposition of biomass or excretion by consumers.

**Decomposition rates largely determine the rates of nutrient cycling.**

- The rates at which nutrients cycle in different ecosystems are extremely variable as a result of variable rates of decomposition.
  - Decomposition takes an average of four to six years in temperate forests, while in a tropical rain forest, most organic material decomposes in a few months to a few years.
  - The difference is largely the result of warmer temperatures and more abundant precipitation in tropical rain forests.
- Like net primary production, the rate of decomposition increases with actual evapotranspiration.
- In tropical rain forests, relatively little organic material accumulates as leaf litter on the forest floor.
  - 75% of the nutrients in the ecosystem are present in the woody trunks of trees.
  - 10% of the nutrients are concentrated in the soil.
- In temperate forests, where decomposition is slower, the soil may contain 50% of the organic material.
- In aquatic ecosystems, decomposition in anaerobic mud of bottom sediments can take 50 years or more.
  - However, algae and aquatic plants usually assimilate nutrients directly from the water.
  - Aquatic sediments may constitute a nutrient sink.

**Nutrient cycling is strongly regulated by vegetation.**

- Long-term ecological research (LTER) monitors the dynamics of ecosystems over long periods of time.
  - The Hubbard Brook Experimental Forest has been studied since 1963.
  - The study site is a deciduous forest with several valleys, each drained by a small creek that is a tributary of Hubbard Brook.
- Preliminary studies confirmed that internal cycling within a terrestrial ecosystem conserves most of the mineral nutrients.
- Some areas were completely logged and then sprayed with herbicides for three years to prevent regrowth of plants.
  - All the original plant material was left in place to decompose.
- Water runoff from the altered watershed increased by 30–40%, apparently because there were no plants to absorb and transpire water from the soil.
  - The concentration of Ca$^{2+}$ in the creek increased four-fold, while concentration of K$^+$ increased by a factor of 15.
  - Nitrate loss was increased by a factor of 60.
• This study demonstrates that the amount of nutrients leaving an intact forest ecosystem is controlled by the plants.
• Results of the Hubbard Brook studies assess natural ecosystem dynamics and provide insight into the mechanisms by which human activities affect ecosystem processes.

**Concept 54.5 The human population is disrupting chemical cycles throughout the biosphere**

• Human activities and technologies have disrupted the trophic structure, energy flow, and chemical cycling of ecosystems worldwide.

**The human population moves nutrients from one part of the biosphere to another.**

• Human activity intrudes in nutrient cycles.
  ° Nutrients from farm soil may run off into streams and lakes, depleting nutrients in one area, causing excesses in another, and disrupting chemical cycles in both places.
  ° Humans also add entirely new materials—many toxic—to ecosystems.
• In agricultural ecosystems, a large amount of nutrients are removed from the area as crop biomass.
  ° After a while, the natural store of nutrients can become exhausted.
  ° The soil cannot be used to grow crops without nutrient supplementation.
• Nitrogen is the main nutrient lost through agriculture.
  ° Plowing and mixing the soil increase the decomposition rate of organic matter, releasing usable nitrogen that is then removed from the ecosystem when crops are harvested.
• Recent studies indicate that human activities have approximately doubled the worldwide supply of fixed nitrogen, due to the use of fertilizers, cultivation of legumes, and burning.
  ° This may increase the amount of nitrogen oxides in the atmosphere and contribute to atmospheric warming, depletion of ozone, and possibly acid precipitation.
• The key problem with excess nitrogen seems to be **critical load**, the amount of added nitrogen that can be absorbed by plants without damaging the ecosystem.
  ° Nitrogenous minerals in the soil that exceed the critical load eventually leach into groundwater or run off into freshwater and marine ecosystems, contaminating water supplies, choking waterways, and killing fish.
• Lakes are classified by nutrient availability as oligotrophic or eutrophic.
  ° In an oligotrophic lake, primary productivity is relatively low because the mineral nutrients required by phytoplankton are scarce.
  ° Overall productivity is higher in eutrophic lakes.
• Human intrusion has disrupted freshwater ecosystems by **cultural eutrophication**.
  ° Sewage and factory wastes and runoff of animal wastes from pastures and stockyards have overloaded many freshwater streams and lakes with nitrogen.
  ° This results in an explosive increase in the density of photosynthetic organisms, released from nutrient limitation.
Shallow areas become choked with weeds and algae.
- As photosynthetic organisms die and organic materials accumulate at the lake bottom, detritivores use all the available oxygen in the deeper waters.
- This can eliminate fish species.

Combustion of fossil fuels is the main cause of acid precipitation.
- The burning of fossil fuels releases oxides of sulfur and nitrogen that react with water in the atmosphere to produce sulfuric and nitric acids.
- These acids fall back to earth as acid precipitation—rain, snow, sleet or fog with a pH less than 5.6.
- Acid precipitation is a regional or global problem, rather than a local one.
  - The tall exhaust stacks built for smelters and generating plans export the problem far downwind.
- Acid precipitation lowers the pH of soil and water and affects the soil chemistry of terrestrial ecosystems.
  - With decreased pH, calcium and other nutrients leach from the soil.
  - The resulting nutrient deficiencies affect the health of plants and limit their growth.
- Freshwater ecosystems are very sensitive to acid precipitation.
  - Lakes underlain by granite bedrock have poor buffering capacity because of low bicarbonate levels.
  - Fish populations have declined in many lakes in Norway, Sweden, and Canada as pH levels fall.
    - Lake trout are keystone predators in many Canadian lakes.
    - When they are replaced by acid-tolerant species, the dynamics of food webs in the lakes change dramatically.
- Environmental regulations and new industrial technologies have led to reduced sulfur dioxide emissions in many developed countries.
  - The water chemistry of many streams and freshwater lakes is slowly improving as a result.
  - Ecologists estimate that it will take another 10 to 20 years for these ecosystems to recover, even if emissions continue to decline.
- Massive emissions of sulfur dioxide and acid precipitation continue in parts of central and eastern Europe.

Toxins can become concentrated in successive trophic levels of food webs.
- Humans introduce many toxic chemicals into ecosystems.
  - These substances are ingested and metabolized by organisms and can accumulate in the fatty tissues of animals.
  - These toxins become more concentrated in successive trophic levels of a food web, a process called biological magnification.
    - Magnification occurs because the biomass at any given trophic level is produced from a much larger biomass ingested from the level below.
    - Thus, top-level carnivores tend to be the organisms most severely affected by toxic compounds in the environment.
Many toxins cannot be degraded by microbes and persist in the environment for years or decades.

Other chemicals may be converted to more toxic products by reaction with other substances or by the metabolism of microbes.

- For example, mercury was routinely expelled into rivers and oceans in an insoluble form.
- Bacteria in the bottom mud converted it to methyl mercury, an extremely toxic soluble compound that accumulated in the tissues of organisms, including humans who fished in contaminated waters.

**Human activities may be causing climate change by increasing atmospheric carbon dioxide.**

- Since the Industrial Revolution, the concentration of CO₂ in the atmosphere has increased greatly as a result of burning fossil fuels and wood removed by deforestation.
  - The average CO₂ concentration in the environment was 274 ppm before 1850.
  - Measurements in 1958 read 316 ppm and have increased to 370 ppm today.
- If CO₂ emissions continue to increase at the present rate, the atmospheric concentration of this gas will be double what it was at the start of the Industrial Revolution by the year 2075.
- Increased productivity by vegetation is one consequence of increasing CO₂ levels.
- Because C₃ plants are more limited than C₄ plants by CO₂ availability, one effect of increasing CO₂ levels may be the spread of C₃ species into terrestrial habitats previously favoring C₄ plants.
  - For example, corn may be replaced on farms by wheat and soybeans.
- To assess the effect of rising levels of atmospheric CO₂ on temperate forests, scientists at Duke University began the Forest-Atmosphere Carbon Transfer and Storage (FACTS-1) experiment.
  - The FACTS-1 study is testing how elevated CO₂ influences tree growth, carbon concentration in soils, insect populations, soil moisture, understory plant growth, and other factors over a ten-year period.
- Rising atmospheric CO₂ levels may have an impact on Earth’s heat budget.
  - When light energy hits the Earth, much of it is reflected off the surface.
    - CO₂ causes the Earth to retain some of the energy that would ordinarily escape the atmosphere.
      - This phenomenon is called the **greenhouse effect**.
      - If it were not for this effect, the average air temperature on Earth would be −18°C.
      - A number of studies predict that by the end of the 21st century, atmospheric CO₂ concentration will have doubled and average global temperature will rise by 2°C.
- An increase of only 1.3°C would make the world warmer than at any time in the past 100,000 years.
  - If increased temperatures caused the polar ice caps to melt, sea levels would rise by an estimated 100 m, flooding coastal areas 150 km inland from current coastlines.
A warming trend would also alter geographic distribution of precipitation, making major U.S. agricultural areas much drier.

- Scientists continue to construct models to predict how increasing levels of CO₂ in the atmosphere will affect Earth.
- Global warming is a problem of uncertain consequences and no certain solutions.
- Stabilizing CO₂ emissions will require concerted international effort and the acceptance of dramatic changes in personal lifestyles and industrial processes.
- Many ecologists think that this effort suffered a major setback in 2001, when the United States pulled out of the Kyoto Protocol, a 1997 pledge by industrialized nations to reduce their CO₂ output by 5% over a ten-year period.

**Human activities are depleting atmospheric ozone.**

- Life on earth is protected from the damaging affects of ultraviolet radiation (UV) by a layer of O₃, or ozone, that is present in the lower stratosphere.
- Studies suggest that the ozone layer has been gradually “thinning” since 1975.
- The destruction of ozone probably results from the accumulation of CFCs, or chlorofluorocarbons—chemicals used in refrigeration, as propellant in aerosol cans, and for certain manufacturing processes.
  - The breakdown products from these chemicals rise to the stratosphere, where the chlorine they contain reacts with ozone to reduce it to O₂.
    - Subsequent reactions liberate the chlorine, allowing it to react with other ozone molecules in a catalytic chain reaction.
    - At middle latitudes, ozone levels have decreased by 2–10% during the past 20 years.
  - The result of a reduction in the ozone layer may be increased levels of UV radiation that reach the surface of the Earth.
    - Some scientists expect increases in skin cancer and cataracts, as well as unpredictable effects on crops and natural communities.
    - Even if all chlorofluorocarbons were banned globally today, chlorine molecules already present in the atmosphere will continue to reduce ozone levels for at least a century.
- The impact of human activity on the ozone layer is one more example of how much we are able to disrupt ecosystems and the entire biosphere.