Advanced Placement Biology

Summer Assignment

Textbook: Biology 5th & **8th** edition and by Campbell, Reece and Mitchell. The **8th** edition book must be checked out from the library by **June 8th**.

Assignment: Read chapters 50-53. Define the Key Terms and answer the Objective Questions for each chapter. All 3 chapters (6 assignments) are due the 1st day of school. There will be a quiz on the 2nd day of school covering chapters 50-53. Join Google Classroom with the code “mexeu8” and access the pdf. Eventually the Key Terms and Objectives can be found at the Haiku website. Click on “AP Biology” and then click on “Ch. 33-55 lecture notes”. Scroll down to Ch.50. The homework will be found on the 1st or 2nd page of each chapter. Please DO NOT type any homework assignments due to rampant plagiarisms in previous years and place each of the 6 assignments on separate pages. Any questions about the assignments can be asked through my email: rreta@tustin.k12.ca.us.

Please note that online homework chapter numbers do not align with new textbook chapter numbers due to the author dying before publishing new homework.

Please realize that Advance Placement Biology is a University level biology class for biology majors. It requires a very significant commitment of time, energy, maturity and dedication to the class to succeed. I hope you have fun and safe summer, see you in September.

Mr. Reta

CHAPTER 33
INVERTEBRATES

OUTLINE

I. The Parazoa
   A. Phylum Porifera: sponges are sessile with porous bodies and choanocytes

II. The Radiata
   A. Phylum Cnidaria: cnidarians have radial symmetry, a gastrovascular cavity, and cnidocytes
   B. Phylum Ctenophora: comb jellies possess rows of ciliary plates and adhesive colloblasts

III. The Acoelomates
   A. Phylum Platyhelminthes: flatworms are dorsoventrally flattened acoelomates

IV. The Pseudocoelomates
   A. Phylum Rotifera: rotifers have jaws and a crown of cilia
   B. Phylum Nematoda: roundworms are unsegmented and cylindrical with tapered ends

V. The Coelomates: Protostomes
   A. Phylum Nemertea: The phylogenetic position of proboscis worms is uncertain
   B. The lophophorate phyla: bryozoans, phoronids, and brachiopods have ciliated tentacles around their mouths
   C. Phylum Mollusca: mollusks have a muscular foot, a visceral mass, and a mantle
   D. Phylum Annelida: annelids are segmented worms
   E. Phylum Arthropoda: arthropods have regional segmentation, jointed appendages, and an exoskeleton

VI. The Coelomates: Deuterostomes
   A. Phylum Echinodermata: Echinoderms have a water vascular system and secondary radial symmetry
   B. Phylum Chordata: the chordates include two invertebrate subphyla and all vertebrates

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. From a diagram, identify the parts of a sponge and describe the function of each including the spongocoel, porocyte, epidermis, choanocyte, mesohyl, amoebocyte, osculum, and spicule.
2. List characteristics of the phylum Cnidaria that distinguish it from the other animal phyla.
3. Describe the two basic body plans in Cnidaria and their role in Cnidarian life cycles.
4. List the three classes of Cnidaria and distinguish among them based upon life cycle and

morphological characteristics.

5. List characteristics of the phylum Ctenophora that distinguish it from the other animal phyla.
6. List characteristics that are shared by all bilaterally symmetrical animals.
7. List characteristics of the phylum Platyhelminthes that distinguish it from the other animal phyla.
8. Distinguish among the four classes of Platyhelminthes and give examples of each.
9. Describe the generalized life cycle of a trematode and give an example of one fluke that parasitizes humans.
10. Describe the anatomy and generalized life cycle of a tapeworm.
11. List distinguishing characteristics descriptive of the phylum Nemertea.
12. Explain why biologists believe proboscis worms evolved from flatworms.
13. Describe features of digestive and circulatory systems that have evolved in the Nemertea and are not found in other acoelomate phyla.
14. Describe unique features of rotifers that distinguish them from other pseudocoelomates.
15. Define parthenogenesis and describe alternative forms of rotifer reproduction.
16. List characteristics of the phylum Nematoda that distinguish it from other pseudocoelomates.
17. Give examples of both parasitic and free-living species of nematodes.
18. List characteristics that distinguish the phylum Mollusca from the other animal phyla.
19. Describe the basic body plan of a mollusk and explain how it has been modified in the Polyplacophora, Gastropoda, Bivalvia, and Cephalopoda.
20. Distinguish among the following four Molluscan classes and give examples of each:

    a. Polyplacophora c. Bivalvia
    b. Gastropoda d. Cephalopoda

21. Explain why some zoologists believe the mollusks evolved from ancestral annelids while others propose that mollusks arose from flatworm-like ancestors.
22. List characteristics that distinguish the phylum Annelida from the other animal phyla.
23. Explain how a fluid-filled septate coelom is used by annelids for burrowing.
24. Distinguish among the classes of annelids and give examples of each.
25. List characteristics of arthropods that distinguish them from the other animal phyla.
26. Describe advantages and disadvantages of an exoskeleton.
27. Distinguish between hemocoel and coelom.
28. Provide evidence for an evolutionary link between the Annelida and Arthropoda.
29. Describe major independent arthropod lines of evolution represented by the subphyla:

    a. Trilobitomorpha c. Crustacea
    b. Cheliceriformes d. Uniramia

30. Explain what arthropod structure was a preadaptation for living on land.
31. Distinguish among the following arthropod classes and give an example of each:

    a. Arachnida d. Chilopoda
    b. Crustacea e. Insecta
    c. Diplopoda

32. Distinguish between incomplete metamorphosis and complete metamorphosis.
33. Define lophophore and list three lophophorate phyla.
34. Explain why lophophorates are difficult to assign as protostomes or deuterostomes.
35. List at least four characteristics shared by the deuterostome phyla that distinguish them from protostomes.

36. List characteristics of echinoderms that distinguish them from other animal phyla.
37. Describe the structures and function of a water vascular system, including ring canal, radial canal, tube feet and ampulla.
38. Distinguish among the classes of echinoderms and give examples of each.

KEY TERMS

invertebrates
spongocoel
osculum
choanocyte
mesohyl
amoebocyte
hermaphrodites
gastrovascular cavity
polyp
medusa
cnidocytes
cnidae
radula
Class Arachnida
complete digestive tract
parthenogenesis
closed circulatory system
lophophorate animals
lophophore
bryozoans
phoronids
brachiopods
foot
visceral mass
mantle
mantle cavity
eurypterids
planarian
ammonites
Class Chilopodia
cuticle
exoskeleton
molting
open circulatory system
trilobite
Chelicerates
Uniramians
Crustaceans
chelicerae
mandibles
antennae
compound eyes
colloblasts
torsion
Class Diplodia
Class Insecta
entomology
Malpighian tubules
tracheal system
incomplete metamorphosis
complete metamorphosis
echinoderms
water vascular system
tube feet
nematocysts
trochophore
book lungs
metanephridia

LECTURE NOTES

Over one million species of animals are living today; 95% of these are invertebrates.

- Most are aquatic.
- The most familiar belong to the subphylum Vertebrata of the phylum Chordata. This is only about 5% of the total.

I. The Parazoa

A. Phylum Porifera: sponges are sessile with porous bodies and choanocytes

The sponges, in the phylum Porifera, are the only members of the subkingdom Parazoa due to their unique development and simple anatomy (see Campbell, Figure 33.1).

- Approximately 9000 species, mostly marine with only about 100 in fresh water
- Lack true tissues and organs, and contain only two layers of loosely associated unspecialized cells
- No nerves or muscles, but individual cells detect and react to environmental changes
- Size ranges from 1 cm to 2 m
- All are suspension-feeders (= filter-feeders)
- Possibly evolved from colonial choanoflagellates

Parts of the sponge include (see Campbell, Figure 33.2):

- *Spongocoel* = Central cavity of sponge
- *Osculum* = Larger excurrent opening of the spongocoel
- *Epidermis* = Single layer of flattened cells which forms outer surface of the sponge

- *Porocyte* = Cells which form pores; possess a hollow channel through the center which extends from the outer surface (incurrent pore) to spongocoel
- *Choanocyte* = Collar cell, majority of cells which line the spongocoel; possess a flagellum which is ringed by a collar of fingerlike projections. Flagellar movement moves water and food particles which are trapped on the collar and later phagocytized.
- *Mesohyl* = The gelatinous layer located between the two layers of the sponge body wall (epidermis and choanocytes)
- *Amoebocyte* = Wandering, pseudopod bearing cells in the mesohyl; function in food uptake from choanocytes, food digestion, nutrient distribution to other cells, formation of skeletal fibers, gamete formation
- *Spicule* = Sharp, calcium carbonate or silica structures in the mesohyl which form the skeletal fibers of many sponges
- *Spongin* = Flexible, proteinaceous skeletal fibers in the mesohyl of some sponges

Most sponges are hermaphrodites, but usually cross-fertilize.

- Eggs and sperm form in the mesohyl from differentiated amoebocytes or choanocytes.
- Eggs remain in the mesohyl.
- Sperm are released into excurrent flow of the spongocoel and are then drawn in with incurrent flow of another sponge.
- Sperm penetrate into mesohyl and fertilize the eggs.
- The zygote develops into a flagellated larva which is released into the spongocoel and escapes with the excurrent water through the osculum.
- Surviving larvae settle on the substratum and develop. In most cases the larva turns inside-out during metamorphosis, moving the flagellated cells to the inside.

Sponges possess extensive regeneration abilities for repair and asexual reproduction.

II. The Radiata

The branch radiata is composed of phylum Cnidaria and phylum Ctenophora

A. Phylum Cnidaria: Cnidarians have radial symmetry, a gastrovascular cavity, and cnidocytes

There are more than 10,000 species in the phylum Cnidaria, most of which are marine. The phylum contains hydras, jellyfish, sea anemones and coral animals.

Some characteristics of cnidarians include:

- Radial symmetry
- Diploblastic
- Simple, sac-like body
- *Gastrovascular cavity*, a central digestive cavity with only one opening (functions as mouth and anus)

There are two possible cnidarian body plans: sessile polyp and motile, floating medusa (see Campbell, Figure 33.3). Some species of cnidarians exist only as polyps, some only as medusae, and others are dimorphic (both polyp and medusa stages in their life cycles).

Polyp = Cylindrical form which adheres to the substratum by the aboral end of the body stalk and extends tentacles around the oral end to contact prey

Medusa = Flattened, oral opening down, bell-shaped form; moves freely in water by passive drifting and weak bell contractions; tentacles dangle from the oral surface which points downward.

Cnidarians are carnivorous.

- Tentacles around the mouth/anus capture prey animals and push them through the mouth/anus into the gastrovascular cavity.
- Digestion begins in the gastrovascular cavity with the undigested remains being expelled through the mouth/anus.
- Tentacles are armed with stinging cells, called cnidocytes—after which the Cnidaria are named.

Cnidocytes = Specialized cells of cnidarian epidermis that contain eversible capsule-like organelles, or *cnidae*, used in defense and capture of prey (see Campbell, Figure 33.4). Nematocysts are stinging capsules.

The simplest forms of muscles and nerves occur in the phylum Cnidaria.

- Epidermal and gastrodermal cells have bundles of microfilaments arranged into contractile fibers.

  The gastrovascular cavity, when filled with water, acts as a hydrostatic skeleton against which the contractile fibers can work to change the animal's shape.

- A simple nerve net coordinates movement; no brain is present.

  The nerve net is associated with simple sensory receptors radially distributed on the body. This permits stimuli to be detected and responded to from all directions.

There are three major classes of cnidarians (see Campbell, Figure 33.5 and Table 33.1):

1. **Class Hydrozoa**

   Most hydrozoans alternate polyp and medusa forms in the life cycle although the polyp is the dominant stage. Some are colonial (e.g., *Obelia*, Campbell, Figure 33.6), while others are solitary (e.g., *Hydra*).

   Hydra is unique in that only the polyp stage is present.

   - They usually reproduce asexually by budding; however, in unfavorable conditions they reproduce sexually. In this case a resistant zygote is formed and remains dormant until environmental conditions improve.

2. **Class Scyphozoa**

   The planktonic medusa (jellyfish) is the most prominent stage of the life cycle.

   - Coastal species usually pass through a small polyp stage during the life cycle.
   - Open ocean species have eliminated the polyp entirely.

3. **Class Anthozoa**

   This class contains sea anemones and coral animals.

   They only occur as polyps.

   Coral animals may be solitary or colonial and secrete external skeletons of calcium carbonate.

   - Each polyp generation builds on the skeletal remains of earlier generations. In this way, coral reefs are formed.
   - Coral is the rock-like external skeletons.

B. Phylum Ctenophora: combjellies possess rows of ciliary plates and adhesive colloblasts

This phylum contains the comb jellies. There are about 100 species, all of which are marine.

Some characteristics of ctenophores include:

- A resemblance to the medusa of Cnidarians in that the body of most is spherical or ovoid; a few are elongate and ribbonlike.
- Transparent body, 1 - 10 cm in diameter (spherical/ovoid forms) or up to 1 m long (ribbonlike forms) (see Campbell, Figure 33.7)
- Eight rows of comblike plates composed of fused cilia which are used for locomotion
- One pair of long retractable tentacles that function in capturing food; these tentacles have adhesive structures called *colloblasts.*
- A sensory organ containing calcareous particles is present.

  The particles settle to the low point of the organ which then acts as an orientation cue.

  Nerves extending from the sensory organ to the combs of cilia coordinate movement.

III. The Acoelomates

A. Phylum Platyhelminthes: flatworms are dorsoventrally flattened acoelomates

The members of the phylum Platyhelminthes differ from the phylum Cnidaria in that they:

- Exhibit bilateral symmetry with moderate cephalization
- Are triploblastic (develop from three-layered embryos: ectoderm, endoderm and mesoderm)
- Possess several distinct organs, organ systems, and true muscles

Although more advanced than cnidarians, two things point to the early evolution of platyhelminths in bilateria history.

- A gastrovascular cavity is present.
- They have an acoelomate body plan.

There are more than 20,000 species of Platyhelminthes which are divided into four classes (see Campbell, Table 33.2):

- Class Turbellaria
- Classes Trematoda and Monogenea
- Class Cestoda

1. Class Turbellaria

Mostly free-living, marine species; a few species are found in freshwater and moist terrestrial habitats (see Campbell, Figure 33.8).

Planarians are familiar and common freshwater forms (see Campbell, Figure 33.9).

- Carnivorous, they feed on small animals and carrion
- Lack specialized organs for gas exchange or circulation

  Gas exchange is by diffusion (flattened body form places all cells close to water).

  Fine branching gastrovascular cavity distributes food throughout the animal.
- Flame cell excretory apparatus present which functions primarily to maintain osmotic balance of the animal.

Nitrogenous waste (ammonia) diffuses directly from cells to the water.

- Move by using cilia on the ventral dermis to glide along a film of mucus. Muscular contractions produce undulations which allow some to swim.
- On the head are a pair of eyespots which detect light and a pair of lateral auricles that are olfactory sensors.

  Possess a rudimentary brain which is capable of simple learning.
- Reproduce either asexually or sexually.

  Asexually by regeneration: mid-body constriction separates the parent into two halves, each of which regenerates the missing portion

  Sexually by cross-fertilization of these hermaphroditic forms

2. Classes Monogenea and Trematoda

All members of these two classes are parasitic.

Flukes are members of the class Trematoda.

- Suckers are usually present for attaching to host internal organs.
- Primary organ system is the reproductive system; a majority are hermaphroditic.
- Life cycles include alternations of sexual and asexual stages with asexual development taking place in an intermediate host.

  Larvae produced by asexual development infect the final hosts where maturation and sexual reproduction occurs (see Campbell, Figure 33.10)
- *Schistosoma* spp. (blood flukes) infect 200 million people worldwide.

Members of the class Monogenea are mostly external parasites of fish.

- Structures with large and small hooks are used for attaching to the host animal.
- All are hermaphroditic and reproduce sexually.

3. Class Cestoidea

Adult tapeworms parasitize the digestive system of vertebrates.

- Possess a scolex (head) which may be armed with suckers and/or hooks that help maintain position by attaching to the intestinal lining (see Campbell, Figure 33.11).
- Posterior to the scolex is a long ribbon of units called proglottids.

  A proglottid is filled with reproductive organs.
- No digestive system is present.

The life cycle of a tapeworm includes an intermediate host.

- Mature proglottids filled with eggs are released from the posterior end of the worm and pass from the body with the feces.
- Eggs are eaten by an intermediate host and a larva develops, usually in muscle tissue.

  The final host becomes infected when it eats an intermediate host containing larvae.
- Humans can become infected with some species of tapeworms by eating undercooked beef or pork containing larvae.

IV. The Pseudocoelomates

The pseudocoelomate body plan probably arose independently several times.

A. Phylum Rotifera: rotifers have jaws and a crown of cilia

There are approximately 1800 species of rotifers. They are small, mainly freshwater organisms, although some are marine and others are found in damp soil.

- Size ranges from 0.05-2.0 mm
- Pseudocoelomate with the pseudocoelomic fluid serving as a hydrostatic skeleton and as a medium which transports nutrients and wastes when the body moves
- *Complete digestive system* is present.

  Rotifer refers to the crown of cilia that draws a vortex of water into the mouth.

  Posterior to the mouth, a jawlike organ grinds the microscopic food organisms suspended in the water.

Reproduction in rotifers may be by *parthenogenesis* or sexual.

- Some species consist only of females with new females developing by parthenogenesis from unfertilized eggs.
- Other species produce two types of eggs, one that develops into females, the other into degenerate males.

  Males produce sperm that fertilize eggs which develop into resistant zygotes that survive desiccation.

  When conditions improve, the zygotes break dormancy and develop into a new female generation that reproduces by parthenogenesis until unfavorable conditions return.

- Rotifers have no regeneration or repair abilities.

Rotifers contain a certain and consistent number of cells as adults. The zygotes undergo a specific number of divisions and the adult contains a fixed number of cells.

B. Phylum Nematoda: roundworms are unsegmented and cylindrical with tapered ends

There are about 90,000 species of roundworms, ranging in size from less than 1.0 mm to more than 1 m.

- Bodies are cylindrical with tapered ends
- Very numerous in both species and individuals
- Found in fresh water, marine, moist soil, tissues of plants, and tissues and body fluids of animals
- A complete digestive tract is present and nutrients are transported through the body in the pseudocoelomic fluid
- A tough, transparent cuticle forms the outer body covering (see Campbell, Figure 33.12a)
- Longitudinal muscles are present and provide for whip-like movements
- Dioecious with females larger than males
- Sexual reproduction only, with internal fertilization
- Female may produce 100,000 or more resistant eggs per day
- Like rotifers, nematodes have a fixed number of cells as adults

Nematodes fill various roles in the community.

- Free-living forms are important in decomposition and nutrient cycling.
- Plant parasitic forms are important agricultural pests.
- Animal parasitic forms can be hazardous to health (*Trichinella spiralis* in humans via undercooked infected pork) (see Campbell, Figure 33.13b).

- One species, *Caenorhabitis elegans*, is cultured extensively and is a model species for the study of development.

V. The Coelomates: Protostomes

The protostome lineage of coelomate animals gave rise to many phyla. In many, the coelom functions as a hydrostatic skeleton (e.g., mollusks, annelids).

A. Phylum Nemertea: the phylogenetic position of proboscis worms is uncertain

There are about 900 species, most are marine with a few in fresh water and damp soil.

The phylum Nemertea contains the proboscis worms (see Campbell, Figure 33.14)

- Sizes range from 1 mm to more than 30 m.
- Some active swimmers, others burrow in sand.
- Possess a long, retractable hollow tube (proboscis) which is used to probe the environment, capture prey, and as defense against predators.
- Excretory, sensory, and nervous systems are similar to planarians.
- Structurally acoelomate, like flatworms.

There are some important differences between the Nemertea and Platyhelminthes:

- Nemertea possess a closed circulatory system, which consists of vessels through which blood flows. Some species have red blood cells containing a form of hemoglobin which transports oxygen. No heart is present, but body muscle contractions move the blood through vessels.
- Nemertea possess a complete digestive system with a mouth and an anus.

The phylogenetic position of the Nemertea is uncertain.

- Although the body is structurally acoelomate, the fluid-filled proboscis sac is considered a true coelom by some researchers.
- A simple blood vascular system and a complete digestive system are characteristics shared with more advanced phyla.

B. The lophophorate phyla: bryozoans, phoronids, and brachiopods have ciliated tentacles around their mouths

The lophophorate animals contain three phyla: Phoronida, Bryozoa and Brachiopoda.

- These three phyla are grouped together due to presence of a lophophore (see Campbell, Figure 33.15)

Lophophore = Horseshoe-shaped or circular fold of the body wall bearing ciliated tentacles that surround the mouth at the anterior end of the animal.

- Cilia direct water toward the mouth between the tentacles which trap food particles for these suspension-feeders.
- The presence of a lophophore in all three groups suggests a relationship among these phyla.

The three phyla also possess a U-shaped digestive tract (the anus lies outside of the tentacles) and have no distinct head—both adaptations for a sessile existence.

Lophophorates are difficult to assign as protostomes or deuterostomes.

- Their embryonic development more closely resembles deuterostomes; however, in the Phoronida, the blastopore develops into the adult mouth.
- Molecular systematics places the lophophorate phyla closer to the protostomes than the deuterostomes.

1. Bryozoans

This phylum contains the moss animals. There are about 5000 species which are mostly marine and are widespread.

Bryozoans are small, colonial forms (see Campbell, Figure 33.15a)

- In most, the colony is enclosed within a hard exoskeleton and the lophophores are extended through pores when feeding.
- Some are important reef builders.

2. Phoronids

This phylum contains about 15 species of tube-dwelling marine worms.

- Length from 1 mm to 50 cm
- Phoronids live buried in sand in chitinous tubes with the lophophore extended from the tube when feeding.

3. Brachiopods

The phylum Brachiopoda contains the lamp shells. There are approximately 330 extant species, all marine.

- More than 30,000 fossil species of the Paleozoic and Mesozoic have been identified.

The body of a brachiopod is enclosed by dorsal and ventral shell halves (see Campbell, Figure 33.15b)

- Attach to the substratum by a stalk
- Open the shell slightly to allow water to flow through the lophophore

C. Phylum Mollusca: mollusks have a muscular foot, visceral mass, and a mantle

There are more than 50,000 species of snails, slugs, oysters, clams, octopuses, and squids.

Mollusks are mainly marine, though some inhabit fresh water and many snails and slugs are terrestrial.

Mollusks are soft-bodied, but most are protected by a hard calcium carbonate shell.

- Squids and octopuses have reduced, internalized shells or no shell.

The molluscan body consists of three primary parts: muscular *foot* for locomotion, a *visceral mass* containing most of the internal organs, and a *mantle,* which is a heavy fold of tissue that surrounds the visceral mass and secretes the shell (see Campbell, Figure 33.16).

A *radula* is present in many and functions as a rasping tongue to scrap food from surfaces.

Some species are monoecious while most are dioecious.

- Gonads are located in the visceral mass.

Some zoologists believe the mollusks evolved from annelid-like ancestors (although true segmentation is absent in mollusca) because the life cycle of many mollusks includes a ciliated larva, called a *trochophore,* which also is characteristic of annelids, while others believe that mollusks arose earlier in the protostome lineage before segmentation evolved.

1. Class Polyplacophora

The class Polyplacophora contains the marine species known as chitons.

- They have an oval shape with the shell divided into eight dorsal plates (see Campbell, Figure 33.17).
- Cling to rocks along the shore at low tide using the foot as a suction cup to grip the rock. This muscular foot also allows it to creep slowly over the rock surface.
- A radula is used to cut and ingest (“graze”) algae.

2. Class Gastropoda

The class Gastropoda contains the snails and slugs.

- Largest molluscan class with more than 40,000 species
- Mostly marine, but many species are freshwater or terrestrial
- *Torsion* during embryonic development is a distinctive characteristic:

  Uneven growth in the visceral mass causes the visceral mass to rotate 180°, placing the anus above the head in adults (see Campbell, Figure 33.18).
- Body protected by a shell (absent in slugs and nudibranchs) which may be conical or flattened (see Campbell, Figure 33.19).
- Many species have distinct heads with eyes at the tips of tentacles.
- Movement results from a rippling motion along the elongated foot.
- Most gastropods are herbivorous, using the radula to graze on plant material; several groups are predatory and possess modified radulae.
- Most aquatic gastropods exchange gases via gills; terrestrial forms have lost the gills and utilize a vascularized lining of the mantle cavity for gas exchange.

3. Class Bivalvia

The class Bivalvia contains the clams, oysters, mussels and scallops.

Possess a shell divided into two halves (see Campbell, Figure 33.20).

- The shell halves are hinged at the mid-dorsal line and are drawn together by two adductor muscles to protect the animal.
- Bivalves may extend the foot for motility or anchorage when the shell is open.
- The mantle cavity (between shells) contains gills which function in gas exchange and feeding.

Most are suspension-feeders and they trap small food particles in the mucus coating of the gills and then use cilia to move the particles to the mouth.

Water enters the mantle cavity through an incurrent siphon, passes over the gills, and then exits through an excurrent siphon.

No radula or distinct head is present.

Bivalves lead sedentary lives. They use the foot as an anchor in sand or mud. Sessile mussels secrete threads that anchor them to rocks, docks or other hard surfaces.

Scallops can propel themselves along the sea floor by flapping their shells.

4. Class Cephalopoda

The Class Cephalopoda contains the squids and octopuses.

Cephalopods are agile carnivores (see Campbell, Figure 33.22).

- Use beak-like jaws to crush prey
- The mouth is at the center of several long tentacles

A mantle covers the visceral mass, but the shell is either reduced and internal (squids) or totally absent (octopuses).

- The chambered nautilus is the only shelled cephalopod alive today.
- Squids swim backwards in open water by drawing water into the mantle cavity, and then firing a jetstream of water through the excurrent siphon which points anteriorly.

  Directional changes can be made by pointing the siphon in different directions.

  Most squid are less than 75 cm long but the giant squid may reach 17 m and weigh 2 tons.

- Octopuses usually don't swim in open water, but move along the sea floor in search of food.

Cephalopods are the only mollusks with a *closed circulatory system* in which the blood is always contained in vessels.

Cephalopods have well developed nervous systems with complex brains capable of learning. They also have well developed sense organs.

The cephalopod ancestors were probably shelled, carnivorous forms - the *ammonites.*

- These cephalopods were the dominant invertebrate predators in the oceans until they became extinct at the end of the Cretaceous.

D. Phylum Annelida: annelids are segmented worms

The presence of a true coelom and segmentation are two important evolutionary advances present in the annelids.

- The coelom serves as a hydrostatic skeleton, permits development of complex organ systems, protects internal structures, and permits the internal organs to function separately from the body wall muscles.
- Segmentation also provided for the specialization of different body regions.

There are more than 15,000 species of annelids.

- They have segmented bodies and range in size from less than 1 mm to 3 m.
- There are marine, freshwater, and terrestrial (in damp soil) annelids.

Annelids have a coelom partitioned by septa. The digestive tract, longitudinal blood vessels, and nerve cords penetrate the septa and extend the length of the animal (see Campbell, Figure 33.23.)

The complete digestive system is divided into several parts, each specialized for a specific function in digestion:

pharynx → esophagus → crop → gizzard → intestine

Annelids have a closed circulatory system.

- Hemoglobin is present in blood cells.
- Dorsal and ventral longitudinal vessels are connected by segmental pairs of vessels.
- Five pairs of hearts circle the esophagus.
- Numerous tiny vessels in the skin permit gas exchange is across the body surface.

An excretory system of paired *metanephridia* is found in each segment; each metanephridium has a nephrostome (which removes wastes from the coelomic fluid and blood) and exits the body through an exterior pore.

The annelid nervous system is composed of a pair of cerebral ganglia lying above and anterior to the pharynx.

- A nerve ring around the pharynx connects these ganglia to a subpharyngeal ganglion, from which a pair of fused nerve cords run posteriorly.
- Along the ventral nerve cords are fused segmental ganglia.

Annelids are hermaphroditic but cross-fertilize during sexual reproduction.

- Two earthworms exchange sperm and store it temporarily.
- A special organ, the clitellum, secretes a mucous cocoon which slides along the worm, picking up its eggs and then the stored sperm.
- The cocoon slips off the worm into the soil and protects the embryos while they develop.

- Asexual reproduction occurs in some species by fragmentation followed by regeneration.

Movement involves coordinating longitudinal and circular muscles in each segment with the fluid-filled coelom functioning as a hydrostatic skeleton.

- Circular muscle contraction makes each segment thinner and longer; longitudinal muscle contraction makes the segment shorter and thicker.
- Waves of alternating contractions pass down the body.
- Most aquatic annelids are bottom-dwellers that burrow, although some swim in pursuit of food.

1. Class Oligochaeta

The class Oligochaeta contains earthworms and a variety of aquatic species.

Earthworms ingest soil, extract nutrients in the digestive system and deposit undigested material (mixed with mucus from the digestive tract) as casts through the anus.

- Important to farmers as they till the soil and castings improve soil texture.
- Darwin estimated that one acre of British farmland had about 50,000 earthworms that produced 18 tons of castings per year.

2. Class Polychaeta

The class Polychaeta contains mostly marine species (see Campbell, Figure 33.24.)

A few drift and swim in the plankton, some crawl along the sea floor, and many live in tubes they construct by mixing sand and shell bits with mucus.

- Tube-dwellers include the fanworms that feed by trapping suspended food particles in their feathery filters which are extended from the tubes.

Each segment has a pair of parapodia which are highly vascularized paddle-like structures that function in gas exchange and locomotion.

- Traction for locomotion is proved by several chitinous setae present on each parapodium.

3. Class Hirudinea

The class Hirudinea contains the leeches.

- A majority of species are freshwater but some are terrestrial in moist vegetation.
- Many are carnivorous and feed on small invertebrates, while some attach temporarily to animals to feed on blood.
- Size ranges from 1 – 30 cm in length.

Some blood-feeding forms have a pair of blade-like jaws that slit the host's skin while others secrete enzymes that digest a hole in the skin.

- An anesthetic is secreted by the leech to prevent detection of the incision by the host.
- Leeches also secrete hirudin which prevents blood coagulation during feeding.
- Leeches may ingest up to ten times their weight in blood at a single meal and may not feed again for several months.
- Leeches are currently used to treat bruised tissues and for stimulating circulation of blood to fingers and toes reattached after being severed in accidents.

E. Phylum Arthropoda: arthropods have regional segmentation, jointed appendages, and exoskeletons

The phylum Arthropoda is the largest phylum of animals with approximately one million described species.

Arthropods are the most successful phylum based on species diversity, distribution, and numbers of individuals.

1. General characteristics of arthropods

The success and great diversity of arthropods is related to their segmentation, jointed appendages, and hard exoskeleton.

The segmentation in this group is much more advanced than that found in annelids.

- In the arthropods, different segments of the body and their associated appendages have become specialized to perform specialized functions.
- Jointed appendages are modified for walking, feeding, sensory reception, copulation and defense.
- Campbell, Figure 33.25 illustrates the diverse appendages and other arthropod characteristics of a lobster.

The arthropod body is completely covered by the *cuticle*, an *exoskeleton* (external skeleton) constructed of layers of protein and chitin.

- The cuticle is thin and flexible in some locations (joints) and thick and hard in others.
- The exoskeleton provides protection and points of attachment for muscles that move the appendages.
- The exoskeleton is also relatively impermeable to water.
- The old exoskeleton must be shed for an arthropod to grow (molting) and a new one secreted.

Arthropods show extensive cephalization with many sensory structures clustered at the anterior end. Well-developed sense organs including eyes, olfactory receptors, and tactile receptors are present.

An *open circulatory system* containing hemolymph is present.

- Hemolymph leaves the heart through short arteries and passes into the sinuses (open spaces) which surround the tissues and organs.
- The hemolymph reenters the heart through pores equipped with valves.
- The blood sinuses comprise the hemocoel. Though the hemocoel is the main body cavity, it is not part of the coelom.
- The true coelom is reduced in adult arthropods.

Gas exchange structures are varied and include:

- Feathery gills in aquatic species
- Tracheal systems in insects
- Book lungs in other terrestrial forms (e.g., spiders)

2. Arthropod phylogeny and classification

Arthropods are segmented protostomes which probably evolved from annelids or a segmented protostome common ancestor.

- Early arthropods may have resembled onychophorans which have unjointed appendages.

    However, many fossils of jointed-legged animals resembling segmented worms support the evolutionary link between the Annelida and Arthropoda (see Campbell, Figure 33.26).

Such comparisons also indicate that annelids and arthropods are *not* closely related.

- Parapodia may have been forerunners of appendages.
- Some systematists suggest that comparisons of ribosomal RNA and other macromolecules indicate that onychophorans are arthropods and not transitional forms.
- This evidence presents an alternative hypothesis that segmentation evolved independently in annelids and arthropods.

  Thus, the most recent common ancestor of these two phyla would have been an unsegmented protostome.

Although the origin of arthropods is unclear, most zoologists agree that four main evolutionary lines can be identified in the arthropods. Their divergence is represented by the subgroups: Trilobites (all extinct), Chelicerates, Uniramians, and Crustaceans (see Campbell, Table 33.5).

3. Trilobites

Early arthropods, called trilobites, were very numerous, but became extinct approximately 250 million years ago (see Campbell, Figure 33.27).

- Trilobites had extensive segmentation, but little appendage specialization.
- As evolution continued, the segments tended to fuse and appendages became specialized for a variety of functions.

4. Spiders and other chelicerates

Other early arthropods included chelicerates, such as the *eurypterids* (sea scorpions) which were predaceous and up to 3 m in length.

The chelicerate body is divided into an anterior cephalothorax and a posterior abdomen.

Their appendages were more specialized than those of trilobites, with the most anterior ones being either pincers or fangs.

Chelicerates are named for their feeding appendages, the *chelicerae*.

Only four marine species remain; one is the horseshoe crab (see Campbell, Figure 33.28).

The bulk of the modern chelicerates are found on land in class Arachnida.

- Includes terrestrial spiders, scorpions, ticks, and mites (see Campbell, Figure 33.29)
- Arachnids possess a cephalothorax with six pairs of appendages: chelicerae, pedipalps (used in sensing and feeding), and four pairs of walking legs (see Campbell, Figure 33.30).

In spiders,

- Fang-like chelicerae, equipped with poison glands, are used to attack prey.
- Chelicerae and pedipalps masticate the prey while digestive juices are added to the tissues. This softens the food and the spider sucks up the liquid.
- Gas exchange is by book lungs (stacked plates in an internal chamber), whose structure provides an extensive surface area for exchange (see Campbell, Figure 33.30b).
- Spiders weave silken webs to capture prey.
  - The proteinaceous silk is produced as a liquid by abdominal glands and spun into fibers by spinnerets. The fibers harden on contact with air.
  - Web production is apparently an inherited complex behavior.
  - Silk fibers are also used for escape, egg covers, and wrapped around food presented to females during courtship.

5. **Millipedes and centipedes**

The class Diplopoda includes the millipedes.

- Wormlike with a large number of walking legs (two pairs per segment) (see Campbell, Figure 33.31a)
- Eat decaying leaves and other plant matter
- Probably among the earliest land animals

The class Chilopoda includes the centipedes.

- They are carnivorous.
- One pair of antennae and three pairs of appendages modified as mouthparts (including mandibles) are located on the head.
- Each trunk segment has one pair of walking legs (see Campbell, Figure 33.31b).
- Poison claws on the most anterior trunk segment are used to paralyze prey and for defense.

6. **Insects**

The class Insecta has a greater species diversity than all other forms of life combined.

- There are about 26 orders of insects (see Campbell, Table 33.6)
- They inhabit terrestrial and freshwater environments, but only a few marine forms exist.

Entomology = The study of insects

The oldest insect fossils are from the Devonian period (about 400 million years ago), and an increase in insect diversity can be attributed to:

- The evolution of flight during the Carboniferous and Permian
- The evolution of specialized mouth parts for feeding on gymnosperms and other Carboniferous plants
  - The fossil record holds examples of a diverse array of specialized mouth parts.

A second major radiation of insects, which occurred during the Cretaceous period, was once thought to have paralleled radiation of flowering plants.

- Current research indicates the major diversification of insects preceded angiosperm radiation during the Cretaceous period (65 million years ago).
- If this is true, insect diversity played a major role in angiosperm radiation, the reverse of the original hypothesis.

Flight is the key to the success of insects, enabling them to escape predators, find food and mates, and disperse more easily than nonflying forms.

- One or two pairs of wings emerge from the dorsal side of the thorax in most species (see Campbell, Figure 33.32).
- Wings are extensions of the cuticle and not modified appendages.
- Wings may have first evolved to help absorb heat, then developed further for flight.
- Other views suggest wings may have initially served for gliding, as gills in aquatic forms, or even as structures for swimming.

Dragonflies were among the first to fly and have two coordinated pairs of wings. Modifications are found in groups which evolved later.

- Bees and wasps hook their wings together (act as one pair).
- Butterflies have overlapping anterior and posterior wings.

- Beetles have anterior wings modified to cover and protect the posterior (flying) wings.

Insects have several complex internal organ systems (see Campbell, Figure 33.33).

- Complete digestive system with specialized regions
- Open circulatory system with hemolymph
- Excretory organs are the *Malpighian tubules*, which are outpocketings of the gut
- Gas exchange is by a tracheal system, which opens to the outside via spiracles that can open or close to regulate air and limit water loss
- Nervous system is composed of a pair of ventral nerve cords (with several segmental ganglia) which meet in the head where the anterior ganglia are fused into a dorsal brain close to the sense organs.

  Insects show complex behavior which is apparently inherited (e.g., social behavior of bees and ants).

Many insects undergo metamorphosis during their development.

Incomplete metamorphosis = A type of development during which young resemble adults but are smaller and have different body proportions

- For example, in grasshoppers a series of molts occur with each stage looking more like an adult until full size is reached.

Complete metamorphosis = A type of development characterized by larval stages (e.g., maggot, grub, caterpillar) which are very different in appearance from adults.

- Larva eat and grow before becoming adults.
- Adults find mates and reproduce with the females laying eggs on the appropriate food source for the larval forms.

Insects are dioecious and usually reproduce sexually with internal fertilization.

- In most, sperm are deposited directly into the female's vagina during copulation. Some males produce spermatophores which are picked up by the female.
- Inside the female, sperm are stored in the spermatheca.
- Most insects produce eggs although some flies are viviparous.
- Many insects mate only once in a lifetime with stored sperm capable of fertilizing many batches of eggs.

Insects impact terrestrial organisms in a number of ways by:

- Competing for food
- Serving as disease vectors
- Pollinating many crops and orchards

7. Crustaceans

There are more than 40,000 species of crustaceans in marine and fresh waters.

The crustaceans have extensive specialization of their appendages.

- Two pairs of antennae, three or more pairs of mouthparts including mandibles, walking legs on the thorax, appendages are present on the abdomen.
- Lost appendages can be regenerated.

Characteristics of their physiology:

- Gas exchange may take place across thin areas of the cuticle (small forms) or by gills (large forms).
- An open circulatory system is present with hemolymph.

- Nitrogenous wastes are excreted by diffusion across thin areas of the cuticle.
- Salt balance of the hemolymph is regulated by a pair of specialized antennal or maxillary glands.

Most are dioecious and some males (e.g., lobsters) have a specialized pair of appendages to transfer sperm to the female's reproductive pore during copulation.

- Most aquatic crustaceans have at least one swimming larval stage.

The decapods are relatively large crustaceans that have a carapace (calcium carbonate hardened exoskeleton over the cephalothorax).

Examples:
- Freshwater crayfish
- Marine lobsters, crabs and shrimp
- Tropical land crabs

The isopods are mostly small marine crustaceans but include terrestrial sow bugs and pill bugs.

- Terrestrial forms live in moist soil and damp areas.

Copepods are numerous small marine and freshwater planktonic crustaceans.

- The larvae of larger crustaceans may also be planktonic.

Barnacles are sessile crustaceans with parts of their cuticle hardened into shells by calcium carbonate.

- Barnacles feed by directing suspended particles toward the mouth with specialized appendages.

VI. The Coelomates: Deuterostomes

The deuterostomes, while a very diverse group, share characteristics which indicate their association: radial cleavage, enterocoelous coelom formation, and the blastopore forms the anus.

A. Phylum Echinodermata: echinoderms have water vascular systems and secondary radial symmetry

Most *echinoderms* are sessile or sedentary marine forms with radial symmetry as adults.

- Internal and external parts radiate from the center, often as five spokes.
- A thin skin covers a hard calcareous platelike exoskeleton.
- Most have bumps and spines which serve various functions.

A unique feature of echinoderms is the *water vascular system*, a network of hydraulic canals which branch into extensions called *tube feet* that function for locomotion, feeding, and gas exchange.

Echinoderms are dioecious with sexual reproduction and external fertilization.

- Bilaterally symmetrical larvae metamorphose into radial adults.
- Early embryonic development exhibits the characteristics of deuterostomes.

There are about 7000 species of echinoderms, all of which are marine. The six recognized classes are:

1. Class Asteroidea

This class includes the sea stars which have five or more arms extending from a central disc (see Campbell, Figure 33.36)

- Tube feet on the undersurface of the arms are extended by fluid forced into them by contraction of their ampulla.
- Suction cups at the end of each tube foot attach to the substratum and muscles in the tube foot wall contract and shorten the foot.

Coordination of extension, attaching, contraction and release allow slow movement and attachment to prey (see Campbell, Figure 33.37).

- Prey are obtained by attaching tube feet to the shells of clams and oysters; the arms of the sea star wrap around the prey and hold tightly using the tube feet.
- The muscles of the mollusk fatigue and the shell is pulled open.
- The sea stars evert their stomachs between the shell halves and secrete digestive juices onto the soft tissues of the mollusk.

Sea stars have a strong ability to regenerate. One species can even regrow an entire body from a single arm. Fishermen chopping up sea stars may actually increase their numbers.

2. Class Ophiuroidea

This class contains the brittle stars which differ from sea stars in that they have:

- Smaller central discs than sea stars
- Longer, more flexible arms than sea stars (see Campbell, Figure 33.37c)
- No suckers on their tube feet
- Locomotion is by serpentine lashing of flexible arms
- Varying feeding mechanisms

3. Class Echinoidea

The class Echinoidea contains the sea urchins and sand dollars.

Sea urchins are spherical in shape, while sand dollars are flattened in the oral-aboral axis.

Echinoideans lack arms but have:

- Five rows of tube feet present that provide slow movement (see Campbell, Figure 33.37d)
- Muscles that pivot their spines to aid in locomotion

Echinoideans have a complex jaw-like structure present around the mouth which is used for feeding on seaweeds and other food.

4. Class Crinoidea

The class Crinoidea contains the sea lilies.

Most sea lilies are sessile, living attached to substratum by stalks.

Motile sea lilies use their arms for a crawling form of locomotion as well as for feeding.

Arms circle the mouth (which points upward) and are used in suspension-feeding (see Campbell, Figure 33.37e).

Crinoids have exhibited a very conservative evolution. Extant forms are very similar to fossilized forms from Ordovician period (500 million years ago).

5. Class Holothuroidea

The class Holothuroidea contains the sea cucumbers which have little resemblance to other echinoderms (see Campbell, Figure 33.37f).

- They lack spines.
- The hard endoskeleton is reduced.
- The body is elongated in the oral-aboral axis.

Species in the Holothuroidea do possess five rows of tube feet, a part of the unique water vascular system.

- Some tube feet around the mouth have developed into feeding tentacles.

6. Class Concentricycloidea

This class contains the sea daisies which are small (less than 1 cm), disc-shaped marine animals.

- They live in deep water.
- They do not possess arms.
- Tube feet are located around the disc margin.
- Possess a rudimentary digestive system or an absorptive velum on the oral surface.
- Water vascular system consists of two concentric ring canals.

B. Phylum Chordata: the chordates include two invertebrate subphyla and all vertebrates

The Chordata diverged from a common deuterostome ancestor with echinoderms at least 500 million years ago.

- The two phyla are grouped together due to similarities in early embryonic development.
- This phylum contains three subphyla: Urochordata, Cephalochordata, and Vertebrata.

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CHAPTER 34
VERTEBRATE EVOLUTION AND DIVERSITY

OUTLINE

I. Invertebrate Chordates and the Origin of Vertebrates
   A. Four anatomical features characterize phylum Chordata
   B. Invertebrate chordates provide clues to the origin of vertebrates

II. Introduction to the Vertebrates
   A. Neural crest, cephalization, a vertebral column, and a closed circulatory system characterize subphylum Vertebrata
   B. Overview of vertebrate diversity

III. Superclass Agnatha: Jawless Vertebrates
   A. Lampreys and hagfishes are the only extant agnathans

IV. Superclass Gnathostomata I: The Fishes
   A. Vertebrate jaws evolved from skeletal supports of the pharyngeal slits
   B. A cartilaginous endoskeleton reinforced by calcified granules is diagnostic of class Chondrichthyes
   C. A bony endoskeleton, operculum, and swim bladder are hallmarks of class Osteichthyes

V. Superclass Gnathastomata II: The Tetrapods
   A. Amphibians are the oldest class of tetrapods
   B. Evolution of the amniotic egg expanded the success of vertebrates on land
   C. A reptilian heritage is evident in all amniotes
   D. Birds began as flying reptiles
   E. Mammals diversified extensively in the wake of the Cretaceous extinctions

VI. Primates and the Phylogeny of *Homo sapiens*
   A. Primate evolution provides a context for understanding human origins
   B. Humanity is one very young twig on the vertebrate tree

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. Describe the four unique characteristics of chordates.
2. Distinguish between the three subphyla of the phylum Chordata and give examples of each.
3. Describe the specialized characteristics found in the subphylum Vertebrata and explain how each is beneficial to survival.
4. Compare and contrast members of Agnatha, Placadermi, and Chondrichthyes.

5. Explain how members of the class Osteichthyes have becomes so diversified.
6. Summarize the evidence supporting the fact that amphibians evolved from crossopterygians.
7. Distinguish between the three orders of living amphibians.
8. List the distinguishing characteristics of members of the class Reptilia and explain any special adaptations to the terrestrial environment.
9. Explain how environmental changes during the Cretaceous Period may have affected the dinosaurs.
10. List the distinguishing characteristics of members of the class Aves and explain any special adaptations for flight.
11. Summarize the evidence supporting the fact that birds evolved from reptilian ancestors.
12. Explain why mammals underwent an adaptive radiation during the Cenozoic.
13. Distinguish between monotreme, marsupial, and placental mammals.
14. Explain how convergent evolution produced marsupial and placental ecological counterparts on different continents.
15. Compare and contrast the four main evolutionary lines of placental mammals.
16. Describe the characteristics found in early primates which indicate an arboreal existence.
17. Appraise the significance of the three most prominent misconceptions about human evolution.
18. Diagram an evolutionary tree for humans.
19. Explain how humans have influenced the extinction rates of other organisms.

KEY TERMS

vertebrates	Superclass Gnathostomata	lungfishes	Chelonia
chordates		Subclass Sarcopterygii	Squamata
notochord	placoderms	Class Amphibia	Crocodilia
urochordates	Class Chondrichthyes	urodeles	Class Aves
tunicates	spiral valve	anurans	ratites
lancelets	lateral line system	apodans	carinates
cephalochordates	oviparous	extraembryonic membranes	Class Mammalia
somites	ovoviviparous	Class Reptilia	placenta
paedogenesis	viviparous	ectotherms	therapsids
neural crest	cloaca	synapsids	monotremes
tetrapods	Class Osteichthyes	sauropods	eutherian mammals
amniotic egg	operculum	anapsids	prosimians
amniotes	swim bladder	diapsids	anthropoids
Superclass Agnatha	ray-finned fishes	therapsids	paleoanthropology
ostracoderms	lobe-finned fishes	endothermic	mosaic evolution
passeriforms			

LECTURE NOTES

I. Invertebrate Chordates and the Origin of Vertebrates

The phylum Chordata includes three subphyla: two invertebrate subphyla, Urochordata, Cephalochordata; and the subphylum Vertebrata.

A. Four anatomical features characterize phylum Chordata

Chordates are deuterostomes with four unique characteristics which appear at some time during the animal's life. These characteristics are the notochord, a dorsal, hollow nerve cord, pharyngeal slits, and a muscular postanal tail (see Campbell, Figure 34.1).

1. Notochord

Notochord = A longitudinal, flexible rod located between the gut and nerve cord

- Present in all chordate embryos
- Composed of large, fluid-filled cells encased in a stiff, fibrous tissue
- Extends through most of the length of the animal as a simple skeleton

In some invertebrate chordates and primitive vertebrates it persists to support the adult.

In most vertebrates, a more complex, jointed skeleton develops and the notochord is retained in adults as the gelatinous material of the discs between the vertebrae.

2. Dorsal, hollow nerve cord

Develops in the embryo from a plate of dorsal ectoderm that rolls into a tube located dorsal to the notochord.

Unique to chordates; other animal phyla have solid, usually ventral, nerve cords.

The brain and spinal cord (central nervous system) develops from this nerve cord.

3. Pharyngeal slits

Chordates have a complete digestive system (mouth and anus). The pharynx is the region just posterior to the mouth and it opens to the outside through several pairs of slits.

- The presence of these pharyngeal slits permits water entering the mouth to exit without passing through the entire digestive system.
- These pharyngeal gill slits function for suspension-feeding in invertebrate chordates.
- They have become modified for gas exchange and other functions during the evolution of vertebrates.

4. Muscular postanal tail

A tail extending beyond the anus, it is found in most chordates and contains skeletal elements and muscles.

- Provides much of the propulsive force in many aquatic species.

The digestive tract in most nonchordates extends nearly the whole length of the body.

II. Invertebrate Chordates Provide Clues to the Origin of Vertebrates

A. Subphylum Urochordata

Species in the subphylum Urochordata (*urochordates*) are commonly called *tunicates.*

Entire animal is cloaked in a tunic made of a celluloselike carbohydrate.

Most are sessile marine animals that adhere to rocks, docks, and boats (see Campbell, Figure 34.2a).

Some species are planktonic, while others are colonial.

The tunicates are filter feeders.

- Seawater enters through an incurrent siphon, passes through the slits of the pharynx into a chamber called the atrium, and exits via an excurrent siphon, the atriopore (see Campbell, Figure 34.2b).
- Food filtered from the water by a mucus net of the pharynx is moved by cilia into the intestine.

- The anus empties into the excurrent siphon.
- When disturbed, tunicates eject a jet of water through the excurrent siphon, so they are commonly called sea squirts.

Adult tunicates bear little resemblance to other chordates.

- They lack a notochord, a nerve cord and tail.
- They possess only pharyngeal slits.

Larval tunicates are free swimmers and possess all four chordate characteristics (see Campbell, Figure 34.2c).

- Larva attach by the head on a surface and undergo metamorphosis to adult form.
- In some species, if the *Manx* gene (named after the tailless cat) is turned off during development, the larvae will be tailless. *Manx* expression also is required for notochord and nerve cord development.
  - These observations remind us that a relatively small number of genes that regulate development may influence the evolution of some basic aspect of an animal body plan.

B. Subphylum Cephalochordata

Animals in the subphylum Cephalochordata (*cephalochordates*) are known as *lancelets* due to their bladelike shape (see Campbell, Figure 34.3). Chordate characteristics are prominent and persist in the adult. These include:

- Notochord
- Dorsal nerve cord
- Numerous gill slits
- Postanal tail

Cephalochordates are marine filter feeders.

- They burrow tail first into the sand with only the anterior exposed.
- Water is drawn into mouth by ciliary action and food is trapped on a mucous net secreted across the pharyngeal slits.
- Water exits through the slits and trapped food passes down the digestive tube.

Cephalochordates are feeble swimmers with fishlike motions.

- Frequently move to new locations
- Muscle segments are serially arranged in chevronlike rows, and coordinated contraction flexes the notochord from side to side in a sinusoidal pattern.
- Muscle segments develop from blocks of mesoderm called *somites* that are arranged along each side of the notochord in the embryo.
- The serial musculature is evidence of the lancelet's segmentation (see Campbell, Figure 34.4).

  Whether segmentation evolved independently in annelids, arthropods, and chordates, or from a common ancestor of all bilateral animals, is currently under debate.

C. Relationship of invertebrate chordates to the vertebrates

Vertebrates first appeared in the fossil records in Cambrian rocks.

- Fossilized invertebrates (about 550 million years old) resembling cephalochordates were found in Burgess Shale of British Columbia.
- This is about 50 million years older than the oldest known vertebrates.

Most zoologists feel the vertebrate ancestors possessed all four chordate characteristics and were suspension-feeders.

- They may have resembled lancelets but were less specialized.
- Information provided by molecular systematics supports the idea that cephalochordates are the closest relatives of vertebrates.

Cephalochordates and vertebrates may have evolved from a sessile ancestor by paedogenesis.

Paedogenesis = Precocious attainment of sexual maturity in a larva

- Cephalochordates more closely resemble urochordate larvae than adult urochordates.
- Changes in the developmental control genes can alter the timing of developmental events (e.g., gonad maturation).
- Zoologists postulate that some early urochordatelike larval forms became sexually mature and reproduced before undergoing metamorphosis.
- If reproducing larvae were successful, natural selection may have reinforced the absence of metamorphosis and a vertebrate life cycle may have evolved.

The divergence of cephalochordates from vertebrates occurred about 500 million years ago.

- The differences between the two groups can be viewed as vertebrate adaptations to larger size and a more mobile life style.

III. Introduction to the Vertebrates

Vertebrates have retained the primitive chordate features while adding other specializations. These synapomorphies distinguish the vertebrates from urochordates and cephalochordates.

A. Neural crest, pronounced cephalization, a vertebral column, and a closed circulatory system characterize subphylum Vertebrata

The unique vertebrate structures probably evolved in association with increased size and more active foraging for food. The unique vertebrate adaptations include:

- The *neural crest*, a group of embryonic cells found only in vertebrates, contributes to the formation of certain skeletal components and many other structures distinguishing vertebrates from other chordates.

  The dorsal, hollow nerve cord develops from an infolding of the edges of an ectodermal plate on the surface of the embryo.

  The neural crest forms near the dorsal margins of the tube resulting from this infolding (see Campbell, Figure 34.5).

  Cells from the neural crest then migrate to various specific areas of the embryo and help form a variety of structures including some of the bones and cartilage of the cranium.

- Vertebrates show a much greater degree of *cephalization* than cephalochordates.

  The brain and sense organs are located at the anterior end which is the portion of the body which is in contact with the most environmental stimuli.

- A skeleton including a cranium and vertebral column is the main axis of the body, replacing the notochord as the basic skeleton.

  The cranium protects the brain.

  The vertebral column provides support and a strong, jointed anchor that provides leverage to the segmental swimming muscles.

  The axial skeleton made larger size and stronger, faster movement possible.

  Most vertebrates also have ribs (anchor muscles and protect internal organs) and an appendicular skeleton supporting two pairs of appendages.

- The vertebrate skeleton may be composed of bone, cartilage, or a combination of the two.
  - A majority of the skeleton is a non-living matrix which is secreted and maintained by living skeletal cells.
  - The living vertebrate endoskeleton can grow with the animal unlike the exoskeleton of arthropods.

Some anatomical adaptations also support the greater metabolic demands of increased activity.

- The generation of ATP by cellular respiration, to replace the energy used by vertebrates in obtaining food or escaping predators, consumes oxygen.
  - The respiratory and circulatory systems of vertebrates show adaptations which support the mitochondria of muscles and other active tissues.
- Vertebrates have a closed circulatory system composed of a ventral chambered (two to four) heart, arteries, capillaries, and veins.
  - The heart pumps the blood through the system.
  - The blood becomes oxygenated as it passes through the capillaries of the gills or lungs.
- The more active the lifestyle, the larger the amounts of organic molecules necessary to produce energy.
  - Vertebrates have several adaptations for feeding, digestion and nutrient absorption.
  - For example, muscles in the walls of the digestive tract move food from organ to organ along the tract.

B. Overview of Vertebrate Diversity

The vertebrates are divided into two major groups, or superclasses: Superclass Agnatha, whose members lack jaws, and Superclass Gnathastomata, whose members possess jaws (see Campbell, Table 34.1)

The gnathostomes are divided into six classes: Chondrichthyes, Osteichthyes, Amphibia, Reptilia, Aves, and Mammalia. The last four classes are collectively known as the tetrapod vertebrates.

- *Tetrapod* = An animal possessing two pairs of limbs that support it on land

In addition to being tetrapods, the reptiles, birds and mammals have other adaptations for a terrestrial lifestyle which are not found in the amphibians.

- The *amniotic egg* (a shelled, water resistant egg) allows completion of the life cycle on land.
- Most mammals do not lay eggs but retain other features of the amniotic condition, consequently, they are also considered *amniotes* along with the birds and reptiles.

Review Figure 34.6 to establish the relationships among the classes of the subphylum Vertebrata.

IV. Superclass Agnatha: Jawless Vertebrates

Vertebrates probably arose in the late Precambrian and early Cambrian. The oldest fossils of vertebrates are of jawless animals found in rock strata 400 to 500 million years old.

Early agnathans were small, less than 50 cm in length.

- They were jawless with oval or slitlike mouths; most lacked paired fins and were bottom-dwellers.

- Some were active and had paired fins.
- Were probably bottom- or suspension-feeders that trapped organic debris in their gill slits.

Ostracoderms and most other agnathans declined and disappeared during the Devonian.

A. Lampreys and hagfishes are the only extant agnathans

Extant forms include about 60 species of lampreys and hagfishes which lack paired appendages and external armor (see Campbell, Figure 34.7).

Lampreys are eel-shaped and feed by clamping their round mouths onto live fish.

- Once attached, they use a rasping tongue to penetrate the skin and feed on the prey's blood.
- Sea lampreys spend their larval development in freshwater streams and migrate to the sea or lakes as they mature.
- Larva are suspension-feeders that resemble lancelets (cephalochordates).
- Some lamprey species feed only as larvae. Once they mature and reproduce, they die within a few days.

Hagfishes superficially resemble lampreys.

- They are scavengers without rasping mouthparts.
- Some species will feed on sick or dead fish while others feed on marine worms.
- Lack a larval stage and are entirely marine (Physiologically, they are the only extant vertebrate that is a true osmoconformer; all other vertebrates are osmoregulators).

V. Superclass Gnathostomata I: The Fishes

The agnathans were gradually replaced by vertebrates with jaws (Superclass Gnathostomata) during the late Silurian and early Devonian. Early gnathostomes included ancestors of class Chondrichthyes and class Osteichthyes and a now extinct group of armored fishes called *placoderms* appeared.

Most placoderms were less than 1 m in length, but some were up to 10 m long.

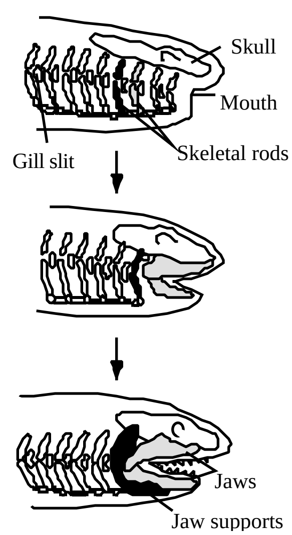
- Differed from agnathans in that they possessed paired fins and hinged jaws.
- Paired fins enhanced swimming ability and hinged jaws allowed more varied feeding habits including predation.

A. Vertebrate jaws evolved from skeletal supports of the pharyngeal slits

Hinged jaws evolved as modifications of the skeletal rods which previously supported the anterior pharyngeal (gill) slits (see Campbell, Figure 34.8).

- Remaining gill slits retained function as major gas exchange sites.
- Hinged jaws of vertebrates work in an up and down direction; those in arthropods work from side to side.

Placoderms and another group of jawed fishes, the acanthodians, radiated during the Devonian period (the Age of Fishes) and many new forms evolved in fresh and salt waters.



- Placoderms and acanthodians disappeared by the start of the Carboniferous period (350 million years ago).
- Ancestors of the placoderms and acanthodians also gave rise to early sharks (class Chondrichthyes) and bony fishes (class Osteichthyes).

B. A cartilaginous endoskeleton reinforced by calcified granules is diagnostic of class Chondrichthyes

The class Chondrichthyes contains about 750 extant species of cartilaginous fishes (e.g., sharks, skates, rays) (see Campbell, Figure 34.9).

Species in the class Chondrichthyes have flexible skeletons composed of cartilage, well-developed jaws and paired fins.

- The ancestors of members of this class had bony skeletons.
- The characteristic cartilaginous skeleton is thus a derived characteristic, having evolved secondarily.
- The developmental sequence in cartilaginous fishes differs from other vertebrates in that the initial (first) cartilaginous skeleton does not become ossified.
- In most species, however, parts of the skeleton are strengthened by calcified granules
- The cartilaginous skeleton is more elastic and lighter than a bone skeleton.

Sharks have streamlined bodies and are swift swimmers.

- The tail provides propulsion.
- The dorsal fins serve as stabilizers.
- Pectoral and pelvic fins produce lift.
- Some buoyancy is provided by large amounts of oil stored in liver, but most must swim continuously to remain in the water column.
  - Continual swimming also produces water flow through mouth and over gills for gas exchange.
  - Some sharks are known to rest on the sea floor and in caves; they use jaw and pharynx muscles to pump water over their gills while resting.

Most sharks are carnivorous, although the largest sharks and rays are suspension-feeders.

- Prey may be swallowed whole or pieces may be torn from large prey.
- Teeth evolved as modified scales.
- The digestive tract is proportionately shorter than in other vertebrates.
  - A *spiral valve*, which increases surface area and slows food movement, is present in the intestine.

Sharks possess sharp vision (cannot distinguish color) and olfactory senses that are adaptations to their lifestyle.

- Electric sensory regions that detect muscle contractions of prey are located on the head.
- A *lateral line system* is present along the flanks.
  - It is composed of rows of microscopic organs sensitive to water pressure changes and detects vibrations.
- A pair of auditory organs also detect sound waves passing through the water.

Sharks reproduce sexually with internal fertilization.

- A pair of claspers on the pelvic fins of males transfers sperm into the female reproductive tract.
- Some species are *oviparous*, some are *ovoviviparous*, and a few are *viviparous*.

- A *cloaca* (common chamber for reproductive, digestive and excretory systems) is present.

Rays are adapted to a bottom-dwelling lifestyle.

- They have dorsoventrally flattened bodies.
- Their jaws are used to crush mollusks and crustaceans.
- Enlarged pectoral fins provide propulsion for swimming.
- The tail in many species is whiplike and, in some, bears venomous barbs.

C. A bony endoskeleton, operculum, and a swim bladder are hallmarks of class Osteichthyes

The class Osteichthyes contains the bony fishes, which are represented by more than 30,000 extant species.

- Abundant in marine and fresh waters (see Campbell, Figure 34.10)
- Range from 1 cm to 6 m in length
- Skeleton is bony, reinforced with a matrix of calcium phosphate
- Skin is covered with flattened bony scales
- Skin glands produce mucus that reduces drag when swimming
- A lateral line system is present as a row of tiny pits in the skin on both sides of the body (see Campbell, Figure 34.11).

Gas exchange occurs by drawing water over the four or five pairs of gills located in chambers covered by an operculum.

- Water is drawn into the mouth, through the pharynx and out between the gills by movement of the operculum and contraction of muscles within the gill chambers.

    Allows bony fishes to breath while stationary.

A *swim bladder*, located dorsal to the digestive tract, provides buoyancy.

- Transfer of gases between blood and swim bladder varies bladder inflation and adjusts the density of the fish.

Bony fishes are very maneuverable swimmers. The flexible fins provide better steering and propulsion than the stiff fins of sharks.

- The fastest bony fish can swim to 80 km per hour in short bursts.
- A fusiform body shape is common to all fast fishes and aquatic mammals.

    This body shape reduces drag produced by the density of water (convergent evolution).

Most bony fish are oviparous and utilize external fertilization.

- Some are ovoviviparous or viviparous and utilize internal fertilization.
- Some display complex mating behavior.

The cartilaginous and bony fishes diversified during the Devonian and Carboniferous periods.

- Sharks arose in the sea, bony fishes probably originated in fresh water.
- The swim bladder was modified from lungs of ancestral fishes which supplemented the gills for gas exchange in stagnant waters.

The two extant subclasses of bony fishes had diverged by the end of the Devonian: Subclass Actinopterygii (ray-finned fishes) and Subclass Sarcopterygii

The *subclass Actinopterygii* includes fish with fins supported mainly by flexible rays.

- These are the most familiar fishes.

- They spread from fresh water to the seas and many returned to fresh water during evolution of the taxon.
- Some bony fish (e.g., salmon and sea-run trout) reproduce in fresh water and mature in the sea.

The *subclass Sarcopterygii* includes lobe-finned fishes (coelocanths and rhipidistans) and lungfishes that evolved in fresh water The ancestors of these fishes continued to use their lungs to aid the gills in gas exchange.

Coelocanths and rhipidistians are referred to as lobe-finned fishes.

- Their fins were fleshy, muscular, and supported by extensions of the bony skeleton.
- Many were large, bottom-dwelling forms that used their paired fins to walk on the substratum.
- The only extant species, the coelocanth, is marine and lungless. It belongs to a lineage that became marine at some point in its evolution.
- All rhipidistians are extinct.

Three genera of lungfishes exist in the Southern Hemisphere.

- They live in stagnant ponds and swamps where they surface to gulp air into lungs connected to the pharynx.
- When ponds dry, lungfishes burrow in the mud and aestivate.

Lobe-finned fishes of the Devonian were numerous and important in vertebrate genealogy because they probably gave rise to amphibians (see Campbell, Figure 34.13).

VI. Superclass Gnathostomata II: The Tetrapods

A. Amphibians are the oldest class of tetrapods

The first vertebrates to move onto land were members of *Class Amphibia.*

Today there are about 4000 extant species of frogs, salamanders, and caecilians.

1. Early amphibians

Some scientists suggest that early amphibians evolved from lobe-finned fishes that adapted to environmental variations (drought and flooding) of the Devonian.

- The skeletal structure of the lobed fins suggest they could have assisted in movement on land.
- Fossil lobe-fins, such as the rhipidistian *Eusthenopteron*, exhibited many anatomical similarities to early amphibians (see Campbell, Figure, 34.14a)

Recent molecular and other data, however, suggest that amphibians are more closely related to lungfishes than they are to lobe-fin fishes.

The oldest amphibian fossils are from the late Devonian (365 million years ago) (see Campbell, Figure 34.14b).

- Early amphibians probably were mostly aquatic and periodically came on land to eat insects and other invertebrates that had moved previously onto land.
- Amphibians were the only vertebrates on land in the late Devonian and early Carboniferous.

Radiation of forms occurred during the early Carboniferous period.

- Some forms reached 4 m in length and some resembled reptiles.
- Amphibians began to decline during the late Carboniferous. At the beginning of the Triassic period (245 million years ago), most of the survivors resembled modern species.

2. Modern amphibians

There are three extant orders of amphibians: Urodela (salamanders), Anura (frogs and toads) and Apoda (caecilians) (see Campbell, Figure 34.15).

The order Urodela (urodeles; e.g., salamanders) contains about 400 species.

- Some are aquatic and some are terrestrial.
- Terrestrial forms walk with a side-to-side bending of the body. Aquatic forms swim sinusoidally or walk along the bottom of streams or ponds.

The order Anura (*anurans*; e.g., frogs and toads) contains about 3500 species, which are better adapted to the terrestrial habitat than urodeles.

- Enlarged hindlegs provide better movement (hopping) than in urodeles.
- They capture prey by flicking the sticky tongue which is attached anteriorly.
- Predator avoidance is aided by camouflage color patterns and distasteful or poisonous mucus secreted by skin glands.

    Bright coloration is common in poisonous species.

The order Apoda (*apodans*; e.g., caecilians) contains about 150 species.

- They are legless and almost blind.
- Most species burrow in moist tropical soils; a few species inhabit freshwater ponds and streams.

Many frogs exhibit a metamorphosis from the larval to adult stage (see Campbell, Figure 34.16):

- The tadpole (larval stage) is usually an aquatic herbivore. It possesses internal gills, a lateral line system, and a long, finned tail.
- The tadpole lacks legs and swims by undulating the tail.
- During metamorphosis, legs develop and the gills and lateral line system disappear.
- A young frog is tetrapod. It has air-breathing lungs, a pair of external eardrums, and a digestive system that can digest animal protein.
- The adult is usually terrestrial or semiaquatic and a predator.

Many amphibians, including some frogs, do not have a tadpole stage.

- Some species in each order are strictly aquatic while others are strictly terrestrial.
- Urodeles and apodans have larva that more closely resemble adults and both larva and adults are carnivorous.
- Paedogenesis is common in some groups of urodeles.

Most amphibians maintain close ties with water and are most abundant in damp habitats.

- Terrestrial forms in arid habitats spend much of their time in burrows where humidity is high.
- Gas exchange is primarily cutaneous and terrestrial forms must keep the skin moist.

    Lungs can aid in gas exchange although most are small and inefficient. Some forms lack lungs.

    Many species also exchange gases across moist surfaces of the mouth.

Amphibians are dioecious.

- The reproduce sexually usually with external fertilization in water (e.g., ponds, streams, temporary pools).

- In frogs, the male grasps the female and sperm are released as the female sheds her eggs (see Campbell, Figure 34.16a)
- Eggs are unshelled and produced in large numbers by most species.

Some species exhibit parental behavior and produce small numbers of eggs.

- Males or females (species dependent) incubate eggs on their back, in the mouth or in the stomach.
- Some tropical species lay eggs in a moist foamy nest that prevents drying.
- Some species are ovoviviparous and a few are viviparous with the eggs developing in the female's reproductive tract.

Amphibians exhibit complex and diverse social behavior especially during breeding season (e.g., vocalization by male anurans, migrations, navigation or chemical signaling).

B. Evolution of the amniotic egg expanded the success of vertebrates on land

Many specialized adaptations for living in a terrestrial habitat were necessary for reptiles to evolve from their amphibian ancestor.

- The amniotic egg was important. Its development broke the last ties with the aquatic environment by allowing life cycles to be completed on land.

  The shell of the amniotic egg helps prevent desiccation, therefore, it can be laid in a dry place.

  Most mammals have dispensed with the shell, instead, the embryo implants in the wall of the uterus and obtains its nutrients from the mother.
- The *extraembryonic membranes* within the egg develop from tissue layers that grow out from the embryo.

  These specialized membranes function in gas exchange, transfer of stored nutrients to the embryo, and waste storage.

  One of these membranes, the amnion, encloses a compartment filled with amniotic fluid that bathes the embryo and provides a cushion against shocks (see Campbell, Figure 34.17).

Reptiles , birds, and mammals make up a monophyletic group, the amniotes.

C. A reptilian heritage is evident in all amniotes

The *class Reptilia* is a diverse group with about 7000 extant species and a wide array of extinct forms.

- This grouping is based on the apparent similarity of the tetrapods (lizards, snakes, turtles, and crocodilians), but cladistic analysis indicates that grouping these vertebrates in a class that does not include birds is inconsistent with phylogeny.
- Birds appear to be more closely related to crocodiles than are turtles.
- Class Reptilia can only be defined by the absence of features that distinguish birds (feathers) and mammals (hair and mammary glands)

1. Reptilian characteristics

Reptiles possess several adaptations for terrestrial living not found in amphibians.

- Scales contain the protein keratin which helps prevent dehydration.
- Gas exchange occurs via lungs although many turtles also use moist cloacal surfaces.
- They are dioecious with sexual reproduction and internal fertilization.

  Most are oviparous and produce an amniotic egg (see Campbell, Figure 34.18).

Some species of snakes and lizards are viviparous with the young obtaining nutrients from the mother across a “placenta” which forms from the extraembryonic membranes.

Reptiles are ectotherms and use behavioral adaptations to regulate their body temperature.

- *Ectotherm* = An animal that uses behavioral adaptations to absorb solar energy and regulate its body temperature.
- Due to ectothermy, reptiles can survive on less than 10% of the calories required by mammals of comparable size.

Reptiles were abundant and diverse in the Mesozoic era.

2. The Age of Reptiles

a. Origin and early evolutionary radiation of reptiles

The oldest reptilian fossils are found in late Carboniferous rock (300 million years old).

- Ancestors were probably Devonian amphibians.
- Two waves of adaptive radiation resulted in reptiles being the dominant terrestrial vertebrates for 200 million years.

The first reptilian radiation was in the early Permian period and gave rise to two main evolutionary branches: the synapsids and sauropsids (see Campbell, Figure 34.19).

- Synapsids were terrestrial predators and gave rise to the therapsid lineage which were mammal-like reptiles.

  Therapsids were large, dog-sized predators from which mammals are believed to have evolved.

- Sauropsids gave rise to the modern amniote groups other than mammals. They split into two lineages early in their history: the anapsids and the diapsids.

  The anapsids are presently represented only by the turtles.

  The extant diapsids are represented by the lizards, snakes, and crocodilians; dinosaurs and some other extinct groups were also diapsids. Cladistic analysis suggests that birds are the closest living relatives of extinct dinosaurs.

b. Dinosaurs and pterosaurs

The second reptilian radiation began in the late Triassic (about 200 million years ago) and several lineages evolved during this event.

- Two groups are most important: the dinosaurs and pterosaurs (flying reptiles).
- Dinosaurs varied in body shape, size, and habitat.

  Some fossilized forms measure 45 meters in length.

- Pterosaurs had wings formed from skin stretched from the body wall, along the forelimb to the tip of an elongate finger and supported by stiff fibers.

Evidence indicates that dinosaurs were agile, fast moving, and social, some may have even exhibited parental care of the young (see Campbell, Figure 34.20).

There is also some anatomical evidence supporting the hypothesis that dinosaurs were endothermic.

- *Endothermy* = The ability to keep the body warm through an animal’s own metabolism

- Skeptics of this hypothesis feel that the Mesozoic climate was warm and consistent, and that basking may have been sufficient for maintaining body temperature.
- Low surface-to-volume ratios of large forms reduced fluctuations of body temperature vs. air temperature; thus, dinosaurs may not have been endothermic.

c. The Cretaceous crisis

In the Cretaceous (last period of the Mesozoic), the climate became cooler and more variable, and mass extinctions occurred.

A few dinosaurs survived into the early Cenozoic, but all these reptiles were gone by the end of the Cretaceous (65 million years ago).

3. Modern reptiles

The largest and most diverse extant orders are the: *Chelonia* (turtles), *Squamata* (lizards and snakes), and *Crocodilia* (alligators and crocodiles).

Turtles of the order Chelonia evolved from anapsids during the Mesozoic.

- They show little change from the earliest forms (see Campbell, Figure 34.21a).
- They are protected from predators by a hard shell.
- All turtles, even aquatic species, lay their eggs on land.

Lizards and snakes are classified in the order Squamata.

Lizards are the most numerous and diverse group of extant reptiles (see Campbell, Figure 34.21b).

- They evolved from the diapsid lineage.
- Most are small.
- Many nest in crevices and decrease activity during cold periods.

Snakes probably descended from burrowing lizards (see Campbell, Figure 34.21c).

- They are limbless and most live above ground.
- Vestigial pelvic and limb bones present in primitive snakes (boas) are evidence of a limbed ancestor.
- Snakes are carnivorous and have a number of adaptations for hunting prey.
    - They have acute chemical sensors.
    - They are sensitive to ground vibrations (although lacking eardrums).
    - Pit vipers have sensitive heat-detecting organs between their eyes and nostrils.
    - Flicking tongue helps transmit odors toward olfactory organs on roof of mouth.
    - Poisonous snakes inject a toxin through a pair of sharp, hollow teeth and loosely articulated jaws allow them to swallow large prey.

Crocodiles and alligators are among the largest living reptiles (see Campbell, Figure 34.21d).

- Crocodilians also evolved from the diapsid lineage.
- The spend most of their time in the water, breathing air through upturned nostrils.
- They are confined to warm regions of Africa, China, Indonesia, India, Australia, South America, and the southeastern United States.
- They are the living reptiles most closely related to dinosaurs.

D. Birds began as flying reptiles

The *class Aves* (birds) evolved during the great reptilian radiation of the Mesozoic era (see Campbell, Figure 34.19).

- They possess distinct reptilian characteristics such as the amniotic egg and scales on the legs, but modern birds also look quite different because of their feathers and other flight equipment.

1. Characteristics of birds

Each part of the bird's anatomy is modified in some way that enhances flight.

- The bones have a honeycombed internal structure that provides strength while reducing weight (see Campbell, Figure 34.22).
- Some organ systems are reduced (only one ovary in females).
- Birds have no teeth (reduces weight) and food is ground in the gizzard.

  The beak is made of keratin and evolution has produced many shapes in relation to the bird's diet.

Flying requires much energy production from an active metabolism.

- Birds are endothermic with insulation provided by feathers and a fat layer.
- Birds have efficient circulatory system with a four-chambered heart that segregates oxygenated blood from unoxygenated blood.
- They have efficient lungs with tubes connecting to elastic air sacs that help dissipate heat and reduce the body density.

Birds also have a very well developed nervous system.

- Acute vision and well-developed visual and coordinating areas of the brain aid in flying.
- They show complex behavior especially during breeding season when elaborate courtship rituals are performed.

Birds are dioecious with sexual reproduction and internal fertilization.

- Sperm are transferred from the cloaca of the male to the cloaca of the female (males of most species lack a penis) during copulation.
- Eggs are laid and must be kept warm through brooding by the female, male or both depending on the species.

Wings are airfoils, formed by the shape and arrangement of the feathers, that illustrate the same aerodynamic principles as airplane wings (see Campbell, Figure 34.23).

- Power is supplied to the wings by contraction of the large pectoral (breast) muscles which are anchored to a keel on the sternum (breastbone).
- Some birds have wings adapted for soaring (hawks) while others must beat their wings continuously to stay aloft (hummingbirds).

Feathers are made of keratin and are extremely light and strong.

- Feathers evolved from the scales of reptiles and may have first functioned as insulation.
- Feathers also function to control air movements around the wing.

Radical alteration of body form was necessary for evolution of flight, but flight provides many benefits.

- Allows aerial reconnaissance that enhances hunting and scavenging.
- Birds can exploit flying insects as an abundant, highly nutritious food resource.
- Flight provides an escape mechanism from land-bound predators.

- Flight also allows migration to utilize different food resources and seasonal breeding areas.

2. The origin of birds

Birds shared a common ancestor with *Archaeopteryx lithographica.*

- Fossils of *Archaeopteryx* have been recovered from limestone dating to the Jurassic period (150 million years ago).
- *Archaeopteryx* had clawed forelimbs, teeth, a long tail containing vertebrae and feathers (see Campbell, Figure 34.24).
- *Archaeopteryx* is not considered the ancestor to modern birds, but a side branch of the avian lineage.

  The skeleton indicates a weak flyer that may have been a tree-dwelling glider.

Cladistic analysis suggests that birds arose from a theropod dinosaur. Some researchers, however, believe that birds arose from early Mesozoic reptiles (thecodonts), a group that also was ancestral to the dinosaurs.

E. Modern birds

There are about 8600 extant species in 28 orders. Most birds can fly but several are flightless (ostrich, kiwi, and emu) (see Campbell, Figure 34.25a).

- Flightless birds are called *ratites* because the breastbone lacks a keel and large breast muscles used for flying are absent.
- Flying birds are referred to as *carinates* due to the presence of a sternal keel (carina) that supports the large breast muscles used in flying.
- Carinate birds exhibit a variety of feather colors, beak and foot shape, behavior and flight ability (see Campbell, Figure 34.25 b and c).

  Penguins are carinate birds that do not fly, but use powerful breast muscles in swimming.
- Almost 60% of extant species belong to one order of carinate birds (the *passeriforms,* or perching birds), which includes the jays, swallows, sparrows, warblers and many others (see Campbell, Figure 34.25d).

F. Mammals diversified extensively in the wake of the Cretaceous extinctions

There are about 4500 species of extant mammals.

Extinction of the dinosaurs and the fragmentation of continents opened new adaptive zones at the end of the Mesozoic era.

Mammals underwent a massive radiation to fill these vacant zones.

1. Mammalian characteristics

Species in *class Mammalia* have the following characteristics:

- Hair that is composed of keratin, but is not believed to have evolved from reptilian scales; it provides insulation
- Endothermic with an active metabolism

  An efficient respiratory system that utilizes a diaphragm for ventilation supports the metabolism.

  A four-chambered heart segregates oxygenated from unoxygenated blood.
- Mammary glands that produce milk to nourish the young
- Teeth that are differentiated into various sizes and shapes, which are adapted to chewing many types of food.

The jaw apparatus of the ancestral reptiles was also modified during evolution with two of the jaw bones becoming incorporated into the middle ear.

Mammals are dioecious with sexual reproduction and internal fertilization.

- Most are viviparous with the developing embryo receiving nutrients from the female across the *placenta*.
- A few are oviparous.

Mammals have large brains in comparison to other vertebrate groups and are capable of learning.

- Parental care of long duration helps young learn from the parents.

2. The evolution of mammals

Mammals evolved from therapsid ancestors (part of the synapsid branch) during the Triassic period.

- The oldest fossil mammals are dated to 220 million years ago.
- Early mammals coexisted with dinosaurs throughout the Mesozoic era.
- Most Mesozoic mammals were small, probably insectivorous and nocturnal.

Mammals continued to diversify during the Cenozoic.

- During the Cretaceous period (last of the Mesozoic), mass extinctions and mass radiations transformed the flora and fauna of Earth.
- By the beginning of the Cenozoic, mammals were undergoing an adaptive radiation, and their diversity is represented today by three major groups: monotremes, marsupials, and eutherian (placental) mammals.

3. Monotremes

The *monotremes* include the platypuses and echidnas, which are characterized by:

- Oviparity
- A reptilian-like egg with large amounts of yolk that nourishes the developing embryos (see Campbell, Figure 34.27a)
- Hair
- Milk production from specialized glands on the belly of females

  After hatching, young suck milk from the fur of the mother who lacks nipples.

The mixture of ancestral reptilian and derived mammalian traits suggests that monotremes descended from an early branch of the mammalian lineage.

- Extant monotremes are found in Australia and New Guinea.

4. Marsupials

The *marsupials* include opossums, kangaroos, koalas, and other mammals that complete their development in a marsupium (maternal pouch).

Marsupial eggs contain a moderate amount of yolk that nourishes the embryo during early development in the mother's reproductive tract.

- Young are born in an early stage of development and are small (about the size of a honeybee in kangaroos).
- The hindlegs are simple buds, but the forelimbs are strong enough for the young to climb from the female reproductive tract exit to the marsupium.
- In the marsupium, the young attaches to a teat and completes its development while nursing.

Convergent evolution in Australian marsupials has produced a diversity of forms which resemble eutherian (placental) counterparts in all ecological roles (see Campbell, Figure 34.28).

- Opossums are the only extant marsupials outside of the Australian region.
- South America had an extensive marsupial fauna during the Tertiary period, as seen in the fossil record.

Plate tectonics and continental drift provide a mechanism which explains the distribution of fossil and modern marsupials.

- Fossil evidence indicates marsupials probably originated in what is now North America and spread southward while the land masses were joined.
- The breakup of Pangaea produced two island continents: South America and Australia.

  With isolation, their marsupial faunas diversified away from the placental mammals that began adaptive radiation on the northern continents.

- Australia has remained isolated from other continents for about 65 million years, thus isolating its developing fauna.
- When North and South America joined at the isthmus of Panama, extensive migrations took place over the land bridge in both directions.

  The most important migrations occurred about 12 million years ago and again about 3 million years ago.

5. Eutherian (placental) mammals

In placental mammals, embryonic development is completed within the uterus where the embryo is joined to the mother by the placenta.

Adaptive radiation during the late Cretaceous and early Tertiary periods (about 70 to 45 million years ago) produced the orders of extant placental mammals (see Campbell, Table 34.2)

- Fossil evidence indicates that placentals and marsupials diverged from a common ancestor about 80 to 100 million years ago; thus, they are more closely related than either is to the monotremes.

Most mammalogists favor a genealogy that recognizes at least four main evolutionary lines of placental mammals.

- One lineage consists of the orders Chiroptera (bats) and Insectivora (shrews) which resemble early mammals.

  The modified forelimbs which serve a wings in bats probably evolved from insectivores that fed on flying insects.

  Some bats feed on fruits while others bite mammals and lap the blood.

  Most bats are nocturnal.

- A second lineage consists of medium-sized herbivores that underwent a massive adaptive radiation during the Tertiary period.

  This led to such modern orders as the Lagomorpha (rabbits), Perissodactyla (odd-toed ungulates), Artiodactyla (even-toed ungulates), Sirenia (sea cows), Proboscidea (elephants) and Cetacea (whales, porpoises).

- The third evolutionary lineage produced the order Carnivora which probably first appeared during the Cenozoic.

  Included in this order are the cats, dogs, raccoons, skunks, and pinnipeds (seals, sea lions, walruses).

  Seals and their relatives evolved from middle Cenozoic carnivores that became adapted for swimming.

- The fourth lineage had the greatest adaptive radiation and produced the primate-rodent complex.

Includes the orders Rodentia (rats, squirrels, beavers) and Primates (monkeys, apes, humans).

VII. Primates and the Phylogeny of *Homo sapiens*

A. Primate evolution provides a context for understanding human origins

The first primates were small arboreal mammals.

- Dental structure suggests they descended from insectivores in the late Cretaceous.
- *Purgatorius unio*, found in Montana, is considered to be the oldest primate.

Primates have been present for 65 million years (end of Mesozoic era) and are defined by characteristics shaped by natural selection for living in trees. These characteristics include:

- Limber shoulder joints which make it possible to *brachiate* (swing from one hold to the next).
- Dexterous hands for hanging on branches and manipulating food.
- Sensitive fingers with nails, not claws.
- Eyes are close together on the front of the face, giving overlapping fields of vision for enhanced depth perception (necessary for brachiating).
- Excellent eye-hand coordination.
- Parental care with usually single births and long nurturing of offspring.

B. Modern primates

Modern primates are divided into two suborders: Prosimii (premonkeys) and Anthropoidea (monkeys, apes, humans).

- Prosimians (lemurs, lorises, pottos, tarsiers) probably resemble early arboreal primates (see Campbell, Figure 34.29).

There is a question as to which early *prosimian* lineage is ancestral to the *anthropoids*.

- Two groups of prosimian fossils are recognized by paleontologists.
  One ancestral to the tarsiers, the other to lemurs, lorises, and pottos (see Campbell, Figure 34.30).
- The divergence of these two groups occurred at least 50 million years ago and it has been debated as to which of these two groups was also ancestral to the anthropoids.
- Recently discovered fossils raise another possibility.
  Fossils found in Asia and Africa, which date at least 50 million years ago, appear to be more similar to anthropoids than to either groups of prosimian fossils.
  These fossils indicate an early divergence of prosimians into three lineages with the third being ancestral to the anthropoids.

Fossils of monkeylike primates indicate anthropoids were established in Africa and Asia by 40 million years ago in Africa or Asia (South America and Africa had already separated).

- Ancestors of New World monkeys may have reached South America by rafting from Africa or migration southward from North America.

New World monkeys and Old World monkeys have evolved along separate pathways for many millions of years (see Campbell, Figure 34.31)

- All New World monkeys are arboreal.
- Old World monkeys include arboreal and ground-dwelling forms.

- Most monkeys, both New and Old World, are diurnal and usually live in social bands.

There are also four genera of apes included in the anthropoid suborder: *Hylobates* (gibbons), *Pongo* (orangutans), *Gorilla* (gorillas) and *Pan* (chimpanzees) (see Campbell, Figure 34.32).

- Apes are confined to the tropical regions of the Old World.
- They are larger than monkeys (except the gibbons) with relatively long legs, short arms, and no tails.
- Only gibbons and orangutans are primarily arboreal although all are capable of brachiation.
- Social organization varies with the gorillas and chimpanzees being highly social.
- Apes have larger brains than monkeys and thus exhibit more adaptable behavior.

C. Humanity is one very young twig on the vertebrate tree

Paleoanthropology concentrates on the small span of geological time during which humans and chimpanzees diverged from a common ancestor.

Paleoanthropology = The study of human origins and evolution

Competition between researchers has often clouded the field of paleoanthropology.

- Researchers gave new names to fossil forms which were actually the same species recovered by others. (This practice ended about 20 years ago.)
- Theories were proposed on insufficient evidence; often a few teeth or a jawbone fragment.
- Such actions resulted in many persistent misconceptions about human evolution even though fossil discoveries have disproved many of the myths.

1. Some common misconceptions

Our ancestors were chimpanzees or other modern apes.

Humans and chimpanzees represent two divergent branches of the anthropoid lineage which evolved from a common, less specialized ancestor.

Human evolution represents a ladder with a series of steps leading directly from an ancestral anthropoid to Homo sapiens.

- This progression is usually shown as a line of fossil hominids becoming progressively more modern.
- Human evolution included many branches which led to dead ends with several different human species coexisting at times (see Campbell, Figure 34.33).
- If punctuated equilibrium applies to humans, most evolutionary change occurred with the appearance of new hominid species, not phyletic (anagenic) change in an unbranched lineage.

Various human characteristics like upright posture and an enlarged brain evolved in unison.

- *Mosaic evolution* occurred with different features evolving at different times.
- Some ancestral forms walked upright but had small brains.

Present understanding of our ancestry remains unclear even after dismissing many of these myths.

2. Early anthropoids

The oldest known fossils of apes are of *Aegyptopithecus*, the "dawn ape," which was a cat-sized tree-dweller from about 35 million years ago.

About 23 million years ago (during the Miocene epoch), descendants of the first apes diversified and spread to Eurasia.

About 20 million years ago, the Indian plate collided with Asia and the Himalayan range formed.

- The climate became drier and the African and Asian forests contracted.
    - This isolated these regions of anthropoid evolution from each other.

Most anthropologists believe that humans and apes diverged from a common African anthropoid ancestor 6 to 8 million years ago.

- Evidence from the fossil record and DNA comparisons between humans and chimpanzees supports this conclusion.

3. The first humans

Australopithecus africanus was discovered by Raymond Dart in 1924.

- Additional fossils proved that *Australopithecus* was a hominid that walked fully erect and had humanlike teeth and hands.
- The brain was about one-third the size of modern humans.
- Various species of *Australopithecus* began appearing about 4 million years ago and existed for over 3 million years.

"Lucy", an *Australopithecus* skeleton, was discovered in 1974 in the Afar region of Ethiopia by paleoanthropologists.

- Lucy is 3.2 million years old.
- The skeleton was 40% complete and small, about one meter tall with a head the size of a softball.
- The structure indicates an upright posture.
- It was different enough to be placed in a different species, *Australopithecus afarensis*.
- Similar fossils have been discovered which indicate the species existed for about one million years.

Since 1994, other hominid bone fragments have been recovered in east Africa areas near the site of Lucy's discovery. These fragments are so different from *A. afarensis* that new hominid species have been named:

- *Australopithecus anamensis,* from about 4 million years ago
- *Australopithecus ramidus*., from about 4.4 million years ago

A. ramidus, which represents the oldest known hominid, exhibited some interesting characteristics.

- Skull fragments indicated the head balanced on top of the spinal column—evidence of the early evolution of upright posture.
- The skeletons of forest-dwelling animals were found among the bones—this challenges the view that bipedalism evolved when humans began living on the savanna.

The discovery of A. ramidus and A. afarensis has raised several questions.

- Is *A. ramidus* the ancestor of *A. afarensis* or an extinct evolutionary branch?
- Is *A. afarensis* ancestral to other hominids or did it share a common ancestor with *Homo*?
    - *A. afarensis* underwent little change during its one million year span.
    - Several new hominid species resulted from an adaptive radiation which began about 3 million years ago.

  - The new species included *A. africanus*, several heavy-boned species of *Australopithecus*, and *Homo habilis* (appeared about 2.5 million years ago).

While the phylogeny of early hominids is uncertain, one fact is clear: hominids walked upright for two million years without a substantial increase in brain size.

- This posture may have freed the hands for other things such as gathering food or caring for infants.

4. Homo habilis

Enlargement of the human brain is first evident in fossils dating to about 2.5 million years ago.

- Skulls with brain capacities of about 650 cubic centimeters have been found compared with the 500 cc capacity of *A. africanus*.
- Simple stone tools have been found at times with the larger-brained fossils.
- Most paleoanthropologists believe these advances warrant placing the larger-brained fossils in the genus *Homo* and naming them *Homo habilis*.
- It is clear from the fossil record that after walking upright for more than two million years, hominids began to use their brains and hands to fashion tools.

Homo habilis and other new hominids were a part of a larger speciation event among African mammals.

- About 2.5 million years ago, Africa's climate began to become drier and savannas started to replace forests.
- The fauna began to adapt to these new conditions.
- *Homo habilis* coexisted with the smaller-brained *Australopithecus* for nearly one million years.
- One hypothesis is that *Australopithecus africanus* (and other australopithecines) and *Homo habilis* were two distinct lines of hominids.

  Australopithecus africanus was an evolutionary dead end, while *Homo habilis* may have been on the line to modern humans, leading first to *Homo erectus* which later gave rise to *Homo sapiens*.

5. *Homo erectus* and descendants

Homo erectus was the first hominid to migrate out of Africa into Europe and Asia.

- Fossils known as Java Man and Beijing Man are examples if *H. erectus*.

Homo erectus lived from about 1.8 million years ago until 250,000 years ago.

- Fossils found in Africa cover the entire span of *H. erectus'* existence.
- These populations existed during the same period as *H. erectus* populations on other continents.
- The spread to new continents may have resulted from a gradual range expansion associated with a shift in diet to include a larger portion of meat.

  In general, carnivores need a larger range than herbivores.

Homo erectus was taller and had a larger brain than *H. habilis*.

- The *H. erectus* brain capacity increased to as large as 1200 cc during the 1.5 million years of its existence.

  This overlaps the normal range of modern humans.

The intelligence that evolved in *H. habilis* allowed early humans to survive in the colder climates to which they migrated.

- *Homo erectus* lived in huts or caves, built fires, wore clothes of skins, and designed more refined stone tools than *H. habilis*.

- *Homo erectus* was poorly equipped in a physical sense to live outside of the tropics but made up for the deficiencies with intelligence and social cooperation.

Some descendants of *H. erectus* developed larger brain capacities and exhibited regional diversity in populations.

- The Neanderthals are the best known descendants of *H. erectus*.
- Neanderthals lived in Europe, the Middle East, and Asia from 130,000 to 35,000 years ago.
- They had heavier brows, less pronounced chins, and slightly larger brain capacities than modern man.
- They were skilled tool makers who participated in burials and other rituals requiring abstract thought.

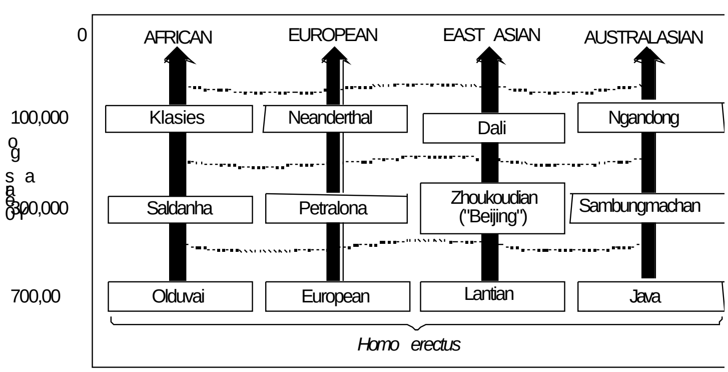
Many paleoanthropologists group the African post-*Homo erectus* fossils with Neanderthals and other descendants from Asia and Australasia. They believe these fossils represent the earliest forms of *Homo sapiens.*

- Some post-*H. erectus* fossils date to 300,000 years ago.

6. The emergence of *Homo sapiens*: Out of Africa...but when? *science as a Process*

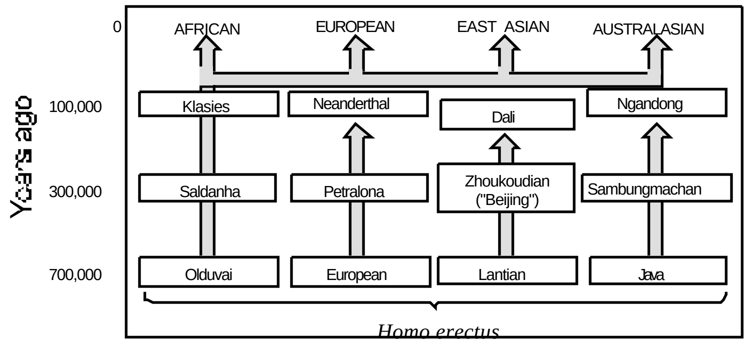
The debate over the origin of modern humans continues unabated with two widely divergent models currently being discussed. These are the multiregional model and the monogenesis model.

The *multiregional model* proposes: 1) Neanderthals and other post-*Homo erectus* hominids were ancestors to modern humans; and 2) modern humans evolved along the same lines in different parts of the world (see also, Campbell, Figure 34.35a).



- If this model is correct, the geographic diversity of humans originated between one and two million years ago when *Homo erectus* spread from Africa to other continents.
- Supporters feel that interbreeding among neighboring populations provided opportunities for gene flow over the entire range and resulted in the genetic similarity of modern humans.

During the 1980s, some paleoanthropologists who interpreted the fossil record in a different way began to develop an alternative to the multiregional model. This alternative became known as the “Out of Africa” or *monogenesis model*.



The *monogenesis model* proposes: 1) *Homo erectus* was the ancestor to modern humans who evolved in Africa; and 2) modern humans dispersed from Africa, displacing the Neanderthals and other post-*H. erectus* hominids (see also Campbell, Figure 34.35b).

- If this model is correct, the diversity of modern humans has developed from geographic diversification within the last 100,000 years.
- To supporters of this model, an exclusively African genesis for modern humans is strongly indicated by the fact that the complete transition from archaic *Homo sapiens* to modern humans is found only in African fossils.
- The focus of their interpretations is on the relationship between Neanderthals and modern humans in Europe and the Middle East.
- The oldest fossils of modern *Homo sapiens* are about 100,000 years old. These were found in Africa and similar fossils have been recovered from caves in Israel.
- The fossils from Israel were found in caves near other caves containing Neanderthal-like fossils which date from 120,000 to 60,000 years ago—overlapping *H. sapiens* by about 40,000 years.
- Supporters of the monogenesis model interpret this information to mean that no interbreeding occurred during the time of coexistence since the two types of hominids persisted as distinct forms.
- This interpretation means the Neanderthals were not ancestors of modern humans since they coexisted and were probably evolutionary dead ends along with other dispersed post-*H. erectus* hominids.

Modern molecular techniques are being used to examine the question of human origins.

- In the late 1980s, a group of geneticists compared the mitochondrial DNA (mtDNA) from a multiethnic group of more than 100 people from four different continents.
- The premise for this analysis is that the greater the differences in the mtDNA of two people, the longer the time of divergence from a common source.
- Analysis of the mtDNA comparisons resulted in the tracing of the source of all human mtDNA back to Africa with the divergence from that common source beginning about 200,000 years ago.

- These results appeared to support the monogenesis model in that the divergence from the common source was too late to represent dispersal of *Homo erectus*, but supported a later dispersal of modern humans.

Several researchers have challenged the interpretation of the mtDNA study, especially the methods used to construct evolutionary trees from this type of data and the reliability of mtDNA as a biological clock.

- This criticism has encouraged advocates of the multiregional model to argue that the fossil evidence supports the multiregional evolution of humans more strongly than African monogenesis.
- These scientists also consider certain fossils from different geographical regions to be links between that region's archaic *Homo sapiens* and the modern humans currently on that continent.

New evidence from comparisons of nuclear DNA and new methods for using the mtDNA data to trace the relationships of populations are stimulating further debate.

- This new information strengthens the monogenesis model.
- Greater genetic diversity is found in African populations south of the Sahara than in other parts of the world.
    - If modern humans evolved in southern Africa, these populations would have the longest history of genetic diversification.
    - If populations of humans in other parts of the world resulted from migrations out of Africa, the smaller genetic diversity could be the result of the founder effect and genetic drift.

Debate continues about whether the multiregional model or the monogenesis model is more accurate.

- New evidence obtained by attempts to extract DNA from fossilized Neanderthal and other archaic *Homo sapiens* skulls may shed new light on this question.

7. Cultural evolution: a new force in the history of life

Erect stance was a very radical anatomical change in our evolution and required major changes in the foot, pelvis and vertebral column.

Enlargement of the brain was a secondary alteration made possible by prolonging the growth period of the skull and its contents.

The brains of nonprimate mammalian fetuses grow rapidly, but growth slows and stops soon after birth.

- The brains of primates continue to grow after birth and the period is longer for a human than other primates.
- Parental care is lengthened due to this extended development and this contributes to the child's learning.

Learning from the experiences of earlier generations is the basis of culture (transmission of accumulated knowledge over generations); the transmission is by written and spoken language.

A cultural evolution is a continuum, but three stages are recognized:

1. Nomads of the African grasslands made tools, organized communal activities and divided labors about 2 million years ago.
2. The development of agriculture in Africa, Eurasia, and the Americas about 10,000 to 15,000 years ago encouraged permanent settlements.
3. The Industrial Revolution began in the eighteenth century. Since then, new technology and the human population have escalated exponentially.

No significant biological change in humans has occurred from the beginning to now.

Evolution of the human brain may have been anatomically simpler than acquiring an upright stance, but the consequences of cerebral growth have been enormous.

- Cultural evolution resulted in *Homo sapiens* becoming a species that could change the environment to meet its needs and not have to adapt to an environment through natural selection.
  - Humans are the most numerous and widespread of large animals.
- Cultural evolution outpaces biological evolution and we may be changing the world faster than many species can adapt.
  - The rate of extinctions this century is 50 times greater than the average for the past 100,000 years.
  - The overwhelming rate of extinction is due primarily to habitat destruction and chemical pollution, both functions of human cultural changes and overpopulation.
  - Global temperature increase and alteration of world climates are a result of escalating fossil fuel consumption.
  - Destruction of tropical rain forests, which play a role in maintenance of atmospheric gas balance and moderating global weather, is startling.

The effect of *Homo sapiens* is the latest and may be the most devastating crisis in the history of life.

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CHAPTER 35
PLANT STRUCTURE AND GROWTH

OUTLINE

I. Introduction to Modern Plant Biology
   A. Molecular biology is revolutionizing the study of plants
   B. Plant biology reflects the major themes in the study of life

II. The Angiosperm Body
   A. A plant's root and shoot systems are evolutionary adaptations to living on land
   B. Structural adaptations of protoplasts and walls equip plant cells for their specialized functions
   C. The cells of a plant are organized into dermal, vascular, and ground tissue systems

III. Plant Growth
   A. Meristems generate cells for new organs throughout the lifetime of a plant: *an overview of plant growth*
   B. Primary growth: apical meristems extend roots and shoots by giving rise to the primary plant body
   C. Secondary growth: lateral meristems add girth by producing secondary vascular tissue and periderm

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. List the characteristics of an angiosperm.
2. Explain the differences between monocots and dicots.
3. Describe the importance of root systems and shoot systems to plants and explain how they work together.
4. Explain how taproot systems and fibrous root systems differ.
5. Explain the differences between stolons and rhizomes.
6. Describe how plant cells grow.
7. Distinguish between parenchyma and collenchyma cells with regards to structure and function.
8. Describe the differences in structure and function of the two types of sclerenchyma cells.
9. Explain the importance of tracheids and vessel elements to plants.
10. Distinguish between water-conducting cells and sieve-tube members with regards to structure and function.
11. Explain the differences between simple tissues and complex tissues.
12. Explain the importance of a cuticle on the aerial parts of a plant and its absence on roots.

13. Describe the functions of the dermal tissue system, vascular tissue system and ground tissue system.
14. Distinguish among annual, biennial, and perennial plants.
15. Explain the importance of the zones of cell division, cell elongation, and cell differentiation in primary growth of roots.
16. Explain the importance of the endodermis to a plant.
17. Describe the importance of an apical meristem to the primary growth of shoots.
18. Distinguish between the arrangement of vascular tissues in roots and shoots.
19. Describe how "wood" forms due to secondary growth of stems.
20. Using a diagram, describe the basic structure of a root, a stem, and a leaf.

KEY TERMS

monocots	petiole	meristem	endodermis
dicots	protoplast	apical meristem	lateral roots
root system	parenchyma cell	primary growth	pericycle
shoot system	collenchyma cell	secondary growth	vascular bundle
xylem	sclerenchyma cell	lateral meristem	stomata
phloem	fiber	primary plant body	guard cells
taproot	sclereids	root cap	transpiration
fibrous root	tracheids	zone of cell division	mesophyll
root hairs	vessel elements	quiescent center	secondary plant body
adventitious	pits	protoderm	vascular cambium
stem	xylem vessels	pericycle	cork cambium
node	sieve-tube members	procambium	ray initials
internode	sieve plates	ground meristem	fusiform initials
axillary bud	companion cell	zone of elongation	periderm
terminal bud	dermal tissue system	zone of maturation	bark
apical dominance	epidermis	stele	lenticel
leaves	annuals	pith	
blade	perennials	cortex	

LECTURE NOTES

Plants form the foundation on which most terrestrial ecosystems are built.

- As the primary producers in most systems (through the process of photosynthesis), plants serve as the first link in the food chain which affects all species of animals in the system.

Plants were first studied by early humans who had to distinguish between edible and poisonous plants.

- These early humans later began to use plant products to make useful tools and other items.
- Modern plant biology continues to center on how to use plants and plant products to benefit humans.

I. Introduction to Modern Plant Biology

A. Molecular biology is revolutionizing the study of plants

New methods and the discovery of unique, interesting experimental organisms has expanded the knowledge base in many areas of plant biology.

Studying organisms such as *Arabidopsis thaliana*, which has a short generation time and a tiny genome, has enabled scientists to gain new insight into the genetic control of plant development.

- For example, researchers have identified the genes responsible for flower development.
- Eventually, researchers may be able to understand the mechanisms that control several basic process, such as how a plant causes water to flow upward, how plants resist disease, and what makes roots grow down and shoots grow up.

B. Plant biology reflects the major themes in the study of life

Plants, as do all living systems, have a hierarchy of structural levels. As research into the biology of plants progresses, the relationships of the molecular and cellular mechanisms to the function of the whole organism will emerge.

Correlating the structure and functions of plants is a second focus of plant biology.

- Structure and function of plants are the result of interactions with the environment over both evolutionary and short-term time scales.

  In their evolutionary journey, plants adapted to the problems of a terrestrial existence as they moved from water to land (e.g., woody tissues provide support).

  Over the short-term, environmental stimuli cause individual plants to exhibit structural and physiological responses (e.g., stomata close during the hottest part of the day, thus conserving water) (see Campbell, Figure 35.2).

While plants and animals faced many of the same problems (e.g., support, internal transport) they solved such problems in different ways.

- The two groups evolved independently from unicellular ancestors which had different modes of nutrition; this alone established a different evolutionary direction.

II. The Angiosperm Body

A. A plant's root and shoot systems are evolutionary adaptations to living on land

Plant biologists study two levels of plant architecture: morphology and anatomy.

Plant morphology = The study of the external structure of plants (e.g., arrangement of the parts of a flower)

Plant anatomy = The study of the internal structure of plants (e.g., arrangement of the cells and tissues in a leaf)

Angiosperms (flowering plants) are the most diverse and widespread of the plants with about 275,000 extant species.

- Characterized by flowers and fruits, which are believed to be adaptations for reproduction and seed dispersal
- Taxonomists divide angiosperms into two taxonomic classes: *monocots* and *dicots* which possess either one or two seed leaves, respectively, in combination with other characteristics (see Campbell, Figure 35.3).

A plant can be divided into two basic systems, a subterranean *root system* and an *aerial shoot system* (stems, leaves, flowers).

- This two system arrangement reflects the evolutionary history of plants as terrestrial organisms (see Campbell, Figure 35.4).
- Unlike the algal ancestors which were completely surrounded by nutrient rich water, terrestrial plants face a divided habitat:
  - Air is the source of CO_2 for photosynthesis, and sunlight cannot penetrate into the soil.
  - Soil provides water and dissolved minerals to the plant.
- Each system depends on the other for survival of the whole plant.
  - Roots depend on shoots for sugar and other organic nutrients.
  - Shoots depend on roots for minerals, water and support.
- Materials are transported through the plant by vascular tissues.
  - *Xylem* conveys water and dissolved minerals to the shoots.
  - *Phloem* conveys food from shoots to roots and other nonphotosynthetic parts, and from storage roots to actively growing shoots.

1. The root system

Root structure is well adapted to:

- Anchor plants
- Absorb and conduct water and nutrients
- Store food

There are two major types of root systems:

1. The *taproot* system is seen in many dicots.
   - One large, vertical root (the taproot) produces many smaller secondary roots.
   - Provides firm anchorage
   - Some taproots, such as carrots, turnips, and sweet potatoes, are modified to store a large amount of reserve food.
2. A *fibrous root* system is found primarily in monocots (palms, bamboo, grasses).
   - A mat of threadlike roots spreads out below the soil surface.
   - Provides extensive exposure to soil water and minerals
   - Roots are concentrated in the upper few centimeters of soil, preventing soil erosion.

Absorption of water is greatly enhanced by *root hairs,* which increase the surface area of the root (see Campbell, Figure 35.5).

- Root hairs are normally most numerous near the root tips.
- Water and mineral absorption are also enhanced by mycorrhizae, symbiotic associations between roots and fungi.

Many plants possess root nodules, which contain symbiotic bacteria capable of converting atmospheric nitrogen to nitrogenous compounds that the plant can use for the synthesis of proteins and other organic molecules.

Adventitious roots = Roots arising above ground from stems or leaves

- Form in addition to the normal root system
- Some, such as prop roots of corn, help support the plant stem

2. The shoot system

Shoot systems are comprised of vegetative shoots and floral shoots.

- Vegetative shoots consist of a stem and attached leaves; may be the main shoot or a vegetative branch.
- Floral shoots terminate in flowers.

a. Stems

Stem morphology includes:(see Campbell, Figure 35.4):

- *Nodes* = The points where leaves are attached to stems
- *Internodes* = The stem segments between the nodes
- *Axillary bud* = An embryonic side shoot found in the angle formed by each leaf and the stem; usually dormant
- *Terminal bud* = The bud on a shoot tip; it usually has developing leaves and a compact series of nodes and internodes

Growth of a shoot is usually concentrated at the apex of the shoot where the terminal bud is located.

- The presence of a terminal bud inhibits development of axillary buds, a condition called *apical dominance.*
- Apical dominance appears to be an evolutionary adaptation to increase exposure of plant parts to light by concentrating resources on increasing plant height.

Axillary buds begin to grow under certain conditions and after damage or removal of the terminal bud.

- Some may develop into floral shoots.
- Others develop into vegetative shoots with terminal buds, leaves, and axillary buds.

  This development results in branching which also increases exposure of plant parts to light.

Some plants have modified stems which are often mistaken for roots. There are several types of modified stems, each of which performs a specific function (see Campbell, Figure 35.6)

- Stolons are horizontal stems growing along the surface of the ground (e.g., strawberry plant runners).
- Rhizomes are horizontal stems growing underground (e.g., irises).

  Some end in enlarged tubers where food is stored (e.g., potatoes)
- Bulbs are vertical, underground shoots with leaf bases modified for food storage (e.g., onions).

b. Leaves

Leaves are the main photosynthetic organs of a plant.

A leaf usually exists in the shape of a flattened blade which is joined to the node of a stem by a petiole.

- Most monocots lack petioles; instead, the leaf base forms a sheath surrounding the stem.

Leaves of monocots and dicots vary in the arrangement of their major veins.

- Monocot leaves have parallel major veins running the length of the blade.
- Dicot leaves have a multi-branched network of major veins; can be palmate or pinnate.
- All leaves have numerous minor cross-veins.

Plant taxonomists use a variety of leaf characteristics to classify plants,

including:
- Leaf shape
- Spatial arrangement of leaves on a stem
- Pattern of a leaf's veins

Campbell, Figure 35.7 illustrates simple vs. compound leaves.

Some plants have leaves that have become adapted for functions other than photosynthesis (see Campbell, Figure 35.8).
- Tendrils are modified leaflets that cling to supports.
- Spines of cacti function in protection.
- Many succulents have leaves modified for storing water.
- Some plants have brightly colored leaves that help attract pollinators to the flower.

B. Structural adaptations of protoplasts and walls equip plant cells for their specialized functions

Each type of plant cell has structural adaptations that make it possible to perform that cell's function. Some are coupled with specific characteristics of the protoplast (see Campbell, Figure 35.9)

Protoplast = Contents of a plant cell exclusive of the cell wall

1. Parenchyma cells

Parenchyma cells are the least specialized plant cells (see Campbell, Figure 35.10a).

Primary walls are thin and flexible.

Most lack secondary walls.

The protoplast usually has a large central vacuole.

They function in synthesizing and storing organic products.

Photosynthesis occurs in the chloroplasts of mesophyll cells.

Some parenchyma cells in stems and roots have colorless plastids that store starch.

Most mature cells do not divide, but retain the ability to divide and differentiate into other cell types under special conditions (e.g., repair and replacement after injury).

2. Collenchyma cells

Collenchyma cells usually lack secondary walls.

The primary cell wall is thicker than in parenchyma cells but is of an uneven thickness (see Campbell, Figure 35.10b).

They are usually grouped in strands or cylinders to support young parts of plants without restraining growth.

They are living cells which elongate as the stems and leaves they support grow.

3. Sclerenchyma cells

Sclerenchyma cells function in support.

They have very rigid, thick secondary walls strengthened by lignin.

Many lack protoplasts at functional maturity, so they cannot elongate. In fact, they may be dead, functioning only as support.

There are two forms: *fibers* (long, slender, tapered cells occurring in bundles) and *sclerids* (shorter, irregularly-shaped cells) (see Campbell, Figure 35.10c).

4. Water-conducting cells of xylem: tracheids and vessel elements

Xylem consists of two cell types, both with secondary walls and both dead at functional maturity.

- Before the protoplast dies, secondary walls are deposited in spiral or ring patterns (which allows them to stretch) in parts of the plant that are still growing.

Tracheids are long, thin, tapered cells having lignin-hardened secondary walls with *pits* (thinner regions where only primary walls are present) (see Campbell, Figure 35.10a)

- Water flows from cell to cell through pits.
- They also function in support.

Vessel elements are wider, shorter, thinner-walled, and less tapered than tracheids.

- Vessel elements are aligned end to end.
- The end walls are perforated, permitting the free flow of water through long chains of vessel elements called xylem vessels.

5. **Food-conducting cells of phloem: sieve-tube members**

Sieve-tube members are chains of phloem cells that transport sucrose, other organic compounds, and some minerals.

- The cells are alive at functional maturity.
- Protoplasts lack a nucleus, ribosomes, and a distinct vacuole.

In angiosperms, the end walls of sieve-tube members have pores and are called *sieve plates*.

- The pores probably facilitate the movement of fluid between cells.
- At least one *companion cell* is connected to each sieve-tube member by many plasmodesmata; the companion's nucleus and ribosomes may also serve the sieve-tube member which lacks these organelles.
  - Companion cells also help load sugar produced in the mesophyll into sieve-tubes of leaves of some plants.

> It is useful to emphasize how close inspection of cell structure often reveals its function, and vice versa.

C. The cells of a plant are organized into dermal, vascular, and ground tissue systems

Each organ of a plant (leaf, stem, root) has three tissue systems: dermal, vascular, and ground tissue systems.

Each of the three systems is continuous throughout the plant, although specific characteristics and spatial relationships vary in different plant organs (see Campbell, Figure 35.12).

1. *Dermal tissue system* (or *epidermis*) = Single layer of tightly packed cells covering and protecting the young parts of the plant
   - Functions in protection and has special characteristics consistent with the function of the organ it covers.
     - Root hairs specialized for water and mineral absorption are extensions of epidermal cells near root tips.
     - The waxy cuticle that helps the plant retain water is secreted by epidermal cells of leaves and most stems.
2. *Vascular tissue system* = The xylem and phloem that functions in transport and support; is continuous throughout the plant
3. *Ground tissue system* = Predominantly parenchyma, with some collenchyma and sclerenchyma present; occupies the space between dermal and vascular tissue systems; functions in photosynthesis, storage, and support

III. Plant Growth

A. Meristems generate cells for new organs throughout the lifetime of a plant: *an overview of plant growth*

Plant growth begins with germination of the seed and continues for the lifespan of the plants.

Plants do not live indefinitely, they have finite life spans.

- Most have genetically determined lifespans.
- Some are environmentally determined.
- *Annuals* complete their life cycle in one year or growing season.
- Biennials typically have life spans of two years.
- *Perennials*, such as trees and some grasses, live many years.

Indeterminate growth is made possible by *meristems* (perpetually embryonic tissues).

- *Indeterminate growth* = Continued growth as long as the plant lives
  - In contrast, most animals cease growing after reaching a certain size (determinate growth).
  - Certain plant organs, such as flower parts, show determinate growth.
- Meristematic cells are unspecialized and divide to generate new cells near the growing point.
  - New meristematic cells formed by division that remain in the region and produce new cells are called initials.
  - New cells are displaced (derivatives), and become incorporated and specialized into tissues.
- *Apical meristems*, located in root tips and shoot buds, supply cells for plants to grow in length.
  - *Primary growth* (elongation) is initiated by apical meristems and forms primary tissues organized into the 3 tissue systems.
  - *Secondary growth* (increased girth) is the thickening of roots and shoots which occurs in woody plants due to development of lateral meristems.
- *Lateral meristems* = Cylinders of dividing cells extending along the lengths of roots and shoots.
  - Cell division in the lateral meristems produces secondary dermal tissues which are thicker and tougher than the epidermis it replaces.
  - Also adds new layers of vascular tissues.

B. Primary growth: apical meristems extend roots and shoots by giving rise to the primary plant body

Primary growth produces the *primary plant body*, which consists of three tissue systems (see Campbell, Figure 35.12).

- The youngest portions of woody plants and herbaceous plants are examples of primary plant bodies.
- Apical meristems are responsible for the primary growth of roots and shoots.

1. Primary growth of roots

Root growth is concentrated near its tip and results in roots extending through the soil.

- The root tip is covered by a *root cap*, which protects the meristem and secretes a polysaccharide coating that lubricates the soil ahead of the growing root.
- The root tip contains three zones of cells in successive stages of primary growth. Although described separately, these zones blend into a continuum (see Campbell, Figure 35.15).

1. Zone of cell division
   - Located near the tip of the root; includes the apical meristem and its derivatives, the primary meristems.
   - The apical meristem is centrally located; it produces the primary meristems and replacement cells of the root cap.
   - A *quiescent center* is located near the center of the apical meristem. It is composed of resistant, slowly dividing cells which may serve as reserve replacement cells in case of damage to the meristem.
   - The primary meristems form as three concentric cylinders of cells (the *protoderm*, *procambium*, and *ground meristem*) that will produce the tissue systems of the roots.
2. Zone of cell elongation
   - In this region, cells elongate to at least ten times their original length.
   - The elongation of cells in this region pushes the root tip through the soil.
   - Continued growth is sustained by the meristem's constant addition of new cells to the youngest end of the elongation zone.
3. Zone of maturation
   - Is located farthest from the root tip
   - Region where the new cells become specialized in structure and function and where the three tissue systems complete their differentiation.

a. Primary tissues of roots

The apical meristem produces three primary meristems, which in turn give rise to the three primary tissues of roots (see Campbell, Figure 35.16).

1. The *protoderm* is the outermost primary meristem.
   - Gives rise to the epidermis over which water and minerals must cross.
   - Root hairs are epidermal extensions which increase surface area, thus enhancing uptake.
2. The *procambium* forms a *stele* (central cylinder) where xylem and phloem develop.
   - In dicots, xylem radiates from the stele's center in two or more spokes, with phloem in between the spokes.
   - In monocots, a central *pith* (core of parenchyma cells) is ringed by vascular tissue in an alternating pattern of xylem and phloem.
3. The ground meristem is located between the protoderm and procambium; it gives rise to the ground tissue system. The ground tissue:
   - Is mostly parenchyma and fills the *cortex* (root area between the stele and epidermis)
   - Stores food; the cell membranes are active in mineral uptake
   - Has *endodermis*, the single-cell thick, innermost layer of the cortex that forms the boundary between the cortex and

the stele; it selectively regulates passage of substances from soil to the vascular tissue of the stele

Lateral roots may sprout from the outermost layer of the stele of a root.

- The *pericycle*, just inside the endodermis, is a layer of cells that may become meristematic and divide to form the lateral root (see Campbell, Figure 35.17).
- A lateral root forms as a clump of cells in the pericycle, then elongates and pushes through the cortex until it emerges from the primary root.
- The lateral root maintains its vascular connection to the stele of the main root.

2. Primary growth of shoots

A shoot's apical meristem is a dome-shaped mass of dividing cells at the tip of the terminal bud (see Campbell, Figure 35.18).

- Forms the primary meristems that differentiate into the three tissue systems.
- On the flanks of the apical meristem dome are *leaf primordia* which form leaves.
- Meristematic cells left by the apical meristem at the base of the leaf primordia develop into axillary buds.

Most shoot elongation actually occurs due to growth of slightly older internodes below the shoot apex.

- Growth is a result of both cell division and elongation within the internode.
- Intercalary meristems are present at the base of each internode in grasses and some other plants.

  These tissues permit prolonged internode elongation along the length of the shoot.

Axillary buds may form branches later in the life of the plant.

- Branches originate at the surface of the shoot and are connected to the vascular system which lies near the surface.
- This is a direct contrast to development of lateral roots which form deep in the pericycle of the root.

a. Primary tissues of stems

The vascular tissue of the stem is organized into strands of *vascular bundles* that run the length of the stem (see Campbell, Figure 35.19).

- They converge at the transition zone (shoot → root) to join the root stele.
- Each bundle is surrounded by ground tissue, including pith and cortex.

In dicots, bundles are arranged in a ring with pith inside and cortex outside.

- Xylem faces the pith, phloem faces the cortex.
- Pith and cortex are connected by pith rays, thin layers of ground tissue.

In monocots, vascular bundles are scattered throughout the ground tissue of the stem.

- The stem ground tissue is mostly parenchyma.
- Ground tissue of stems is mostly parenchyma, strengthened in many plants by collenchyma located beneath the epidermis.

The protoderm of the terminal bud gives rise to the epidermal portion of the dermal tissue system.

b. Tissue organization of leaves

Leaves are cloaked by an epidermis of tightly interlocked cells (see also Campbell, Figure 35.20).

- It protects against physical damage and pathogens.
- A waxy cuticle prevents water loss.
- *Stomata* are pores flanked by *guard cells* which regulate gas exchange with the surrounding air and photosynthetic cells inside the leaf.
- Stomata also allow *transpiration* (water loss from plant by evaporation).
- Stomata are usually more numerous on the bottom surface of the leaf. This location minimizes water loss.

The ground tissue of a leaf is *mesophyll.*

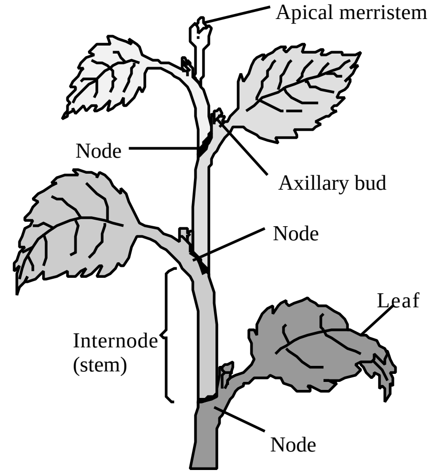
- Consists mainly of parenchyma cells equipped with chloroplasts for photosynthesis
- Dicots usually have two distinct regions of mesophyll:
    1. *Palisade parenchyma* = One or more layers of columnar cells of the upper half of a leaf
    2. *Spongy parenchyma* = Irregularly shaped cells surrounded by air spaces through which oxygen and carbon dioxide circulate. Located in the lower half of the leaf

The leaf vascular tissue is continuous with that of the stem through leaf traces which are branches from the stem vascular bundles.

- Leaf traces continue in the petiole as a vein, which branches repeatedly throughout the mesophyll of the leaf blade.
- This arrangement brings the photosynthetic tissue of the leaf into close contact with xylem and phloem.
- Functions also as a skeleton to support the shape of the leaf.

c. Modular shoot construction and phase changes during development

Shoots are constructed of a series of modules produced by the serial development of nodes and internodes within the shoot apex (see also Campbell, Figure 35.21).



- Each module consists of a stem, one or more leaves, and an axillary bud associated with each leaf.
- Elongation of the internode provides for primary growth of the plant.

Modules found in the body of a plant represent various ages of tissue. The age of a module is proportional to its distance from the apical meristem.

- The developmental phase of each module changes over time.
- There is a gradual change from a juvenile vegetative state to a mature vegetative state.

  Leaf morphology usually changes during this transition (see Campbell, Figure 35.22).
- In some plants, the mature shoot apex may undergo a second phase change to a flower-producing (reproductive) state.

  Primary growth of these shoot tips is terminated since the apical meristem is consumed in production of the flower.

C. Secondary growth: lateral meristems add girth by producing secondary vascular tissue and periderm

A *secondary plant body* results from secondary growth.

- The secondary plant body is comprised of the secondary tissues produced during growth in diameter.
- Secondary growth results from two lateral meristems: the *vascular cambium* and the *cork cambium.*

  Vascular cambium produces secondary xylem and phloem.

  Cork cambium produces a tough, thick covering for roots and stems that replaces the epidermis.
- Secondary growth occurs in all gymnosperms and most dicot angiosperms.

  It is rare in monocots.

1. Secondary growth of stems

a. Vascular cambium and the production of secondary vascular tissue

Vascular cambium forms when meristemic parenchyma cells develop between the primary xylem and primary phloem of each vascular bundle and in the rays of ground tissue between the bundles (see Campbell, Figures 35.23 and 35.24)

Fasicular cambium = Cambium within the vascular bundle

Interfasicular cambium = Cambium in the rays between vascular bundles

- Together, meristematic bands in the fasicular and interfasicular regions form a continuous cylinder of dividing cells around the xylem and pith of the stem.

- *Ray initials* (meristematic cells of the interfasicular cambium) produce radial files of parenchyma cells (= xylem and phloem rays) which permit lateral transport of water and nutrients as well as storage of starch and other reserves.
- *Fusiform initials* (cells of fasicular cambium) produce new vascular tissues; secondary xylem to the inside of the vascular cambium and secondary phloem to the outside.

Accumulated layers of secondary xylem produces wood that consists mostly of tracheids, vessel elements and fiber.

- The hardness and strength of wood results from these cells which, while dead at maturity, have thick, lignified walls.
- Forms annual growth rings due to yearly activity: cambium dormancy, spring wood production and summer wood production.

The secondary phloem does not accumulate extensively. The secondary phloem, and all tissues external to it, develop into bark which eventually sloughs off the tree trunk.

It is important to note that primary and secondary growth occur simultaneously, but in different regions of the stem.

b. Cork cambium and the production of periderm

Cork cambium is a cylinder of meristematic tissue that forms protective layers of the secondary plant body.

- It first forms in the outer cortex of the stem.
- Phelloderm (parenchyma cells) forms to the inside of cork cambium initials as they divide.
- Cork cells form to the outside of cork cambium initials as they divide.
- As cork cells mature, they deposit suberin (a waxy material) in their walls and die.
- These dead cork tissues protect the stem from damage and pathogens while reducing water loss.
- The combination of cork cambium, layers of cork, and phelloderm form the *periderm* (the protective coat of the secondary plant body that replaces primary epidermis).
- The term *bark* refers to all the tissues external to the vascular cambium (phloem, phelloderm, cork cambium and cork) (see Campbell, Figure 35.25).

Cork cambium is a cylinder of fixed size and does not grow in diameter.

- As continued secondary growth splits it, it is replaced by new cork cambium formed deeper in the cortex.
- When no cortex is left, it develops from parenchyma cells in the secondary phloem (only the youngest secondary phloem, internal to cork cambium, functions in sugar transport).
- Lenticels are present in the bark.

Lenticel = Spongy region in the bark which permit gas exchange by living cells within the trunk

2. Secondary growth of roots

Vascular cambium and cork cambium also function in secondary growth of roots.

- The vascular cambium produces secondary xylem to its inside and secondary phloem to its outside.

  It is first located between xylem and phloem of the stele.

The cortex and epidermis split and are shed as the stele grows in diameter.

- Cork cambium forms from the pericycle of the stele and produces the periderm, which becomes secondary dermal tissue.

  Periderm is impermeable to water, consequently, the roots with secondary growth function to anchor the plant and transport water and solutes between the younger roots and the shoot system.

Older roots become woody, and annual rings appear in the secondary xylem.

- Old roots and old stems may look very similar.

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CHAPTER 36

TRANSPORT IN PLANTS

OUTLINE

I. An Overview of Transport Mechanisms in Plants
   A. Transport at the cellular level depends on the selective permeability of membranes
   B. Proton pumps play a central role in transport across plant membranes
   C. Differences in water potential drive water transport
   D. Vacuolated cells have three major compartments
   E. The symplast and apoplast both function in transport within tissues and organs
   F. Bulk flow functions in long-distance transport

II. Absorption of Water and Mineral by Roots
   A. Root hairs, mycorrhizae, and a large surface area of cortical cells enhance water and mineral absorption
   B. The endodermis functions as a selective sentry between the root cortex and vascular tissue

III. Transport of Xylem Sap
   A. The ascent of xylem sap depends mainly on transpiration and the physical properties of water
   B. Review: xylem sap ascends by solar-powered bulk flow

IV. The Control of Transpiration
   A. Guard cells mediate the photosynthesis-transpiration compromise
   B. Xerophytes have evolutionary adaptations that reduce transpiration

V. Translocation of Phloem Sap
   A. Phloem translocates its sap from sugar sources to sugar sinks
   B. Pressure flow is the mechanism of translocation in angiosperms

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. List three levels in which transport in plants occurs and describe the role of aquaporins.
2. Trace the path of water and minerals from outside the root to the shoot system.
3. Provide experimental evidence that links plant cellular respiration to mineral accumulation.
4. Explain how a proton pump may affect mineral transport in plants.
5. Describe the symplast and apoplast routes for the transit of water and minerals across the root cortex from the epidermis to the stele.
6. Explain the function of the Casparian strip.
7. Explain how solutes are transferred between the symplast and apoplast.

8. Define water potential.
9. Explain how solute concentration and pressure affects water potential.
10. Predict the direction of net water movement based upon differences in water potential between a plant cell and a hypoosmotic environment, a hyperosmotic environment or an isosmotic environment.
11. Explain how root pressure is created by some plants and how it causes guttation.
12. According to the transpiration-cohesion-adhesion theory, describe how xylem sap can be pulled upward in xylem vessels.
13. Explain why a water potential gradient is required for the passive flow of water through a plant, from soil.
14. Compare the transpiration-to-photosynthesis ratio between C_3 and C_4 plants.
15. Describe both the disadvantages and benefits of transpiration.
16. Explain how guard cells control the stomatal aperture and how this, in turn, can affect photosynthetic rate and transpiration.
17. Explain how K^+ fluxes across the guard cell membrane affects guard cell function.
18. List three cues that contribute to stomatal opening at dawn.
19. Describe environmental stresses that can cause stomata to close during the daytime.
20. Explain how xerophytes can be adapted to arid climates.
21. Explain how crassulacean acid metabolism allows CAM plants to reduce the transpiration rate.
22. Describe source-to-sink transport in phloem and explain what determines the direction of phloem sap flow.
23. Compare the process of phloem loading between plants such as corn and squash.
24. Give one explanation for how a proton pump can allow for selective accumulation of sucrose in the symplast.
25. Explain what causes phloem sap to flow from source to sink and describe how a scientist can study pressure-flow in phloem.

KEY TERMS

transport proteins	turgor pressure	endodermis	circadian rhythms
selective channels	turgid	Casparian strip	translocation
chemiosmosis	aquaporins	transpiration	sugar source
osmosis	tonoplast	cohesion	sugar sink
water potential	symplast	root pressure	transfer cells
megapascals	apoplast	guttation	
tension	bulk flow	transpiration-to- photosynthesis ratio	
plasmolyze	mycorrhizae		

LECTURE NOTES

Land plants require a transport system, because unlike their aquatic ancestors, photosynthetic plant organs have no direct access to water and minerals.

I. An Overview of Transport Mechanisms in Plants

Three levels of transport occur in plants:

1. Uptake and release of water and solutes by individual cells
2. Short-distance cell-to-cell transport at the level of tissues and organs
3. Long-distance transport of sap in xylem and phloem at the whole-plant level

Campbell, Figure 36.1 provides an overview of these transport functions.

A. Transport at the cellular level depends on the selective permeability of membranes

Water and solute transport is covered in detail in Chapter 8. This section highlights a few of the transport processes in the context of plant cells.

The plasma membrane's selective permeability controls the movement of solutes between a plant cell and the extracellular fluids. Solutes may move by passive or active transport.

Passive transport occurs when a solute molecule diffuses across a membrane down a concentration gradient.

- Requires no direct expenditure of energy by the cell
- Transport proteins embedded in the membrane may increase the speed at which solutes cross.
  - *Transport proteins* may facilitate diffusion by serving as carrier proteins or forming selective channels.
  - Carrier proteins bind selectively to a solute molecule on one side of the membrane, undergo a conformational change, and release the solute molecule on the opposite side of the membrane.
  - *Selective channels* are simply passageways by which selective molecules may enter and leave a cell; some gated selective channels are stimulated to open or close by environmental conditions.

Active transport occurs when a solute molecule is moved across a membrane against the concentration gradient.

- Energy requiring process
- Active transport is not accomplished by the use of transport proteins, such as those involved in facilitated diffusion, but is conducted by active transporters, a special class of membrane proteins (e.g., the proton pump is an active transporter important to plants).

B. Proton pumps play a central role in transport across plant membranes

A *proton pump* hydrolyzes ATP and uses the energy to pump hydrogen ions (H^+) out of the cell.

- Produces a proton gradient with a higher concentration outside of the cell
- Produces a membrane potential, since the inside of the plant cell is negative in relation to the outside

This membrane potential and the stored energy of the proton gradient are used by the plant to transport many different molecules (see Campbell, Figure 36.2).

- Potassium ions (K^+) are pulled into the cells because of the electrochemical gradient.
- Nitrate (NO_3^-) enters plant cells against the electrochemical gradient by in exchange for hydrogen ions by a process known as *cotransport.*

The involvement of proton pumps in the transport processes of plant cells is a specific application of *chemiosmosis.*

C. Differences in water potential drive water transport in plant cells

Osmosis results in the net uptake or loss of water by the cell and depends on which component, the cell or extracellular fluids, has the highest water potential.

Water potential (Ψ) = The free energy of water that is a consequence of solute concentration and applied pressure; physical property predicting the direction water will flow

- Water will always move across the membrane from the solution with the higher water potential to the one with lower water potential.
- Water potential is measured in units of pressure called *megapascals* (MPa); one MPa is equal to ten atmospheres of pressure.

1. How solutes and pressure affect water potential

Pure water in an open container has a water potential of zero megapascals ($\Psi = 0$ MPa).

- Addition of solutes to water lowers the Ψ into the negative range.
- Increased pressure raises the Ψ into the positive range.
- A negative pressure, or *tension*, may also move water across a membrane; this *bulk flow* (movement of water due to pressure differences) is usually faster than the movement caused by different solute concentrations.

Campbell, Figure 36.3 illustrates water potential and water movement.

2. Quantitative analysis of water potential

The effects of pressure and solute concentration on water potential are represented by:

$$\Psi = \Psi_P + \Psi_S$$

- Ψ_P = Pressure potential
- Ψ_S = Solute potential or osmotic potential

> Example: A 0.1M solution has a Ψ_S of -0.23 MPa; in the absence of physical pressure, the water potential is −0.23 MPa ($\Psi = 0 + (-0.23) = -0.23$ MPa).
>
> The addition of pressure to the solution could counter the effects of osmotic pressure by stopping net water movement (if P = 0.23) or by forcing water from the solution back into the pure water (if $P \geq 0.3$).
>
> Similar changes would result if a negative pressure were applied to the pure water side of the membrane.

Plant cells will gain or lose water to intercellular fluids depending upon their water potential.

- A flaccid cell (P = 0) placed in a hyperosmotic solution will lose water by osmosis; the cell will *plasmolyze* (protoplast pulls away from the cell wall) in response (see Campbell, Figure 36.4a).
- A flaccid cell placed in a hypoosmotic solution will gain water by osmosis; the cell will swell and a *turgor pressure* develops; when pressure from the cell wall is equal to the osmotic pressure, an equilibrium is reached and no net water movement occurs ($\Psi = 0$) (see Campbell, Figure 36.4b).

3. Aquaporins

Until recently, most biologists accepted the hypothesis that leakage of water through the lipid bilayer accounted for the flux of water across plasma membranes.

Recent experimental data suggests that water transport is too specific and too rapid to be explained entirely by diffusion through the lipid bilayer,

- Water-specific channels made up of transport proteins, called *aquaporins*, have been discovered in plant and animal cells.
- Aquaporins do not actively transport water, but rather facilitate its diffusion (osmosis).

D. Vacuolated cells have three major compartments

The three major compartments of a plant cell are the 1) cell wall, 2) cytosol of the protoplast, and 3) tonoplast (see Campbell, Figure 36.5).

Tonoplast = Membrane surrounding the large central vacuole found in plant cells; important in regulating intracellular conditions

- Contains integral transport proteins that control the movement of solutes between the cytosol and the vacuole
- Has a membrane potential; proton pumps in the tonoplast help the plasma membrane maintain a low H^+ concentration in the cytosol by moving H^+ into the vacuole
- Several solutes are transported between the cytosol and vacuole due to this membrane potential and proton gradient.

Two of the three cellular compartments of plants are continuous between cells.

- Plasmodesmata connect the cytosolic compartments of neighboring cells; this cytoplasmic continuum is called the *symplast.*
- The walls of adjacent cells are connected to forming a continuum of cell walls called the *apoplast.*

E. The symplast and apoplast both function in transport within tissues and organs

Lateral transport is short-distance transport, usually along the radial axis of plant organs.

It can occur by three routes in plant tissues and organs (see Campbell, Figure 36.5):

1. Across the plasma membranes and cell walls. Solutes move from one cell to the next by repeatedly crossing plasma membranes and cell walls.
2. The symplast route. A symplast is the continuum of cytoplasm within a plant tissue formed by the plasmodesmata which passes through pores in the cell walls. Once water or a solute enters a cell by crossing a plasma membrane, the molecules can enter other cells by traveling through the plasmodesmata.
3. The apoplast route. An apoplast is the continuum between plant cells which is formed by the continuous matrix of cell walls. Water and solute molecules can move from one area of a root or other organ via the apoplast without entering a cell.

Water and solute molecules can move laterally in a plant organ by any one of these routes or by switching from one route to another.

F. Bulk flow function in long-distance transport

This type of transport is usually along the vertical axis of the plant (up and down) from the roots to the leaves and vice versa.

Vascular tissues are involved in this type of transport as diffusion would be too slow.

- *Bulk flow* (movement due to pressure differences) moves water and solutes through xylem vessels and sieve tubes.
- Transpiration reduces pressure in the leaf xylem; this creates a tension which pulls sap up through the xylem from the roots.
- Hydrostatic pressure develops at one end of the sieve tubes in the phloem; this forces the sap to the other end of the tube.

II. Absorption of Water and Minerals by Roots

Water and minerals enter plants through the following transport pathway (see Campbell, Figure 36.6):

Soil → Epidermis → Root cortex → Xylem

A. Root hairs, mycorrhizae, and a large surface area of cortical cells enhance water and mineral absorption

Soil ⟶ Epidermis:

- Most absorption occurs near root tips where the epidermis is permeable to water.
- Root hairs, extensions of epidermal cells, increase the surface area available for absorption.
- Most plants form symbiotic relationships with fungi; the "infected" roots form *mycorrhizae*, a structure made from the plant roots and the hyphae of fungi. Water and minerals absorbed by the hyphae are transferred to the host plant.

Epidermis ⟶ Root cortex:

Lateral transport of minerals and water through the root is usually by a combination of apoplastic and symplastic routes.

- The apoplastic route exposes parenchymal cortex cells to soil solution.

  Soil solution, containing soil particles, water and dissolved minerals, flows into hydrophilic walls of epidermal cells and passes freely along the apoplast into root cortex.

  Compared to the epidermis, the apoplastic route exposes greater membrane surface area for water and mineral uptake into cytoplasm.

- The symplastic route makes selective mineral absorption possible.

  As soil solution moves along cell walls, some water and solutes cross the plasma membrane of epidermal and cortex cells.

  Cells cannot absorb a sufficient supply of mineral ions by diffusion alone—the soil solution is too dilute. Active transport permits root cells to accumulate essential minerals in very high concentrations.

  For example, transport proteins of the plasma membrane and tonoplast actively transport K^+ into root cells as Na^+ is pumped out.

B. The endodermis functions as a selective sentry between the root cortex and vascular tissue

Root Cortex ⟶ Xylem:

- Only minerals using the symplastic route may move directly into the vascular tissues. They have been previously selected by a membrane.
- Minerals and water passing through apoplasts are blocked at the *endodermis* (the innermost layer of cells in the root cortex) by a *Casparian strip* (a ring of suberin around each cell in the endodermis) and must enter an endodermal cell (see Campbell, Figure 36.6).

Water and minerals enter into the stele through the cells of the endodermis.

- Casparian strips ensure that all substances entering the stele pass through at least one membrane, allowing only selected ions to pass into the stele. Also prevents stele contents from leaking back into the apoplast and out into the soil.
- Water and minerals enter the stele via symplast, but tracheids and xylem vessels are part of the apoplast.
- Endodermal and parenchymal cells selectively discharge minerals into the apoplast so they may enter the xylem. This action probably involves diffusion and active transport.
- Those minerals and water that move into the apoplast are free to enter the tracheids and xylem vessels.

III. Transport of Xylem Sap

A. The ascent of xylem sap depends mainly on transpiration and the physical properties of water

The shoot depends upon an efficient delivery of its water supply.

- Xylem sap flows upward at 15m per hour or faster.
- Xylem vessels are close to each leaf cell, because veins branch throughout the leaves.

Water transported up from roots must replace that lost by *transpiration*.

- Transpiration is the evaporation of water from the aerial parts of a plant.
- The upward flow of xylem sap also provides nutrients (minerals) to the shoot system.

1. Pushing xylem sap: root pressure

When transpiration is low, active transport of ions into the xylem decreases the stele's water potential and causes water flow into the stele. This osmotic water uptake increases pressure which forces fluid up the xylem (= *root pressure*).

- Root pressure causes *guttation* (exudation of water droplets at leaf margins).
- The water droplets escape through specialized structures called hydrathodes, which relieve the pressure caused by more water entering the leaves than is lost by transpiration.

Root pressure is not the major mechanism driving the ascent of xylem sap.

- Cannot keep pace with transpiration
- Can only force water up a few meters

2. Pulling xylem sap: the transpiration-cohesion-tension mechanism

Transpiration pulls xylem sap upward, and cohesion of water transmits the upward-pull along the entire length of xylem.

a. Transpirational pull

Transpirational pull depends upon the creation of negative pressure.

Gaseous water in damp intercellular leaf spaces diffuses into the drier atmosphere through stomata (see Campbell, Figure 36.8).

The lost water vapor is replaced by evaporation from mesophyll cells bordering the airspaces.

The remaining water film, adhering to the hydrophilic cell walls, retreats into the cell wall pores (see Campbell, Figure 36.9).

Cohesion in this surface film of water resists an increase in the surface area of the film—a surface tension effect.

The water film forms a meniscus due to the negative pressure caused by the adhesion and cohesion.

This negative pressure pulls water from the xylem, through the mesophyll, toward the surface film on cells bordering the stomata.

Water moves through symplasts and apoplasts to a region of low water potential.

Mechanism results in water from the xylem replacing water transpired through the stomata.

b. Cohesion and adhesion of water

The transpirational pull on the xylem sap is transmitted to the soil solution (see Campbell, Figure 36.10). Cohesion of water due to H bonds allows for the pulling of water from the top of the plant without breaking the "chain."

The adhesion of water (by H bonds) to the hydrophilic walls of xylem cells also helps pull against gravity.

The small diameter of vessels and tracheids is important to the adhesion effect.

The upward pull of sap causes tension (negative pressure) in xylem, which decreases water potential and allows passive flow of water from soil into stele.

Transpirational pull can extend down to the roots only through an unbroken chain of water molecules.

Cavitation (formation of a water vapor pocket in xylem) breaks the chain of water molecules and the pull is stopped.

- Vessels cannot function again unless refilled with water by root pressure. (This can only occur in small plants.)
- Pits between adjacent xylem vessels allow for detours around a cavitated area.
- Secondary growth also adds new xylem vessels each year.

B. Review: xylem sap ascends by solar-powered bulk flow

Bulk flow is the movement of fluid due to pressure differences at opposite ends of a conduit.

The ascent of xylem sap is ultimately powered by the sun, which causes evaporative water loss, and thus, negative pressure.

- Xylem vessels or chains of tracheids serve as the conduits in plants.
- Transpirational pull lowers the pressure at the upper (leaf) end of the conduit.
- Osmotic movement of water from cell to cell in roots and leaves are due to small gradients in water potential caused by both solute and pressure gradients.

In contrast, bulk flow through the xylem vessels depends only on pressure.

IV. The Control of Transpiration

A. Guard cells mediate the photosynthesis-transpiration compromise

Transpiration results in a tremendous water loss from the plant. This water is replaced by the upward movement of water through the xylem. Guard cells surrounding stomata balance the requirements for photosynthesis with the need to conserve water.

1. The photosynthesis-transpiration compromise

Large surface areas along a leaf's airspaces are needed for CO_2 intake for photosynthesis, but also results in greater surface area for evaporative water loss.

- Internal surface area of a leaf may be 10 to 30 times the external surface area.
- Stomata are more concentrated on the bottom of leaves, away from the sun; this reduces evaporative loss.
- The waxy leaf cuticle prevents water loss from the rest of the leaf surface.

Transpiration-to-photosynthesis ratios measure efficiency of water use. This ratio is g H_2O lost/g CO_2 assimilated into organic material.

- Ratio of 600:1 is common in C_3 plants; 300:1 in C_4 plants.
- C_4 plants can assimilate CO_2 at greater rates than C_3 plants.

Benefits of transpiration:

- It assists in mineral transfer from roots to shoots.
- Evaporative cooling reduces risk of leaf temperatures becoming too high for enzymes to function.

If transpiration exceeds delivery of water by xylem, plants wilt.

- Plants can adjust to reduce risk of wilting.
- Regulating the size of stomatal openings also reduces transpiration.

2. How stomata open and close

Guard cells = Cells that flank stomata and control stomatal diameter by changing shape

- When turgid, guard cells "buckle" due to radially-arranged microfibrils and stomata open
- When flaccid, guard cells sag and stomatal openings close

The change in turgor pressure that regulates stomatal opening results from reversible uptake and loss of K^+ by guard cells.

- Uptake of K^+ decreases guard cell water potential so H_2O is taken up, cells become turgid, and stomata open. The tonoplast plays a role as most of the K^+ and water are stored in the vacuole.
- The increase in positive charge is countered by the uptake of chloride (Cl^-), export of H^+ ions released from organic acids, and the negative charges acquired by organic acids as they lose their protons.
- Closing of the stomata results when K^+ exits the guard cells and creates an osmotic loss of water.

Evidence from studies using patch clamping techniques indicates that K^+ fluxes across the guard cell membrane are likely coupled to membrane potentials created by proton pumps.

- Stomatal opening correlates with active transport of H^+ out of the guard cell.
- The resulting membrane potential drives K^+ into the cell through specific membrane channels.

By integrating internal and external environmental cues, guard cells open and close, balancing the requirements for photosynthesis with the need to conserve water from transpirational loss.

Stomata open at dawn in response to three cues:

1. Light. Induces guard cells to take up K^+ by:
   - Activating a blue-light receptor which stimulates proton pumps in the plasma membrane
   - Driving photosynthesis in guard cell chloroplasts, making ATP available for the ATP-driven proton pumps
2. Decrease of CO_2 in leaf air spaces due to photosynthesis in the mesophyll
3. An internal clock in the guard cells. This will make them open even if plant is kept in dark (a *circadian rhythm* approximates a 24-hour cycle)

Guard cells may close stomata during the daytime if:

- There is a water deficiency resulting in flaccid guard cells.
- Mesophyll production of abscisic acid (a hormone) in response to water deficiency signals guard cells to close.
- High temperature increases CO_2 in leaf air spaces due to increased respiration, closing guard cells.

B. Xerophytes have adaptations that reduce transpiration

Xerophytes, plants adapted to arid climates, have some of the following evolutionary adaptations that reduce transpiration:

- Small, thick leaves (reduced surface area:volume, so less H_2O loss)
- A thick cuticle
- Stomata are in depressions on the underside of leaves to protect from water loss due to drying winds (see Campbell, Figure 36.12)
- Some shed leaves in the driest time of the year.
- Cacti and others store water in stems during the wet season.

Plants of family Crassulaceae use CAM (crassulacean acid metabolism) to assimilate CO_2.

- At night, mesophyll cells assimilate CO_2 into organic acids.
- During the day, the acids are broken down, releasing CO_2, which is used to synthesize sugars by the conventional C_3 pathway.
- Thus, stomata can close during the day, the plant conserves water, and there is still an ample supply of CO_2 for photosynthesis.

V. Translocation of Phloem Sap

Translocation = The transport of the products of photosynthesis by phloem to the rest of the plant

- In angiosperms, sieve-tube members are the specialized cells of phloem that function in translocation.
  - Sieve-tube members are arranged end-to-end forming long sieve tubes.
  - Porous cross walls called sieve plates are in between the members and allow phloem to move freely along the sieve tubes.

Phloem sap contains primarily sucrose, but also minerals, amino acids, and hormones.

A. Phloem translocates its sap from sugar sources to sugar sinks

Phloem sap movement is not unidirectional; it moves through the sieve tubes from a source (production area) to a sink (use or storage area).

Sugar source = Organ where sugar is produced by photosynthesis or by the breakdown of starch (usually leaves).

Sugar sink = Organ that consumes or stores sugar (growing parts of plants, fruits, non-green stems and trunks, and others)

Sugar flows from source to sink.

- Source and sink depend on season. A tuber is the sink when stockpiling in the summer, but is the source in the spring.
- Minerals may also be transported to sinks.
- The sink is usually supplied by the nearest source.
- Direction of flow within a phloem element can change, depending on locations of the source and sink.

B. Phloem loading and unloading

Sugar produced at a source must be loaded into sieve-tube members before it can be translocated to a sink.

- In some plant species, the sugar may move through the symplast from mesophyll cells to the sieve members.
- In other species, the sugar uses a combination of symplastic and apoplastic routes (see Campbell, Figure 36.13a)
- Some plants have *transfer cells*. These are modified companion cells which have numerous ingrowths of their walls. These structures increase the cells' surface area and enhances solute transfer between apoplast and symplast.

- In plants such as corn, active transport accumulates sucrose in sieve-tube members to two to three the concentration in mesophyll cells.
    - Proton pumps power this transport by creating a H^+ gradient (see Campbell, Figure 36.13b).
    - A membrane protein uses the potential energy stored in the gradient to drive the cotransport of sucrose by coupling sugar transport to the diffusion of H^+ back into the cell.

Sucrose is unloaded at the sink end of sieve tubes.

- In some plants, sucrose is unloaded from the phloem by active transport.
- In other species diffusion moves the sucrose from the phloem into the cells of the sink.
- Both symplastic and apoplastic routes may be involved.

C. Pressure flow is the mechanism of translocation in angiosperms

Phloem sap flows up to 1 m per hour, too fast for just diffusion or cytoplasmic streaming.

The flow is by a bulk flow (pressure-flow) mechanism; buildup of pressure at the source and release of pressure at the sink causes source-to-sink flow (see Campbell, Figure 36.14).

- At the source end, phloem loading causes high solute concentrations.
    - Water potential decreases, so water flows into tubes creating hydrostatic pressure.
    - Hydrostatic pressure is greatest at the source end of the tube.
- At the sink end, the water potential is lower outside the tube due to the unloading of sugar; osmotic loss of water releases hydrostatic pressure.
- Xylem vessels recycle water from the sink to the source.

Aphids have been used to study flow in phloem (see Campbell, Figure 36.15).

- The aphid stylet punctures phloem and the aphid is "force-fed" by the pressure.
- The aphid is severed from its stylet and flow is measured through the stylet.
- The flow exerts greater pressure and has a higher sugar concentration the closer to the source.

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CHAPTER 37
PLANT NUTRITION

OUTLINE

I. Nutritional Requirements of Plants
   A. The chemical composition of plants provides clues to nutritional requirements
   B. Plants require nine macronutrients and at least eight micronutrients
   C. The symptoms of mineral deficiency depend on the function and mobility of the element
II. Soil
   A. Soil characteristics are key environmental factors of terrestrial ecosystems
   B. Soil conservation is one step toward sustainable agriculture
III. The Special Case of Nitrogen As a Plant Nutrient
   A. The metabolism of soil bacteria makes nitrogen available to plants
   B. Improving the protein yield of crops is a major goal of agricultural research
IV. Nutritional Adaptations: Symbiosis of Plants and Soil Microbes
   A. Symbiotic nitrogen fixation results from intricate interactions between roots and bacteria
   B. Mycorrhizae are symbiotic associations of roots and fungi that enhance plant nutrition
   C. Mycorrhizae and root nodules may have an evolutionary relationship
V. Nutritional adaptations: Parasitism and Predation By Plants
   A. Parasitic plants extract nutrients from other plants
   B. Carnivorous plants supplement their mineral nutrition by preying on animals

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. Describe the chemical composition of plants including:
   a. Percent of wet weight as water
   b. Percent of dry weight as organic substances
   c. Percent of dry weight as inorganic minerals
2. Explain how hydroponic culture is used to determine which minerals are essential nutrients.
3. Distinguish between macronutrient and micronutrient.
4. Recall the nine macronutrients required by plants and describe their importance in normal plant structure and metabolism.
5. List seven micronutrients required by plants and explain why plants need only minute quantities of these elements.

6. Explain how a nutrient's role and mobility determine the symptoms of a mineral deficiency.
7. Explain how soil is formed.
8. Explain what determines the texture of topsoil and list the type of soil particles from coarsest to smallest.
9. Describe the composition of loams and explain why they are the most fertile soils.
10. Explain how humus contributes to the texture and composition of soil.
11. Explain why plants cannot extract all of the water in soil.
12. Explain how the presence of clay in soil helps prevent the leaching of mineral cations.
13. Define cation exchange, explain why it is necessary for plant nutrition, and describe how plants can stimulate the process.
14. Explain why soil management is necessary in agricultural systems but not in natural ecosystems such as forests and grasslands.
15. List the three mineral elements that are most commonly deficient in farm soils.
16. Describe the environmental consequence of overusing commercial fertilizers.
17. Explain how soil pH determines the effectiveness of fertilizers and a plant's ability to absorb specific mineral nutrients.
18. Describe problems resulting from farm irrigation in arid regions and list several current approaches to solving these problems.
19. Describe precautions that can reduce wind and water erosion.
20. Define nitrogen fixation and write the overall equation representing the conversion of gaseous nitrogen to ammonia.
21. Distinguish between nitrogen-fixing bacteria and nitrifying bacteria.
22. Recall the forms of nitrogen that plants can absorb and describe how they are used by plants.
23. Beginning with free-living rhizobial bacteria, describe the development of a root nodule.
24. Explain why the symbiosis between a legume and its nitrogen-fixing bacteria is considered to be mutualistic.
25. Recall two functions of leghemoglobin and explain why its synthesis is evidence for coevolution.
26. Describe the basis for crop rotation.
27. Describe agricultural research methods used to improve the quality and quantity of proteins in plant crops.
28. Discuss the relationships between root nodule formation and mycorrhizae development
29. Describe modifications for nutrition that have evolved among plants including parasitic plants, carnivorous plants, and mycorrhizae.

KEY TERMS

mineral nutrients	topsoil	cation exchange	nodules
essential nutrient	horizons	nitrogen-fixing bacteria	bacteroids
macronutrients	loams	nitrogen fixation	mycorrhizae
micronutrients	humus	nitrogenase	ectomycorrhizae

LECTURE NOTES

I. Nutritional Requirements of Plants

Plants and other photosynthetic autotrophs play a critical role in the energy flow and chemical cycling of ecosystems by transforming:

- Light energy into chemical bond energy
- Inorganic compounds into organic compounds

To accomplish these tasks, plants require:

- Sunlight as the energy source for photosynthesis
- Inorganic, raw materials, such as:
  - Carbon dioxide
  - Water
  - Variety of inorganic, mineral ions in the soil

To acquire the resources of light and inorganic nutrients, plants have highly ramified root and shoot systems with large surface areas for exchange with their environment—soil and air.

A. The chemical composition of plants provides clues to nutritional requirements

Early ideas about plant nutrition:

- In the fourth century B.C., Aristotle thought that soil was the substance for plant growth and that leaves only provided shade for fruit.
- In the 1600s, Jean-Baptiste Van Helmont wanted to discover if plants grew by absorbing soil, so he:
  - Planted a seed in a measured amount of soil
  - Weighed the grown plant
  - Measured how much soil was left.

The soil did not decrease proportionately. Van Helmont concluded plants grew mainly from the water they absorbed

- In the 1700s, Stephen Hales postulated plants were nourished mostly by air.

Although certain minerals taken up from the soil are essential to the growth of plants (e.g., nitrogen taken up in the form of nitrate ions), these mineral nutrients make up only a tiny fraction of a plant's mass

Plants grow mainly by accumulating water in their cells' central vacuoles.

- Water is a nutrient since it supplies most of the hydrogen and some oxygen incorporated into organic compounds by photosynthesis.
- 80–85% of an herbaceous plant is water.
- More than 90% of the water absorbed is lost by transpiration.
- Retained water functions as a solvent, allows cell elongation, and keeps cells turgid.

By weight, the bulk of a plant's organic material is from assimilated CO_2 (taken from air) (see Campbell, Figure 37.1). The composition of the dry weight of plants is:

- 95% organic substances, mostly carbohydrates
- 5% minerals, to some extent determined by soil composition

B. Plants require nine macronutrients and at least eight micronutrients

An *essential nutrient* is one that is required for a plant to grow from a seed and complete its life cycle (see Campbell, Table 37.1) .

- Determined by hydroponic culture, in which roots are bathed in an aerated aqueous solution of known mineral content. If a mineral is omitted and plant growth is abnormal, it is essential (see Campbell, Figure 37.2).

*Macronutrient*s = Elements required by plants in large amounts

Micronutrients = Elements required by plants in small amounts

- These function primarily as cofactors of enzymatic reactions.
- Optimal concentrations vary for different plant species.

C. The symptoms of a mineral deficiency depend on the function and mobility of the element

Symptoms of mineral deficiencies depend on:

1. The role of the nutrient in the plant
2. Its mobility within the plant
    - Deficiencies of nutrients mobile in the plant appear in older organs first since some are preferentially shunted to growing parts.
    - Deficiencies of immobile nutrients affect young parts of plant first because older tissues may have adequate reserves.

Deficiencies of N, K, and P are the most common.

- Shortages of micronutrients are less common and often localized.
- Overdoses of some micronutrients can be toxic.

II. Soil

A. Soil characteristics are key environmental factors in terrestrial ecosystems

Plants growing in an area are adapted to the texture and chemical composition of the soil.

1. Texture and composition of soils

Soil is produced by the weathering of solid rock. Living organisms may accelerate the process once they become established.

Horizons = Distinct soil layers

Topsoil = Mixture of decomposed rock of varying texture, living organisms, and humus.

The texture of a topsoil depends on the particle size.

- Coarse sand has diameter of 0.2 – 2 mm.
- Sand is 20 – 200 mm.
- Silt is 2 – 20 mm.
- Clay is less than 2 mm.

The most fertile soils are *loams*, a mixture of sand, silt and clay.

- Fine particles retain water and minerals.
- Coarse particles provide air spaces with oxygen for cellular respiration.

Soil contains many bacteria, fungi, algae, protists, insects, earthworms, nematodes, and plant roots. These affect the soil composition. For example, earthworms aerate soil; bacteria alter soil mineral composition.

Humus = Decomposing organic material

- Prevents clay from packing together
- Builds a crumbly soil that retains water but is still porous for good root aeration
- Acts as a reservoir of mineral nutrients

Soil composition determines which plants may grow in it, and plant growth, in turn, affects soil characteristics.

2. The availability of soil water and minerals

Some water is bound so tightly to hydrophilic soil that it cannot be extracted by plants.

Water bound less tightly is generally available to the plant as a soil solution containing minerals. This solution is absorbed into the root hairs and passes via the apoplast to the endodermis (see Campbell, Figure 37.6a)

Positively charged minerals (K^+, Ca^+, Mg^+) adhere by electrical attraction to negatively charged clay particles.

- Clay provides much surface area for binding
- Prevents leaching of mineral nutrients

Cation exchange = H ions in soil displace positively charged mineral ions from clay, making them available to plants (see Campbell, Figure 37.6b).

- Stimulated by roots which release acids to add H^+ to the soil solution.

Negatively charged minerals (NO_3^-, $H_2PO_4^-$, SO_4^-) are not tightly bound to soil particles.

- Tend to leach away more quickly.

B. Soil conservation is one step toward sustainable agriculture

Good soil management is necessary to maintain soil fertility, which may have taken centuries to develop through decomposition and accumulation of organic matter.

Agriculture is unnatural and depletes the mineral content of the soil, making soil less fertile. Crops also use more water than natural vegetation.

Three important aspects of soil management are:

1. Fertilizers
2. Irrigation
3. Erosion prevention

1. Fertilizers

Fertilizers may be mined, chemically produced, or organic.

- Usually enriched in N, P, K
- Marked with three numbers corresponding to percentage of nitrogen (as ammonium or nitrate), percentage of phosphorus (as phosphoric acid), and percentage of potassium (as potash).
- Organic fertilizers are manure, fishmeal, and compost. Release minerals more gradually than chemical fertilizers, thus, soil retains minerals longer. Excess minerals from chemical fertilizers may be leached from soil and may pollute streams and lakes.

To properly use fertilizers, one must consider the soil pH.

- Acidity affects cation exchange and the chemical form of the minerals.
- A change in soil pH may make one essential element more available while causing another to adhere so tightly to soil particles that it is unavailable.

2. Irrigation

Availability of water limits plant growth in many environments.

Problems of irrigation arid land:

- Huge drain of water resources.
- Can gradually make soil salty and infertile.

Solutions to these problems:

- Use of drip irrigation. Perforated pipes slowly drip water close to plant roots, which reduces water evaporation and drainage.
- Development of plant varieties that require less water or can tolerate more salinity.

3. Erosion

Wind and water erode away much of the topsoil each year. Measures to prevent these losses include:

- Rows of trees to divide fields act as windbreaks.
- Terracing hillsides helps prevent water erosion.
- Planting alfalfa and wheat provide good ground cover and protection.

Proper management makes soil a renewable resource that will remain fertile for many generations.

III. The Special Case of Nitrogen as a Plant Nutrient

A. The metabolism of soil bacteria makes nitrogen available to plants

Plants require nitrogen to produce proteins, nucleic acids and other organic molecules.

- Plants can not use nitrogen in gaseous form (N_2).
- To be assimilated by plants, nitrogen must be in the form of ammonium (NH_4^+) or nitrate (NO_3^-).

There is a complex cycling of nitrogen in ecosystems:

- Over the short term, the main source of nitrogenous minerals is the decomposition of humus by microbes.
  - For example, ammonifying bacteria (see Campbell, Figure 37.8)
  - Nitrogen in organic compounds is repackaged into inorganic compounds that can be absorbed as minerals by roots.
- Nitrogen is lost from this local cycle when soil denitrifying bacteria convert NO_3^- to N_2, which diffuses form the soil to the atmosphere.
- *Nitrogen-fixing bacteria* restock nitrogenous minerals in the soil by converting N_2 to NH_3 (ammonia), a metabolic process called nitrogen fixation.
  - *Nitrogen fixation* = The process of converting atmospheric nitrogen (gaseous state) to nitrogenous compounds that can be directly used by plants (nitrate or ammonia) (see Campbell, Chapter 49, for more details)•
    The process is catalyzed by the enzyme nitrogenase:

$$N_2 + 8e^- + 8H^+ + 16ATP \xrightarrow{\text{nitrogenase}} 2NH_3 + H_2 + 16ADP + 16\ P_i$$

  - Some soil bacteria possess nitrogenase.
  - Very energy consuming process, costing the bacteria at least 8 ATPs for each ammonia molecule synthesized.
  - In the soil, ammonia is converted to the ammonium ion which plants can absorb:

$$NH_3 + H^+ \longrightarrow NH_4^+$$

  - Plants acquire most of their nitrogen in the form of nitrate (NO_3^-), which is produced in soil by nitrifying bacteria that oxidize ammonium (see Campbell, Figure 37.8). Other species of nitrogen-fixing bacteria live in plant roots in symbiotic relationships (see below).
  - Nitrogen absorbed by the plant is incorporated into organic compounds.

- Most plant species export nitrogen from the roots to the shoots (through xylem) in the form of nitrate or of organic compounds (e.g., amino acids) that were synthesized in the roots.

B. Improving the protein yield of crops is a major goal of agricultural research

A majority of the world's population depends mainly on plants for protein. Some food plants have a low protein content while others may be deficient in certain amino acids.

Ways in which to increase the protein content of plants include:

1. Plant breeding to create new varieties enriched in protein
    - Unfortunately these "super" varieties require large quantities of nitrogen in the form of commercial fertilizer, which is too expensive for many countries to afford.
2. Improving the productivity of symbiotic nitrogen fixation
    - Mutant strains of *Rhizobium* have been isolated that continue to produce nitrogenase even after fixed nitrogen accumulates, thus releasing the excess into the soil.
    - *Rhizobium* varieties may be selected that fix N_2 at a lower cost in photosynthetic energy, yielding a higher total food content in the plant.

IV. Nutritional Adaptations: Symbiosis of Plants and Soil Microbes

A. Symbiotic nitrogen fixation results from intricate interactions between roots and bacteria

Legumes (e.g., peas, beans, soybeans, peanuts, alfalfa, clover) have a built-in source of fixed nitrogen because they possess root nodules.

Nodules = Root swellings composed of plant cells that contain nitrogen-fixing bacteria of the genus *Rhizobium*. Each species of legume is associated with a particular species of *Rhizobium* (see Campbell, Figure 37.10).

Nodules form as follows:

- Roots secrete chemicals that attract nearby bacteria.
- Attracted bacteria emit chemicals that stimulate root hairs to elongate and curl to prepare for bacterial infection.
- Bacteria enter the root through an "infection thread" that carries them to the root cortex.
- Bacteria become enclosed in vesicles and assume a form called *bacteroids* (see Campbell, Figure 37.9).
    - Bacteroids produce a chemical that induces the host's cells to divide and form a nodule.
- Nodules continue to grow and a connection with the xylem and phloem develops.

This association is mutualistic; the bacteria supplies fixed nitrogen, and the plant supplies carbohydrates and other organic compounds.

Leghemoglobin = An iron-containing protein that binds oxygen

- The plant and the bacteria each make a part of the molecule.
- Releases oxygen for the intense respiration needed to produce ATP for nitrogen fixation.
- Keeps the free oxygen concentration low in root nodules so that the oxygen cannot inhibit the function of nitrogenase.

Most of the ammonium produced is used by the nodules to make amino acids for export to the shoots and leaves.

1. Symbiotic nitrogen fixation and agriculture

The basis for crop rotation is that, under favorable conditions, root nodules fix more nitrogen than the legume uses. The excess is secreted as ammonium into the soil.

- One year a nonlegume crop is planted, and the next year a legume is planted to restore the fixed nitrogen content of the soil.
- Legumes may be plowed under to further increase the fixed nitrogen content of the soil.

Some nonlegumes host nitrogen-fixing symbionts.

- Alders and tropical grasses may host nitrogen-fixing actinomycetes.
- Rice farmers culture a fern (*Azolla*), containing symbiotic nitrogen-fixing cyanobacteria, with the rice.

2. The molecular biology of root nodule formation in legumes

Chemical signals between plant roots and bacteria direct their association and the formation of nodules (see Campbell, Figure 37.11).

The specificity of the interaction between a plant and a particular bacterial species (e.g., *Rhizobium*) in the soil results from the unique chemical structure of the signal molecules.

- The initial signal molecule is produced by the plant.
- In response to the plant signal, bacteria produce an "answering" signal.
- The signals alter gene expression in cell of the recipient that results in the production of enzymes and other signal molecules (e.g., bacterial Nod factors; named for their action on nodulation and similar in structure to chitins).
  - Recent evidence reveals that plants produce chitin-like growth factors and that the bacterial Nod factors "cross-talk" with signal systems in the plant.

Through genetic engineering, scientists may:

- Create varieties of *Rhizobium* that can infect nonlegumes
- Transfer the genes required for nitrogen-fixation directly into plant genomes, using bacterial plasmids as vectors (see Campbell, Chapter 20).

B. Mycorrhizae are symbiotic associations of roots and fungi that enhance plant nutrition

Mycorrhizae = Symbiotic associations (mutualistic) between plant roots and fungi; the fungus either forms a sheath around the root or penetrates root tissue

- Help the plant absorb water
- Absorb minerals, and may secrete acid that increases mineral solubility and converts minerals to forms easily used by the plant
- May help protect the plant against certain soil pathogens
- The plant nourishes the fungus with photosynthetic products.

Almost all plants are capable of forming mycorrhizae if exposed to the proper species of fungi. Plants grow more vigorously when mycorrhizae are present.

Mycorrhizae may have permitted early plants to colonize land.

- Fossils indicate the earliest land plants possessed mycorrhizae.
- This mutualistic association may have allowed the early plants to obtain enough nutrients to survive colonization.

1. Two main types of mycorrhizae

In *ectomycorrhizae*, the mycelium forms a sheath over the root, but does not penetrate it (see Campbell, Figure 37.12a).

- Hyphae increase absorptive surface
- Common in woody plants (e.g., pine, oak, walnut)

Endomycorrhizae do not form a sheath surrounding the root and hyphae extend into root cell walls (but do not penetrate plasma membrane) (see Campbell, Figure 37.12b).

- More common that ectomycorrhizae; found in over 90% of plant species, including crop plants (e.g., wheat, corn)

2. Agricultural importance of mycorrhizae

Mycorrhizae can only form if the plant is exposed to the appropriate species of fungus.

- In agriculture, seeds are often collected in one environment to be planted in foreign soil devoid of the correct fungus and the resulting plant may display symptoms of malnutrition.
- Inoculating seeds with the spores of mycorrhizal fungi promotes the formation of mycorrhizae and helps to assure good plant health.

C. Mycorrhizae and root nodules may have an evolutionary relationship

Recent research indicates that the molecular biology of root nodule formation is closely related to the mechanisms involved with mycorrhizae formation.

- The same plant genes that are activated in the early stages of nodule formation are the same genes activated during the early development of endomycorrhizae.
- The chemical cues produced by the microbes appear structurally related and activate plant gene expression through the same signal transduction pathway.

Mycorrhizae probably evolved over 400 million years ago in the earliest vascular plants, whereas root nodules most likely emerged some 65 to 130 million years ago, during the evolution of angiosperms

The recent observations concerning the molecular mechanisms associated with the symbiotic relationships of roots suggests that root nodule development is partially adapted from a signaling pathway already in place in mycorrhizae (e.g., an exaptation).

V. Nutrition Adaptations: Parasitism and Predation By Plants

Some plant adaptations enhance nutrition through interactions with other organisms.

A. Parasitic plants extract nutrients from other plants

Some parasitic plants:

- Are photosynthetic, and only supplement nutrition by using haustoria (*not* homologous to those of parasitic fungi) to obtain xylem sap from their host plant (e.g., mistletoe)
- Have lost photosynthesis entirely, drawing all nutrients from the host plant by tapping into the phloem (e.g., dodder) (see Campbell, Figure 37.13)

Epiphytes are plants that:

- Grow on the surface of other plants, anchored by roots, but are *not parasitic*
- Nourish themselves from the water and minerals absorbed from rain
- Examples include Spanish moss and staghorn ferns

B. Carnivorous plants supplement their mineral nutrition by digesting animals

Carnivorous plants:

- Live in habitats with poor (usually nitrogen deficient) soil conditions
- Are photosynthetic, but obtain some nitrogen and minerals by killing and digesting insects

Most insect traps evolved by modification of leaves and are usually equipped with glands that secrete digestive juices.

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CHAPTER 38
PLANT REPRODUCTION AND DEVELOPMENT

OUTLINE

I. Sexual Reproduction
- A. Sporophyte and gametophyte generations alternate in the life cycles of plants: *a review*
- B. Male and female gametophytes develop within anthers and ovaries, respectively
- C. Pollination brings female and male gametes together
- D. Researchers are unraveling the molecular mechanisms of self-incompatibility
- E. Double fertilization gives rise to the zygote and endosperm
- F. The ovule develops into a seed containing an embryo and a supply of nutrients
- G. The ovary develops into a fruit adapted for seed dispersal
- H. Evolutionary adaptations of seed germination contribute to seedling survival

II. Asexual Reproduction
- A. Many plants can clone themselves by asexual reproduction
- B. Vegetative propagation of plants is common in agriculture
- C. Sexual and asexual reproduction are complementary in the life histories of many plants: *a review*

III. Cellular Mechanisms of Plant Development
- A. Growth, morphogenesis, and differentiation produce the plant body: *an overview*
- B. The cytoskeleton guides cell division and expansion
- C. Cell differentiation depends on gene regulation
- D. Pattern formation determines the location and tissue organization of plant organs

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. Outline the angiosperm life cycle.
2. List the four floral parts in their order from outside to inside of the flower.
3. From a diagram of an idealized flower, correctly label the following structures and describe their function:
   - a. Sepals
   - b. Petals
   - c. Stamen: filament and anther
   - d. Carpel: style, ovary, ovule and stigma
4. Distinguish between complete and incomplete flowers.
5. Distinguish between a perfect and imperfect flower.
6. Distinguish between monoecious and dioecious.

7. Explain by which generation, structure, and process spores are produced.
8. Explain by which generation, structures, and process gametes are produced.
9. Explain why it is technically incorrect to refer to stamens and carpels as male and female sex organs.
10. Describe the formation of a pollen grain in angiosperms.
11. With reference to the developing pollen grain, distinguish among generative nucleus, tube nucleus, and sperm nucleus.
12. Describe the development of an embryo sac, and explain what happens to each of its cells.
13. Distinguish between pollination and fertilization.
14. Describe how pollen can be transferred between flowers.
15. Describe mechanisms that prevent self-pollination, and explain how this contributes to genetic variation.
16. Outline the process of double fertilization, and describe the function of endosperm.
17. Describe the development of a plant embryo from the first mitotic division to an embryonic plant with rudimentary organs.
18. From a diagram, identify the following structures of a seed and recall a function for each:

a.	Seed coat	d.	Radicle	g.	Endosperm
b.	Embryo	e.	Epicotyl	h.	Cotyledons
c.	Hypocotyl	f.	Plumule	i.	Shoot apex

19. Explain how a monocot and dicot seed differ.
20. Describe several functions of fruit and explain how fruits form.
21. Distinguish among simple, aggregate, and multiple fruits and give examples of each.
22. Explain how seed dormancy can be advantageous to a plant and describe some conditions for breaking dormancy.
23. Using a cereal as an example, explain how a seed mobilizes its food reserves and describe the function of aleurone, α-amylase, and gibberellic acid.
24. Describe variations in the process of germination including the fate of the radicle, shoot tip, hypocotyl, epicotyl, and cotyledons.
25. Distinguish between sexual reproduction and vegetative reproduction.
26. Describe natural mechanisms of vegetative reproduction in plants including fragmentation and apomixes.
27. Describe various methods horticulturists use to vegetatively propagate plants from cuttings.
28. Explain how the technique of plant tissue culture can be used to clone and genetically engineer plants.
29. Describe the process of protoplast fusion and its potential agricultural impact.
30. Define monoculture and list its benefits and risks.
31. Compare sexual and asexual reproduction in plants and explain their adaptive roles in plant populations.

KEY TERMS

alternation of generations	monoecious	scutellum	stock
	dioecious	coleorhiza	scion
sporophyte	microspore	coleoptile	protoplast fusion
gametophyte	megaspore	fruit	monoculture

sepal	embryo sac	pericarp	development
petal	pollination	simple fruit	growth
stamen	self-incompatible	aggregate fruit	morphogenesis
ovules	endosperm	multiple fruit	cellular differentiation
complete flower	double fertilization	imbibition	preprophase band
incomplete flower	seed coat	vegetative reproduction	pattern formation
perfect flower	hypocotyl	fragmentation	positional information
imperfect flower	radicle	apomixis	
organ-identity genes	epicotyl	callus	

LECTURE NOTES

Modifications in reproduction were key adaptations enabling plants to spread into a variety of terrestrial habitats.

- Water has been replaced by wind and animals as a means for spreading gametes.
- Embryos are protected in seeds.
- Vegetative reproduction is an asexual mechanism for propagation in many environments.

I. Sexual Reproduction

A. Sporophyte and gametophyte generations alternate in the life cycles of plants: *a review*

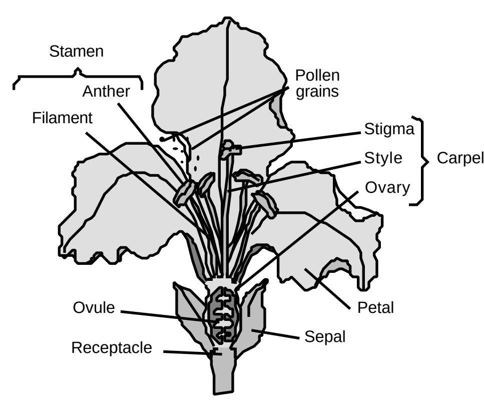
The angiosperm (flowering plant) life cycle includes *alternation of generations* during which multicellular haploid gametophyte generations alternate with diploid sporophyte generations (see Campbell, Figure 38.1).

- The *sporophyte* is the recognizable "plant" most familiar to us. It produces haploid spores by meiosis in sporangia.
- Spores will undergo mitotic division and develop into a multicellular male or female *gametophyte.*
- Gametophytes produce gametes (sperm and egg) by mitosis. The gametes fuse to form a zygote that develops into a multicellular sporophyte.
- The sporophyte is dominant in the angiosperm life cycle with the gametophyte stages being reduced and totally dependent on the sporophyte.

B. Male and female gametophytes develop within anthers and ovaries, respectively

Flowers are the reproductive structure of angiosperm sporophytes.

- Develop from compressed shoots with four whorls of modified leaves separated by very short internodes.
- The four sets of modified leaves are the: *sepals*, *petals*, *stamens*, and *carpels* (see also Campbell, Figure 38.2).



  - Stamens and carpels contain the sporangia and are the reproductive parts of the flower.
- Female gametophytes develop in carpel sporangia as *embryo sacs*, which contain the eggs. This occurs inside the *ovules*, which are at the base of the carpel and surrounded by ovaries.
- Male gametophytes develop in the stamen sporangia as pollen grains. These form at the stamen tips within chambers of the anthers.

Pollination occurs when wind- or animal-born pollen released from anthers lands on the stigma at the tip of a carpel.

- A pollen tube grows from the pollen grain, down the carpel, into the embryo sac.
- Sperm are discharged resulting in fertilization of the eggs.
- The zygote will develop into an embryo; as the embryo grows, the ovule surrounding it develops into a seed.
- While seed formation is taking place, the entire ovary is developing into a *fruit*, which will contain one or more seeds.

Seeds are dispersed from the source plant when fruits are moved about by the wind or animals.

- Seeds deposited in soil of the proper conditions (moisture, nutrients) will germinate.
- The embryo starts growing and develops into a new sporophyte.
- After flowers are produced by the sporophyte, a new generation of gametophytes develop and the life cycle continues.

Several variations on the basic flower structure have evolved during the angiosperm evolutionary history.

Complete flower = A flower with sepals, petals, stamens and carpels

Incomplete flower = A flower that is missing one or more of the parts listed for a complete flower (e.g., most grasses do not have petals on their flowers)

Perfect flower = A flower having both stamens and carpels (may be incomplete by lacking either sepals or petals)

Imperfect flower = A flower that is either *staminate* (having stamens but no carpels) or carpellate (having carpels but no stamens); a unisex flower

Monoecious = Plants having both staminate flowers and carpellate flowers on the same individual plant

Dioecious = Plants having staminate flowers and carpellate flowers on separate individual plants of the species

See Campbell, Figure 34.3, for examples of floral diversity.

1. Development of male gametophyte (pollen)

Pollen grain = The immature male gametophyte that develops within the anthers of stamens in an angiosperm

- They are extremely durable; their tough coats are resistant to biodegradation.
- Fossilized pollen has provided many important evolutionary clues.
- Formation of a pollen grain is as follows (see also Campbell, Figure 38.4a):

Within the sporangial chamber of an anther, diploid microsporocytes undergo meiosis to form four haploid microspores.

↓

The haploid microspore nucleus undergoes mitotic division to give rise to a generative cell and a tube cell.

↓

The wall of the microspore then thickens and becomes sculptured into a species-specific pattern.

↓

These two cells and the thickened wall are the pollen grain, an immature male gametophyte.

2. Development of female gametophyte (embryo sac)

Ovule = Structure which forms within the chambers of the plant ovary and contains the female sporangium

The female gametophyte is the *embryo sac*, and it generally develops as follows (see also Campbell, Figure 38.4b):

A megasporocyte in the sporangium of each ovule grows and goes through meiosis to form four haploid *megaspores* (only one usually survives).
(Details of next steps vary extensively, depending on species.)

↓

The remaining megaspore grows and its nucleus undergoes three mitotic divisions, forming one large cell with eight haploid nuclei.

↓

Membranes partition this into a multicellular *embryo sac*.

Within the embryo sac:

- The egg cell is located at one end and is flanked by two other cells (synergids).
- At the opposite end are three antipodal cells.
- The other two nuclei (polar nuclei) share the cytoplasm of the large central cell.
- At the end containing the egg is the micropyle (an opening through the integuments surrounding the embryo sac).

C. Pollination brings female and male gametophytes together

1. Pollination

Pollination = The placement of pollen onto the stigma of a carpel

- Some plants use wind to disperse pollen.
- Other plants interact with animals that transfer pollen directly between flowers.
- Some plants self-pollinate, but most cross-pollinate.

Most monoecious angiosperms have mechanisms to prevent self-pollination. These mechanisms thus contribute to genetic variation in the species by ensuring sperm and eggs are from different plants.

- The stamens and carpels mature at different times in some species.
- Structural arrangement of the flower in many species pollinated by animals reduces the chance that pollinators will transfer pollen from anthers to the stigma of the same flower.
- Other species are *self-incompatible*. If a pollen grain lands on the stigma of the same flower, a biochemical block prevents the pollen grain from developing and fertilizing the egg.

D. Researchers are unraveling the molecular mechanisms of self-incompatibility

Self-incompatibility = The rejection of pollen from the same, or closely related, plant by the stigma

The recognition of "self" pollen is based on S-genes (named for self-incompatibility).

- Many alleles for the S-locus are found in a plant population’s gene pool (see Campbell, Figure 38.5).
- A pollen grain that lands on a stigma with matching alleles at the S-locus is self-incompatible.
  - The pollen grain will either not initiate or complete formation of the pollen tube.
  - This prevents self-fertilization and fertilization between plants with a common S-locus (usually closely related plants).

Although all self-compatibility genes are described as being S-loci, such genes appear to have evolved independently in numerous plant families. As a consequence, the mechanism underlying inhibition of pollen tube formation varies.

- In some cases, the block occurs in the pollen grain (e.g., gametophyte self-incompatibility). RNAases from the carpel enter the pollen grain (only if the pollen is identified as a "self") and destroy RNA (e.g., legumes).
- In other cases, the block is caused by cells in the stigma of the carpel (e.g., sporophyte incompatibility). For example, in members of the mustard family, self recognition activates a signal transduction system in epidermal cells of the carpel that inhibits germination of the pollen grain (see Campbell, Figure 38.6).

Studies on self-incompatibility may lead to benefits for agricultural production.

- Many important agricultural plants are self-compatible.

  Different varieties of these crop plants are hybridized to combine the best traits of the varieties and prevent loss of vigor from excessive inbreeding.

  To maximize the numbers of hybrids, plant breeders prevent self-fertilization by laboriously removing the anthers from parent plants that provide the seeds.
- If the molecular mechanism responsible for self-incompatibility can be imposed on normally self-compatible crop species, production of hybrids would be simplified.

E. Double fertilization gives rise to the zygote and endosperm

When a compatible pollen grain (different S-locus alleles) lands on a stigma of an angiosperm, double fertilization occurs.

- *Double fertilization* = The union of two sperm cells with two cells of the embryo sac
- After adhering to a stigma, the pollen grain germinates and extends a pollen tube between the cells of the style toward the ovary (see Campbell, Figure 38.7).
- The generative cell divides (mitosis) to form two sperm. (A pollen grain with a tube enclosing two sperm = mature male gametophyte.)
- Directed by a chemical attractant (usually calcium), the tip of the pollen tube enters through the micropyle and discharges its two sperm nuclei into the embryo sac.
- One sperm unites with the egg to form the zygote.
- The other sperm combines with the two polar nuclei to form a 3*n* nucleus in the large central cell of the embryo sac.

This central cell will give rise to the *endosperm*, which is a food storing tissue.

After double fertilization is completed, each ovule will develop into a seed and the ovary will develop into a fruit surrounding the seed(s).

F. The ovule develops into a seed containing an embryo and a supply of nutrients

1. Endosperm development

Endosperm development begins before embryo development.

The triploid nucleus divides to form a milky, multinucleate "supercell" after double fertilization.

This endosperm undergoes cytokinesis to form membranes and cell walls between the nuclei, thus becoming multicellular.

Endosperm is rich in nutrients, which it provides to the developing embryo.

In most monocots, the endosperm stocks nutrients that can be used by the seedling after germination.

In many dicots, food reserves of the endosperm are exported to the cotyledons, thus mature seeds have no endosperm.

2. Embryo development (embryogenesis)

The zygote's first mitotic division is transverse, creating a larger basal cell and a smaller terminal cell (see Campbell, Figure 38.8).

- The basal cell divides transversely to form the *suspensor*, which anchors the embryo and transfers nutrients to it from the parent plant.
- The terminal cell divides several time to form a spherical proembryo attached to the suspensor.

Cotyledons appear as bumps on the proembryo and the embryo elongates.

- The apical meristem of the embryonic shoot is located between the cotyledons.

The suspensor (the opposite end of the axis) attaches at the apex of the embryonic root with its meristem.

- The basal cell gives rise to part of the root meristem in some species.

After germination, the apical meristems at the root and shoot tips will sustain primary growth.

- The embryo also contains protoderm, ground meristem, and procambium.

Two features of plant form are established during embryogenesis.

1. The root-shoot axis with meristems at opposite ends
2. A radial pattern of protoderm, ground meristem, and procambrium ready to produce the dermal, ground, and vascular tissue systems

As the embryo develops, proteins, oil, and starch accumulate and are stored until the seed germinates.

3. **Structure of the mature seed**

In mature seeds, the embryo is quiescent until germination.

- The seed dehydrates until its water content is only 5% to 15% by weight.
- The embryo is surrounded by endosperm, enlarged cotyledons, or both.
- The seed coat is formed from the integuments of the ovule.

The arrangement within the seed of a dicot is shown in Campbell, Figure 38.9a.

- Below the cotyledon attachment point, the embryonic axis is called the *hypocotyl*, which terminates in the *radicle*, or embryonic root.
- Above the cotyledons, the embryonic axis is called the *epicotyl*, which terminates in the *plumule* (shoot tip with a pair of tiny leaves).
- Fleshy cotyledons are present in some dicots before germination due to their absorption of nutrients from the endosperm.
- In other dicots, thin cotyledons are found, and nutrient absorption and transfer occur only after germination (see Campbell, Figure 38.9b).

A monocot seed has a single cotyledon (see Campbell, Figure 38.9c). Members of the grass family, including wheat and corn, have a specialized cotyledon called the *scutellum*.

- The scutellum has a large surface area and absorbs nutrients from the endosperm during germination.
- The embryo is enclosed in a sheath comprised of the *coleorhiza* (covers the root) and the *coleoptile* (covers the shoot).

G. The ovary develops into a fruit adapted for seed dispersal

A fruit develops from the ovary of the flower while seeds are developing from the ovules.

- A *fruit* protects the seeds and aids in their dispersal by wind or animals.
- In some angiosperms, other floral parts also contribute to formation of what we call fruit:

  The core of an apple is the true fruit.

  The fleshy part of the apple is mainly derived from the fusion of flower parts located at the base of the flower.

A true fruit is a ripened ovary.

- Pollination triggers hormonal changes that cause the ovary to grow (see Campbell, Figure 38.10).
- The wall of the ovary thickens to become the *pericarp*.
- Transformation of a flower into a fruit parallels seed development.
- In most plants, fruit does not develop without fertilization of ovules. (In parthenocarpic plants, fruit does develop without fertilization.)

Depending upon their origin, fruits can be classified as (see Campbell, Table 38.1):

1. *Simple fruits*. Fruit derived from a single ovary; for example, cherries (fleshy) or soybeans (dry).
2. *Aggregate fruits*. Fruit derived from a single flower with several separate carpels; for example, strawberries.
3. *Multiple fruits*. Fruit derived from an *inflorescence* or separate tightly clustered flowers; for example, pineapple.

Fruits ripen about the time seeds are becoming fully developed.

- In dry fruits, such as soybean pods, the fruit tissues age and the fruit (pod) opens and releases the seeds.
- Fleshy fruits ripen through a series of steps guided by hormonal interactions.
    - The fruit becomes softer as a result of enzymes digesting the cell wall components.
    - Colors usually change and the fruit becomes sweeter as organic acids or starch are converted to sugar.
    - These changes produce an edible fruit which entices animals to feed, thus dispersing the seeds.

H. Evolutionary adaptations contribute to seedling survival

Seed germination represents the continuation of growth and development, which was interrupted when the embryo became quiescent at seed maturation.

- Some seeds germinate as soon as they reach a suitable environment.
- Other seeds require a specific environmental cue before they will break dormancy.

1. Seed dormancy

The evolution of the seed was an important adaptation by plants to living in terrestrial habitats.

- The environmental conditions in terrestrial habitats fluctuate more often than conditions in aquatic habitats.

Seed dormancy prevents germination when conditions for seedling growth are unfavorable.

- It increases the chance that germination will occur at a time and place most advantageous to the success of the seedling.

Conditions for breaking dormancy vary depending on the type of environment the plant inhabits.

- Seeds of desert plants may not germinate unless there has been heavy rainfall (not after a light shower).
- In chaparral regions where brushfires are common, seeds may not germinate unless exposed to intense heat, after a fire has cleared away older, competing vegetation.
- Other seeds may require exposure to cold, sunlight, or passage through an animal's digestive system before germination will occur.

A dormant seed may remain viable for a few days to a few decades (most are viable for at least a year or two). This provides a pool of ungerminated seeds in the soil, which is one reason vegetation appears so rapidly after environmental disruptions.

2. From seed to seedling

The first step in seed germination in many plants is *imbibition* (absorption of water).

- Hydration causes the seed to swell and rupture the seed coat.
- Hydration also triggers metabolic changes in the embryo that cause it to resume growth.
- Storage materials of the endosperm or cotyledons are digested by enzymes and the nutrients transferred to the growing regions of the embryo.

> Example: The embryo of a cereal grain releases a hormone (a gibberellin) as a messenger to the aleurone (outer layer of endosperm) to initiate production of α-amylase and other enzymes that digest starch stored in the endosperm (see Campbell, Figure 38.11).

- The radicle (embryonic root) then emerges from the seed.

The next step in the change from a seed to a seedling is the shoot tip breaking through the soil surface.

- In many dicots, a hook forms in the hypocotyl.

  Growth pushes the hypocotyl above ground.
- Light stimulates the hypocotyl to straighten, raising the cotyledons and epicotyl.
- The epicotyl then spreads the first leaves which become green and begin photosynthesis.

Germination may follow different methods depending on the plant species (see Campbell, Figure 38.12).

- In peas, a hook forms in the epicotyl and the shoot tip is lifted by elongation of the epicotyl and straightening of the hook. The cotyledons remain in the ground.
- In monocots, the coleoptile pushes through the soil and the shoot tip grows up through the tunnel of the tubular coleoptile.

Only a small fraction of the seedlings will survive to the adult plant stage.

- Large numbers of seeds and fruits are produced to compensate for this loss.
- This utilizes a large proportion of the plant's available energy.

II. Asexual Reproduction

A. Many plants can clone themselves by asexual reproduction

Asexual reproduction (or *vegetative reproduction*) = The production of offspring from a single parent; occurs without genetic recombination, resulting in a clone

- Meristematic tissues composed of dividing, undifferentiated cells can sustain or renew growth indefinitely.
- Parenchyma cells can also divide and differentiate into various types of specialized cells.

There are two major natural mechanisms of vegetative reproduction:

1. *Fragmentation* = Separation of a parent plant into parts that re-form whole plants (see Campbell, Figure 38.13a)
   - The most common form of vegetative reproduction
   - Some species of dicots exhibit a variation of fragmentation during which the parental root system develops adventitious shoots that become separate shoot systems.
2. *Apomixis* = The production of seeds without meiosis and fertilization
   - A diploid cell in the ovule gives rise to an embryo.
   - The ovules mature into seeds which are dispersed.
   - An example would be a dandelion.

B. Vegetative propagation of plants is common in agriculture

Most methods of vegetative propagation in agriculture are based on the ability of plants to form adventitious roots or shoots.

The objective is to improve crops, orchards, and ornamental plants.

1. Clones from cuttings

Clones may be obtained from either shoot or stem cuttings (plant fragments).

- At the cut end of the shoot, a mass of dividing, undifferentiated cells form (called a *callus*).
- If the shoot fragment includes a node, then adventitious roots can form without a callus stage.
- Cuttings may come from stems, leaves (African violets), or specialized storage stems (potatoes).

It is possible to combine the best qualities of different varieties or species by grafting a twig of one plant onto a closely related species or different variety of the same species.

- The plant providing the root system is the *stock*.
- The twig grafted onto the stock is the *scion*.
- The quality of a fruit is usually determined by the scion, although sometimes the stock can alter the characteristics of the shoot system that develops from the scion.

2. Test-tube cloning and related techniques

Test-tube cloning makes it possible to culture small explants (pieces of parental tissue) or single parenchyma cells on an artificial medium containing nutrients and hormones (see Campbell, Figure 38.14)

- The cultured cells divide to form an undifferentiated callus.
- The callus sprouts fully differentiated roots and shoots when the hormone balance of the culture media is manipulated.
- A single plant can be cloned into thousands of copies by subdividing calluses as they grow.

Tissue culture is often used to regenerate genetically engineered plants.

- Foreign genes are typically introduced into small pieces of plant tissue or into single plant cells.
- The use of test-tube culture techniques permits the regeneration of genetically altered plants from a single plant cell that received foreign DNA.

    The protein quality of sunflower seeds has been improved in transgenic plants that received a gene for bean protein as cultured cells.

Protoplast fusion, coupled with tissue culture methods, can produce new plant varieties that can be cloned.

- Protoplasts are plant cells which have had their cell walls removed.
- Protoplasts may be fused to form hybrid protoplasts.
- Protoplast can be screened for mutations that will improve the agricultural value of the plant.
- Protoplasts regenerate cell walls and become hybrid plantlets.

3. Benefits and risks of monoculture

Monoculture = The cultivation of large areas of land with a single plant variety

Genetic variability in many crops has been purposefully reduced by plant breeders who have selected for self-pollinating varieties or used vegetative reproduction to clone exceptional plants.

- Benefits of such genetic unity are: plant growth is uniform; fruits ripen in unison; crop yields are dependable.
- A great disadvantage is that little genetic variability means little adaptability. One disease could destroy a whole plant variety.
- "Gene banks," where seeds of many plant varieties are stored, are maintained to retain diverse varieties of crop plants.

C. Sexual and asexual reproduction are complementary in the life histories of many plants: *a review*

Both sexual and asexual reproduction have had featured roles in the adaptation of plant populations to their environments.

Benefits of sexual reproduction:

- Generates variation, an asset when the environment (biotic and abiotic) changes
- Produces seeds, which can disperse to new locations and wait until hostile environments become favorable

Benefits of asexual reproduction:

- In a stable environment, plants can clone many copies of themselves in a short period.
- Progeny are mature fragments of the parent plant, and not as fragile as seedlings produced by sexual reproduction.

III. Cellular Mechanisms of Plant Development

Regardless of whether a plant is sexually produced or results from vegetative reproduction, the initial individual will go through a series of changes that will produce a whole plant.

Development = The sum of all changes that progressively elaborate an organism's body.

- These changes include a number of mechanisms that shape the leaves, roots, and other organs into functional structures.

A. Growth, morphogenesis, and differentiation produce the plant body: *an overview*

The change from a fertilized egg to a plant involves growth, morphogenesis, and cellular differentiation.

Growth is an irreversible increase in size resulting from cell division and cell enlargement.

- The zygote divides mitotically to produce a multicellular embryo in the seed.
- Mitosis resumes in the root and shoot apical meristems after germination.
- Enlargement of the newly produced cells results in most of the actual size increase.

Morphogenesis is the development of body shape and organization.

- Begins in the early divisions of the embryo to produce the cotyledons and rudimentary roots and shoots
- Continues to shape the root and shoot systems as the plant grows
  - The meristems, which remain embryonic, continue growth and morphogenesis throughout the life of the plant.

Cellular differentiation is the divergence in structure and function of cells as they become specialized during the plant's development.

- Every organ of the plant body has a diversity of cells within its total structure.
- Each cell of each organ is fixed in a certain location and performs a specific function (e.g., guard cells, xylem).

B. The cytoskeleton guides cell division and expansion

Plant shape depends on the spatial orientations of cell divisions and cell expansions.

- Plant cells cannot move about as individuals within a developing organ due to their cell walls being cemented to those of neighboring cells.
- Since movement is eliminated, when the cell elongates, its growth is perpendicular to the plane of division.

1. Orienting the plane of cell division

During late interphase (G_2), the cytoskeleton of the cell is rearranged and the microtubules of the cortex become concentrated into the *preprophase band* (see Campbell, Figure 38.17).

The microtubules of the preprophase band disperse leaving behind an array of actin microfilaments.

- These microfilaments hold the nucleus in a fixed orientation until the spindle forms and then direct movement of the vesicles that produce the cell plate.

The walls that develop at the end of cell division form along the plane established by the preprophase band.

2. Orienting the direction of cell expansion

Plant cells expand (elongate) when the cell wall yields to the turgor pressure of the cell.

- Crosslinks between cellulose microfibrils in the cell wall are weakened (via broken hydrogen bonds) by acid-inducible enzymes in the cell wall upon secretion of acids from the cell.
- The loosened wall permits uptake of water by the hypertonic cell; water uptake causes the cell to expand.
- Growth continues until the crosslinks become re-established firmly enough to offset the turgor pressure.
- About 90% of the cell's expansion is due to water uptake, although some cytoplasm is also produced by the cell.
- Most of the water entering the cell is stored in the large central vacuole which forms due to coalescence of small vacuoles as the cell grows.

Plant cells show very little increase in width as they elongate.

- Cellulose microfibrils in the innermost cell wall layers stretch very little; consequently, the cell expands in the direction perpendicular to the orientation of the microfibrils.
- Alignment of microfibrils in the wall mirrors the microtubule orientation found in the cortex (see Campbell, Figure 38.15). This is believed to result from microtubular control of the flow of cellulose-producing enzymes in a specific direction along the membrane.

C. Cell differentiation depends on gene regulation

The progressive development of specialized structures and functions in plant cells reflects the different types of proteins synthesized by different types of cells. It should be noted that differentiative processes continue throughout the life of a plant because meristems sustain indeterminate growth (see Campbell, Figure 38.20).

Xylem cells function in both transport within the plant and structural support.

- Cell walls are hardened by lignin, which is produced by enzymes made by the cell.
- The final stage of differentiation includes the production of hydrolytic enzymes which destroy the protoplast.

  This leaves only the cell walls intact and permits the movement of xylem sap through the cells.

Guard cells regulate the size of the stomatal opening.

- Must have flexible walls, thus the enzymes that produce lignin are not produced.
- The protoplast remains intact and regulates ion exchange necessary to increase and decrease turgor.

All cells in a plant possess a common genome. This has been proven by cloning whole plants from single somatic cells.

- All the genes necessary are present since these cells dedifferentiate in tissue cultures and then redifferentiate to produce the diversity of cells found in the plant.
- This ability indicates that cellular differentiation is controlled by gene expression leading to the production of specific proteins.
- Different cell types (like xylem and guard cells) selectively express certain genes at different times during their differentiation; this results in the different developmental pathways that gives rise to the diverse cell types.

D. Pattern formation determines the location and tissue organization of plant organs

The organization in a plant can be seen in the characteristic pattern of cells in each tissue, the pattern of tissues in each organ, and the spatial organization of the organs on the plant.

Pattern formation = The development of specific structures in specific locations

1. Positional information

Pattern formation depends on positional information.

Positional information = Signals indicating a cell's location relative to other cells in an embryonic mass

- Genes respond to these signals and their response affects the localized rates and planes of cell division and expansion.
- This signal detection continues in each cell as the organs develop and cells respond by differentiating into particular cell types.

Several hypotheses have been proposed as to how embryonic cells detect their positions. One hypothesis about positional information transmission is that it relies on gradients of chemical signals.

- A chemical signal might diffuse from a shoot's apical meristem and the decreasing gradient farther from the source would indicate to cells their relative position from the tip.
- A second chemical signal released from the outermost lateral cells would diffuse inward indicating the radial position to each cell.

- Each cell could thus determine its relative longitudinal and radial position from the gradients of these two chemical signals.

2. Clonal analysis of the shoot apex

Positional information is the basis for the processes involved in plant development: growth, morphogenesis, and differentiation. Plant developmental biologists have developed the technique of clonal analysis to study the relationships of these processes.

- Clonal analysis involves mapping the cell lineages derived from each cell of the apical meristem, noting their position as the plant organs develop.
- Mapping is possible due to induced somatic mutations in each cell which can be used to distinguish that cell and its derived cells from neighboring cells.

This technique has been used to determine that the developmental fates of cells in the apex are somewhat predictable.

- For example, almost all cells developing from the outermost meristematic cells become part of the dermal tissues of leaves and stems.

It is not currently possible to predict what meristematic cells will develop into specific tissues and organs.

- The outermost cells usually divide on a plane perpendicular to the shoot surfaces, thus adding cells to the surface layer.
- Random changes can result in one of these cells dividing on a plane parallel to the surface; this indicates meristematic cells are not dedicated early in their development to forming specific tissues and organs.
- Consequently, it is the cell's final position in a developing organ which determines what type of cell it becomes, not the particular cell lineage to which it belongs.

3. The genetic basis of pattern formation in flower development

The shoot tip in flowering plants shifts from indeterminate growth to determinate growth when the flower is produced.

- The meristem is consumed during the formation of primordia for sepals, petals, stamens, and carpels.

Positional information commits each primordium to develop into an organ of specific structure and function.

- Some *organ-identity genes* that function in development of the floral pattern and are regulated by positional information have been identified.
- Mutations in these organ-identity genes can cause abnormal floral patterns.
    - For example, an extra whorl of sepals may develop instead of petals.
    - Such abnormal patterns indicate wild-type alleles are responsible for normal floral pattern development.

Arabidopsis thaliana is the experimental organism many plant biologists are now using to study plant development.

- It is a small plant with a relatively rapid life cycle.
- It also has a small genome that simplifies the search for specific genes.
- Several organ-identity genes affecting floral pattern development have been identified and a few have been cloned.
- Similar organ-identity genes have been found in a distantly related plant, the snapdragon.

This finding suggests a conservative evolution of the genes controlling basic angiosperm body plan development.

One hypothesis about how positional information influences a particular floral-organ primordium is based on the overall genetic basis of pattern formation (see Campbell, Figure 38.21).

- Organ-identity genes code for transcription factors that are regulatory proteins that help control expression of other genes.
- This control involves binding of the transcription factor to specific sites on the DNA, which affects transcription.
- It is believed that positional information determines which organ-identity gene is expressed, and the resulting transcription factor induces expression of these genes controlling development of specific organs.

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CHAPTER 39

CONTROL SYSTEMS IN PLANTS

OUTLINE

I. Plant Hormones
   - A. Research on how plants grow toward light led to the discovery of plant hormones: *science as a process*
   - B. Plant hormones help coordinate growth, development, and responses to environmental stimuli
   - C. Analysis of mutant plants is enhancing plant research
   - D. Signal-transduction pathways link cellular responses to hormone signals and environmental stimuli

II. Plant Movements as Models for Studying Control Systems
   - A. Tropisms orient the growth of plant organs
   - B. Turgor movements are relatively rapid, reversible plant responses

III. Control of Daily and Seasonal Responses
   - A. Biological clocks control circadian rhythms
   - B. Photoperiodism synchronizes many plant responses to changes of season

IV. Phytochromes
   - A. Phytochromes function as photoreceptors in many plant responses to light and photoperiod
   - B Phytochromes may help entrain the biological clock

V. Plant Responses to Environmental Stress
   - A. Plants cope with environmental stress through a combination of developmental and physiological responses

VI. Defense Against Pathogens
   - A. Resistance to disease depends on a gene-for-gene recognition between plant and pathogen
   - B. The hypersensitive response (HR) contains an infection
   - C. Systemic acquired resistance (SAR) extends protection against pathogens to the whole plant

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. For each of the following scientists, describe their hypothesis, experiments, and conclusions about the mechanism of phototropism:
   - a. Charles Darwin
   - b. Francis Darwin
   - c. Peter Boysen Jensen
   - d. F.W. Went

2. List five classes of plant hormones, describe their major functions, and recall where they are produced in the plant.
3. Explain how a hormone may cause its effect on plant growth and development.
4. Describe a possible mechanism for polar transport of auxin.
5. According to the acid-growth hypothesis, explain how auxin can initiate cell elongation.
6. Explain why 2,4-D is widely used as a weed killer.
7. Explain how the ratio of cytokinin to auxin affects cell division and cell differentiation.
8. Define apical dominance and describe the check-and-balance control of lateral branching by auxins and cytokinins.
9. List several factors besides auxin from the terminal bud that may control apical dominance.
10. Describe how stem elongation and fruit growth depend upon a synergism between auxin and gibberellins.
11. Explain the probable mechanism by which gibberellins trigger seed germination.
12. Describe how abscisic acid (ABA) helps prepare a plant for winter.
13. Explain the antagonistic relationship between ABA and gibberellins, and how it is possible for growing buds to have a higher concentration of ABA than dormant buds.
14. Give an example of how ABA can act as a "stress hormone".
15. Describe the role of ethylene in plant senescence, fruit ripening and leaf abscission.
16. Discuss how the study of mutant varieties of plants has heightened our understanding of plant hormones
17. Describe the components of a signal-transduction pathway.
18. List two environmental stimuli for leaf abscission.
19. Define tropism and list three stimuli that induce tropisms and a consequent change of body shape.
20. Explain how light causes a phototropic response.
21. Describe how plants apparently tell up from down, and explain why roots display positive gravitropism and shoots exhibit negative gravitropism.
22. Distinguish between thigmotropism and thigmomorphogenesis.
23. Describe how motor organs within pulvini can cause rapid leaf movements and sleep movements.
24. Provide a plausible explanation for how a stimulus that causes rapid leaf movement can be transmitted through the plant.
25. Define circadian rhythm and explain what happens when an organism is artificially maintained in a constant environment.
26. List some common factors that entrain biological clocks.
27. Define photoperiodism.
28. Distinguish among short-day plants, long-day plants, and day-neutral plants; give common examples of each; and explain how they depend upon critical night length.
29. Provide evidence for the existence of a florigen.
30. Explain how the interconversion of phytochrome can act as a switching mechanism to help plants detect sunlight and trigger many plant responses to light.
31. Using photoperiodism as an example, explain how an integrated control system can regulate a plant process such as flowering.

32. Explain the molecular basis of resistance to nonvirulent pathogens.
33. Describe the local and systemic response to virulent pathogens.

KEY TERMS

hormone	oligosaccharins	circadian rhythm	phytoalexins
phototropism	brassinosteroids	photoperiodism	PR proteins
auxin	tropisms	short-day plant	hypersensitive response
cytokinins	gravitropism	long-day plants	systemic acquired
gibberellin	statoliths	day-neutral plants	resistance (SAR)
abscisic acid (ABA)	thigmomorphogenesis	phytochrome	
ethylene	action potentials	heat-shock proteins	
senescence	sleep movements	gene-for-gene recognition	

LECTURE NOTES

Control systems in plants are adaptations that evolved over time in response to interactions with their environment. Plants respond to environmental stimuli by:

- Sending signals between different parts of the plant.
- Tracking the time of day and the time of year.
- Sensing and responding to gravity and direction of light, etc.
- Adjusting their growth pattern and development.

I. Plant Hormones

Hormone = A compound produced by one part of an organism that is transported to other parts where it triggers a response in target cells and tissues

A. Research on how plants grow toward light led to the discovery of plant hormones: *science as a process*

Phototropism = Growth toward or away from light

- Growth of a shoot toward light is positive phototropism; growth away from the light is negative phototropism.
- Results form differential growth of cells on opposite sides of a shoot, or in the case of a grass seedling, coleoptile.
- Cells on the darker side elongate faster than those on the light side (see Campbell, Figure 39.1).

Experiments on phototropism led to the discovery of a plant hormone.

Charles and Francis Darwin removed the tip of the coleoptile from a grass seedling (or covered it with an opaque cap) and it failed to grow toward light (see Campbell, Figure 39.2). They concluded that:

- The coleoptile tip was responsible for sensing light.
- Since the curvature occurs some distance below the tip, the tip sends a signal to the elongating region.

Peter Boysen-Jensen separated the tip from the remainder of the coleoptile by a block of gelatin, preventing cellular contact, but allowing chemical diffusion.

- Seedlings behaved normally.
- If an impenetrable barrier was substituted, no phototropic response occurred.
- These experiments demonstrated that the signal was a mobile substance.

In 1926, F.W. Went removed the coleoptile tip, placed it on an agar block, and then put the agar (without the tip) on decapitated coleoptiles kept in the dark (see Campbell, Figure 39.3).

- A block centered on the coleoptile caused the stem to grow straight up.
- If the block was placed off-center, the plant curved away from the side with the block.
- Went concluded the agar block contained a chemical that diffused into it from the coleoptile tip, and that this chemical stimulated growth.
- Went called this chemical an *auxin.*

Kenneth Thimann later purified and characterized auxin.

B. Plant hormones help coordinate growth, development, and responses to environmental stimuli

Plant hormones control plant growth and development by affecting division, elongation, and differentiation of cells.

- Effects depend on site of action, stage of plant growth and hormone concentration.
- The hormonal signal is amplified, perhaps by affecting gene expression, enzyme activity, or membrane properties.
- Reaction to hormones depends on hormonal balance (relative concentration of one hormone compared with others).

Major classes of plant hormones include (see also Campbell, Table 39.1):

1. Auxin (such as IAA)
2. Cytokinins (such as zeatin)
3. Gibberellins (such as GA_3)
4. Abscisic acid
5. Ethylene

1. Auxin

Auxin = A hormone that promotes elongation of young developing shoots or coleoptiles

The natural auxin found in plants is a compound named indoleacetic acid (IAA).

a. Auxin and cell elongation

The apical meristem is a major site of auxin production.

Auxin stimulates cell growth only at concentrations between 10^{-8} to 10^{-3} M.

Auxin moves from the apex down to the zone of cell elongation at a rate of about 10 mm per hour.

- This is faster than would be found in diffusion but much slower than in phloem translocation.
- Polar transport of auxin is unidirectional and requires metabolic energy (see Campbell, Figure 39.4).
- Energy for auxin transport is provided by chemiosmosis.
- IAA is actively transported down a stem by auxin carriers located on the basal ends of cells (carriers are absent on the apical ends).
- Movement of auxin is aided by the differences in pH between the acidic cell wall and the neutral cytoplasm.
    - ATP-driven pumps maintain a proton gradient across the plasma membrane (see Campbell, Figure 39.4).

- As auxin passes through the acidic cell wall, it picks up a proton to become electrically neutral, which allows it to pass through the plasma membrane.
- Auxin is ionized in the neutral intracellular environment which temporarily traps it within the cell since the plasma membrane is less permeable to ions.
- Auxin can only exit the cell by the basal end, where specific carrier proteins are built into the membrane. The proton gradient contributes to auxin efflux by favoring the transport of anions out of the cell.

The acid-growth hypothesis states that cell elongation is due to stimulation of a proton pump that acidifies the cell wall (see Campbell, Figure 39.5).

- Acidification causes the crosslinks between the cellulose myofibrils of the cell walls to break (via disruption of hydrogen bonds).
- This loosens the wall, allowing water uptake, which results in elongation of the cell.

b. Other effects of auxin

Affects secondary growth by inducing vascular cambium cell division and differentiation of secondary xylem

Promotes formation of adventitious roots

Promotes fruit growth in many plants

Auxins are used as herbicides. 2,4-D is a synthetic auxin which affects dicots selectively, allowing removal of broadleaf weeds from a lawn or grain field.

2. Cytokinins

Cytokinins = Modified forms of adenine that stimulate cytokinesis

Cytokinins function in several areas of plant growth:

- Cell division and differentiation
- Apical dominance
- Anti-aging hormones

a. Control of cell division and differentiation

Move from the roots to target tissues by moving up in the xylem sap.

Stimulate RNA and protein synthesis. The new proteins produced by stimulation of RNA appear to be involved in cell division.

Cytokinins, in conjunction with auxin, control cell division and differentiation.

- Stem parenchyma cells cultured without cytokinins grow very large and do not divide.
- Cytokinins added alone have no effect on cells grown in tissue culture.
- Equal concentrations of cytokinins and auxins stimulate cells to grow and divide, but they remain an undifferentiated callus.
- More cytokinin than auxin causes shoot buds to develop from the callus.
- More auxin than cytokinin causes roots to form.

b. Control of apical dominance

Cytokinins and auxin contribute to apical dominance through an antagonistic mechanism.

- Auxin from the terminal bud restrains axillary bud growth, causing the shoot to lengthen.

- Cytokinins (from the roots) stimulate axillary bud growth.
- Auxin cannot suppress axillary bud growth once it has begun.
- Lower buds thus grow before higher ones since they are closer to the cytokinin source than the auxin source.

Auxin stimulates lateral root formation while cytokinins restrain it.

This stimulation-inhibition action may help balance plant growth since an increase in the root system would signal the plant to produce more shoots.

c. Cytokinins as anti-aging hormones

Cytokinins can retard aging of some plant organs, perhaps by inhibiting protein breakdown, stimulating RNA and protein synthesis, and mobilizing nutrients.

May slow leaf deterioration on plants since detached leaves dipped in a cytokinin solution stay green longer.

3. Gibberellins

More than 80 different gibberellins, many naturally occurring, have been identified.

a. Stem elongation

Gibberellins are produced primarily in roots and young leaves. They:

- Stimulate growth in leaves and stems but show little effect on roots
- Stimulate cell division and elongation in stems, possibly in conjunction with auxin
- Cause bolting (rapid growth of floral stems, which elevates flowers)

b. Fruit growth

Fruit development is controlled by both gibberellins and auxin.

- In some plants, both must be present for fruit set.

The most important commercial application of gibberellins is in the spraying of Thompson seedless grapes (see Campbell, Figure 39.8). The hormones cause the grapes to grow larger and farther apart after treatment.

c. Germination

The release of gibberellins signals seeds to break dormancy and germinate.

- A high concentration of gibberellins is found in many seeds, especially in the embryo.
- Imbibed water appears to stimulate gibberellin release.
- Environmental cues may also cause gibberellin release in seeds which require special conditions to germinate.

In cereal grains, gibberellins stimulate germination and support growth by stimulating synthesis of mRNA coding for α-amylase. The α-amylase then digests the stored nutrients, making them available to the embryo and seedling.

In breaking both seed dormancy and apical bud dormancy, gibberellins act antagonistically with abscisic acid, which inhibits plant growth.

4. Abscisic acid (ABA)

Abscisic acid is produced in the terminal bud and helps prepare plants for winter by suspending both primary and secondary growth.

- Directs leaf primordia to develop scales that protect dormant buds.
- Inhibits cell division in vascular cambium.

The onset of seed dormancy is another time it is advantageous to suspend growth.

- In most cases, the ratio of ABA:gibberellins determines whether seeds remain dormant or germinate.

- In other plants, seeds germinate when ABA is washed out of the seeds (desert plants) or degraded by some other stimulus such as sunlight.

ABA also acts as a stress hormone, closing stomata in times of water-stress thus reducing transpirational water loss.

5. Ethylene

Ethylene = A gaseous hormone that diffuses through air spaces between plant cells

- Ethylene can also move in the cytosol, traveling from cell to cell in the phloem or symplast.

High auxin concentrations induce release of ethylene, which acts as a growth inhibitor.

a. Senescence in plants

Senescence (aging) is a natural process in plants that may occur at the cellular, organ, or whole plant level. Ethylene probably plays an important role at each level.

Examples:
- Xylem vessel elements and cork cells that die before becoming fully functional
- Leaf fall in the autumn
- Withering of flowers
- Death of annuals after flowering

The best studied forms of senescence are fruit ripening and leaf abscission.

b. Fruit ripening

During fruit ripening, ethylene triggers senescence, and then the aging cells release more ethylene.

- The breakdown of cell walls and loss of chlorophyll are considered aging processes.
- The signal to ripen spreads from fruit to fruit since ethylene is a gas.

c. Leaf abscission

Leaf abscission is an adaptation that prevents deciduous trees from desiccating during winter when roots cannot absorb water from the frozen ground.

- Before abscission, the leaf's essential elements are shunted to storage tissues in the stem from which they are recycled to new leaves in the spring.
- Environmental stimuli are shortening days and cooler temperatures.

When a leaf falls, the breakpoint is an abscission layer near the petiole base (see Campbell, Figure 39.10).

- Weak area since the small parenchyma cells have very thin walls and there are no fiber cells around the vascular tissue.

Mechanics of abscission are controlled by a change in the balance of ethylene and auxin.

- Auxin decrease makes cells in the abscission layer more sensitive to ethylene. Cells then produce more ethylene which inhibits auxin production.
- Ethylene induces synthesis of enzymes that digest the polysaccharides in the cell walls, further weakening the abscission layer.

Wind and weight cause the leaf to fall by causing a separation in the abscission layer.

Even before the leaf falls, a layer of cork forms a protective scar on the twig's side of the abscission layer. The cork prevents pathogens from entering the plant.

D. Analysis of mutant plants is extending the list of hormones and their functions

Until recently, plant hormone research was conducted mainly by applying compounds to whole plants or tissue cultures and measuring their effects on growth and development.

Recently, researchers have gained new insight into hormone synthesis and action by studying mutant varieties that grow or develop abnormally.

Studies with mutant also has led to the discovery of new plant hormones.

- *Oligosaccharides* = Short chains of sugars released from cell walls by the hydrolytic action of enzymes on cell wall polysaccharide; these compounds function in pathogen defense, cell growth and differentiation, and flower development
- *Brassinosteroids* = Steroids that are critical for normal growth

E. Signal-transduction pathways link cellular responses to hormonal signals and environmental stimuli

Chemical signaling was covered in detail in Chapter 11. It may be useful to review highlights in the special context of plant systems, which are discussed at various points in the remainder of this chapter.

Plant cell responses to hormones and environmental stimuli are mediated by intracellular signals (signal-transduction pathways).

- *Signal-transduction pathway* = A mechanism linking a mechanical or chemical stimulus to a cellular response
- Three steps are involved in each pathway: reception, transduction, and induction (see Campbell, Figure 39.11).

Reception is the detection of a hormone or environmental stimulus by the cell.

- May take various forms depending on the stimulus.

  Examples:
  - Absorption of a particular wavelength of light by a pigment within a cell
  - The binding of a hormone to a specific protein receptor in the cell or on its membrane

- Reception of a hormone only occurs in *target cells* for that hormone.
  - Target cells possess the specific protein receptor to which the hormone must bind; other cells do not possess the receptor.

Transduction in the pathway results in an amplification of the stimulus and its conversion into a chemical form that can activate the cell's responses.

- The hormone (first messenger) binds to a specific receptor and the hormone-receptor combination stimulates the second messenger (a substance that increases in concentration within a cell stimulated by the first messenger).
- The receptor may be bound to the cell membrane and its activation results in a chemical change to the cell.
- Amplification of the signal results from a single first messenger molecule binding to its receptor giving rise to many second messengers, which activate an even larger number of proteins and other molecules.

- Calcium ions appear to be important second messengers in many plant responses. Calcium ion concentration increases in the cell and the ions bind to the protein calmodulin.
- The calmodulin-calcium complex then activates other target molecules within the cell.
- A second part of transduction that is important is the specificity of the responses.
  - Two cell types both may have receptors for a hormone but respond differently, because each contains different target proteins for the second messenger.

Induction is the pathway step in which the amplified signal induces the cell's specific response to the stimulus.

- Some responses occur rapidly. For example,
  - ABA stimulation of stomatal closing
  - Auxin-induced acidification of cell walls during cell elongation
- Other responses take longer, especially if they require changes in gene expression (thigmomorphogenesis).

II. Plant Movements As Models for Studying Control Systems

A. Tropisms orient the growth of plant organs toward or away from stimuli

Tropisms = Growth responses that result in curvatures of whole plant organs toward or away from stimuli.

- Mechanism is a differential rate of cell elongation on opposite sides of the organ.

Three primary stimuli that result in tropisms are light (phototropism), gravity (gravitropism), and touch (thigmotropism).

1. Phototropism

Phototropism = Growth either toward or away from light

It is generally accepted that cells on the darker side of a grass coleoptile elongate faster than cells on the bright side due to asymmetric distribution of auxins moving down from the shoot tip.

- For organs, other than grass coleoptiles, the mechanism may be different.

No evidence exists that unilateral light causes an asymmetric distribution of auxins in the stems of many dicots.

There is evidence that other substances that act as growth inhibitors do have an asymmetric distribution toward the lighted side of the stem.

Regardless of the mechanism, the shoot tip is the site of the photoreception that triggers the growth response.

- A photoreceptor sensitive to blue light is present in the shoot tip; this receptor is believed to be a yellow pigment related to riboflavin.
- The same receptor may be involved in other plant responses to light.

2. Gravitropism

Gravitropism = Orientation of a plant in response to gravity

Roots display positive gravitropism (curve downward).

Shoots display negative gravitropism (bend upward).

The possible mechanisms of gravitropism in roots:

- Specialized plastids containing dense starch grains (*statoliths*) aggregate in the low points of plant cells (see Campbell, Figure 39.12).

- In roots, statoliths occur in certain root cap cells.
  - Aggregating statoliths trigger calcium redistribution, which results in lateral transport of auxin in the root.
  - Calcium and auxin accumulate on the lower side of the elongation zone.
  - Roots curve down, because at high concentrations, auxin *inhibits* root cell elongation, so cells on the upper side elongate faster than those on the lower side.

Researchers are challenging the falling statolith hypothesis for positive gravitropism in root growth.

- Insufficient energy is released by starch grains settling to the bottom of cells to account for gravitational detection.
- Many plants lacking starch grains distinguish up from down.
- Studies on *Chara*, a green alga closely related to plants, indicate the settling of the entire protoplasm provides a cell with its up-down orientation.
  - The protoplast is attached to the inside of the cell wall by proteins.
  - When the protoplast settles, the protein tethers at the top of the cell are stretched and those at the bottom are compressed.
  - The sense of up and down is related to this stretching and compressing of the proteins.
  - Experiments where *Chara* was placed in a solution more dense than the protoplast resulted in the protoplast floating upward and an upside down growth pattern.
  - Whether this mechanism is at work in true plants is currently under investigation.

3. Thigmotropism

Thigmotropism = Directional growth in response to touch

- Contact of tendrils stimulates a coiling response caused by differential growth of cells on opposite sides of the tendril.

Thigmomorphogenesis = Developmental response to mechanical perturbation

- Usually results from increased ethylene production in response to chronic mechanical stimulation.
- Stem lengthening decreases while stem thickening increases.

B. Turgor movements are relatively rapid, reversible plant responses

Turgor movements = Reversible movements caused by changes in turgor pressure of specialized cells in response to stimuli

1. Rapid leaf movements

Rapid leaf movements occur in plants such as *Mimosa*.

- When the compound leaf is touched, it collapses and folds together (see Campbell, Figure 39.14).
- Results from rapid a loss of turgor within pulvini (special motor organs located in leaf joints).
- Motor cells lose potassium, which causes water loss by osmosis.
- Turgor pressure is regained and natural leaf form restored in about ten minutes.

Rapid leaf movements travel from the leaf that was stimulated to adjacent leaves along the stem.

- This may be a response to reduce water loss or protect against herbivores.
- The stimulus and response travel wavelike through the plant at 1 cm/sec.

- This transmission is correlated with *action potentials* (electrical impulses) resembling those in animals, but thousands of times slower.
- Action potentials may be widely used as a form of internal communication since they have been found in many algae and plants.

2. Sleep movements

Sleep movements = Lowering of leaves to a vertical position in evening and raising of leaves to a horizontal position in morning (see Campbell, Figure 39.15)

Occurs in many legumes.

Due to daily changes in turgor pressure of motor cells of pulvini.

Cells on one side of the pulvinus are turgid while those on the other side are flaccid.

Migration of potassium ions from one side of the pulvinus to the other is the osmotic agent leading to reversible uptake and loss of water by motor cells.

III. Control of Daily and Seasonal Responses

A. Biological clocks control circadian rhythms in plants and other eukaryotes

Biological clocks (internal oscillators that keep accurate time) are common in all eukaryotes and control many rhythmic phenomena.

- Many human features (e.g., blood pressure, temperature, metabolic rate) fluctuate with the time of the day.
- Certain fungi produce spores for only certain hours during the day.
- Plants display sleep movements and a rhythmic pattern of opening and closing stomata.

Circadian rhythm = A physiological cycle with a frequency of about 24 hours

- Persists even when an organism is sheltered from environmental cues.
- The oscillator is probably endogenous and is set to a 24-hour period by daily signals from the environment.
- When the organism is sheltered from environmental cues, rhythm may deviate from 24 hours (called free-running periods) and can vary from 21 to 27 hours.

Deviation of a free-running period from 24 hours does not indicate erratic drift of a biological clock, just absence of a synchronizing cue.

- Most biological clocks are cued to the light-dark cycle resulting from the Earth's rotation.
- The clock may take days to reset once the cues change.
- Jet lag is a human condition resulting from a lack of synchronization of the internal clock to the time zone.

The nature of the internal oscillator is still currently of great research interest.

- Recent research suggests that the clock is a molecular mechanism common to all eukaryotes. Timekeeping appears to be related to the synthesis of a protein that regulates its own production through feedback.
  - The protein is a transcription factor that inhibits the gene that encodes for the transcription factor; it has been suggested that cyclic changes in the level of the protein form the basis for the internal clock.
  - Such genes have been found in a wide range of organisms, including fruit flies and bread mold, but not plants as of yet.

B. Photoperiodism synchronizes many plant responses to changes of season

Photoperiodism = A physiological response to day length

Seasonal events (seed germination, flowering) are important in plant life cycles.

Plants detect the time of year by the photoperiod (relative lengths of night and day).

1. **Photoperiodism and the control of flowering**

W.W. Garner and H.A. Allard (1920) postulated that the amount of day length controls flowering. Based on their studies, they classified plants into three categories:

1. *Short-day plants* require a light period shorter than a critical length and generally flower in late summer, fall and winter.
2. *Long-day plants* flower only when the light period is longer than a certain number of hours, generally in late spring and summer.
3. *Day-neutral plants* are unaffected by photoperiod and flower when they reach a certain stage of maturity.

a. Critical night length

It was discovered in the 1940s that night length, not day length, actually controls flowering and other responses to photoperiod.

- If the daytime period is broken by a brief exposure to darkness, there is no effect on flowering.
- If the nighttime period is interrupted by short exposure to light, photoperiodic responses are disrupted and the plants do not flower (see Campbell, Figure 39.16).
- Therefore, short-day plants flower if night is longer than a critical length, and long-day plants need a night shorter than a critical length.

Some plants flower after a single exposure to the proper photoperiod.

Some require several successive days of the proper photoperiod to bloom.

Others respond to photoperiod only if they have been previously exposed to another stimulus. For example, vernalization is a requirement for pretreatment with cold before flowering.

b. Is there a flowering hormone?

There is evidence that a "flowering hormone" is present in plants since leaves detect the photoperiod while buds produce flowers.

- Only requires one leaf for a plant to detect photoperiod and for floral buds develop.
- If all leaves are removed, no photoperiod detection occurs.

Most plant physiologists believe an unidentified hormone is produced in the leaves and moves to the buds or there is a change in the relative concentrations of two more hormones (see Campbell, Figure 39.17).

The hormone (or mixture of hormones) appears to be the same in both long-day and short-day plants.

c. Meristem transition from vegetative growth to flowering

A combination of environmental cues (e.g., photoperiod) and internal signals (e.g., hormones) induces the transition of a bud's meristem from a vegetal state into a flowering state.

The transition requires the coordinate expression of genes that control pattern formation.

IV. Phytochromes

A. Phytochromes function as a photoreceptors in many plant responses to light and photoperiod

Pigments named phytochromes help plants measure the length of darkness in a photoperiod.

- *Phytochrome* = A protein containing a chromophore (light-absorbing component) responsible for a plant's response to photoperiod (see Campbell, Figures 39.18 and 39.19)

- Discovered during studies on how different colors of light affect responses to photoperiod.

Red light (λ of 660 nm) is most effective in interrupting night length.

- Brief exposure of short-day plants to red light prevents flowering even if the plant is kept at critical night length conditions.
- A long-day plant is induced to flower by a brief exposure to red light even if kept at a night length exceeding the critical number of hours.
- If a flash of red light (R flash) is followed by a flash of far-red (FR) light (λ of 730 nm), the plant perceives no interruption of night length.
- Only the wavelength of the last flash affects the plant's measurement of night length, regardless of the number of alternating flashes (see Campbell, Figure 39.18).

Phytochromes alternate between two photoreversible forms: P_r (red absorbing) and P_{fr} (far-red absorbing). The P_r and P_{fr} interconversion is a switching mechanism controlling various plant events (see Campbell, Figure 39.20).

1. The ecological significance of phytochrome as a photoreceptor

Phytochrome functions as a photodetector that tells the plant if light is present.

- Plants synthesize phytochrome as P_r, and if kept in dark, it remains as P_r, but if the phytochrome is illuminated, some P_r is converted to P_{fr}.
- P_{fr} triggers many plant responses to light (e.g., seed germination).
- A shift in the P_r and P_{fr} equilibrium indicates the relative amounts of red and far-red light present in the sunlight.
- Shifts in the P_r and P_{fr} ratio may cause changes (e.g., increased growth) which would adjust a plant's growth and development in response to some environmental changes.

Photoreception by phytochrome has a large effect on the whole plant even though very little of the pigment is present in plant cells.

- This fact implies the photoconversion from P_r to P_{fr} produces a signal that is amplified in some way.
- The amplification may be by either an alteration of membrane permeability and/or by affecting gene expression.

  Photoconversion of phytochrome triggers the potassium fluxes in cells of the pulvini that produces the sleep movements in legumes.

  Light induces the synthesis of starch digesting α-amylase required for seed germination in some species.

Complementing phytochrome’s effect, other photoreceptors help coordinate a plant’s growth and development with its environment.

B. Phytochromes may help entrain the biological clock

P_{fr} gradually reverts to P_r.

- This occurs every day after sunset.
- The pigment is synthesized as P_r and degradative enzymes destroy more P_{fr} than P_r.
- At sunrise, the P_{fr} level increases due to photoconversion of P_r.

Plants do not use the disappearance of P_{fr} to measure night length since:

- The conversion is complete within a few hours after sunset.
- Temperature affects the conversion rate, thus, it would not be reliable.

Night length is measured by the biological clock, not by phytochrome.

- Perhaps phytochrome synchronizes the clock to the environment.
- The clock measures night length very accurately (some short-day plants will not flower if night is even one minute shorter than the critical length).

V. Plant Responses to Environmental Stress

A. Plants cope with environmental stress through a combination of developmental and physiological responses

A plant must adjust to environmental fluctuations every day of its life. Severe fluctuations may put plants under stress.

- *Stress* = An environmental condition that can have an adverse effect on a plant's growth, reproduction, and survival

Some plants have evolutionary adaptations that enable them to live in environments that are stressful to other plants.

- For example, halophytes have special anatomical and physiological adaptations that permit them to grow best in salty soils.
  - Salt glands on the leaves eliminate excess salt from the plants, thus the saline environment is not an environmental stress.

1. Responses to water deficit

Plants have control systems in both the leaves and roots that help them cope with water deficits.

Most control systems in leaves help the plant conserve water by reducing transpirational water loss.

- Guard cells lose turgor and the stomata close when a leaf faces a water deficit.
- Mesophyll cells in the leaf are also stimulated to increase synthesis and release abscisic acid which acts on guard cell membranes to help keep the stomata closed.
- Growth of young leaves is inhibited by a water deficit since cell expansion is a turgor-dependent process.
  - This reduces transpiration by slowing the increase in leaf surface area.
- The leaves of many grasses and other plants wilt; they roll into a shape that reduces the surface area exposed to the sun, thus reducing transpiration.

Roots respond to water deficits by reducing growth.

- Drying of the soil from the surface down inhibits the growth of shallow roots.
  - The cells cannot retain the turgor necessary for elongation.
- Deeper roots surrounded by moist soil continue to grow.
  - This maximizes root exposure to soil moisture.

2. Responses to oxygen deprivation

Waterlogged soil lacks the air spaces that provide oxygen for cellular respiration in the roots.

- Some plants form air tubes that extend from submerged roots to the surface, thus oxygen can reach the roots (see Campbell, Figure 39.21).
- Mangroves are structurally adapted to their coastal marsh environments in that their submerged roots are continuous with aereal roots that provide access to oxygen.

3. Responses to salt stress

Excess salts (sodium chloride or others) in the soil may:

1. Lower the water potential of the soil solution causing a water deficit even though sufficient water is present
   - A water potential in the soil that is more negative than that of the root tissue will cause roots to lose water instead of absorb it.
2. Have a toxic effect on the plant at relatively high concentrations
   - The uptake of most harmful ions is impeded by the selectively permeable membranes of root cells.
   - This causes a problem with acquiring water from solute rich soils.

Many plants produce compatible solutes in response to moderately saline soils.

- *Compatible solute* = An organic compound that keeps the water potential of cells more negative than the soil solution without admitting toxic quantities of salt

With the exception of halophytes, most plants cannot survive extended periods of salt stress.

4. Responses to heat stress

Transpiration is one mechanism that helps plants respond to excessive heat and prevent the denaturing of enzymes and damage to metabolism.

- The evaporative cooling associated with transpiration keeps the temperature of the leaf 3° to 10°C lower than ambient temperature.
- Cooling via transpiration will continue while stomata remain open; however, if a water deficit occurs, the stomata close and the cooling function is lost in order to conserve water.

Most plants will begin producing *heat-shock proteins* when exposed to excessive temperatures (40°C or above for temperate zone plants).

- This is a back-up system to transpiration.
- Some heat-shock proteins are identical to chaperone proteins found in unstressed cells.

  Chaperone proteins serve as temporary supports which help other proteins fold into their functional conformations.
- Heat-shock proteins may help enzymes and other proteins maintain their conformation, thus preventing denaturation.

5. Responses to cold stress

Chilling of a plant (reduction of ambient temperature to a non-freezing level) causes a change in the fluidity of cell membranes.

- *Fluidity* = The lateral drifting of proteins and lipids in the plane of the membrane; a result of the fluid mosaic structure of membranes
- At a critical point, lipids become locked into crystalline structures causing a loss of fluidity.
- Solute transport and membrane protein function are adversely affected by the loss of fluidity.

Plants respond to the cold stress of chilling by altering the lipid composition of their membranes.

- The proportion of saturated fatty acids in the membrane is increased.

  The shape of the fatty acids reduces crystal formation, thus maintaining fluidity at lower temperatures.

- This modification works best for gradual temperature changes as it takes several hours to days to occur.

Subfreezing temperatures are the most severe form of cold stress because ice crystals begin to form in the plant.

- Less threat to plant survival occurs if the ice crystals form only in the cell walls and intracellular spaces.
- When ice crystals form in the protoplasts, the cell usually dies.
    - The ice crystals perforate the membranes and organelles.
- Wood plants which are native to regions where cold winters occur have adaptations to cope with the stress of freezing.
    - The solute composition of live cells is changed in a way that prevents ice crystal formation even when the cytosol is supercooled.
    - This is effective even when ice crystals form in the cell walls.

6. Responses to herbivores

Plants counter excessive grazing by herbivores with both physical and chemical defense measures.

- Physical defenses include structures such as thorns and spines.
- Chemical defenses take the form of distasteful or toxic compounds such as canavanine.
    - Similar to arginine, canavanine is an unusual amino acid produced by some plants.
    - When ingested by insects, it is incorporated in place of arginine in the insect's proteins.
    - Incorporation of canavanine disrupts protein conformation and the insect dies.

Some plants even recruit predatory animals to help defend against herbivores.

- Certain wasps inject their eggs into their prey (e.g., caterpillars). Upon hatching, the larvae feed upon, and eventually kill, the caterpillar (this benefits the plant).
- The plant attracts wasps via volatile chemical signals released from caterpillar-induced wounded plant tissue.

VI. Defense Against Pathogens

Plants, like animals, are subject to infection from various pathogens. Plant structure (epidermis and periderm) offers the first line of defense. Plants also posses a chemical-based second line of defense akin to the immune system of animals.

A. Resistance to disease depends on a gene-for-gene recognition between plant and pathogen

Most pathogen-plant interactions are nonvirulent, meaning that the pathogen gains access to the host to perpetuate itself without causing severe damage to the plant.

Specific resistance to disease is based on a *gene-for-gene recognition* in which a precise match-up occurs between an allele in the plant and an allele in the pathogen (see Campbell, Figure 39.23).

- A plant is resistant if one of its *R* (resistance) genes is a dominant allele that corresponds to a dominant *Avr* (avirulent) allele in the pathogen.
- The molecular mechanisms actually involve the products of the *R* and *Avr* genes, a receptor and a signal molecule, respectively. (The *Avr* product most likely mimics the action of an endogenous signal molecule of the plant.)

B. The hypersensitive response (HR) contains the infection

Plants infected by a virulent pathogen are capable of resisting infection through a localized chemical signaling system. The response involves the following factors:

- *Phytoalexins* = Antimicrobial compounds released from wounded cells
- Activation of genes encoding *PR proteins* (for pathogenesis-related), some of which are antimicrobial, and others of which act as signals to adjacent cells
- Lignin synthesis and cross-linking of cell wall components, actions aimed at isolating the infection

If the pathogen is a virulent based on an R-Avr match, the local response is more vigorous and is referred to as a *hypersensitive response* (HR).

C. Systemic acquired resistance (SAR) helps prevent infection throughout the plant

Although an HR response is local and specific, signals produced from an HR are conveyed throughout the plant.

Such signals, or "alarm hormones," initiate a non-specific *systemic acquired resistance* (SAR) response to help protect uninfected tissue from a pathogen that might spread from its point of invasion.

- The SAR includes production of phytoalexin and PR proteins.
- A possible alarm hormone is salicylic acid. A modified form of this compound, acetylsalicylic acid, is the active component of aspirin.

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CHAPTER 40

AN INTRODUCTION TO ANIMAL STRUCTURE AND FUNCTION

OUTLINE

I. Levels of Structural Organization
   A. Function correlates with structure in the tissues of animals
   B. The organ systems of an animal are interdependent

II. Introduction to the Bioenergetics of Animals
   A. Animals are heterotrophs that harvest chemical energy from the food they ingest
   B. Metabolic rate provides clues to an animal's bioenergetic "strategy"
   C. Metabolic rate per gram is inversely related to body size among similar animals

III. Body Plans and the External Environment
   A. Physical support on land depends on adaptations of body proportions and posture
   B. Body size and shape affect interactions with the environment

IV. Regulating the Internal Environment
   A. Mechanisms of homeostasis moderate changes in the internal environment
   B. Homeostasis depends on feedback circuits

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. Define tissue and explain where it falls in the hierarchy of structural organization.
2. From micrographs or diagrams, correctly identify the following animal tissues, explain how their structure relates to function and give examples of each.
   a. Epithelial tissue: cuboidal, columnar, squamous
   b. Connective tissue: adipose, cartilage, bone
   c. Muscle: skeletal (striated), cardiac, smooth, nervous
3. Describe how metabolic rate can be determined for animals, and distinguish between basal metabolic rate and standard metabolic rate.
4. Describe several body shapes that maximize external surface area in contact with the environment.
5. Explain how animals with complex internal organization and relatively small surface area to volume ratio can have adequate surface area for materials exchange with the environment.
6. Describe the location and function of interstitial fluid.
7. Define homeostasis.
8. Distinguish between negative and positive feedback.

KEY TERMS

tissues	elastic fibers	osteoblasts	abdominal cavity
epithelial tissue	reticular fibers	Haversian systems	organ systems
basement membrane	fibroblasts	blood	metabolic rate
simple epithelium	macrophages	nervous tissue	calories (cal)
stratified epithelium	adipose tissue	neuron	kilocalories (kcal)
cuboidal	tendons	muscle tissue	basal metabolic rate
columnar	fibrous connective tissue	skeletal muscle	standard metabolic rate
squamous		striated muscle	interstitial fluid
mucous membrane	ligaments	cardiac muscle	homeostasis
connective tissue	cartilage	organs	negative feedback
loose connective tissue	chondrocytes	mesenteries	positive feedback
collagenous fibers	bone	thoracic cavity	

LECTURE NOTES

There are several unifying themes in the study of animal anatomy and physiology.

- There is a correlation between form and function; functions are properties that emerge from the specific shape and order of body parts.
- A comparative approach allows us to see how species of diverse evolutionary history and varying complexity solve problems common to all.
- Animals, as all living organisms, have the capacity to respond and adjust to environmental change in two temporal scales:
    - Over the long term by adaptation due to natural selection
    - Over the short term by physiological responses

The objectives of this chapter are to:

- Illustrate the hierarchy of structural order characterizing animals
- Emphasize the importance of energetics in animal life (how animals obtain, process, and use chemical energy)
- Examine how animal body forms affect their interactions with the environment
- Preview how regulatory systems maintain favorable internal environments

I. Levels of Structural Organization

There is a structural hierarchy of life:

- Atoms → molecules → supramolecular structures → cell
- The cell is the lowest level of organization that can live as an organism.

The hierarchy of multicellular organisms is: cell → tissues → organs → organ systems.

A. Function correlates with structure in the tissues of animals

Tissues = Groups of cells with common structure and function

- Cells may be held together by a sticky coating or woven together in a fabric of extracellular fibers.

There are four main categories of tissues: epithelial tissue, connective tissue, muscle tissue, and nervous tissue.

1. Epithelial Tissue

Formed from sheets of tightly packed cells, *epithelial tissue* covers the outside of the body and lines organs and body cavities. Characteristics of epithelium include:

- Cells are closely joined and are riveted by tight junctions in some tissue types (see Campbell, Chapter 7).
- It functions as a barrier against mechanical injury, invading microbes, and fluid loss.
- Its free surface is exposed to air or fluid. Cells at the base are attached to a *basement membrane,* which is a dense layer of extracellular material.

Epithelial tissue cells are categorized by the number of layers and shape of the free surface cells:

- *Simple epithelium* is one layer of cells.
- *Stratified epithelium* has multiple tiers of cells.
- Pseudostratified epithelium is one layer of cells that appear to be multiple because the cells vary in length.
- Cell shapes are *cuboidal* (like dice), *columnar* (bricks on end), or *squamous* (like flat floor tiles).
- A tissue may be described by a combination of terms such as stratified squamous epithelium (see Campbell, Figure 40.1).

Some epithelia are specialized for absorption or secretion of chemical solutions, in addition to their protective role.

- Some epithelia are ciliated (e.g., the lining of the respiratory system).
- The *mucous membranes* lining the oral cavity and nasal passageways secrete mucus which moistens and lubricates the surfaces.
- The structure fits function. For example, simple squamous epithelium is leaky and is specialized for exchange of materials by diffusion. It is found in blood vessel linings and air sacs in the lungs.

2. Connective tissue

Connective tissue is characterized by a sparse cell population scattered through an extensive extracellular matrix.

- Functions to bind and support other tissues.
- Matrix is a web of fibers embedded in a homogenous ground substance.
- Consists of a loose weave of three types of proteinaceous fibers:
    - *Collagenous fibers* are bundles of fibers containing three collagen molecules each. They have great tensile strength and resist stretching (see Campbell, Figure 40.2).
    - *Elastic fibers* are long threads of the protein elastin. Elastic properties lend tissue a resilience to quickly return to the original shape.
    - *Reticular fibers* are branched and form a tightly woven fabric joining connective tissue to adjacent tissues.

Major types of connective tissue include (see Campbell, Figure 40.3):

- Loose connective tissue
- Adipose tissue
- Fibrous connective tissue
- Cartilage
- Bone
- Blood

Loose connective tissue holds organs in place and attaches epithelia to underlying tissues.

- Consists of two types of cells
    1. *Fibroblasts secrete the proteins of the extracellular fibers.*

2. *Macrophages are phagocytic amoeboid cells that function in immune defense of the body.*

- Has all three fiber types

Adipose tissue is loose connective tissue specialized to store fat in adipose cells distributed throughout its matrix.

- Insulates the body and stores fuel molecules.
- Each adipose cell has one large fat droplet which can vary in size as fats are stored or utilized.

Fibrous connective tissue is dense due to the arrangement of a large number of collagenous fibers in parallel bundles, which impart great tensile strength.

- Found in *tendons* (attach muscles to bones) and *ligaments* (attach bones together at joints).

Cartilage is composed of collagenous fibers embedded in chondroitin sulfate, a protein-carbohydrate ground substance.

- *Chondrocytes* secrete both collagen and chondroitin sulfate, which make cartilage both strong and flexible:

  Chondrocytes are confined to lacunae, scattered spaces within the ground substance.

- Cartilage comprises the skeleton of all vertebrate embryos.

  Some vertebrates (e.g., sharks) retain the cartilaginous skeleton in adults.

  Most vertebrates eventually replace most of the cartilage with bone. Cartilage is retained in areas such as the nose, ears, trachea, intervertebral discs and ends of some bones.

Bone is a mineralized connective tissue.

- *Osteoblasts*, bone-forming cells, deposit a matrix of collagen and calcium phosphate, which hardens into the mineral hydroxyapatite. The combination of collagen and hydroxyapatite makes the bone harder than cartilage, but not brittle.
- Bone consists of repeating *Haversian systems* (concentric layers or lamellae deposited around a central canal containing blood vessels and nerves).
- Once osteoblasts are trapped in their secretions, they are called osteocytes. Osteocytes are located in spaces called *lacunae* surrounded by a hard matrix and are connected to each other by cell extensions called canaliculi.
- In long bones, only the outer area is hard and compact; the inner area is filled with spongy bone tissue called marrow.

Blood is a connective tissue composed of:

- Liquid extracellular matrix of plasma that contains water, salts, and proteins.
- Cellular component that contains:

  Leukocytes, white blood cells that function in immune defense

  Erythrocytes, red blood cells that transport oxygen

  Platelets, cell fragments that function in blood clotting

- Blood cells are made in red marrow near the ends of long bones.

3. Nervous tissue

Nervous tissue senses stimuli and transmits signals from one part of the animal to another.

Neuron = Nerve cell specialized to conduct an impulse or bioelectric signal (see Figure 40.4); consists of:

- Cell body
- Dendrites, extensions that conduct impulses to the cell body
- Axons, extensions that transmit impulses away from the cell body (see Campbell, Chapter 48)

4. Muscle tissue

Muscle tissue consists of long, excitable cells capable of contraction.

In the muscle cell cytoplasm are parallel bundles of microfilaments made of the contractile proteins, actin and myosin.

Muscle is the most abundant tissue in most animals.

There are three types of vertebrate muscle tissue (see Campbell, Figure 40.5):

1. *Skeletal muscle* is responsible for voluntary movements.

   Attached to bones by tendons

   Microfilaments are aligned to form a banded or striated appearance (hence, skeletal muscle is also called *striated muscle*).

2. *Cardiac muscle* forms the contractile wall of the heart.

   Cells are striated and branched.

   Ends of cells are joined by *intercalated disks*, which relay the contractile impulse from cell to cell.

3. *Smooth muscle* is so named because it is unstriated.

   - Found in the walls of internal organs (e.g., digestive tract, bladder) and arteries
   - Spindle-shaped cells contract slowly, but can retain contracted condition longer than skeletal muscle
   - Responsible for involuntary movements (e.g., churning of the stomach)

B. The organ systems of an animal are interdependent

Tissues are organized into *organs* in all but the simplest animals.

In some organs, the tissues may be layered; for example, the vertebrate stomach (see Campbell, Figure 40.6)

Many organs are suspended by sheets of connective tissue called *mesenteries*.

- In mammals, for example, the heart and lungs are suspended in the *thoracic cavity*; the thoracic cavity is separated from the *abdominal cavity* by the diaphragm.

Organs may be organized into organ systems.

- *Organ systems* = Several organs with separate functions that act in a coordinated manner (e.g., digestive, circulatory, and respiratory systems) (see Campbell, Table 40.1)
- Systems are interdependent: an organism is a living whole greater than the sum of its parts.

II. Introduction to the Bioenergetics of Animals

A. Animals are heterotrophs that harvest chemical energy from the food they ingest

Animals, as living organisms, exchange energy with the environment. Since they are heterotrophic, animals acquire energy from organic molecules synthesized by other organisms (see also Campbell, Figure 40.7).

Energy input – Ingestion of food

↓

Digestion – Enzymatic hydrolysis of food

↓

Absorption – Absorption of small energy-containing molecules by body cells

↓

Catabolism – Cellular respiration and fermentation harvests chemical energy from food molecules.

↙ ↘

Some **energy stored** in ATP

Some **energy lost** as heat to surroundings

↓ (from energy stored in ATP)

Energy used – Chemical energy of ATP powers cellular work. After the needs of staying alive are met, leftover chemical energy and carbon skeletons from food molecules can be used in biosynthesis.

↓

Energy lost – Cellular work generates heat, which is lost to the surroundings.

B. Metabolic rate provides clues to an animal's bioenergetic "strategy"

Bioenergetics, the study of the dynamic balance between energy intake and loss in an organism, gives clues to how an animal adapts to its environment. By measuring the rate of energy use, physiologists can determine:

- How much food energy an animal needs just to stay alive
- The energy costs for specific activities such as walking or running

Metabolic rate = Total amount of energy an animal uses per unit of time; usually measured in *calories* or *kilocalories* (kcal or CAL = 1000 calories).

- Can be determined by measuring:
  - The amount of oxygen used for an animal's cellular respiration
  - An animal's heat loss per unit of time

    Heat loss, a byproduct of cellular work, is measured with a calorimeter (a closed, insulated chamber with a device that records heat production).

    Calorimeters are effectively used with small animals that have high metabolic rates, but are less precise with small animals that have low metabolic rates and with large animals.

Every animal has a range of metabolic rates.

- Minimal rates support basic life functions, such as breathing.

- Maximal rates occur during peak activity, such as all-out running.
- Between these extremes, metabolic rates can be influenced by many factors, including:
    - Age, sex, and size
    - Body temperature
    - Environmental temperature
    - Food quality and quantity
    - Activity level
    - Amount of available oxygen
    - Hormonal balance
    - Time of day

Endotherms = Animals that generate their own body heat metabolically

- Examples include birds and mammals
- Require more kilocalories to sustain minimal life functions that ectotherms
- Many are also homeothermic, that is, their body temperature must be maintained within narrow limits

Basal metabolic rate (BMR) = An endothermic animal's metabolic rate measured under resting, fasting and stress-free conditions

- Average human BMR is 1600-1800 kcal/day for adult males; 1300-1500 kcal/day for adult females.

Ectotherms = Animals that acquire most of their body heat from the environment

- Include most fish, amphibians, reptiles, and invertebrates
- Are energetically different from endotherms; body temperature and metabolic rate changes with environmental temperature
- Because it is influenced by temperature, an ectotherm's minimal metabolic rate (SMR) must be determined at a specific temperature.
    - *Standard metabolic rate (SMR)* = An ectotherm's metabolic rate measured under controlled temperature and under resting, fasting, and stress-free conditions

C. Metabolic rate per gram is inversely related to body size among similar animals

There is an inverse relationship between metabolic rate and size.

- Smaller animals consume more calories per gram than larger animals
- Correlated with a higher metabolic rate and need for faster O_2 delivery to the tissues, small animals also have higher:
    - Breathing rates
    - Blood volume
    - Heart rates
- This inverse relationship between metabolic rate and body size holds true for both endotherms and ectotherms, and is not simply a function of surface area to volume ratio.

III. Body Plans and the External Environment

An animal's body plan results from a developmental pattern programmed by its genome—a product of millions of years of evolution due to natural selection.

A. Physical support on land depends on adaptations of body proportions and posture

Body proportions and size-weight relationships change in animal bodies as they become larger.

- Body design must accommodate the greater demand for support that comes with increasing size. (The strain on body supports depends on an animal's weight, which increases as the cube of its height or other linear dimension.)
- In mammals and birds, the most important design feature in supporting body weight is posture—leg position relative to the main body—rather than leg bone size (see Campbell, Figure 40.8).

> Examples:
> - The legs of an elephant are in a more upright position than those of small mammals.
> - Large mammals run with legs nearly extended, which reduces strain; small mammals run with legs bent and crouch when standing.

Bioenergetics also plays an important role in load-bearing, since crouched posture is partly a function of muscle contraction, powered by chemical energy.

B. Body size and shape affect interactions with the environment

Animal cells must have enough surface area in contact with an aqueous medium to allow adequate environmental exchange of dissolved oxygen, nutrients, and wastes. This requirement imposes constraints on animal size and shape.

- Single-celled organisms, such as protozoans, must have sufficient surface area of plasma membrane to service the entire volume of cytoplasm and are thus limited in size (see Campbell, Figure 40.9a). Recall that:

  The upper limits of cells size are imposed by the surface area to volume ratio.

  As cell size increases, volume increases proportionately more than surface area.
- Some multicellular animals have a body plan that places all cells in direct contact with their aqueous environments. Two such body plans include:
  1. *Two-layered sac.* A body wall only two cell layers thick (see Campbell, Figure 40.9b); for example, the body cavity of *Hydra* opens to the exterior, so both outer and inner layers of cells are bathed in water.
  2. *Flat-shaped body with maximum surface area exposed to the aqueous environment.* For example, tapeworms are thin and flat, so most cells are bathed in the intestinal fluid of the worm's vertebrate host.
- Most complex animals have a smaller surface area to volume ratio and thus lack adequate exchange area on the outer surface.

  Instead, highly folded, moist, internal surfaces exchange materials with the environment (see Campbell, Figure 40.10).

  The circulatory system shuttles materials between these specialized exchange surfaces.

Though logistical problems exist with environmental exchange, there are some distinct advantages to a complex body form.

- Environmental exchange surfaces are internal and protected from desiccation, so the animal can live on land.
- Cells are bathed with internal body fluid, so the animal can control the quality of the cells' immediate environment.

IV. Regulating the Internal Environment

A. Mechanisms of homeostasis moderate changes in the internal environment

Interstitial fluid = The internal environment of vertebrates, composed of fluid between the cells

- Fills spaces between cells
- Exchanges nutrients and wastes with blood carried in capillaries

Homeostasis = Dynamic state of equilibrium in which internal conditions remain relatively stable; steady state (see Campbell, Figure 40.11)

- French physiologist Claude Bernard first described the "constant internal milieu" in animals; he recognized many animals can maintain constant conditions in their internal environment—even when the external environment changes.

B. Homeostasis depends on feedback circuits

Homeostatic control systems have three functional components:

1. *Receptor* detects internal change.
2. *Control center* processes information from the receptor and directs the effector to respond.
3. *Effector* provides the response.

As a control system operates, the effector's response feeds back and influences the magnitude of the stimulus by either depressing it (negative feedback) or enhancing it (*positive feedback*).

Negative feedback = Homeostatic mechanism that stops or reduces the intensity of the original stimulus and consequently causes a change in a variable that is opposite in direction to the initial change

- Most common homeostatic mechanism in animals
- There is a lag time between sensation and response, so the variable drifts slightly above and below the *set point.*
- A nonbiological example is the thermostatic control of room temperature (see Campbell, Figure 40.12.)
- Human examples include hormonal control of blood glucose levels and the regulation of body temperature by the hypothalamus.
  - If the human hypothalamus detects a high blood temperature, it sends nerve impulses to sweat glands, which increase sweat output and cause evaporative cooling.
  - When the body temperature returns to normal, no additional signals are sent.

Set point = A variable's range of values that must be maintained to preserve homeostasis

Positive feedback = Homeostatic mechanism that enhances the initial change in a variable

- Rarer than negative feedback and usually controls only episodic events
- Examples include blood clotting and the heightening of labor contractions during childbirth.

  During childbirth, the baby's head against the uterine opening stimulates contractions which cause greater pressure of the head against the uterine opening.

  The greater pressure, in turn, further enhances uterine contractions.

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CHAPTER 41
ANIMAL NUTRITION

OUTLINE

I. Nutritional Requirements
   A. Animals are heterotrophs that require food for fuel, carbon skeletons, and essential nutrients: *an overview*
   B. Homeostatic mechanisms manage an animal's fuel
   C. An animal's diet must supply essential nutrients and carbon skeletons for biosynthesis

II. Food Types and Feeding Mechanisms
   A. Most animals are opportunistic feeders
   B. Diverse feeding adaptations have evolved among animals

III. Overview of Food Processing
   A. The four main stages of food processing are ingestion, digestion, absorption, and elimination
   B. Digestion occurs in specialized compartments

IV. The Mammalian Digestive System
   A. The oral cavity, pharynx, and esophagus initiate food processing
   B. The stomach stores food and performs preliminary digestion
   C. The small intestine is the major organ of digestion and absorption
   D. Hormones help regulate digestion
   E. Reclaiming water is a major function of the large intestine

V. Evolutionary Adaptations of Vertebrate Digestive Systems
   A. Structural adaptations of the digestive system are often associated with diet
   B. Symbiotic microorganisms help nourish many vertebrates

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. Distinguish among herbivores, carnivores, and omnivores.
2. Describe the following feeding mechanisms and give examples of animals that use each:
   a. Filter-feedingb.   b. Substrate-feeding
   c. Deposit-feeding   d. Fluid-feeding
3. Define digestion and describe why it is a necessary process.
4. Explain how anhydro bonds are formed and describe the role of hydrolysis in digestion.
5. Distinguish between intracellular and extracellular digestion.
6. Explain why intracellular digestion must be sequestered in a food vacuole, and give examples of organisms which digest their food in vacuoles.

7. Define gastrovascular cavity and explain why extracellular digestive cavities are advantageous.
8. Using *Hydra* as an example, describe how a gastrovascular cavity functions in both digestion and distribution of nutrients.
9. List major animal phyla which use gastrovascular cavities for digestion.
10. Describe some distinct advantages that complete digestive tracts have over gastrovascular cavities, and list the major animal phyla with alimentary tracts.
11. Define peristalsis and describe its role in the digestive tract.
12. Describe how salivation is controlled and list the functions of saliva.
13. Describe the role of salivary amylase in digestion.
14. Describe the sequence of events which occur as a result of the swallowing reflex.
15. Describe the function of the esophagus, and explain how peristalsis in the esophagus is controlled.
16. Describe the role of the cardiac and pyloric sphincters.
17. List the three types of secretory cells found in stomach epithelium and what substances they secrete.
18. Recall the normal pH of the stomach, and explain the function of stomach acid.
19. Describe the function of pepsin.
20. Explain why the stomach normally does not digest itself.
21. Explain how pepsin and acid secretion are regulated and describe the roles of the hormones gastrin and enterogastrone.
22. Describe the cause of ulcers, and explain why they are frequently found in the duodenum.
23. Explain how chyme is moved through the small intestine.
24. Describe the sequence of events which occur in response to acid chyme entering the duodenum and include the roles of:
    a. Secretin
    b. Bicarbonate
    c. Cholecystokinin (CCK)
    d. Gall bladder
    e. Bile
    f. Pancreatic enzymes
    g. Enterogastrone
25. Describe how pancreatic zymogens for proteolytic enzymes are activated in the duodenum and include the role of the intestinal enzyme enterokinase.
26. Describe enzymatic digestion of carbohydrates, proteins, lipids and nucleic acids, including the reactants and products for each enzymatic reaction and whether they occur in the:
    a. Oral cavity
    b. Stomach
    c. Lumen of small intestine
    d. Brush border of small intestine
27. Explain the function of bile, describe where it is produced and stored, and describe its composition.
28. State whether the lumen of the digestive tract is technically inside or outside the body.
29. Explain where most nutrient absorption occurs.
30. Explain why the many folds, villi, and microvilli are important in the small intestine.
31. Describe how specific nutrients are absorbed across the intestinal epithelium and across the capillary or lacteal wall, and indicate whether the transport is with or against the concentration gradient.
32. Explain what happens to glycerol and fatty acids after they are absorbed into the intestinal epithelium, and describe the fate of chylomicrons and lipoproteins.
33. Explain the function of the hepatic portal vein.

34. Explain where in the digestive tract that most reabsorption of water occurs.
35. Describe the composition of feces, and explain what the main source of vitamin K isfor humans.
36. Give examples of vertebrates with the following digestive adaptations and explain how these adaptations are related to diet:
    a. Variation in dentition
    b. Variation in length of the digestive tract
    c. Fermentation chambers
37. Explain why animals need a nutritionally adequate diet
38. Describe the effects of undernourishment or starvation.
39. List some of the risks of obesity.
40. Distinguish between malnourished and undernourished.
41. List four classes of essential nutrients, and describe what happens if they are deficient in the diet.
42. List and distinguish between water-soluble and fat-soluble vitamins, and explain how they are used by the body.
43. Describe the dietary sources, major body functions and effects of deficiency for the following required minerals in the human diet: calcium, phosphorus, sulfur, potassium, chlorine, sodium, magnesium, and iron.

KEY TERMS

undernourished	bulk-feeders	gastric juice	villi
essential nutrients	intracellular digestion	pepsin	microvilli
malnourished	extracellular digestion	pepsinogen	brush border
essential amino acids	gastrovascular cavity	acid chyme	lacteal
essential fatty acids	complete digestive tract	pyloric sphincter	chylomicrons
vitamins	alimentary canal	small intestine	hepatic portal vessel
minerals	peristalsis	duodenum	gastrin
herbivores	sphincters	bile	secretin
carnivores	salivary gland	trypsin	cholecystokinin (CCK)
omnivores	pancreas	chymotrypsin	enterogastrone
ingestion	liver	carboxypeptidase	large intestine
digestion	gallbladder	aminopeptidase	colon
enzymatic hydrolysis	oral cavity	dipeptidase	cecum
absorption	salivary amylase	enteropeptidase	appendix
elimination	bolus	nucleases	feces
suspension-feeders	pharynx	emulsification	rectum
substrate-feeders	epiglottis	lipase	ruminant
deposit-feeders	esophagus	jejunum	anus
fluid-feeders	stomach	ileum	

LECTURE NOTES

I. Nutritional Requirements

A. Animals are heterotrophs that require food for fuel, carbon skeletons, and essential nutrients: *an overview*

Like all heterotrophs, animals must rely on organic compounds in their food to supply energy and the raw materials for growth and repair.

A nutritionally adequate diet provides an animal with:

- Fuel (chemical energy) for cellular respiration
- Raw organic materials for biosynthesis
- Essential nutrients which must be obtained in prefabricated form

B. Homeostatic mechanisms manage an animal's fuel

Chemical energy is obtained from the oxidation of complex organic molecules.

- Monomers from any of the complex organic molecules can be used to produce energy, although those from carbohydrates and fats are used first.
- Oxidation of a gram of fat liberates 9.5 kcal, twice that of a gram of carbohydrate or protein.

The basal energy requirements of an animal must be met to sustain their metabolic functions.

- When an animal takes in more calories than it consumes, the liver and muscles store the excess in the form of glycogen; further excess is stored in adipose tissue in the form of fat.
- When the diet is deficient in calories, glycogen stored in the liver and muscles is utilized first and fat is then withdrawn from adipose tissues.
    - An *undernourished* person or animal is one whose diet is deficient in calories.
        - If starvation persists, the body begins to breakdown its own proteins as a source of energy.
        - The breakdown of the body's own proteins can cause muscles to atrophy and can result in the consumption of the brain's proteins.
    - Obesity (overnourishment) is a greater problem in the United States and other developed countries than undernourishment.
        - It increases the risk of heart attack, diabetes, and other disorders.

C. An animal's diet must supply essential nutrients and carbon skeletons for biosynthesis

Heterotrophs cannot use inorganic materials to make organic molecules; they must obtain organic precursors for these molecules from the food they ingest.

Given a source of carbon and nitrogen, heterotrophs can fabricate a great variety of organic molecules by using enzymes to rearrange the molecular skeletons of precursors acquired from food.

- A single type of amino acid can supply the nitrogen necessary to build other amino acids.
- Fats can be synthesized from carbohydrates.
- The liver is responsible for most of the conversion of nutrients from one type of organic molecule to another.

An animal’s diet also must include essential nutrients, in addition to providing fuel and carbon skeletons.

Essential nutrients = Chemicals an animal requires but cannot synthesize

- Vary from species to species
- An animal is malnourished if its diet is missing one or more essential nutrients (see Campbell, Figure 41.2).
- Includes essential amino acids, essential fatty acids, vitamins, and minerals

Essential amino acids are those that must be obtained in the diet in a prefabricated form.

- Most animals can synthesize about half of the 20 kinds of amino acids needed to make proteins.
- Human adults can produce 12, leaving eight as essential in the diet. (Human infants can only produce 11.)
- Protein deficiency results when the diet lacks one or more essential amino acids.

  The syndrome known as kwashiorkor is a form of protein deficiency in some parts of Africa.
- The human body cannot store essential amino acids, thus a deficiency retards protein synthesis.

  This is most frequent in individuals, who for economic or other reasons, have unbalanced diets.

Essential fatty acids are those unsaturated fatty acids that cannot be produced by the body.

- An example in humans is linoleic acid, which is required to produce some of the phospholipids necessary for membranes.
- Fatty acid deficiencies are rare, as most diets include sufficient quantities.

Vitamins are organic molecules required in the diet in much smaller quantities (0.01 to 100 mg/day) than essential amino acids or fatty acids.

- Many serve a catalytic function as coenzymes or parts of coenzymes.
- Vitamin deficiencies can cause very severe effects as shown in Table 41.1.
- Water-soluble vitamins are not stockpiled in the body tissues; amounts ingested in excess of body needs are excreted in the urine.
- Fat-soluble vitamins (vitamins A, D, E, and K) can be held in the body; excess amounts are stored in body fat and may accumulate over time to toxic levels.
- If the body of an animal can synthesize a certain compound, it is not a vitamin.

  A compound such as ascorbic acid is a vitamin for humans (vitamin C) and must be included in our diets; it is not a vitamin in rabbits where the normal intestinal bacteria produce all that is needed.

Minerals are inorganic nutrients required in the diet in small quantities ranging from 1 mg to 2500 mg per day, depending on the mineral.

- Some minerals serve structural and maintenance roles in the body (calcium, phosphorous) while others serve as parts of enzymes (copper) or other molecules (iron).
- Refer to Table 41.2 for the mineral requirements of humans.

II. Food Types and Feeding Mechanisms

A. Most animals are opportunistic feeders

Animals usually ingest other organisms.

- The food organism may be either dead or alive.
- The food organism may be ingested whole or in pieces.

- Some parasitic animals (e.g., tapeworms) are exceptions.

Animals are categorized based on the kinds of food they usually eat and their adaptations for obtaining and processing food items.

- Herbivores eat autotrophic organisms (plants, algae, and autotrophic bacteria).
- Carnivores eat other animals.
- Omnivores eat other animals and autotrophs.

Animals are opportunistic and may eat foods outside their principal dietary category.

- For example, most carnivores obtain some nutrients from plants that remain in the digestive tract of their prey.
- All animals consume bacteria along with their other food items.

B. Diverse feeding adaptations have evolved among animals

The varied diets exhibited by animals are accompanied by a variety of mechanisms used to obtain food.

- *Suspension-feeders* sift small food particles from the water.

  Many are aquatic animals such as clams and oysters (trap food on gills) and baleen whales (strain food from water forced through the screen-like plates on their jaws) (see Campbell, Figure 41.4).
- *Substrate-feeders* live on or in their food source and eat their way through the food.

  Leaf miners (larvae of various insects) tunnel through the interior of leaves (see Campbell, Figure 41.5).
- *Deposit-feeders* are a type of substrate-feeder that ingests partially decayed organic materials along with their substrate.

  Earthworms ingest soil and their digestive systems extract the organic materials.
- *Fluid-feeders* suck nutrient-rich fluids from a living host (see Campbell, Figure 41.6).

  Aphids ingest the phloem sap from plants; leeches and mosquitoes suck blood from animals; hummingbirds and bees ingest nectar from flowers.
- *Bulk-feeders* eat relatively large pieces of food (see Campbell, Figure 41.7).

  Most animals; they possess various adaptations to kill prey or tear off pieces of meat or vegetation.

III. Overview of Food Processing

A. The four main stages of food processing are ingestion, digestion, absorption, and elimination

Ingestion, the act of eating, is the first stage.

Digestion, the process of breaking down food into small molecules the body can absorb, is the second stage.

- Organic food material is composed of macromolecules (proteins, fats, carbohydrates) that are too large to cross the membranes and enter an animal's cells.
- Digestion enzymatically cleaves these macromolecules into component monomers that can be used by the animal (polysaccharides and disaccharides to simple sugars; proteins to amino acids; fats to glycerol and fatty acids).
- Digestion uses *enzymatic hydrolysis* to break bonds in macromolecules.

  Hydrolytic enzymes catalyze the digestion of each class of macromolecule by adding water.

The chemical digestion is usually preceded by mechanical fragmentation (e.g., chewing) that increases the surface area exposed to digestive juices.

Occurs in a specialized compartment where the enzymes are contained so they don't damage the animal's own cells.

Absorption is the third stage, and it involves the uptake of the small molecules resulting from digestion.

Elimination is the fourth and final stage in which undigested material passes out of the digestive compartment.

B. Digestion occurs in specialized compartments

1. Intracellular digestion

Food vacuoles are the simplest digestive compartments.

- They are organelles in which a single cell digests its food without hydrolytic enzymes mixing with the cell’s cytoplasm.
- Protozoa have food vacuoles that form around food by endocytosis.
- Hydrolytic enzymes are secreted into the food vacuole and digestion occurs; this is referred to as *intracellular digestion* (see Campbell, Figure 41.8)
- Sponges differ from other animals in that all digestion is by the intracellular mechanism.

2. Extracellular digestion

Extracellular digestion occurs within compartments that are continuous, via passages, with the outside of the body.

- At least some hydrolysis occurs in most animals by this mechanism.

Gastrovascular cavity = Digestive sac with a single opening; functions in both digestion and nutrient distribution

- Most animals that have simple body plans possess a gastrovascular cavity.

Digestion in *Hydra* involves both extracellular and intracellular digestion (see Campbell, Figure 41.9).

- *Hydra* is a carnivore that captures prey.
- Food items are immobilized by stings from nematocysts on the tentacles.
- Tentacles then force prey through the mouth into the gastrovascular cavity.
- Specialized gastrodermal cells secrete digestive enzymes that fragment the soft tissues of the prey into tiny pieces.
- Some gastrodermal cells also possess flagella, whose movement prevents settling of food particles and distributes them through the cavity.
- The small pieces are phagocytized by nutritive gastrodermal cells and surrounded by food vacuoles.
- Hydrolysis is completed by intracellular digestion.
- Undigested materials are expelled from the gastrovascular cavity through the single opening.

The combination of extracellular and intracellular digestion that occurs in most animals permits these organisms to feed on larger prey items.

- Phagocytosis is limited to microscopic food.
- Extracellular digestion begins the digestive process by breaking down large food items into smaller particles.

Animals with body plans more complex than cnidarians and platyhelminths have *complete digestive tracts* or *alimentary canals.*

- *Alimentary canal* = Digestive tube running between two openings: the mouth (where food is initially ingested) and the *anus* (where undigested wastes are eliminated) (see Campbell, Figure 41.10)
- Since food moves in one direction along the tube, the tube can be organized into specialized regions that carry out digestion and absorption of nutrients in a stepwise fashion.
- The unidirectional passage of food and the specialization of function for different regions makes the alimentary canal more efficient.

IV. The Mammalian Digestive System

The digestive system in mammals includes the alimentary canal and accessory glands that secrete digestive juices into the canal through ducts.

- *Peristalsis* (rhythmic smooth muscle contractions) pushes food along the tract.
- *Sphincters* (modifications of the muscle layer into ringlike valves) occur at some junctions between compartments and regulate passage of materials through the system.
- The accessory glands are: three pairs of *salivary glands,* the *pancreas,* the *liver,* and the *gallbladder.*

Refer to Campbell, Figure 41.11, for an orientation to the specialized compartments in the human system.

A. The oral cavity, pharynx, and esophagus initiate food processing

1. The oral cavity

Physical and chemical digestion begin in the oral cavity.

- Chewing breaks down large pieces of food into smaller pieces.
- This makes food easier to swallow and increases the surface area available for enzyme action.

The presence of food in the oral cavity stimulates the salivary glands to secrete saliva into the oral cavity.

- Saliva contains mucin (protects the mouth from abrasion and lubricates food); buffers that neutralize acids; antibacterial agents; and salivary amylase, an enzyme that hydrolyzes starch and glycogen to the disaccharide maltose or small polysaccharides.

The tongue tastes and manipulates food during chewing and forms it into a *bolus*, which it pushes to the back of the oral cavity and into the pharynx.

2. The pharynx

The pharynx is an intersection for both the digestive and respiratory systems.

- The movement of swallowing moves the *epiglottis* to block the entrance of the windpipe (the glottis).
- This directs food through the pharynx and into the esophagus (see Campbell, Figure 41.12 a and b)

3. The esophagus

The esophagus is a muscular tube that conducts food from the pharynx to the stomach.

- Peristalsis moves the bolus along the esophagus to the stomach (see Campbell, Figure 41.12 c).
- The initial entrance of the bolus into the esophagus is voluntary (swallowing); once in, the peristalsis results from involuntary contraction of the smooth muscles.
- Salivary amylase remains active as the bolus moves through the esophagus.

B. The stomach stores food and performs preliminary digestion

The stomach is a large, saclike structure located just below the diaphragm on the left side of the abdominal cavity. It functions in:

Food storage

The stomach has an elastic wall with rugae, folds that can expand to accommodate up to 2 L of food.

Storage capacity permits periodic feeding (meals).

Churning

The stomach's longitudinal, vertical, and diagonal muscles contract in churning movements that mix the food.

Stomach contents are mixed about every 20 minutes.

Churning and enzyme action convert food to a nutrient broth called *acid chyme*.

◊ The passage of acid chyme into the small intestine is regulated by the *pyloric sphincter* at the bottom of the stomach.

◊ The pyloric sphincter relaxes at intervals and permits small quantities of chyme to pass.

Secretion

- Gastric secretion is controlled by nerve impulses and the hormone *gastrin*. The stomach epithelium contains three types of secretory cells.
  1. Mucous cells, which secrete:
     - Mucin, a thin mucus that protects the stomach lining from being digested
     - *Gastrin*, a hormone produced by the stomach; gastrin is released into the bloodstream and its action is to stimulate further secretion of gastric juice (HCl and pepsin).
  2. Chief cells, which secrete:
     - *Pepsinogen*, an inactive protease or zymogen that is the precursor to pepsin
     - *Zymogen*, an inactive form of a protein-digesting enzyme
  3. Parietal cells, which secrete HCl
- Protein digestion. Both components of *gastric juice*, HCl and pepsin, are involved with protein digestion:

  HCl provides acidity (pH 1 - 4) which:

  ◊ Kills bacteria

  ◊ Denatures protein

  ◊ Starts the conversion of pepsinogen to pepsin; newly formed pepsin can also catalyze this reaction:

  Pepsin splits peptide bonds next to some amino acids.

  ◊ Does not hydrolyze protein completely

  ◊ Is an endopeptidase that splits peptide bonds located within the polypeptide chain

C. The small intestine is the major organ of digestion and absorption

The human *small intestine* is about 6 m in length and is the site of most enzymatic hydrolysis of food and absorption of nutrients.

- Remember, only limited digestion of carbohydrates occurs in the oral cavity and esophagus (by salivary amylase) and of proteins in the stomach (by pepsin).

The pancreas, liver, gall bladder, and small intestine all contribute to the digestion that occurs in the small intestine. Their products are released into the *duodenum*, the first 25 cm of the small intestine.

- The (exocrine) *pancreas* produces:

  Hydrolytic enzymes that break down all major classes of macromolecules—carbohydrates, lipids, proteins, and nucleic acids.

  Bicarbonate buffer that helps neutralize the acid chyme coming from the stomach.

> NOTE: The typical vertebrate pancreas is a compound gland, having both an exocrine, ducted component as noted above and an endocrine, ductless component that produces and secretes hormones, such as insulin and glucagon.

- The *liver* performs many functions including the production of bile, which:

  Is stored in the *gallbladder*

  Does not contain digestive enzymes

  Contains bile salts which emulsify fat

  Contains pigments that are byproducts of destroyed red blood cells

1. Enzymatic action in the small intestine

a. Carbohydrate digestion

Begins with the action of salivary amylase in the mouth.

Begins again in the duodenum where pancreatic amylases hydrolyze starch and glycogen into disaccharides.

Disaccharidases attached to the surface of the duodenal epithelium hydrolyze disaccharides into monosaccharides.

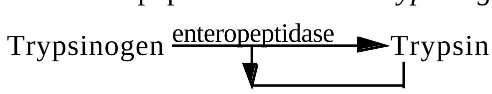
Each disaccharide has its own disaccharidase. For example, maltose is hydrolyzed by maltase, sucrose by sucrase, lactose by lactase, etc.

Since the disaccharidases are on the surface of the epithelium, the final breakdown of carbohydrates occurs where the sugars will be absorbed.

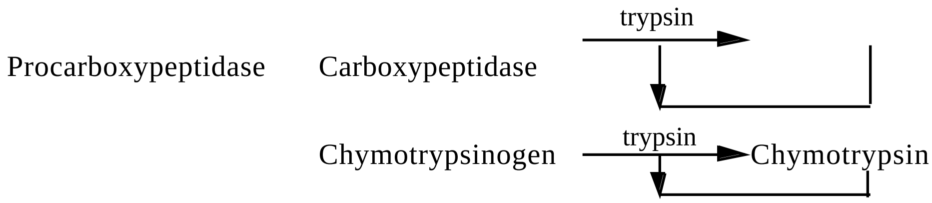
b. Protein digestion

Protein digestion involves the efforts of teams of enzymes (see Campbell, Figure 41.13b):

- Pepsin, an endopeptidase, begins protein digestion in the stomach.
- The pancreas secretes proteases in the form of zymogens that will be activated only in the lumen of the duodenum by the intestinal enzyme, *enteropeptidase.*
  - Enteropeptidase converts *trypsinogen* to *trypsin.*



  - Trypsin the catalyzes the conversion of more trypsinogen to trypsin.
  - Trypsin catalyzes conversion of the other zymogens.



- Trypsin and chymotrypsin (endopeptidases) digest large polypeptides into shorter chains by breaking internal peptide bonds adjacent to certain amino acids.
- *Carboxypeptidase* (exopeptidase) splits amino acids, one at a time, off the end of a polypeptide that has a free carboxyl group.
- The lining of the small intestine also secretes protein-digesting enzymes, *aminopeptidase* and *dipeptidases*.

  Aminopeptidase begins at the end of a polypeptide that has a free amino group and splits off one amino acid at a time.

  Dipeptidases attached to the intestinal lining split small polypeptides.
- Since the protein-digesting enzymes from the pancreas and small intestine break bonds in specific areas of the polypeptide, protein digestion to amino acids is a combined effort from all of these enzymes.

c. Nucleic acid digestion

Nucleic acid digestion also involves teams of enzymes.

- *Nucleases* hydrolyze DNA and RNA into nucleotides (see Campbell, Figure 41.13c).
- Other hydrolytic enzymes (nucleotidases and nucleosidases) break nucleotides into nucleosides and nitrogenous bases, sugars and phosphates.

d. Fat digestion

Fat digestion occurs only in the small intestine, so most fat in food is undigested when it reaches the duodenum. If fat is present in chyme,

- *Emulsification* produces many small fat droplets that collectively have a large surface area exposed for digestion.
- Pancreatic *lipase*, secreted into the duodenum, hydrolyzes fats into the building blocks, glycerol and fatty acids(see Campbell, Figure 41.13d).

Macromolecules are completely hydrolyzed as peristalsis moves the digestive juice-chyme mixture through the duodenum. See Campbell, Figures 41.11 and 41.12 for a summary of digestion.

The remaining areas of the small intestine, the *jejunum* and *ileum*, are specialized for absorption of nutrients.

2. Absorption of nutrients

Nutrients resulting from digestion must cross the digestive tract lining to enter the body. While a small number of nutrients are absorbed by the stomach and large intestine, most absorption occurs in the small intestine.

- Large folds in the walls are covered with projections called villi, which in turn have many microscopic microvilli; this results in a surface area for absorption of about 300 m^2 (see Campbell, Figure 41.15).

  This *brush border* (microvillar surface) is exposed to the lumen of the intestine.

- Penetrating the hollow core of each villus are capillaries and a tiny lymph vessel called a *lacteal*.
- Nutrients are absorbed by diffusion or active transport across the two cell-thick epithelium and into the capillaries or lacteals.
  - Amino acids and sugars enter the capillaries and are transported by the blood.
  - Absorbed glycerol and fatty acids are recombined in epithelial cells to form fats; most are coated with proteins to form *chylomicrons* which enter the lacteals.
- Capillaries and veins draining nutrients away from the villi converge into the *hepatic portal vessel*, which leads directly to the liver.
  - Here various organic molecules are used, stored, or converted to different forms.
  - Blood flows at a rate of about 1 L per minute through the hepatic portal vessel.

D. Hormones help regulate digestion

Hormonal control of digestion involves many different factors; chief among them are the four following regulatory hormones (see Campbell, Table 41.3):

1. *Gastrin*. Released from the stomach in response to presence of food; stimulates the stomach to release gastric juice (HCl and pepsin); stimulates mitosis and development of new mucosa cells.
2. *Secretin*. Released from the duodenum in response to acid chyme entering from the stomach; signals the pancreas to release bicarbonate buffer to neutralize acid chyme.
3. *Cholecystokinin (CCK)*. Released from the duodenum in response to chyme entering from the stomach; signals the gall bladder to release bile and the pancreas to release pancreatic enzymes into the duodenum; also may be involved with the satiety reflex of the brain.
4. *Enterogastrone*. Released from the duodenum in response to the presence of fat in the chyme; inhibits peristalsis in the stomach, and slows digestion.

E. Reclaiming water is a major function of the large intestine

The *large intestine*, or colon, connects to the small intestine at a T-shaped junction containing a sphincter; the blind end of the T is called the *cecum* (see Campbell, Figure 41.11).

- The *appendix* is a fingerlike extension of the cecum and is composed of lymphoid tissue.
- The *colon* is about 1.5 m long and is in the shape of an inverted "U". Its major function is water reabsorption.

Feces (wastes of the digestive tract) are moved through the colon by peristalsis.

- Intestinal bacteria live on organic material in the feces, and some produce vitamin K which is absorbed by the host.
- Feces may also contain an abundance of salts.
- Feces are stored in the rectum and pass through the two sphincters (one involuntary, one voluntary) to the anus for elimination.

V. Evolutionary Adaptations of Vertebrate Digestive Systems

A. Structural adaptations of the digestive system are often associated with diet

The digestive systems of vertebrates are variations on a common plan, and many adaptations associated with diet are found.

Variation in the dentition (assortment of teeth) of mammals reflects the animal's diet (see Campbell, Figure 41.16).

- Carnivores (e.g., dogs and cats) generally have pointed canines and incisors.
  - These teeth are used to kill prey and rip away pieces of flesh.
  - Premolars and molars are jagged and used to crush and shred the food.
- Herbivores (e.g., cows) have teeth with broad, ridged surfaces that are used for grinding vegetation.
  - Incisors and canines are modified for biting off pieces of vegetation.
- Omnivores (e.g., humans) have relatively unspecialized dentition.
  - They are adapted to eat both vegetation and meat and teeth similar to those of both herbivores and carnivores are found.

Nonmammalian vertebrates typically have less specialized dentition, although there are exceptions.

- Poisonous snakes have fangs which are teeth modified to inject venom into prey.
  - Some fangs are hollow, others are grooved.
  - Snakes can also swallow very large prey items due to the loosely hinged lower jaw-skull articulation.

A correlation is also found between length of the vertebrate digestive system and diet.

- Herbivores and omnivores have longer alimentary canals than carnivores relative to size (see Campbell, Figure 41.17).
  - The cell walls in vegetation make it more difficult to digest than meat, and nutrients are less concentrated.
  - The longer tract allows for more time for digestion and provides a greater surface area for absorption.
- The functional length of an alimentary canal may be longer than superficial appearance reveals, as it is with the spiral valve structure in sharks.

B. Symbiotic microorganisms help nourish many vertebrates

Special fermentation chambers are present in the alimentary canals of many herbivores.

- Symbiotic bacteria and protozoa present in these chambers produce cellulase which can digest the cellulose. (Animals do not produce cellulase.)
- The microorganisms digest cellulose to simple sugars and convert the sugars to nutrients essential to the animal.
- The microorganisms may be housed in the cecum (e.g., horses), cecum and colon (e.g., rabbit), or the much more elaborate structure found in ruminants (see Campbell, Figure 41.18).

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CHAPTER 42
CIRCULATION AND GAS EXCHANGE

OUTLINE

I. Circulation in Animals
   A. Transport systems functionally connect the organs of exchange with the body cells: an overview
   B. Most invertebrates have a gastrovascular cavity or a circulatory system for internal transport
   C. Closed cardiovascular systems accommodate gill breathing or lung breathing in the vertebrates
   D. Rhythmic pumping of the mammalian heart drives blood through pulmonary and systemic circuits
   E. Structural differences among the blood vessels correlate with regional functions of the circulatory system
   F. Natural laws governing the movement of fluids in pipes effect blood flow and blood pressure
   G. Transfer of substances between the blood and the interstitial fluid occurs across the thin walls of capillaries
   H. The lymphatic system returns fluid to the blood and aids in body defense
   I. Blood is a connective tissue with cells suspended in plasma
   J. Cardiovascular diseases are the leading cause of death in the United States and many other developed nations

II. Gas Exchange in Animals
   A. Gas exchange supplies oxygen for cellular respiration and disposes of carbon dioxide: *an overview*
   B. Gills are respiratory adaptations of most aquatic animals
   C. Tracheal systems and lungs are respiratory adaptations of terrestrial animals
   D. Control centers in the brain regulate the rate and depth of breathing
   E. Gases diffuse down pressure gradients in the lungs and other organs
   F. Respiratory pigments transport gases and help buffer the blood
   G. Deep-diving mammals stockpile oxygen and consume it slowly

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. List the major animal phyla with gastrovascular cavities, and explain why they do not need a circulatory system.
2. Distinguish between open and closed circulatory systems.
3. Using an arthropod as an example, describe the circulation of hemolymph.

4. Explain how hemolymph differs from blood.
5. Using an earthworm as an example, describe circulation of blood, and explain how it exchanges materials with interstitial fluid.
6. List the components of a vertebrate cardiovascular system.
7. Distinguish between an artery and a vein.
8. Using diagrams, compare and contrast the circulatory schemes of birds, amphibians, and mammals.
9. Distinguish between pulmonary and systemic circuits, and explain the function of each.
10. Explain the advantage of double circulation over a single circuit.
11. Trace a drop of blood through the human heart, listing the structures it passes through en route.
12. List the four heart valves, describe their location, and explain their function.
13. Distinguish between systole and diastole.
14. Describe the events of the cardiac cycle, and explain what causes the first and second heart sounds.
15. Define heart murmur, and explain its cause.
16. Define pulse, and describe the relationship between size and pulse rate among different mammals.
17. Define cardiac output, and explain how it is affected by a change in heart rate or stroke volume.
18. Define myogenic, and describe some unique properties of cardiac muscle which allows it to contract in a coordinated manner.
19. Define pacemaker, and describe the location of two patches of nodal tissue in the human heart.
20. Describe the origin and pathway of the action potential (cardiac impulse) in the normal human heart.
21. Explain why it is important that the cardiac impulse be delayed at the AV node.
22. Explain how the pace of the SA node can be modulated by sympathetic and parasympathetic nerves, changes in temperature, physical conditioning, and exercise.
23. Compare the structures of arteries and veins, and explain how differences in their structures are related to differences in their functions.
24. Describe how capillary structure differs from other vessels, and explain how this structure relates to its function.
25. Recall the law of continuity, and explain why blood flow through capillaries is substantially slower than it is through arteries and veins.
26. Define blood pressure and describe how it is measured.
27. Explain how peripheral resistance and cardiac output affect blood pressure.
28. Explain how blood returns to the heart, even though it must travel from the lower extremities against gravity.
29. Define microcirculation and explain how blood flow through capillary beds is regulated.
30. Explain how osmotic pressure and hydrostatic pressure regulate the exchange of fluid and solutes across capillaries.
31. Describe the composition of lymph, and explain how the lymphatic system helps the normal functioning of the circulatory system.
32. Explain why protein deficiency can cause edema.
33. Explain how the lymphatic system helps defend the body against infection.
34. Explain why vertebrate blood is classified as connective tissue.

35. List the components of blood and describe a function for each.
36. Outline the formation of erythrocytes from stem cells to destruction by phagocytic cells.
37. Outline the sequence of events that occur during blood clotting, and explain what prevents spontaneous clotting in the absence of injury.
38. Explain how atherosclerosis affects the arteries.
39. Distinguish between thrombus and embolus; atherosclerosis and arteriosclerosis; low-density lipoproteins (LDLs) and high-density lipoproteins (HDLs).
40. List the factors that have been correlated with an increased risk of cardiovascular disease.
41. Describe the general requirements for a respiratory surface and list the variety of respiratory organs adapted for this purpose.
42. Describe respiratory adaptations of aquatic animals.
43. Describe countercurrent exchange, and explain why it is more efficient than concurrent flow of water and blood.
44. Describe the advantages and disadvantages of air as a respiratory medium, and explain how insect tracheal systems are adapted for efficient gas exchange in a terrestrial environment.
45. For the human respiratory system, describe the movement of air through air passageways to the alveolus, listing the structures it must pass through on the journey.
46. Define negative pressure breathing, and explain how respiratory movements in humans ventilate the lungs.
47. Define the following lung volumes, and give a normal range of capacities for the human male:
    a. Tidal volume
    b. Vital capacity
    c. Residual volume
48. Explain how breathing is controlled.
49. List three barriers oxygen must cross from the alveolus into the capillaries, and explain the advantage of having millions of alveoli in the lungs.
50. Describe how oxygen moves from the alveolus into the capillary, and explain why a pressure gradient is necessary.
51. Distinguish between hemocyanin and hemoglobin.
52. Describe the structure of hemoglobin, explain the result of cooperative binding, and state how many oxygen molecules a saturated hemoglobin molecule can carry.
53. Draw the Hb-oxygen dissociation curve, explain the significance of its shape, and explain how the affinity of hemoglobin for oxygen changes with oxygen concentration.
54. Describe the Bohr effect, and explain how the oxygen dissociation curve shifts with changes in carbon dioxide concentration and changes in pH.
55. Explain the advantage of the Bohr shift.
56. Describe how carbon dioxide is picked up at the tissues and deposited in the lungs, describe the role of carbonic anhydrase, and state the form most of the carbon dioxide is in as it is transported.
57. Explain how hemoglobin acts as a buffer.
58. Describe respiratory adaptations of diving mammals including the role of myoglobin.

KEY TERMS

open circulatory system
hemolymph
sinuses
closed circulatory system
cardiovascular system
atrium
ventricles
arteries
arterioles
capillaries
capillary bed
venules
veins
systemic circuit
double circulation
pulmonary circuit
atrioventricular valve
semilunar valves
pulse
heart rate
cardiac cycle
systole
hemocyanin
diastole
cardiac output
stroke volume
sinoatrial (SA) node
pacemaker
atrioventricular (AV) node
electrocardiogram
endothelium
blood pressure
peripheral resistance
lymphatic system
lymph
lymph nodes
plasma
red blood cells
erythrocytes
hemoglobin
white blood cells
leukocytes
platelets
pluripotent stem cells
dissociation curve
erythropoietin
fibrinogen
fibrin
hemophilia
thrombus
cardiovascular disease
heart attack
stroke
artherosclerosis
arteriosclerosis
hypertension
low-density lipoproteins (LDLs)
high-density lipoproteins (HDLs)
gas exchange
respiratory medium
respiratory surface
gills
ventilation
countercurrent exchange
myoglobin
tracheal system
lungs
vocal cords
larynx
trachea
bronchi
bronchioles
alveoli
breathing
positive pressure breathing
negative pressure breathing
diaphragm
tidal volume
vital capacity
residual volume
parabronchi
breathing control centers
partial pressure
respiratory pigments

LECTURE NOTES

The exchange of materials (whether nutrients, gases, or waste products) between an organism and its environment must take place across a moist cell membrane.

- The molecules must be dissolved in water in order to diffuse or be transported across the membrane.
- In protozoans, the entire external surface may be used for this exchange.
- The simple, multicellular animals (sponges, cnidarians) have body structures such that each cell is exposed to the surrounding waters.

Three-dimensional animals face the problem that some of their cells are isolated from the surrounding environment.

- These animals have specialized organs, where exchange with the environment occurs, coupled with special systems for the internal transport through body fluids to the cells.
- The association of specialized organs with an internal transport system not only reduces the distance over which molecules must diffuse to enter or leave a cell, but permits regulation of internal fluid composition.

I. Circulation in Animals

A. Transport systems functionally connect body cells with the organs of exchange: *an overview*

Diffusion is too slow of a process to transport chemicals through the body of an animal.

- Time of diffusion is proportional to the square of the distance the chemical must travel.
- If a glucose molecule takes 1 second to diffuse 100 μm, it will take 100 seconds to diffuse 1 mm.

The presence of a circulatory system reduces the distance a substance must diffuse to enter or leave a cell.

- The distance is reduced because the circulatory system connects the aqueous environment of the cell with organs specialized for exchange.
- Molecules will diffuse or be transported into the blood, which carries these molecules to the cells or to the exchange surface, depending on whether the molecules are used (nutrients) or produced (wastes) by the cells.

    Oxygen diffuses from air in the lungs across the thin lung epithelium into the blood.

    This oxygenated blood is carried by the circulatory system to all parts of the body.

    As the blood passes through capillaries in the tissues, oxygen diffuses from the blood into the cells across the cells' plasma membranes.

    Carbon dioxide is produced by the cells and moves in the opposite direction through the same system.

The circulatory system does more than move gases, it is a critical component to maintaining homeostasis of the body.

- The chemical and physical properties of the immediate surroundings of the cells can be controlled using the carrying capacity of the blood.

    The blood passes from the cells through organs (liver, kidneys) that regulate the nutrient and waste content of the blood.

B. Most invertebrates have a gastrovascular cavity or a circulatory system for internal transport

1. Gastrovascular cavities

The cnidarian body plan does not require a specialized internal transport system. The body wall is only two cells thick and encloses a central gastrovascular cavity.

- The water inside the gastrovascular cavity is continuous with the surrounding water.
- The gastrovascular cavity functions in digestion and distribution of nutrients.
- Gastrodermal cells lining the cavity have direct access to the nutrients produced by digestion, however, the structure of the body is such that nutrients only have a short distance to diffuse to the outer cell layer (see Campbell, Figure 42.1).

Planarians and other flatworms also have a gastrovascular cavity.

- The highly ramified structure of the cavity and the flattened body shape ensure all cells are exposed to cavity contents.

A gastrovascular cavity cannot perform the necessary internal transport required by more complex animals, especially if they are terrestrial.

- These animals have some type of circulatory system.

C. Open and closed circulatory systems

Open and closed circulatory systems are alternative solutions for moving materials efficiently through the bodies of animals.

They usually function in combination with other organ systems, which increases the efficiency of the overall body.

1. *Open circulatory system* = Circulatory system in which hemolymph bathes internal organs directly while moving through sinuses (see Campbell, Figure 42.2a)
   - *Hemolymph* is a body fluid which acts as both blood and interstitial fluid.
   - Circulation results from contractions of the dorsal vessel (heart) and body movements.
   - Relaxation of the "heart" draws blood through the ostia (pores) into the vessel.
   - Chemical exchange between the hemolymph and cells occurs in the *sinuses*, which are an interconnected system of spaces surrounding the organs.
   - Insects, other arthropods, and mollusks have an open circulatory system.
2. *Closed circulatory system* = Circulatory system in which blood is confined to vessels and a distinct interstitial fluid is present
   - The heart (or hearts) pumps blood into large vessels.
   - The major vessels branch into smaller vessels, and they supply blood to organs (see Campbell, Figure 42.2b)
   - In the organs, materials are exchanged between the blood and the interstitial fluid bathing the cells.
   - A closed circulatory system is found in annelids, squids, octopuses, and vertebrates.

D. Closed cardiovascular systems accommodate gill-breathing or lung-breathing in the vertebrates

A *cardiovascular system* consists of a heart, blood vessels, and blood.

- The heart has of one *atrium* or two *atria*, chambers that receive blood, and one or two *ventricles*, chambers that pump blood out.
- *Arteries* carry blood away from the heart to organs where they branch into smaller *arterioles* that give rise to microscopic *capillaries* (the site of chemical exchange between blood and interstitial fluid).

  Capillaries have thin, porous walls and are usually arranged into networks called *capillary beds* that infiltrate each tissue.
- Capillaries rejoin to form *venules*, which converge to form the veins that return blood to the heart.

An examination of vertebrate circulatory systems shows various adaptations have evolved within this taxon.

Fish have a two-chambered heart with one atrium and one ventricle (see Campbell, Figure 42.3a)

- Blood pumped from the ventricle goes to the gills. Here, oxygen diffuses into the gill capillaries and CO_2 diffuses out. Gill capillaries converge into arteries that carry blood to capillary beds in other organs. Blood from the organs travel through veins to the atrium of the heart, then into the ventricle.
- Blood flows through two capillary beds during each complete circuit: one in the gills and a second in the organ systems (systemic capillaries).
  - As blood flows through a capillary bed, blood pressure drops substantially.
- Blood flow to the tissues and back to the heart is aided by swimming motions.

Amphibians have a three-chambered heart with two atria and one ventricle (see Campbell, Figure 42.3b)

- Blood flows through a *pulmocutaneous circuit* (to the lungs and skin) and a *systemic circuit* (to all other organs) in a scheme called *double circulation.*
- Blood flow pattern: ventricle → lungs and skin to become oxygenated → left atrium → ventricle → all other organs → right atrium.
  - The second passage through the ventricle ensures sufficient blood pressure for the systemic circulation.
- There is some mixing of oxygen-rich and oxygen-poor blood in the single ventricle although a ridge present in the ventricle diverts most of the oxygenated blood to the systemic circuit and most of the deoxygenated blood to the pulmonary circuit.

Most reptiles (excluding crocodilians) have a three-chambered heart; although, the ventricle is partially divided.

- The anatomical arrangement provides for double circulation: a systemic circuit and a *pulmonary circuit.*
- The partially divided ventricle reduces mixing of oxygenated and deoxygenated blood (even more than in amphibians).

Birds and mammals have a four-chambered heart with two atria and two ventricles (see Campbell, Figure 42.3c). (Crocodiles have a four-chambered heart.)

- Double circulation is similar to that of amphibians except that oxygenated and deoxygenated blood do not mix due to the presence of two separate ventricles.
- The complete separation of oxygenated and deoxygenated blood increases the efficiency of oxygen delivery to the cells.

E. Rhythmic pumping of the mammalian heart drives blood through pulmonary and systemic circuits

1. The mammalian heart

To fully understand the double circulation, consider the human heart (see Campbell Figure 42.5)

- Located beneath the sternum
- Cone-shaped and about the size of a clenched fist
- Surrounded by a sac with a two-layered wall
- Comprised mostly of cardiac muscle tissue
- The two atria have thin walls and function as collection chambers for blood returning to the heart
- The ventricles have thick, powerful walls that pump blood to the organs

There are four valves in the heart which prevent backflow of blood during systole.

- The valves consist of flaps of connective tissue.
- *Atrioventricular valves* are found between each atrium and ventricle and keep blood from flowing back into the atria during ventricular contraction.
- *Semilunar valves* are located where the aorta leaves the left ventricle and where the pulmonary artery leaves the right ventricle; these prevent blood from flowing back into ventricles when they relax.
- A heart murmur is a defect in one or more of the valves that allows backflow of blood. Serious defects are usually corrected by surgical replacement of the valve.

Heart rate = The number of heartbeats per minute

- Usually measured by taking the *pulse* (the sensation you feel is the rhythmic stretching of the arteries caused by the increased pressure of blood during systole).
- In humans, the average resting heart rate of a young adult is 60-70 beats per minute; rates vary depending on the individual's activity level.
- It is not uncommon for heart rates to change during the day.
- There is an inverse relationship between animal body size and pulse; elephants have a rate of 25 beats per minute while some shrews have 600 beats per minute.

The heart chambers alternately contract and relax in a rhythmic cycle (see Campbell, Figure 42.6).

- A complete sequence of contraction and relaxation is the *cardiac cycle*.
- During *systole*, heart muscle contracts and the chambers pump blood.
- During *diastole*, the heart muscles relax and the chambers fill with blood.

Cardiac output = The volume of blood per minute that the left ventricle pumps into the systemic circuit; depends on heart rate and stroke volume

- *Stroke volume* is the amount of blood pumped by the left ventricle each time it contracts. The average human stroke volume is about 75 mL per beat.
- The cardiac output of an average human is 5.25 L/ min.

2. Maintaining the heart's rhythmic beat

Cardiac muscle cells are myogenic (self-excitable) and can contract without input from the nervous system. The tempo of contraction is controlled by the *sinoatrial (SA) node*, a specialized region of the heart, sometimes called the *pacemaker*.

- Located in the right atrium wall near the entrance of the superior vena cava (see Campbell, Figure 42.7).
- The SA node is composed of specialized muscle tissue, which has characteristics of both muscle and nerve tissue.
- Contraction of the SA node initiates a wave of excitation that spreads rapidly from the node and causes the two atria to contract in unison.
- This wave of contraction will pass down the atria until it reaches the *atrioventricular (AV) node*; a second mass of specialized muscle tissue located near the base of the wall separating the atria.
- The impulse is delayed at the AV node for 0.1 second to ensure the atria are completely empty before the ventricles contract.
- The impulse is then carried by a mass of specialized muscle fibers throughout the walls of the ventricle.
- The impulses produce electrical currents as they pass through the cardiac muscle.
    - The currents can be detected by electrodes placed on the skin and recorded as an *electrocardiogram (ECG or EKG).*

Although the SA node controls the rate of heartbeat, it is influenced by several factors:

- Two antagonistic sets of nerves influence the heart rate; one speeds up contractions in the SA node, the other slows contractions.
- Hormones influence the SA node; for example, epinephrine increases heart rate.
- Others factors, including body temperature changes and exercise, also have an influence.

- Exercise creates a greater demand for oxygen in the muscles and an increase in heart rate is an adaptation to meet this demand.

F. Structural differences among the blood vessels correlate with regional functions of the circulatory system

The walls of arteries and veins have three layers:

- An outer layer of connective tissue with elastic fibers that permits stretching and recoil of the vessel
- A middle layer of smooth muscle and elastic fibers
- An inner *endothelium* of simple squamous epithelium (see Campbell, Figure 42.8)

The middle and outer layers of arteries are thicker than those in veins.

- The thicker walls of arteries provide the strength necessary to accommodate the high force with which the heart pumps the blood; the elasticity helps to even out the flow of blood so that it is not pulsatile.
- The thinner-walled veins accommodate the low pressure and low velocity of blood following emergence from capillary beds; flow is facilitated by muscular activity.

Capillaries are comprised only of the endothelial lining, which permits the exchange of chemicals with the interstitial fluids.

G. Natural laws governing the movement of fluids in pipes effect blood flow and blood pressure

1. Blood flow velocity

There is a great difference in the speed at which blood flows through the various parts of the circulatory system. Blood travels about 30 cm/sec in the aorta and about 0.026 cm/sec in capillaries.

- The velocity decreases in accordance with the *law of continuity* which states that a fluid will flow faster through narrow portions of a pipe than wider portions if the volume of flow remains constant.
- An artery gives rise to so many arterioles and then capillaries that the total diameter of vessels is much greater in capillary beds than in the artery, thus blood flows more slowly in capillaries.
- Resistance to blood flow is greater in the smaller vessels since the blood contacts more epithelial surface area.
- Blood flows faster as it enters the venules and veins since the cross-sectional area is decreased (see Campbell, Figure 42.10).

2. Blood pressure

Fluids are driven through pipes by hydrostatic pressure, which is the force exerted by fluids against the surfaces they contact.

Blood pressure = The hydrostatic force that blood exerts against a vessel wall

- Pressure is greater in arteries than in veins and greatest during ventricular systole.

  This is the main force propelling blood from the heart through the vessels.

- *Peripheral resistance* results from impedance by arterioles; blood enters the arteries faster than it can leave.

  Thus, there is a pressure even during diastole, driving blood into capillaries continuously.

- Determined by cardiac output and degree of peripheral resistance

Stress may trigger neural and hormonal responses that cause the smooth muscles of vessel walls to contract, constricting blood vessels and increasing resistance.

- In veins, blood pressure is near zero; blood returns to the heart by the action of skeletal muscles around the veins.

  Veins have valves that allow blood to flow only toward the heart.

- Breathing also helps return blood to the heart, since the pressure change in the thoracic cavity during inhalation cause the vena cava and large veins near the heart to expand and fill.

H. Transfer of substances between the blood and the interstitial fluid occurs across the thin walls of capillaries

1. Blood flow through capillary beds

All tissues and organs receive a sufficient supply of blood even though only 5% to 10% of the capillaries are carrying blood at any one time; the supply is adequate due to the vast number of capillaries present in each tissue.

- Capillaries in the brain, heart, kidneys, and liver usually carry a full load of blood.

Two mechanisms regulate the distribution of blood in capillary beds. Both are controlled by nerve signals and hormones.

1. One mechanism involves the contraction and relaxation of the smooth muscle layer in the walls of arterioles.

   Contraction of the muscle layer constricts the arteriole and reduces the blood flow from it into the capillary bed.

   Relaxation of the muscle layer dilates the arteriole and increases the blood flow into the capillary bed (see Campbell, Figure 42.11).

2. The second mechanism involves the contraction and relaxation of precapillary sphincters, which are rings of smooth muscle located at the entrance to capillary beds.

   Contraction of these sphincters reduces blood flow into the capillary bed; relaxation increases blood flow into the capillary bed.

The diversion of blood from one area of the body to another changes the blood supply to capillary beds.

- After ingesting food, the digestive tract receives a large supply of blood due to dilation of arterioles and the opening of precapillary sphincters associated with the system.
- During exercise, blood is diverted to the skeletal muscles.

2. Capillary exchange

The exchange of materials between the blood and interstitial fluids that are in direct contact with the cells occurs across the thin walls of capillaries.

- The capillary wall is a single, "leaky" layer of flattened endothelial cells that overlap at their edges.
- Materials may cross these cells in vesicles (via endocytosis and exocytosis), by diffusion through the cell, or by bulk flow between the cells due to hydrostatic pressure.

Direction of fluid movement at any point along a capillary depends on the relative forces of hydrostatic pressure and osmotic pressure (see Campbell, Figure 42.12).

- Fluid flows out of a capillary at the upstream end near an arteriole and into a capillary at the downstream end near a venule.

- About 85% of the fluid which leaves the blood at the arteriole end of the capillary, re-enters from the interstitial fluid at the venous end.
- The remaining 15% of the fluid is eventually returned by the lymphatic system.

I. The lymphatic system returns fluid to the blood and aids in body defense

Capillary walls leak fluid and some blood proteins, which return to the blood via the *lymphatic system*. This is the 15% (4 L/day) of fluid that does not re-enter the capillaries.

- The fluid, *lymph*, is similar in composition to interstitial fluid.
- The lymph enters the system by diffusing into lymph capillaries which intermingle with the blood capillaries.
- The lymphatic system drains into the circulatory system at two locations near the shoulders.

Lymph vessels have valves that prevent backflow and depend mainly on movement of skeletal muscles to squeeze the fluid along.

- Rhythmic contractions of vessel walls also help draw fluid into the lymphatic capillaries.

Lymph nodes are specialized swellings along the system that filter the lymph and attack viruses and bacteria.

This defense is conducted by specialized white blood cells inhabiting the lymph nodes.

The nodes become swollen and tender during an infection due to rapid multiplication of the white blood cells present.

Lymph capillaries penetrate small intestine villi and absorb fats, thus transporting them from the digestive system to the circulatory system.

J. Blood is a connective tissue with cells suspended in plasma

Vertebrate blood is connective tissue with several cell types suspended in a liquid matrix called *plasma*.

- The average human has 4 to 6 L of whole blood (plasma + cellular elements).
- Cellular elements are the cells and cell fragments of the blood and represent about 45% of the blood volume (see Figure 42.13).

1. Plasma

Water accounts for 90% of plasma, which also contains electrolytes and plasma proteins.

- *Electrolytes* = Inorganic salts in the form of dissolved ions that help maintain osmotic balance of the blood; some also help buffer the blood
- Electrolyte balance in the blood is maintained by the kidneys.

Plasma proteins help buffer blood, help maintain the osmotic balance between blood and interstitial fluids, and contribute to its viscosity.

- Some escort lipids through blood, some are immunoglobulins, some (fibrinogens) are clotting factors.
- Serum is blood plasma that has had the clotting factors removed.

Plasma also contains substances in transit through the body such as nutrients, metabolic wastes, respiratory gases, and hormones.

2. Cellular elements

Erythrocytes = Red blood cells (RBC); biconcave discs that function in transport of oxygen.

- Each cubic millimeter of human blood contains 5 to 6 million erythrocytes.

- In mammals, RBCs lack nuclei and mitochondria; they generate ATP exclusively by anaerobic metabolism.
- They contain *hemoglobin*, an iron-containing protein that reversibly binds oxygen. About 250 million molecules of hemoglobin are in each erythrocyte.

Leukocytes = *White blood cells* that function in defense and immunity.

- There are five major types of leukocytes: basophils, eosinophils, neutrophils, lymphocytes and monocytes.
- There are usually 5000 to10,000 leukocytes per cubic millimeter of blood, although this number increases during an infection.
- Actually spend most of their time outside the circulatory system in the interstitial fluid and lymphatic system; large numbers are found in the lymph nodes.
- Lymphocytes become specialized during an infection and produce the body's immune response.

Platelets = Fragments of cells 2 to 3 μm in diameter

- Originate as pinched-off cytoplasmic fragments of large cells in the bone marrow
- Lack nuclei
- Function in blood clotting

3. Replacement of cellular elements

The cellular elements of the blood must be replaced as they wear out.

- The average erythrocyte circulates in the blood for 3 to 4 months before being destroyed by phagocytic cells in the liver and spleen.
- The components are usually recycled with new molecules being constructed from the macromolecule components of the old cells.

The *pluripotent stem cells* give rise to all three of the cellular elements.

- These are found in the red marrow of bones, especially the ribs, vertebrae, breastbone, and pelvis.
- Form in the early embryo and are renewed by mitosis (see Campbell, Figure 42.14).
- Produce a number of new blood cells equivalent to the number of dying cells.

Erythrocyte production is controlled by a negative-feedback mechanism. If tissues are not receiving enough oxygen, the kidneys convert a plasma protein to the hormone *erythropoietin*, which stimulates production of erythrocytes in the bone marrow.

Using DNA technology to correct genetic defects in pluripotent stem cells may provide a treatment for such diseases as leukemia and sickle-cell anemia.

4. Blood clotting

A clot forms when platelets clump together to form a temporary plug and release clotting factors (some are also released from damaged cells) that initiate a complex reaction resulting in conversion of inactive *fibrinogen* to active *fibrin* (see Campbell, Figure 42.15)

- Fibrin aggregates into threads that form the clot.

An inherited defect in any of the steps involved in clot formation results in *hemophilia*, a disorder characterized by excessive bleeding from minor injuries.

Anticlotting factors normally prevent spontaneous clotting in the absence of injury.

- On occasion, spontaneous clots called a *thrombus* form from platelets aggregating with coagulated fibrin. Such clots are more likely to form in individuals with cardiovascular disease.

K. Cardiovascular diseases are the leading cause of death in the United States and many other developed nations

Diseases of the heart and blood vessels are referred to as *cardiovascular diseases.*

- Account for more than 50% of all deaths in the United States
- May culminate in a heart attack or stroke
  - *Heart attack* = Death of the cardiac muscle resulting from prolonged blockage of one or more coronary arteries
  - *Stroke* = Death of nervous tissue in the brain often resulting from blockage of arteries in the brain

A thrombus is often associated with a heart attack or stroke.

- *Thrombus* = A blood clot that blocks a key blood vessel
- If it blocks the coronary arteries, a heart attack occurs.
- An *embolus* is a moving clot.
- If the thrombus or embolus blocks an artery in the brain, a stroke results.

Arteries may gradually become impaired by atherosclerosis (see Campbell, Figure 42.16).

- *Atherosclerosis* = Chronic cardiovascular disease characterized by plaques that develop on the inner walls of arteries and narrow the bore of the vessels
- Decreases blood flow through the vessels.
- Increase the risk of clot formation and heart attack.

Arteriosclerosis = Degenerative condition of arteries (form of atherosclerosis) in which plaques become hardened by calcium deposits

Angina pectoris = Chest pains that occur when the heart receives insufficient oxygen due to the build up of plaques in the arteries

- An indicator that the heart is not receiving sufficient oxygen

Hypertension = High blood pressure; may promote atherosclerosis

- Increases risk of heart attack and stroke

Smoking, lack of exercise, and a diet rich in animal fats correlate with increased risk of cardiovascular disease.

Abnormally high concentrations of low density lipoproteins (LDLs) in the blood correlate with atherosclerosis; high density lipoproteins(HDLs) may reduce deposition of cholesterol in arterial plaques.

- Exercise tends to increase HDL concentration.
- Smoking increases the LDL to HDL ratio.

II. Gas Exchange in Animals

A. Gas exchange supplies oxygen for cellular respiration and disposes of carbon dioxide: *an overview*

Circulatory systems transport oxygen and carbon dioxide between respiratory organs and other parts of the body.

Gas exchange = The movement of O_2 and CO_2 between the animal and its environment (see Campbell, Figure 42.17)

- Supports cellular respiration by supplying O_2 and removing CO_2.

The *respiratory medium* (source of oxygen) is air for terrestrial animals and water for aquatic animals.

- Air is 21% oxygen, while the amount of dissolved oxygen in water varies due to temperature, solute concentrations, and other factors.

Respiratory surface = Portion of the animal surface where gas exchange with the respiratory medium occurs. Oxygen diffuses in; carbon dioxide diffuses out

- O_2 and CO_2 can only diffuse through membranes if they are first dissolved in the water that coats the respiratory surface.
- This surface must be large enough to provide O_2 and expel CO_2 for the entire body.

A variety of respiratory surfaces have evolved that are adaptive for organism size and environment.

- Protozoa and other unicellular organisms exchange gases over their entire surface area.
- Animals such as sponges, cnidarians, and flatworms have body structures such that the plasma membrane of each body cell contacts the outside environment and can function in exchange.
- In animals with a more three-dimensional body plan, most of the body cells are isolated from the environment and the respiratory surfaces are generally thin, moist epithelium with a rich blood supply.
    - Usually only a single cell layer separates the respiratory medium from the blood or capillaries.

Animals that are relatively small or have a shape (long, thin) that results in a high surface area to volume ratio may use their outer skin as a respiratory organ.

- Earthworms have moist skin which overlays a dense network of capillaries.
- Gases diffuse across the entire surface (O_2 in; CO_2 out) and into the circulatory system.
- Earthworms and other animals (some amphibians) that use their skin for gas exchange must live in water or damp places in order to keep the exchange surface moist.

Most other animals lack sufficient body surface area to exchange gases for the entire body. These animals possess a region of the body surface that is extensively branched or folded, thus providing a large enough respiratory surface area for gas exchange.

- In most aquatic animals, external *gills* are present and are in direct contact with the water.
- Terrestrial animals have internal respiratory surfaces that open to the atmosphere through narrow tubes.
    - Air lacks the supportive density and moisturizing qualities of water.
    - Lungs and insect tracheae are two variations.

B. Gills are respiratory adaptations of most aquatic animals

Gills are outfoldings of the body surface specialized for gas exchange (see Campbell, Figure 42.18).

- In some invertebrates (e.g., echinoderms), gills have simple shapes and are distributed over the entire body.
- In other invertebrates (e.g., annelids), gills may be flap-like and extend from each body segment or be clustered at one end and be long and feathery.
- Other animals (mollusks, fishes) have gills that are localized on a body region where the surface is finely subdivided to provide a large amount of surface area.

- The gills must be efficient; although water keeps the respiratory surface wet, it has a lower oxygen concentration than air.

Ventilation = Any method of increasing the flow of the respiratory medium over the respiratory surface; brings in a fresh supply of O_2 and removes CO_2

Due to the density and low oxygen concentration of water, fish must expend a large amount of energy to ventilate water.

- Fish have a unique arrangement of blood vessels in their gills, which maximizes O_2 uptake from H_2O.
- Called *countercurrent exchange*, blood flows opposite to the direction in which water passes over gills, maintaining a constant concentration gradient for oxygen between the blood and the water passing over the gill surface (see Campbell, Figures 42.19 and 42.20)

C. Tracheal systems and lungs are respiratory adaptations of terrestrial animals

Air has several advantages over water as a respiratory medium:

- A higher oxygen concentration
- Oxygen and carbon dioxide diffuse faster through air than water.
- Respiratory surfaces do not have to be ventilated as thoroughly.

The major disadvantage is that respiratory surfaces are continually desiccated.

- The evolution of respiratory surfaces within the body (tracheae, lungs) helped solve this problem.

1. Tracheal systems

Tracheae are tiny air tubes that branch throughout the insect body; air enters the system through pores called spiracles and diffuses through the small branches which extend to the surface of nearly every cell (see Campbell, Figure 42.21).

- Some small insects rely on diffusion alone to move O_2 into the system and CO_2 out; others use rhythmic body movements for ventilation.
- Cells are exposed directly to the respiratory medium so insects do not use their circulatory systems to transport O_2 and CO_2.
  - This is a major reason why the open circulatory system works so well in insects.

2. Lungs

Lungs are highly vascularized invaginations of the body surface that are restricted to one location.

- The circulatory system must transport oxygen from the lungs to the rest of the body.

Land snails use an internal mantle as a lung.

Spiders possess booklungs.

Various degrees of lung development are found in terrestrial vertebrates: frogs have simple balloonlike lungs with limited surface area; mammals have highly subdivided lungs with a large surface area.

3. Mammalian respiratory systems: *a closer look*

Located in the thoracic cavity, mammalian lungs are enclosed in a sac consisting of two layers held together by the surface tension of fluid between the layers.

Air entering the nostrils is filtered by hairs, warmed and moistened.

The air then travels through the pharynx, then through the glottis, and into *larynx* (which possesses vocal cords and functions as a voice box).

The flow then enters the cartilage-lined *trachea* that forks into two *bronchi* which further branch into finer *bronchioles* that dead-end in *alveoli*.

Alveoli are lined with a thin layer of epithelium which serves as the respiratory surface.

Oxygen dissolves in the moist film covering the epithelium and diffuses across to the capillaries covering each alveolus; carbon dioxide moves in the opposite direction by diffusion.

4. Ventilating the lungs

Vertebrates ventilate lungs by *breathing* (alternate inhalation and exhalation of air).

Maintains a maximum O_2 concentration and minimum CO_2 concentration in the alveoli.

Frogs ventilate the lungs by *positive pressure breathing.*

- Air is pushed down the windpipe into the lungs.
- Air is pulled into the mouth by lowering the floor region; this enlarges the oral cavity.
- The nostrils and mouth are closed and the floor of the mouth is raised, forcing air down the trachea.
- Air is exhaled by elastic recoil of lungs and by compression of the lungs by the muscular body wall.

Mammals ventilate their lungs by *negative pressure breathing.*

- During inhalation, air is pulled into the lungs by the negative pressure created as the thoracic cavity enlarges by two possible mechanisms:
- When a mammal is at rest, most of the shallow inhalation results from contraction of the *diaphragm.*

  The diaphragm is a dome-shaped, thin sheet of muscle that forms the bottom wall of the thoracic cavity (see Campbell, Figure 42.23). When it contracts, it pushes downward towards the abdomen, enlarging the thoracic cavity.

  This lowers the air pressure in the lungs below atmospheric pressure and causes inhalation.

- Action of the rib muscles in increasing lung volume is important during vigorous exercise.

  Contraction of the rib muscles pulls the ribs upwards, which expands the rib cage.

  As the thoracic cavity enlarges, the lungs also expand, since the surface tension of the fluid between the layers of the lung sac causes the lungs to follow.

  Lung volume increases, resulting in negative pressure within the alveoli, causing air to rush in.

Exhalation occurs when the diaphragm and/or the rib muscles relax, decreasing the volume of the thoracic cavity.

The amount of air inhaled and exhaled depends upon size, activity level, and state of health.

- *Tidal volume* is the volume of air an animal inhales and exhales with each breath during normal quiet breathing. Averages about 500 mL in humans.
- *Vital capacity* is the maximum air volume that can be inhaled and exhaled during forced breathing; averages 3400 mL to 4800 mL in college-age females and males, respectively.
- *Residual volume* is the amount of air that remains in the lungs even after forced exhalation.

Birds have a more complex process for ventilation (see Campbell, Figure 42.24):

- Besides lungs, birds have 8 or 9 air sacs in their abdomen, neck and wings that serve to trim the density of the body and act as sinks for the heat dissipation by metabolism of flight muscles.
- The air sacs do not exchange gases, they serve as bellows to keep the air moving.
- The lungs also have tiny channels called *parabronchi*; air flows through the entire system, lungs and air sacs, in only one direction regardless of whether it is inhaling or exhaling.
- The continuous flow of air through the parabronchi provides a constant supply of oxygen to the blood whether the bird is inhaling or exhaling.

D. Control centers in the brain regulate the rate and depth of breathing

Breathing is an automatic action. We inhale when nerves in the *breathing control centers* of the medulla oblongata and pons send impulses to the rib muscles or diaphragm, stimulating the muscles to contract (see Campbell, Figure 42.25).

- This occurs about 10 to 14 times per minute and the degree of lung expansion is controlled by a negative-feedback mechanism involving stretch receptors in the lungs.
- The medulla's control center also monitors blood and cerebrospinal fluid pH, which drops as blood CO_2 concentrations increase. When it senses a drop in pH (increased CO_2 level), the tempo and depth of breathing are increased and the excess CO_2 is removed in exhaled air.

O_2 concentration in the blood only affects the breathing control centers when it becomes severely low.

O_2 sensors in the aorta and carotids send signals to the breathing control centers and the centers respond by increasing the breathing rate.

The breathing control centers thus respond to a variety of neural and chemical signals.

- The response is an adjustment in the rate and depth of breathing to meet the demands of the body.
- The control is effective since it is coordinated with control of the circulatory system.

E. Gases diffuse down pressure gradients in the lungs and other organs

The diffusion of gases, whether in air or water, depends on differences in *partial pressure* (e.g., P_{O2} = partial pressure of oxygen; note similarity to the diffusion of solutes being dependent on solute concentration). Oxygen comprises about 21% of the atmosphere and carbon dioxide about 0.03%.

- The partial pressure of a gas is the proportion of the total atmospheric pressure (760 mm) contributed by the gas; P_{O2} = 160 mm Hg (0.21 × 760) and P_{CO2} = 0.23 mm Hg.

Gases always diffuse from areas of high partial pressure to those of low partial pressure (see Campbell, Figure 42.26).

- Blood arriving at the lungs from the systemic circulation has a lower P_{O2} and a higher P_{CO2} than air in the alveoli.

  Thus, the blood exchanges gases with air in the alveoli and the P_{O2} of the blood increases while the P_{CO2} decreases.
- In systemic capillaries gradients of partial pressure favor diffusion of oxygen out of the blood and diffusion of CO_2 into it, since cellular respiration rapidly depletes interstitial fluid of O_2 and adds CO_2.

F. Respiratory pigments transport gases and help buffer the plasma

1. Oxygen transport

Oxygen is carried by *respiratory pigments* in the blood of most animals since oxygen is not very soluble in water.

- The pigments are proteins which contain metal atoms; the metal atoms are responsible for the color of the protein.

In arthropods and mollusks, *hemocyanin* is the O_2 carrying pigment.

- The oxygen-binding component is copper and results in a blue color.
- It is dissolved directly in plasma, not confined to cells.

Hemoglobin is the oxygen-transporting pigment in almost all vertebrates.

- Consists of four subunits, each containing a heme group that bonds O_2; an iron atom is at the center of each heme group and actually binds to oxygen.
- The binding of oxygen to hemoglobin is reversible. (Binding occurs in the lungs; release occurs in the tissues.)
- Binding of O_2 to one subunit induces a shape change that increases the affinity of the other three subunits for oxygen (cooperativity).
- The unloading of oxygen from one heme group results in a conformational change that stimulates unloading from the other three.
- The cooperative nature of this mechanism is evident in the *dissociation curve* depicted in Figure 42.27.
- Bohr shift is the lowering of hemoglobins' affinity for oxygen upon a drop in pH (see Campbell, Figure 42.27b) This occurs in active tissues due to the entrance of CO_2 into the blood.

2. Carbon dioxide transport

Hemoglobin not only transports oxygen, but it also helps the blood transport carbon dioxide and assists in buffering the blood against harmful pH changes (see Campbell, Figure 42.28).

Carbon dioxide is transported by the blood in three forms:

- Dissolved CO_2 in the plasma (7%)
- Bound to the amino groups of hemoglobin (23%)
- As bicarbonate ions in the plasma (70%)

Carbon dioxide from cells diffuses into the blood plasma and then into erythrocytes. In the erythrocytes, carbonic anhydrase catalyzes a reversible reaction wherein CO_2 is converted into bicarbonate.

- The CO_2 reacts with water to form carbonic acid.
- The carbonic acid quickly dissociates to bicarbonate and hydrogen ions.
- Bicarbonate then diffuses out of the erythrocyte and into the blood plasma (in exchange for a chloride ion = chloride shift).
- The hydrogen ions attach to hemoglobin and other proteins which results in only a slight change in the pH and the dissociation of oxygen from hemoglobin.
- The process is reversed in the lungs.

G. Deep-diving mammals stockpile oxygen and consume it slowly

Diving mammals such as seals, dolphins, and whales have special adaptations which allow them to make long underwater dives.

Weddell seals, which make dives to 200 to 500 m depths for 20 minutes or more, have been extensively studied (see Campbell, Figure 42.29).

- These mammals can store large amounts of oxygen, about twice as much per kilogram body weight as humans.

  70% of the oxygen load is found in the blood (51% in humans) and 5% in the lungs (36% in humans).

  They also possess a higher *myoglobin* (a respiratory pigment similar to hemoglobin except that it is comprised of a single subunit contains one heme unit) concentration in their muscles.

- The high oxygen load in the blood may be due to the higher blood volume in these seals (twice the amount of blood per kilogram of body weight as humans).
- The seals also have a very large spleen which can store about 24 L of blood.

  The spleen probably contracts after a dive and forces more erythrocytes loaded with oxygen into the blood.

- The high concentration of myoglobin permits these seals to store about 25% of their oxygen in muscles (compared to 13% in humans).

These adaptations provide diving mammals with a large oxygen reservoir at the beginning of a dive, but they also have several adaptations to conserve oxygen during the dive.

- A diving reflex slows the pulse, and oxygen consumption declines as the cardiac output slows.
- Most of the blood is routed to the brain, spinal cord, eyes, adrenal glands, and placenta due to regulatory mechanisms that reduce blood flow to the muscles.
- The reduced blood flow to the muscles results in a depletion of the myoglobin oxygen reserves after about 20 minutes, the muscles then shift to anaerobic production of ATP.

The special adaptations found in diving mammals emphasizes that animals can respond to environmental pressures in the short term through physiological adaptation as well as in the long term by natural selection.

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CHAPTER 43
THE BODY'S DEFENSES

OUTLINE

I. Nonspecific Defenses Against Infection
   - A. The skin and mucous membranes provide first-line barriers to infection
   - B. Phagocytic cells, inflammation, and antimicrobial proteins function early in infection

II. How Specific Immunity Arises
   - A. Lymphocytes provide the specificity and diversity of the immune system
   - B. Antigens interact with specific lymphocytes, inducing immune responses and immunological memory
   - C. Lymphocyte development gives rise to an immune system that distinguishes self from nonself

III. Immune Responses
   - A. Helper T lymphocytes function in both humoral and cell-mediated immunity
   - B. In the cell-mediated response, cytotoxic T cells defend against intracellular pathogens
   - C. In the humoral response, B cells produce antibodies against extracellular pathogens

IV. Immunity in Health and Disease
   - A. Immunity can be achieved naturally or artificially
   - B. The immune system's capacity to distinguish self from nonself limits blood transfusion and transplantation
   - C. Abnormal immune function can lead to disease
   - D. Invertebrates have a rudimentary immune system

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. Explain what is meant by nonspecific defense, and list the nonspecific lines of defense in the vertebrate body.
2. Explain how the physical barrier of skin is reinforced by chemical defenses.
3. Define phagocytosis, and list two types of phagocytic cells derived from white blood cells.
4. Explain how the function of natural killer cells differs from the function of phagocytes.
5. Describe the inflammatory response including how it is triggered.
6. Explain how the inflammatory response prevents the spread of infection to surrounding tissue.
7. List several chemical signals that initiate and mediate the inflammatory response.

8. Describe several systemic reactions to infection, and explain how they contribute to defense.
9. Describe a plausible mechanism for how interferons can fight viral infections and might act against cancer.
10. Explain how complement proteins may be activated and how they function in cooperation with other defense mechanisms.
11. Explain how the immune response differs from nonspecific defenses.
12. Distinguish between active and passive immunity.
13. Explain how humoral immunity and cell-mediated immunity differ in their defensive activities.
14. Outline the development of B and T lymphocytes from stem cells in red bone marrow.
15. Describe where T and B cells migrate, and explain what happens when they are activated by antigens.
16. Characterize antigen molecules, in general, and explain how a single antigen molecule may stimulate the immune system to produce several different antibodies.
17. Describe the mechanism of clonal selection.
18. Distinguish between primary and secondary immune response.
19. Describe the cellular basis for immunological memory.
20. Describe the cellular basis for self-tolerance.
21. Explain how the humoral response is provoked.
22. Explain how B cells are activated.
23. Diagram and label the structure of an antibody, and explain how this structure allows antibodies to perform the following functions:
    a. Recognize and bind to antigens
    b. Assist in destruction and elimination of antigens
24. Distinguish between variable (V) regions and constant (C) regions of an antibody molecule.
25. Compare and contrast the structure and function of an enzyme's active site and an antibody's antigen-binding site.
26. List the five major classes of antibodies in mammals and distinguish among them.
27. Describe the following effector mechanisms of humoral immunity triggered by the formation of antigen-antibody complexes:
    a. Neutralization
    b. Agglutination
    c. Precipitation
    d. Activation of complement system
28. Explain how monoclonal antibodies are produced and give examples of current and potential medical uses.
29. Explain how T-cell receptors recognize "self" and how macrophages, B cells, and some T cells recognize one another in interactions.
30. Describe an antigen-presenting cell (APC).
31. Design a flow chart describing the sequence of events that follows the interaction between antigen presenting macrophages and helper T cells, including both cell-mediated and humoral immunity.
32. Define cytokine, and distinguish between interleukin I and interleukin II.
33. Distinguish between T-independent antigens and T-dependent antigens.
34. Describe how cytotoxic T cells recognize and kill their targets.
35. Explain how the function of cytotoxic T cells differs from that of complement and natural killer cells.

36. Describe the function of suppressor T cells.
37. Distinguish between complement's classical and alternative activation pathways.
38. Describe the process of opsonization.
39. For ABO blood groups, list all possible combinations for donor and recipient in blood transfusions; indicate which combinations would cause an immune response in the recipient; and state which blood type is the universal donor.
40. Explain how the immune response to Rh factor differs from the response to A and B blood antigens.
41. Describe the potential problem of Rh incompatibility between a mother and her unborn fetus, and explain what precautionary measures may be taken.
42. Explain why, other than with identical twins, it is virtually impossible for two people to have identical MHC markers.
43. Describe the rejection process of transplanted tissue in terms of normal cell-mediated immune response, and describe how the immune system can be suppressed in transplant patients.
44. List some known autoimmune disorders, and describe possible mechanisms of autoimmunity.
45. Explain why immunodeficient individuals are more susceptible to cancer than normal individuals.
46. Describe an allergic reaction including the role of IgE, mast cells, and histamine.
47. Explain what causes anaphylactic shock and how it can be treated.
48. Recall the infectious agent that causes AIDS and explain how it weakens the immune system.
49. Explain how AIDS is transmitted and why it is difficult to produce vaccines to protect uninfected individuals.
50. Describe what it means to be HIV-positive.
51. Explain how general health and mental well being might affect the immune system.

KEY TERMS

lysozyme
phagocytosis
macrophages
eosinophils
natural killer cells
inflammatory response
histamine
basophils
mast cells
prostaglandins
chemokines
pyrogens
complement system
interferon
B lymphocytes (B cells)
T lymphocytes (T cells)
antigens
antibodies
effector cells
memory cells
clonal selection
primary immune response
plasma cells
secondary immune response
major histocompatibility complex (MHC)
Class I MHC
Class II MHC
antigen presentation
cytotoxic T cells (T_C)
helper T cells (T_H)
humoral immunity
cell-mediated immunity
antigen-presenting cells (APCs)
interleukin-1 (IL-1)
suppressor T cells (T_S)
CD8
CD4
target cell
perforin
tumor antigen
T-dependent antigens
T-independent antigens
epitope
immunoglobulins (Ig)
heavy chains
light chains
monoclonal antibodies
neutralization
opsonization
agglutination
complement fixation
immune adherence
active immunity
immunization
vaccination
passive immunity
transfusion reaction
Rh factor
graft versus host reaction
anaphylactic shock
acquired immunodeficiency syndrome (AIDS)
opportunistic diseases
human immunodeficiency

antigen receptors	cytokines	membrane attack	virus (HIV)
T cell receptors	interleukin-2 (IL-2)	complex (MAC)	HIV-positive

LECTURE NOTES

The vertebrate body possesses two mechanisms which protect it from potentially dangerous viruses, bacteria, other pathogens, and abnormal cells which could develop into cancer (see Campbell, Figure 43.1 for an overview diagram).

1. One of these mechanisms is *nonspecific*, that is, it does not distinguish between infective agents.
2. The second mechanism is *specific* in that it responds in a very specific manner (e.g., production of antibodies) to the particular type of infective agent.

I. Nonspecific Defense Against Infection

Nonspecific defense mechanisms help prevent entry and spread of invading microbes in an animal's body.

- An invading microbe must cross the external barrier formed by the skin and mucous membranes.
- If the external barrier is penetrated, the microbe encounters a second line of defense: interacting mechanisms of phagocytic white blood cells, antimicrobial proteins, and the inflammatory response.

A. The skin and mucous membranes provide first-line barriers to infection

The skin and mucous membranes act as physical barriers preventing entry of pathogens, and as chemical barriers of anti-pathogen secretions.

- In humans, oil and sweat gland secretions acidify the skin (pH 3 to 5), which discourages microbial growth.
- The normal bacterial flora of the skin (adapted to the acidity) may release acids and other metabolic wastes to further inhibit pathogen growth.
- Saliva, tears, and mucous secretions contain antimicrobial proteins and wash away potential invading microbes.
- An enzyme (*lysozyme*) in perspiration, tears, and saliva attacks the cell walls of many bacteria and destroys other microbes entering the respiratory system and eyes.
- In the respiratory tract, nostril hairs filter inhaled particles and mucus traps microorganisms that are then swept out of the upper respiratory tract by cilia, thus preventing their entrance into the lungs (see Campbell, Figure 43.2).
- In the digestive tract, stomach acid kills many bacteria that enter with foods or those trapped in swallowed mucus from the upper respiratory system.

B. Phagocytic cells, inflammation, and antimicrobial proteins function early in infection

Microbes that penetrate the skin or mucous membranes encounter amoeboid white blood cells capable of *phagocytosis* or cell lysis.

1. Phagocytic and natural killer cells

Neutrophils are cells that become phagocytic in infected tissue.

- Comprise 60% – 70% of total white cells
- Attracted by chemical signals, they enter infected tissues by amoeboid movement
- Only live a few days as they destroy themselves when destroying pathogens

Monocytes comprise only about 5% of the white blood cells, but they provide an even more effective phagocytic defense. They mature, circulate for a few hours, then migrate to the tissues where they enlarge and become macrophages.

Macrophages are large amoeboid cells that use pseudopodia to phagocytize microbe, which is then destroyed by digestive enzymes and reactive forms of oxygen within the cell (see Campbell, Figure 43.3).

- Most wander through interstitial fluid phagocytosing bacteria, viruses, and cell debris.
- Some reside permanently in organs and connective tissues. They are fixed in place, but are located where they will have contact with infectious agents circulating in the blood and lymph.
- Fixed macrophages are especially numerous in the lymph nodes and spleen (see Campbell, Figure 43.4)..

Eosinophils represent about 1.5% of the total white cell count and have limited phagocytic activity.

- Contain destructive enzymes in cytoplasmic granules, which are discharged against the outer covering of the invading pathogen.
- Main contribution is defense against larger invaders such as parasitic worms.

Natural killer (NK) cells destroy the body's own infected cells, especially those harboring viruses.

- Also assault abnormal cells that could form tumors
- Are not phagocytic, but attack the membrane, causing cell lysis

2. The inflammatory response

A localized *inflammatory response* occurs when there is damage to a tissue due to physical injury or entry of microorganisms.

- Vasodilation of small vessels near the injury increases the blood supply to the area, which produces the characteristic redness.
- The dilated vessels become more permeable allowing fluids to move into surrounding tissues resulting in localized edema.

Chemical signals are important in initiating an inflammatory response (see Campbell, Figure 43.5)

- *Histamine* is released from injured circulating *basophils* and *mast cells* in the connective tissue.
    - Released histamine causes localized vasodilation, and the capillaries in the area become leakier.
- Prostaglandins are also released from white blood cells and damaged tissues.
    - These and other substances promote increased blood flow to the injured area.
    - Increased blood flow to the site of injury delivers clotting elements that help block the spread of pathogenic microbes and begin the repair process.

Migration of phagocytic cells into the injured area is also a result of increased blood flow and increased leakage from the capillaries.

- Phagocytes are attracted to the damaged tissues by several chemical mediators including chemotactic factors called *chemokines*.
- Neutrophils arrive first, followed closely by monocytes which develop into macrophages.
- The neutrophils eliminate microorganisms and then die.

- Macrophages destroy pathogens and clean up the remains of damaged tissue cells and dead neutrophils.
- Dead cells and fluid leaked from the capillaries may accumulate as pus in the area before it is absorbed by the body.

More widespread (systemic) inflammatory responses may also occur in cases of severe infections (meningitis, appendicitis).

- The bone marrow may be stimulated to release more neutrophils by molecules emitted by injured cells.
- There may also be a severalfold increase in the number of leukocytes within a few hours of response onset.
- A fever may develop in response to toxins produced by pathogens or due to *pyrogens* released by leukocytes.
- While a high fever is dangerous, moderate fevers inhibit the growth of some microorganisms.
- Moderate fevers may also facilitate phagocytosis and speed up tissue repairs.

3. Antimicrobial proteins

A number of proteins function in nonspecific defense by either directly attacking microorganisms or impeding their reproduction.

The two most important nonspecific protein groups are *complement proteins* and the interferons.

The *complement system* is a group of at least 20 proteins that interact with other defense mechanisms.

- These proteins interact in a series of steps that results in lysis of the invading microbes.
- Some components of the system function along with chemotaxin to help attract phagocytes to the infected site.

The *interferons* are substances produced by virus-infected cells that help other cells resist infection by the virus.

- They are secreted by infected cells as a nonspecific defense earlier than specific antibodies appear.
- Cannot save the infected cell, but their diffusion to neighboring cells stimulates production of proteins in those cells that inhibit viral replication.
- Not a virus-specific defense; interferon produced to infection by one strain of virus produces resistance in cells to other unrelated viruses.
- Most effective against short-term infections (colds and influenza).
- One type of interferon activates phagocytes, which enhances their ability to ingest and kill microorganisms.
- Interferons are now being mass produced using recombinant DNA technology and are being tested as treatments for viral infections and cancer.

II. How Immunity Arises

The *immune system* is the body's third line of defense and is very specific in its response. It is distinguished from nonspecific defenses by:

- Specificity
- Diversity

- Self/nonself recognition
- Memory

A. Lymphocytes provide the specificity and diversity of the immune system

Lymphocytes are responsible for both humoral and cell-mediated immunity

The different responses are due to the two main classes of lymphocytes in the body: *B cells* and *T cells*.

- Early B and T cells (as well as other lymphocytes) develop from multipotent stem cells in the bone marrow and are very much alike. They only differentiate after reaching their site of maturation.
- B cells (B lymphocytes) are responsible for the humoral immune response.
    - They form in the bone marrow and remain there to complete their maturation.
- T cells (T lymphocytes) are responsible for the cell-mediated immune response.
    - They also form in the bone marrow, then migrate to the thymus gland to mature.

Specificity refers to the immune system's ability to recognize and eliminate particular microorganisms and foreign molecules.

Antigen = A foreign substance that elicits a specific response by lymphocytes

Antibody = An antigen-binding immunoglobulin (protein), produced by B cells, that functions as the effector in an immune response

- Antigens may be molecules exhibited on the surface of, produced by, or released from bacteria, viruses, fungi, protozoans, parasitic worms, pollen, insect venom, transplanted organs, or worn-out cells.
- Each antigen has a unique molecular shape and stimulates production of an antibody that defends specifically against that particular antigen.
- *Antigen receptors* on the plasma membranes of lymphocytes recognize and distinguish among antigens.
    - Antigen receptors on B cells are actually transmembrane forms of antibodies and are sometimes referred to as *membrane antibodies.*
    - Antigen receptors on T cells, called *T cell receptors,* are similar in structure to those of B cells, but are never produced in a secreted form.
- The immune response is thus very specific and distinguishes between even closely related invaders.

Diversity refers to the immune system's ability to respond to numerous kinds (millions) of invaders, which are recognized by their antigenic markers.

- Based on the wide variety of lymphocyte populations in the immune system.
- Each population of antibody-producing lymphocytes is stimulated by a specific antigen; the stimulated lymphocytes synthesize and secrete the appropriate antibody.

B. Antigens interact with specific lymphocytes, inducing immune responses and immunological memory

The ability of the immune system to respond to the wide variety of antigens which enter the body is based in the enormous diversity of antigen-specific lymphocytes present in the system.

- Each lymphocyte will recognize and respond to only one antigen.

- This specificity is determined during embryonic development before any antigens are encountered, and is the consequence of the antigen receptor on the lymphocyte's surface.

When an antigen enters the body and binds to receptors on the specific lymphocytes, those lymphocytes are activated and begin to divide and to differentiate.

- The divisions produce a large number of identical effector cells (clones), which bind to the antigen that stimulated the response.
- If, for example, a B cell is activated, it will proliferate to produce a large number of plasma cells that will each secrete an antibody that functions as an antigen receptor for the specific antigen that activated the original B cell.

Thus, each antigen activates only a small number of the diverse group of lymphocytes. The activated cells proliferate to produce a clone of millions of effector cells which are specific for the original antigen (clonal selection) (see Campbell, Figure 43.6).

- *Clonal selection* = Antigenic-specific selection of a lymphocyte that activates it to produce clones of effector cells dedicated to eliminating the antigen that provoked the initial immune response. One clone of cells consists of effector cells. Another clone of cells consists of memory cells.
- *Effector cells* are the short-lived cells that actually defend the body during an immune response.
  - Effector cells are populations of cells resulting from division of lymphocytes that were activated by the binding of antigens to their antigen receptors.

The *primary immune response* is the proliferation of lymphocytes to form clones of effector cells specific to an antigen during the body's first exposure to the antigen.

- There is a 10- to 17-day lag period between initial exposure and maximum production of effector cells.
- The lymphocytes selected by the antigen are differentiating into effector B cells and T cells during the lag period.
  - Activated B cells give rise to effector cells called *plasma cells*, which secrete antibodies (humoral response) that eliminate the activating antigen.

A *secondary immune response* occurs when the body is exposed to a previously encountered antigen.

- The response is faster (2 to 7 days) and more prolonged than a primary response.
- The antibodies produced are more numerous, and they are more effective at binding the antigen (see Campbell, Figure 43.7).

This ability to recognize a previously encountered antigen is known as immunological memory.

- Based on memory cells, which are produced during clonal selection for effectors in a primary immune response.
- Memory cells are not active during the primary response and survive in the system for long periods. (Effector cells produced in the primary response are active, and thus, short-lived.)
- When the same antigen that caused a primary immune response again enters the body, the memory cells are activated and rapidly proliferate to form a new clone of effector cells and memory cells.
- These new clones of effector and memory cells are the secondary immune response.
- This acquired immunity has long been recognized as a resistance to some infections encountered earlier in life (e.g., chicken pox).

C. Lymphocyte development gives rise to an immune system that distinguishes self from nonself

Like all blood cells, lymphocytes derive from pluripotent stem cells in bone marrow or liver of a developing embryo. Initially, all lymphocytes are alike, but depending on the site of maturation, they develop into T cells or B cells (see Campbell, Figure 43.8).

- Cells that remain in the bone marrow develop into B cells
- Cells that migrate to the thymus develop into T cells

1. Immune tolerance for self

Self/nonself recognition is the ability of the immune system to distinguish between the body's own molecules and foreign molecules (antigens).

- Develops before birth when T and B lymphocytes begin to mature in the thymus and bone marrow of the embryo.

Antigen receptors on the surfaces of lymphocytes are responsible for detecting foreign molecules that enter the body. There are no lymphocytes reactive against the body's own molecules under normal conditions.

Self-tolerance = The lack of a destructive immune response to the body's own cells.

- Failure of this system leads to autoimmune disorders that destroy the body's own tissues.

2. The role of cell surface markers in T cell function and development

The *major histocompatibility complex* (MHC; sometimes referred to as human leukocyte antigens or HLA in humans) is a group of glycoproteins embedded in the plasma membranes of cells.

- Important "self-markers" coded for by a family of genes
- There are at least 20 MHC genes and at least 100 alleles for each gene.
- The probability that two individuals will have matching MHC sets is virtually zero unless they are identical twins.

There are two main classes of MHC molecules in the body:

- *Class I MHC* molecules are located on all nucleated cells of the body.
- *Class II MHC* molecules are found only on specialized cells, such as macrophages, B cells, and activated T cells.

MHCs function in antigen presentation by binding to an antigen, thereby facilitating antigen binding to a T cell

- Class MHC I molecules facilitate antigen binding to cytotoxic T cells (see Campbell, Figure 43.9a).
- Class MHC II molecules facilitate antigen binding to helper T cells (see Campbell, Figure 43.9b).

III. Immune Responses

The body will mount either a *humoral* response or a *cell-mediated* response, depending on the antigen which stimulates the system (see Campbell, Figure 43.10).

Humoral immunity produces antibodies in response to toxins, free bacteria, and viruses present in the body fluids.

- Antibodies to these types of antigens are synthesized by certain lymphocytes and then secreted as soluble proteins which circulate through the body in blood plasma and lymph.

Cell-mediated immunity is the response to intracellular bacteria and viruses, fungi, protozoans, worms, transplanted tissues, and cancer cells.

- Depends on the direct action of certain types of lymphocytes rather than antibodies.

A. Helper T lymphocytes function in both humoral and cell-mediated immunity

Cells that take up antigens, such as B cells and macrophages, are known as *antigen-presenting cells (APC)*. They alert the immune system, via helper T cells, of the presence of a foreign antigen (see Campbell Figure 43.11).

- Such cells engulf foreign material (e.g., bacteria)
- Foreign protein (e.g., from broken down bacteria) binds to a newly synthesized class II MHC molecule and is conveyed to the outside of the APC.
- The class II MHC bound foreign antigen is recognized by a helper T cell.
- The interaction between the APC and the helper T cell is enhanced by the presence of a T cell membrane protein, *CD4*.

Helper T cells that bind to a class II MHC-antigen complex on an APC are induced to differentiate into either of two clones of cells:

1. *Activated helper T cells.* Secrete *cytokines*, factors that stimulate other lymphocytes (e.g., interleukin-2 (IL-2) stimulates differentiation of B cells into antibody-secreting plasma cells and induces cytotoxic T cells to become active killers).
2. *Memory helper T cells*
   - Interleukin-1 (IL-1), secreted from APCs, promotes activation of the helper T cell and the subsequent secretion of IL-2 from the activated helper T cell.
   - Helper T cells themselves are regulated by cytokines

Another type of T lymphocyte, *suppressor T cells*, may function to suppress the immune system when an antigen is no longer present.

- Action is not well understood and some immunologists feel T_S cells are actually a form of T_H cells.

B. In the cell-mediated response, cytotoxic T cells defend against intracellular pathogens

Antigen-activated cytotoxic T cells kills cells that are infected by pathogens (e.g., viruses, bacteria).

- Host cells infected by viruses and other pathogens display antigens complexed with class I MHC molecules on their surfaces.
- T_C cells have specific receptors that recognize and bind to antigen-class I MHC markers. (Note that this differs from T_H cells which bind to antigen-class II MHC complexes.)
- The T_C receptor can bind to any cell in the body displaying the antigen-class I MHC marker since class I MHC is present on all nucleated cells.

  T_C cells carry a surface molecule called CD8, which has an affinity for class I MHC molecules, and facilitates the interaction between an APC and the cytotoxic T cell (see Campbell, Figure 43.12).
- When a T_C cell binds to an infected cell (*target cell*), it releases *perforin* which is a protein that forms a lesion in the infected cell's membrane.
- Cytoplasm escapes through the lesion and eventually cell lysis occurs.
- Destruction of the host cell not only removes the site where pathogens can reproduce, but also exposes the pathogens to circulating antibodies from the humoral response.
- T_C cells continue to live after destroying the infected cell and may kill many others displaying the same antigen-class I MHC marker.

Cytotoxic T cells also function to destroy cancer cells, which develop periodically in the body.

- Cancer cells possess distinctive markers not found on normal cells, known as *tumor antigen.*
- T_C cells recognize these markers as nonself and attach and lyse the cancer cells.
- Cancers develop primarily in individuals with defective or declining immune systems.
- Certain types of cancers and viruses have diminish the amounts of class I MHC proteins on affected cells, thereby reducing the ability of cytotoxic T cell to recognize and destroy them.

C. In the humoral response, B cells produce antibodies against extracellular pathogens

The humoral response occurs when an antigen binds to B cell receptors that are specific for the antigen epitopes.

- The B cells differentiate into a clone of plasma cells which begin to secrete antibodies that are most effective against pathogens circulating in the blood or lymph.
- Memory cells are also produced and form the basis for secondary immune responses.

The selective activation of a B cell results from one of two mechanisms:

1. *T-dependent antigens* = Antigens that evoke the cooperative response involving macrophages, helper T cells, and B cells
   - These antigens cannot stimulate antibody production without T_H cell involvement (via cytokines such as IL-2).
   - Most antigens are T-dependent.
   - Memory cells are produced in T-dependent responses.
2. *T-independent antigens* = Antigens that trigger humoral immune responses without macrophages or T cell involvement
   - These antigens usually are long chains of repeating units, such as polysaccharides or protein subunits often found in bacterial capsules and flagella.
   - B cells are stimulated directly by the antigen, which probably binds simultaneously to several antigen receptors on the B cell surface.
   - The antibody production (humoral response) is usually much weaker than that of T-dependent antigens.
   - No memory cells are generated in T-independent responses.

Whether activated by T-dependent or T-independent antigens, a B cell gives rise to a clone of plasma cells.

- Each of these effector cells secretes up to 2000 antibodies per second into the body fluids for its 4- to 5-day lifespan.
- The specific antibodies help eliminate the foreign invader from the body.

1. Antibody structure and function

Antigens are usually proteins or large polysaccharides that make up a portion of the outer covering of pathogens or transplanted cells.

- May be components of the coats of viruses, capsules and cell walls of bacteria, or surface molecules of other cell types.
- Molecules on the cell surface of transplanted tissues and organs or blood cells from other individuals are also recognized as foreign.

Antibodies recognize a localized region on the surface of an antigen (epitope), not the entire antigen molecule (see Campbell, Figure 43.14).

- *Epitope* = On an antigen's surface, a localized region that is chemically recognized by antibodies; also called an antigenic determinant
- Several types of antibodies from several different B cells may be produced by a single bacterial cell since it may have different antigens on different areas and each bacterial antigen may possess more than one recognizable epitope.

Antibodies comprise a specific class of proteins called *immunoglobulins* (Igs) (see Campbell, Figure 43.15a).

The structure of the immunoglobulin is associated with its function.

- Antibodies are Y-shaped molecules comprised of four polypeptide chains: two identical *light chains* and two identical *heavy chains*.
- All four chains have constant (C) regions that vary little in amino acid sequence among antibodies that perform a particular type of defense.
- At the tips of the Y are found variable (V) regions in all four chains; the amino acid sequences in the variable region show extensive variation from antibody to antibody.
- The variable regions function as antigen-binding sites and their amino acid sequences result in specific shapes that fit and bind to specific antigen epitopes.

The antigen-binding site is responsible for the antibody's ability to identify its specific antigen epitope and the stem (constant) regions are responsible for the mechanism by which the antibody inactivates or destroys the antigenic invader.

There are five types of heavy-chain constant regions, and these determine the five major classes of antibodies (see Table 43.1 for a summary):

1. IgM. Consists of five Y-shaped monomers arranged in a pentamer structure; they are circulating antibodies that appear in response to an initial exposure to an antigen.
2. IgG. A Y-shaped monomer; most abundant circulating antibody; readily crosses blood vessels and enters tissue fluids; protects against bacteria, viruses, and toxins circulating in blood and lymph; triggers complement system action.
3. IgA. A dimer consisting of two Y-shaped monomers; produced primarily by cells abundant in mucous membranes; prevents attachment of bacteria and viruses to epithelial surfaces; also found in saliva, tears, perspiration, and colostrum.
4. IgD. A Y-shaped monomer; found primarily on external membranes of B cells; probably functions as an antigen-receptor that initiates differentiation of B cell
5. IgE. A Y-shaped monomer; stem regions attach to receptors on mast cells and basophils; stimulates these cells to release histamine and other chemicals that cause allergic reactions when triggered by an antigen

The specificity of antigen-antibody interactions has formed the bases of laboratory technologies used in research and clinical diagnosis.

- The production of monoclonal antibodies has made significant contributions to biomedical science (see Campbell, Methods box).

2. Antibody-mediated disposal of antigen

Antibodies do not directly destroy an antigenic pathogen. The antibody binds to the antigen to form an antigen-antibody complex, which tags the invader for destruction by one of several effector mechanisms (see Campbell, Figure 43.16).

- *Neutralization* is the simplest mechanism.

    - The antibody blocks viral attachment sites or coats bacterial toxins, making them ineffective. Phagocytic cells eventually destroy the complex.
- In *opsonization*, bound antibodies enhance macrophage attachment to and phagocytosis of microbes.
- Antibody-mediated *agglutination* neutralizes and opsonizes the microbes. Each antibody has two or more antigen-binding sites and can cross-link adjacent antigens. The cross-linking can result in clumps of a bacteria being held together by the antibodies, making it easier for phagocytes to engulf the mass.
- Precipitation is similar to agglutination but involves the cross-linking of soluble antigen molecules instead of cells; these immobile precipitates are easily engulfed by phagocytes.
- In *complement fixation*, antibodies combine with complement proteins; this combination activates the complement proteins, which produce lesions in the foreign cell's membrane that result in cell lysis.

The 20 or so complement proteins circulate in the blood in inactive forms.

- In an infection, these proteins become activated in a cascading fashion, with each component activating the next in the series.
- Completion of the complement cascade results in lysis of many types of viruses and pathogenic cells. Lysis by complement can be achieved two ways:

1. The classical pathway describes complement's activation in the specific defense mechanism (see Campbell, Figure 43.17)
    - Initiated when IgM or IgG antibodies bind to a specific pathogen; this targets the cell for destruction.
    - A complement protein attaches to and bridges the gap between two adjacent antibody molecules.
    - The antibody-complement association activates complement proteins to form in a step-by-step sequence, generating a *membrane attack complex*, which forms a 7 to 10 nm-diameter pore in the bacterial membrane.
    - The MAC pore allows ions and water to rush into the cell, causing it to swell and lyse.
2. The *alternative pathway* is how complement is activated in nonspecific defense mechanisms.
    - Does not require cooperation with antibodies.
    - Complement proteins are activated by substances that are naturally present on many pathogens (yeasts, viruses, virus-infected cells, protozoans) to form a membrane attack complex.
    - The complex lyses the pathogen without the aid of antibodies.

Complement proteins also contribute to inflammation by binding to histamine-containing cells; this association triggers the release of histamine from those cells.

Several complement proteins also attract phagocytic cells to infected sites.

Complement and phagocytes also work together in two ways to destroy pathogens.

1. *Opsonization* is a cooperative mechanism in which complement proteins attach to a foreign cell and stimulate phagocytes to engulf the cell.
2. In *immune adherence*, complement proteins and antibodies coat a microbe, which causes it to adhere to blood vessel walls and other surfaces; this makes the cell easy prey for circulating phagocytes.

IV. Immunity and Health and Disease

A. Immunity can be achieved naturally or artificially

Active immunity is the immunity conferred by recovery from an infectious disease.

- Depends on response by the person's own immune system
- May be acquired naturally from an infection to the body or artificially by *immunization,* also known as *vaccination*
    - Vaccines may be inactivated bacterial toxins, killed microbes, parts of microbes, or viable but weakened microbes.
    - In all cases the organisms can no longer cause the disease but can act as antigens and stimulate an immune response.
    - A person vaccinated against an infectious agent who encounters the pathogen will show the same rapid, memory-based secondary response as someone who has had the disease.

Passive immunity is immunity which has been transferred from one individual to another by the transfer of antibodies.

- Naturally occurs when IgG antibodies cross the placenta from a pregnant woman to her fetus.
- Some antibodies are transferred to nursing infants though breast milk.
- Provides temporary protection to newborns whose immune systems are not fully operational at birth.
- Persists as long as the antibodies last (a few weeks or months), but it can provide protection from infections until a baby’s own immune system has matured.
- May also be transferred artificially from an animal or human already immune to the disease.
    - Rabies is treated by injecting antibodies from people vaccinated against rabies; produces an immediate immunity important to quickly progressing infections.
    - Artificial passive immunity is of short duration but permits the body’s own immune system to begin to produce antibodies against the rabies virus.

B. The immune system’s capacity to distinguish self from nonself limits blood transfusion and tissue transplantation

The body's immune system distinguishes between self (the body's own cells) and nonself (foreign cells).

- Nonself includes pathogens and cells from other individuals of the same species.

1. Blood groups and blood transfusion

The human ABO blood groups provide a good example of nonself recognition. The antigen present on the surface of the erythrocytes is not antigenic to that person but may be recognized as foreign if placed in the body of another individual.

- Individuals of blood type A have the A antigen and make anti-B antibodies.
- Individuals of blood type B have the B antigen and make anti-A antibodies.
- Individuals of blood type AB have the A and B antigen and make no antibodies.
- Individuals of blood type O have neither the A nor B antigen and make anti-A and anti-B antibodies.

Blood group antibodies can cause blood of a different antigenic type to agglutinate, resulting in a life-threatening *transfusion reaction.*

- Type O individuals are universal donors since their blood has neither antigen.
- Type AB individuals are universal recipients since they produce neither antibody A or antibody B.

The blood group antibodies are present in the body before a transfusion occurs because they form in response to the body's normal bacterial flora that have epitopes very similar to blood group antigens.

Usually IgM class antibodies do not cross the placenta, thus they present no harm to a developing fetus with a blood type different from the mother.

The *Rh factor* is another blood group antigen. Rh factor causes problems when a mother is Rh negative and her fetus is Rh positive (inherited from the father).

- When small amounts of fetal blood cross the placenta and come into contact with the mother's lymphocytes, the mother develops antibodies against the Rh factor.
- Usually only a problem in the second child since the response will be quick due to sensitization and formation of memory cells during the first baby's gestation.

  Unlike blood group antibodies, Rh antibodies are IgG class, which can cross the placenta.

  The mother's antibodies cross the placenta and destroy the red blood cells of the Rh positive fetus.
- Can be prevented by injection of anti-Rh antibodies which destroy Rh-positive red cells before the mother develops immunological memory.

2. Tissue grafts and organ transplantation

The MHC is a biochemical fingerprint unique to each individual.

- Complicates tissue grafts and organ transplants since foreign MHC molecules are antigens and cause cytotoxic T cells to mount a cell-mediated response.
- Cyclosporin A and FK506 suppress cell-mediated immunity without crippling humoral immunity, thus increasing the chance of successful grafts and transplants.

In the case of bone marrow transplants, which are used to treat leukemia and other cancers, the graft rather than the host is the source of immune rejection

- The donated bone marrow contains lymphocytes that will react against the recipient. This graft versus host rejection is limited if the MHC molecules of the donor and recipient are well matched.

The reactions of the immune system to transfusions, tissue grafts, and organ transplants are normal reactions of a healthy immune system, not disorders of the system.

C. Abnormal immune function can lead to disease

1. Allergies

Allergy = A hypersensitivity of the body's defense system to an environmental antigen called an allergen

Some believe these reactions to be evolutionary remnants to infection by parasitic worms due to similarities in the responses.

IgE class antibodies are commonly involved in allergic reactions; these antibodies recognize pollen as allergens (see Campbell, Table 43.1)

- IgE antibodies attach by their tails to noncirculating mast cells found in connective tissues.

- When a pollen grain bridges the gap between two adjacent IgE monomers, the mast cell responds with a reaction called *degranulation* (see Campbell, Figure 43.18).
- Degranulation involves the release of histamine and other inflammatory agents.
- Histamine causes dilation and increased permeability of small blood vessels, which results in the common symptoms of an allergy.
- Antihistamines are drugs used to treat allergies since they interfere with the action of histamine.

Anaphylactic shock is a life-threatening reaction to injected or ingested antigens; it is the most serious type of acute allergic response.

- Occurs when mast cell degranulation causes a sudden dilation of peripheral blood vessels and a drastic drop in blood pressure.
- Death may occur in a few minutes.
- This hypersensitivity may be associated with foods (peanuts, fish) or insect venoms (wasp or bee stings).
- Epinephrine may be injected to counteract the allergic response.

2. Autoimmune diseases

Autoimmune disease = An immune system reaction against self

Examples:

- Some cases involve immune reactions against components of the body's own cells, which are released by the normal breakdown of skin and other tissues, especially nucleic acids in lupus erythematous.
- Rheumatoid arthritis is an autoimmune disease in which inflammation damages cartilage and bones in joints.
- Destruction of insulin-producing pancreas cells by an autoimmune reaction appears to cause insulin-dependent diabetes.
- In multiple sclerosis, T cells reactive against myelin infiltrate the central nervous system and destroy the myelin of neurons.
- Antibodies produced to repeated streptococcal infections may react with heart tissues and cause valve damage in some people.
- Other autoimmune diseases are Grave's disease and rheumatic fever.

3. Immunodeficiency diseases

Immunodeficiency refers to a condition where an individual is inherently deficient in either humoral or cell-mediated immune defenses.

- Severe combined immunodeficiency (SCID) is a congenital disorder in which both the humoral and cell-mediated immune defenses fail to function.
- Gene therapy has had some success in the treatment of a type of SCID where there is a deficiency of the enzyme adenosine deaminase.

Not all cases of immunodeficiency are inborn conditions.

- Some cancers, like Hodgkin's disease, damage the lymphatic system and make the individual susceptible to infection.
- Some viral infections cause depression of the immune system (e.g., AIDS).

Physical and emotional stress may compromise the system.

- Adrenal hormones secreted by stressed individuals affect the number of leukocytes and may suppress the system in other ways.
- Physiological evidence suggests direct links between the nervous system and the immune system.

- There is a network of nerve fibers that penetrates deep into the thymus.
- Lymphocytes have also been found to possess surface receptors for chemical signals secreted by nerve cells.

4. Acquired immunodeficiency syndrome (AIDS)

Acquired immunodeficiency syndrome is a severe immune system disorder caused by infection with the *human immunodeficiency virus (HIV).*

Individuals with AIDS are highly susceptible to *opportunistic diseases*, infections, and cancers that take advantage of a deficient immune system.

Mortality rate approaches 100%.

HIV probably evolved from another virus in central Africa and may have gone unrecognized for many years.

There are two major strains: HIV-1 and HIV-2.

HIV infects cells, including T_H cells, which carry the CD4 receptor on their surface.

- Entry by the virus requires CD4 and a coreceptor, such as fusin or CCR5.
- After entry, HIV RNA is reverse-transcribed and the product DNA is integrated into the host cell genome.
- In this provirus form, the viral genome directs the production of new virus particles.

HIV is not eliminated from the body by antibodies for several reasons:

- The latent provirus is invisible to the immune system.
- The virus undergoes rapid mutational changes in antigens during replication which eventually overwhelms the immune system.
- The population of helper T-cells eventually declines to the point where cell-mediated immunity collapses.
- Secondary infections characteristic of HIV infection develop (*Pneumocystis pneumonia* and Kaposi's sarcoma).

A person who tests positive for the presence of antibodies to the virus is *HIV-positive*.

AIDS is the late stage of HIV infection and is defined by a reduced T cell population and the appearance of secondary infections.

- Takes an average of about ten years to reach this stage of infection.
- During most of this time, only moderate symptoms are shown.
- Changes in the level of T cells can be monitored as an indication of disease progression, however, recently it has been shown that measures of viral load may be a better indicator of disease progress and the effectiveness of anti-HIV treatment.

HIV is only transmitted through the transfer of body fluids, such as blood or semen, containing infected cells.

- Most commonly transmitted in the U.S. and Europe through unprotected sex between male homosexuals and unsterilized needles in intravenous drug users.
- In Africa and Asia, transmission through unprotected heterosexual sex is rapidly increasing; especially in areas with a high incidence of other sexually transmitted diseases.
- Transmission during fetal development occurs in 25% of HIV-infected mothers.
- Transmission through blood transfusions has also been reported, but the incidence has declined greatly with implementation of screening procedures.

HIV infection is currently considered an incurable disease.

New drug combinations designed to slow the progression of the disease to AIDS are expensive and not available to all HIV-positive people.

- Drugs that slow viral replication (when used in combinations) include DNA-synthesis inhibitors, reverse transcriptase inhibitors (e.g., AZT, ddI), and protease inhibitors.
- Other drugs are used to fight opportunistic infections common in AIDS patients.

The best way to prevent additional infections is to educate people on how the disease is transmitted and how to protect themselves.

D. Invertebrates have a rudimentary immune system

How invertebrates react against pathogens that enter their bodies is poorly understood, although it is known that they have a well developed ability to distinguish self from nonself.

- Experiments have shown that if the cells from two sponges of the same species are mixed, the cells from each individual will aggregate in separate groups, excluding cells from the other individual.
- Coelomocytes, amoeboid cells that destroy foreign materials, have been found in many invertebrates.

A memory response has also been identified in earthworms.

- A body wall graft from one worm to another will survive for about eight months before rejection if the worms are from the same population.
- A graft involving worms from different populations is rejected in two weeks.
- A second graft from the same donor to the same recipient is rejected in less than one week due to coelomocyte activity.

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CHAPTER 44

CONTROLLING THE INTERNAL ENVIRONMENT

OUTLINE

I. Regulation of Body Temperature
   A. Four physical processes account for heat gain or loss
   B. Ectotherms derive body heat mainly from their surroundings; endotherms derive it mainly from metabolism
   C. Thermoregulation involves physiological and behavioral adjustments
   D. Most animals are ectothermic, but endothermy is widespread
   E. Torpor conserves energy during environmental extremes

II. Water Balance and Waste Disposal
   A. Water balance and waste disposal depend on transport epithelia
   B. An animal's nitrogenous wastes are correlated with its phylogeny and habitat
   C. Cells require a balance between osmotic gain and loss of water
   D. Osmoregulators expend energy to control their internal osmolarity; osmoconformers are isoosmotic with their surroundings

III. Excretory Systems
   A. Most excretory systems produce urine by refining a filtrate derived from body fluids: *an overview*
   B. Diverse excretory systems are variations on a tubular theme
   C. Nephrons and associated blood vessels are the functional units of the mammalian kidney
   D. From blood filtrate to urine: a closer look
   E. The mammalian kidney's ability to conserve water is a key terrestrial adaptation
   F. Nervous and hormonal feedback circuits regulate kidney functions
   G. Diverse adaptations of the vertebrate kidney have evolved
   H. Interacting regulatory systems maintain homeostasis

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. Distinguish between osmoregulators and osmoconformers.
2. Discuss the problems that marine organisms, freshwater organisms, and terrestrial organisms face in maintaining homeostasis, and explain what osmoregulatory adaptations serve as solutions to these problems.
3. Explain the role of transport epithelia in osmoregulation.
4. Describe how a flame-bulb (protonephridial) excretory system functions.

5. Explain how the metanephridial excretory tubule of annelids functions, and describe any structural advances over a protonephridial system.
6. Explain how the Malpighian tubule excretory system contributed to the success of insects in the terrestrial environment.
7. Using a diagram, identify and give the function of each structure in the mammalian excretory system.
8. Using a diagram, identify and give the function of each part of the nephron.
9. Describe and show the relationship among the processes of filtration, secretion, and reabsorption.
10. Explain the significance of the fact that juxtamedullary nephrons are only found in birds and mammals.
11. Explain how the loop of Henle enhances water conservation by the kidney.
12. Describe the mechanisms involved in the hormonal regulation of the kidney.
13. Describe structural and physiological adaptations in the kidneys of non-mammalian species that allow them to osmoregulate in different environments.
14. Explain the correlation between the type of nitrogenous waste produced (ammonia, urea, or uric acid) by an organism and its habitat.
15. Describe the adaptive advantages of endothermy.
16. Discuss the four general categories of physiological and behavioral adjustments used by land mammals to maintain relatively constant body temperatures.
17. Distinguish between the two thermoregulatory centers of the hypothalamus.
18. Describe the thermoregulatory adaptations found in animals other than terrestrial mammals.
19. Describe several mechanisms for physiological acclimatization to new temperature ranges.
20. Distinguish between hibernation and aestivation.

KEY TERMS

thermoregulation
osmoregulation
excretion
conduction
convection
radiation
evaporation
ectotherm
endotherm
vasodilation
vasoconstriction
countercurrent heat exchanger
nonshivering thermogenesis
brown fat
acclimatization
stress-induced proteins
heat-shock proteins
torpor
hibernation
estivation
transport epithelium
ammonia
uric acid
osmolarity
osmoconformer
osmoregulator
stenohaline
euryhaline
anhydrobiosis
filtration
secretion
reabsorption
protonephridium
metanephridium
Malpighian tubules
renal artery
renal vein
ureter
urinary bladder
urethra
renal cortex
renal medulla
nephron
glomerulus
Bowman's capsule
podocytes
proximal tubule
loop of Henle
distal tubule
collecting duct
cortical nephrons
juxtamedullary nephrons
afferent arteriole
efferent arteriole
peritubular capillaries
vasa recta
antidiuretic hormone
juxtaglomerular apparatus
angiotensin II
aldosterone
renin
renin-angiotensin-aldosterone system
atrial natriuretic factor

LECTURE NOTES

Most animals can survive environmental fluctuations more extreme than any of their individual cells could tolerate. This is possible because mechanisms of homeostasis maintain internal environments within ranges tolerable to body cells.

Homeostatic mechanisms include:

- Adaptation to the thermal environment (*thermoregulation*)
- Adaptation to the osmotic environment (*osmoregulation*)
- Strategies for the elimination of waste products of protein catabolism (*excretion*)

They are long-term adaptations that evolved in populations facing environmental problems.

They include cellular mechanisms and short-term physiological adjustments.

I. Regulation of Body Temperature

Metabolism and membrane properties are very sensitive to changes in an animal's internal temperature.

- Each animal lives in, and is adapted to, an optimal temperature range in which it can maintain a constant internal temperature when external temperatures fluctuate.
- Maintaining the body temperature within a range that permits cells to function efficiently is known as *thermoregulation.*

A. Four physical processes account for heat gain or loss

An organism exchanges heat with its environment by four physical processes (see Campbell, Figure 44.1):

1. *Conduction* is the direct transfer of thermal motion (heat) between molecules of the environment and a body surface.
   - Heat is always conducted from a body of higher temperature to one of lower temperature.
   - Water is 50 to 100 times more effective than air in conducting heat.
   - For example, on a hot day, an animal in cold water cools more rapidly than one on land.
2. *Convection* is the transfer of heat by the movement of air or liquid past a body surface.
   - For example, breezes contribute to heat loss from an animal with dry skin.
3. *Radiation* is the emission of electromagnetic waves produced by all objects warmer than absolute zero.
   - It can transfer heat between objects not in direct contact.
   - For example, an animal can be warmed by the heat radiating from the sun.
4. *Evaporation* is the loss of heat from a liquid's surface that is losing some molecules as gas.
   - Production of sweat greatly increases evaporative cooling.
   - Can only occur if surrounding air is not saturated with water molecules

Evaporation and convection are the most variable causes of heat loss.

Terrestrial animals are affected by all four of the above processes; aquatic animals are impacted minimally by radiation and not at all by change of state.

B. Ectotherms derive body heat mainly from their surroundings; endotherms derive it mainly from metabolism

Animals may be classified as either ectotherms or endotherms depending on their major source of body heat.

Ectotherm = An animal that warms its body mainly by absorbing heat from surroundings

- Includes most invertebrates, fishes, reptiles and amphibians
- May derive a small amount of body heat from metabolism.

Endotherm = An animal that derives most or all of its body heat from its own metabolism

- Includes mammals, birds, some fishes, and numerous insects.
- Many maintain a consistent internal temperature even as the environmental temperature fluctuates (see Campbell, Figure 44.2).

The main source of body heat distinguishes endotherms from ectotherms, not the body temperature.

- Distinction is not absolute.
  - Most ectothermic insects and some fishes are partial endotherms. These organisms retain metabolic heat to warm only certain body parts (e.g., locomotor muscles).
  - Some birds and mammals acquire additional body heat by basking in the sun.

A terrestrial lifestyle presents certain problems that have been solved by the evolution of endothermy.

Environmental temperatures fluctuate more in terrestrial habitats than in aquatic habitats.

Endothermic vertebrates are usually warmer than their surroundings, but also have mechanisms to cool their bodies.

- Maintaining a warm body temperature requires an active metabolism which contributes to a high level of cellular respiration
- This permits endotherms to be more physically active for a longer period of time in comparison to most ectotherms.

Endothermy requires more energy than ectothermy.

- At 20°C, a human has a resting metabolic rate of 1300 to 1800 kcal/day while an alligator (ectotherm) of similar weight has a resting metabolic rate of about 60 kcal/day.
- Endotherms usually consume more food than ectotherms of similar size to offset the energy requirements.

The bioenergetic connections between body temperature, an active metabolism, and mobility were important to the evolution of endothermy.

- The evolution of endothermy and a high metabolic rate were accompanied by an increase in efficiency in circulatory and respiratory systems as seen in the birds and mammals.
- Terrestrial ectotherms exhibit their own adaptations for adjusting to temperature changes in the terrestrial environment.

C. Thermoregulation involves physiological and behavioral adjustments

Endotherms and ectotherms use a combination of strategies to thermoregulate.

1. *Adjusting the rate of heat exchange between the animal and its surroundings*

   Heat loss is reduced by the presence of hair, feathers, and fat just below the skin.

   Adaptations found in the circulatory system also help regulate heat exchange.

   - The amount of blood flowing to the skin can be changed by many endotherms and some ectotherms.

    - *Vasodilation* increases the blood flow to the skin due to an increase in the diameter of blood vessels near the body surface.
    - Nerve signals cause muscles in the walls of the blood vessels to relax which permits more blood to flow through the vessel.
    - As blood flow increases, more heat is transferred to the environment by conduction, convection, and radiation.
    - *Vasoconstriction* reduces blood flow to the skin due to a decrease in the diameter of blood vessels near the body surface.
    - Reduced blood flow decreases the amount of heat transferred to the environment.
  - Heat exchange with the environment is also altered by a *countercurrent heat exchanger* (see Campbell, Figure 44.3).
    - This is a special arrangement of arteries and veins found in the extremities of many endothermic animals.
    - Arteries carrying warm blood from the body to the legs of a bird or flipper of a dolphin are in close contact with veins carrying blood from the appendage into the body.
    - This vessel arrangement enhances heat transfer from arteries to veins along the entire length of the vessel.
    - This is possible since venous blood returning from the tip of the appendage is always cooler than the arterial blood.
    - The venous blood entering the body has been warmed to almost core temperature by the exchange.
    - In some species, an alternative set of vessels which bypass the exchanger is present.
    - The rate of heat loss is controlled by the relative amount of blood that enters the appendage by the two paths.

2. *Cooling by evaporative heat loss*

   Water is lost by terrestrial endotherms and ectotherms through breathing and across the skin.

   - In low humidity, water evaporates and heat is lost by evaporative cooling.
   - Panting increases evaporation from the respiratory system.
   - Sweating or bathing in mammals increases evaporative cooling across the skin (see Campbell, Figure 44.4).

3. *Behavioral responses*

   Relocating allows animals to increase or decrease heat loss from the body.

   - In winter, many animals bask in the sun or on warm rocks.
   - In summer, many animals burrow or move to damp areas.
   - Some animals migrate to more suitable climates.

4. *Changing the rate of metabolic heat production*

   This is found only in birds and mammals.

   Increased skeletal muscle activity and non-shivering thermogenesis can greatly increase the amount of metabolic heat produced.

D. Most animals are ectothermic, but endothermy is widespread

1. Invertebrates

Most invertebrates have little control over body temperature, but some do adjust temperature by behavioral or physiological mechanisms.

- The desert locust orients the body to maximize heat absorption from the sun.
- Some large flying insects (e.g., bees) can generate internal heat by contracting all flight muscles in synchrony (functionally analogous to shivering).
  - Little wing movement occurs but large amounts of heat are produced.
  - Allows activity even on cold days and at night (see Campbell, Figure 44.5a).
- Endothermic insects such as honeybees, bumblebees, and noctuid moths have a countercurrent heat exchanger that maintains a high temperature in the thorax where flight muscles are located.

Honeybees also use social organization to regulate temperature.

- They increase movements and huddle to retain heat in cold weather.
  - Maintain constant temperature by changing the density of huddling; heat is distributed by the movement of individuals from the core to the margins of the huddle.
- In warm weather, they cool hives by transporting water to it and fanning with their wings to promote evaporation and convection.

2. Amphibians and reptiles

Amphibians produce little heat and most lose heat rapidly by evaporative cooling from their body surface, making thermoregulation difficult.

- The optimal temperature range varies greatly depending on the species.
- Seek cooler or warmer microenvironments as necessary (behavioral adaptation).
- Some can vary the amount of mucus they secrete to regulate evaporative cooling.

Reptiles are generally ectotherms that warm themselves mainly by behavioral adaptations.

- Orient the body toward the heat sources to increase uptake and maximize the body surface exposed to the heat source.
- They regulate temperature by alternately seeking sun or shade (for example, by turning direction to reduce surface area exposed to the sun).

Some reptiles have physiological adaptations that help regulate heat loss.

- When swimming in cold water, the Galapagos iguana utilizes superficial vasoconstriction to reduce heat loss.
- Female pythons that are incubating eggs increase their metabolic rate by shivering.
  - This maintains their body temperature 5° to 7°C above ambient temperature.

3. Fishes

Fish are generally ectotherms although some are endothermic.

The body temperature of most is within 1° to 2°C of the water temperature.

- Metabolic heat produced by the swimming muscles is lost to the water as blood passes through the gills.

The dorsal aorta carries blood directly from the gills to the tissues, cooling the body core.

Endothermic fishes have an adaptation to reduce heat loss (see Campbell, Figure 44.6).

- Includes large active species such as the bluefin tuna, swordfish, and great white shark.
- Large arteries carry most of the blood from the gills to tissues just under the skin.
- Branches carry blood to the deep muscles where smaller vessels are arranged into a countercurrent heat exchanger.
- The swimming muscles produce enough metabolic heat to raise temperatures at the body core.
- Endothermy enhances the activity level of these fishes by keeping the swimming muscles several degrees warmer than tissues closer to the animal's surface.

4. Mammals and birds

These organisms maintain high body temperatures within a narrow range.

- 36° – 38°C for most mammals
- 40° – 42°C for most birds

Maintaining these narrow ranges requires the ability to closely balance the rate of metabolic heat production with the rate of heat loss or gain from the outside environment.

The rate of heat production may be increased by:

1. The increased contraction of muscles

   Moving or shivering produces metabolic heat

2. The action of hormones that increase the metabolic rate and the production of heat instead of ATP.
   - *Nonshivering thermogenesis* is the hormonal triggering of heat production.
     - Found in numerous mammals and a few birds
     - Occurs throughout the body
   - Some mammals have *brown fat* between the shoulders and in the neck that is specialized for rapid heat production.

Birds and mammals also use other mechanisms to regulate environmental heat exchange.

- Vasodilation and vasoconstriction permit the maintenance of a proper core temperature even when the extremities are cooler.
- Fur and feathers trap a layer of insulating air next to the body.

  Most land mammals and birds raise their hair or feathers, thereby trapping a thicker layer of air, in response to cold.

- A layer of fat just below the human skin provides insulation (see Campbell, Figure 44.7).

Marine mammals live in water colder than their body temperature, but their adaptations to conserve heat are more effective than those of land mammals.

- They are insulated by a very thick layer of fat called blubber under the skin.

  Helps them maintain a body temperature of 36° – 38°C even in Arctic and Antarctic waters.

- Countercurrent heat exchangers reduce heat loss in the extremities where no blubber is found.

Thermoregulation by endotherms also involves cooling the body. Many birds and mammals have behavioral and physiological adaptations to cool the body.

- When whales and other marine mammals move into warm waters, excess heat is eliminated by vasodilation.
  - A large number of blood vessels in the outer skin dilate which permits increased blood flow (and heat loss by conduction) to occur.
- Terrestrial birds and mammals depend on evaporative cooling.
  - Panting increases heat loss.
  - The fluttering of vascularized pouches in the floor of the mouth in some birds increases evaporative cooling.
- Many terrestrial mammals have sweat glands.
- Some mammals spread saliva (some kangaroos and rodents) or a combination of saliva and urine (some bats) over the body to increase evaporative heat loss.

5. Feedback mechanisms in thermoregulation

Thermoregulation in humans and other terrestrial mammals involves a complex homeostatic system and feedback mechanisms (see Campbell, Figure 44.8).

- The hypothalamus contains nerve cells that control thermoregulation and many other aspects of homeostasis.
- The hypothalamus responds to changes in body temperature that are above or below the normal range (36.1° – 37.8°C).

The body's temperature is monitored by nerve cells in the skin, hypothalamus, and other parts of the body.

- Some nerve cells function as warm receptors that signal the hypothalamus when the skin or blood temperature increases.
- Others function as cold receptors that signal the hypothalamus when there is a decrease in temperature of the skin or blood.

When the body's temperature increases above the normal range, cooling mechanisms are activated.

- Vasodilation of skin vessels occurs and capillaries fill with blood; the heat radiates from the skin's surface.
- Sweat glands are activated which increases evaporative cooling.
- These changes result in a decrease in body temperature to within the normal range.
- The cooling mechanisms are "turned off" by the hypothalamus when normal body temperature is achieved.

When the body's temperature decreases below the normal range due to a cold environment, warming mechanisms are activated.

- Vasoconstriction of skin vessels occurs.
  - A smaller volume of blood passes to the skin, thus reducing heat loss from the body surface.
  - The warm blood is diverted from the skin to deeper tissues.
- Skeletal muscles are activated and shivering occurs, which generates metabolic heat.
- Nonshivering thermogenesis increases heat production.

- Changes resulting in an increase in body temperature to within the normal range.
- The warming mechanisms are "turned off" by the hypothalamus when normal body temperature is achieved.

6. Temperature range adjustments

A physiological response called *acclimatization* allows many animals to adjust to a new range of environmental temperature.

- The adjustment takes place over a period of days or weeks.
- The process is important to animals that must adjust to seasonal changes in temperature.

Acclimatization of an animal to a new external temperature range may involve several physiological changes.

- May involve changes in the cooling and warming mechanisms which maintain the internal temperature.
- May involve adjustments at the cellular level.
  - Cells may increase production of certain enzymes to compensate for the lowered activity of each molecule at lower temperatures.
  - Cells may produce enzyme variants having the same function but different temperature optima.
- Membranes may remain fluid by changing the proportions of saturated and unsaturated lipid in their composition.

Cells can also make rapid adjustments to temperature changes.

- Shock due to a large temperature increase (or other stress) stimulates the accumulation of a class of factors called *stress-induced proteins*, including *heat-shock proteins.*
  - Found in animal cells, yeast, and bacteria
  - Help prevent denaturation of other proteins by high temperatures
  - Help prevent cell death and may help maintain homeostasis while the organisms is adjusting to the external environment

E. Torpor conserves energy during environmental extremes

When food supply is low and/or environmental temperatures are extreme, many endotherms will enter a state of torpor.

- *Torpor* = Alternative physiological state in which metabolism decreases and the heart and respiratory systems slow down
- This is a mechanism to conserve energy.

Torpor may be a long-term state (hibernation, estivation) or short-term as in the daily period of torpor seen in many small mammals and birds.

Hibernation and estivation are often triggered by seasonal changes in day length.

- In *hibernation,* the body temperature is lowered; this allows an animal to survive long periods of cold and diminished food supplies.
  - Some animals will begin to eat huge quantities of food as the amount of daylight decreases.
- *Estivation* is characterized by slow metabolism and inactivity.
  - Allows the animal to survive long periods of high temperature and diminished water supply.
  - Also known as summer torpor.

Daily periods of torpor appear to be adapted to feeding patterns.

- They allow many relatively small endotherms to survive on stored energy during hours when they cannot feed.
  - These animals have a very high metabolic rate and rate of energy consumption when active.
- Most bats and shrews feed at night and enter torpor during daylight hours.
- Chickadees and hummingbirds feed during the day and undergo torpor on cold nights.
  - The body temperature of chickadees in the cold, northern forests may drop 10°C during winter nights.

An animal's biological clock appears to control its daily cycle and torpor.

- For example, shrews continue to undergo a daily torpor even when food is continually available.
- Human sleep periods and the corresponding drop in body temperature may be a remnant of a daily torpor in ancestral mammals.

Many animals can tolerate wide fluctuations in their body temperature, but no animal can withstand high concentrations of its own metabolic wastes or much change in the relative amounts of dissolved solutes and water in its cellular environment.

II. Water Balance and Waste Disposal

The majority of cells in most animals (all but sponges and cnidarians) are not exposed to the external environment, but are bathed by an extracellular fluid.

- Animals with open circulatory systems have an extracellular compartment containing hemolymph which bathes the cells.
- Animals with closed circulatory systems have two extracellular compartments—interstitial fluid and blood plasma.

By balancing water gain and loss and disposing of metabolic wastes, an animal's homeostatic mechanisms prevent environmental fluctuations from having a harmful impact.

A. Water balance and waste disposal depend on transport epithelia

The maintenance of water and ion balance as well as the excretion of metabolic wastes is managed by *transport epithelia,* which regulate the movement of solutes between their internal fluids and the external environment (see Campbell, Figure 44.9).

- Usually a single layer of cells, joined by impermeable tight junctions, facing the external environment
- May face a channel that leads to the exterior through an opening on the body surface

In most animals, transport epithelia are arranged into tubular networks with extensive surface areas.

- The transport epithelia in the nasal glands of marine birds are very efficient at eliminating the excess salts obtained from drinking seawater.

The molecular composition of the epithelium's plasma membrane determines the specific osmoregulatory functions.

- For example, the gill epithelium pumps salt out of marine fishes and pumps salts into freshwater fishes.
- May also function in excretion of metabolic wastes in some animals.

B. An animal's nitrogenous wastes are correlated with its phylogeny and habitat

The metabolism of proteins and nucleic acids produces ammonia, a small and very toxic waste product. Some animals excrete the ammonia directly, while others first convert it to urea or uric acid, which are less toxic, but require ATP to produce.

The kind of nitrogenous wastes an animal excretes depends on its evolutionary history and habitat (see Campbell, Figure 44.10).

1. **Ammonia**

Most aquatic animals excrete wastes as ammonia.

Easily permeates membranes since molecules are very water soluble.

In soft-bodied invertebrates, ammonia just diffuses across the body surface and into the surrounding water.

In fishes, ammonia is excreted as ammonium ions across gill epithelium.

The gill epithelium of freshwater fishes exchanges Na^+ from the water for NH_4^+, thus maintaining a higher Na^+ concentration in the blood.

2. **Urea**

Ammonia excretion is unsuitable for animals in a terrestrial habitat.

- It requires large amounts of water and is so toxic it must be eliminated quickly.

Urea is the nitrogenous waste excreted by mammals and most adult amphibians.

- Can be more concentrated in the body since it is about 100,000 times less toxic than ammonia; reduces water loss for terrestrial animals.
- Produced in liver by a metabolic cycle combining ammonia with CO_2. It is transported to kidneys via the circulatory system.
- Sharks produce and retain urea in the blood as an osmoregulatory agent.
- Amphibians that undergo metamorphosis and move to land as adults switch from excreting ammonia to excreting urea.

3. **Uric acid**

Uric acid is the primary form of nitrogenous waste excreted by land snails, insects, birds, and many reptiles.

- Much less soluble in water than ammonia or urea, it can be excreted as a precipitate after reabsorption of nearly all the water from the urine.
- Eliminated in a pastelike form through the cloaca (mixed with feces) in birds and reptiles.

The mode of reproduction is an important factor in determining whether uric acid or urea excretion evolved in a particular group.

- If an embryo released ammonia or urea within a shelled egg, the soluble waste would accumulate to toxic concentrations: uric acid precipitates out of solution and can be stored as a solid within the egg.

The animal's habitat, along with the phylogenetic position, influences the type of nitrogenous waste produced.

- Terrestrial reptiles excrete mostly uric acid; crocodiles excrete ammonia and uric acid; aquatic turtles excrete urea and ammonia.
- Some animals can modify their nitrogenous wastes when the temperature or water availability changes.

C. Cells require a balance between osmotic gain and loss of water

Animals cells cannot survive a net gain (swell and burst) or loss (shrivel and die) of water.

Osmosis = Diffusion of water across a selectively permeable membrane

Occurs when two solutions separated by a membrane differ in *osmolarity* (total solute concentration).

If a selectively permeable membrane separates two solutions of differing osmolarities, water flows from the hypoosmotic solution to the hyperosmotic solution.

Hyperosmotic solution = When comparing two solutions, the solution with a greater solute concentration; net water movement occurs into the solution.

Hypoosmotic solution = When comparing two solutions, the solution with a lower solute concentration; *net* water movement occurs out of the solution.

Isoosmotic solution = When comparing two solutions, a solution with a solute concentration equal to the other solution; no net water movement occurs between the solutions.

D. Osmoregulators expend energy to control their internal osmolarity; osmoconformers are isoosmotic with their surroundings

Water may enter the body of a terrestrial animal through food, drinking, and oxidative metabolism; water exits the body via evaporation and excretion. Aquatic animals are not affected by evaporation, but face the problem of osmosis where water may enter (fresh water) or leave (marine) the body.

- Even animals with specialized body coverings that retard water gain or loss have some unprotected structures exposed to the environment for gas exchange (lungs, gills).

An animal may be an osmoconformer or osmoregulator depending on their strategy for adaptation to the osmotic environment.

Osmoconformers = Animals that do not actively adjust their internal osmolarity

- Most marine invertebrates
- Body fluids are isoosmotic with surroundings

> Although these animals have an internal osmolarity that is equal to that of their surroundings, they do adjust the specific ion composition of their body fluids. For example, the osmolarity of starfish hemolymph is ca. 1000 mosm, identical to that of the seawater in which it lives. The magnesium ion concentration in the hemolymph of the starfish, however, is substantially lower than that in seawater.

Osmoregulators = Animals that regulate internal osmolarity by discharging excess water or taking in additional water

- Many marine animals, all freshwater animals, terrestrial animals, and humans.
- Net movement of water requires an osmotic gradient, the maintenance of which requires energy.
- Osmoregulation permits animals to live in a variety of habitats, but the tradeoff is that it requires an energy expenditure by the animal.

A large change in external osmolarity is fatal to most animals, although some can survive radical fluctuations.

- *Stenohaline animal* = Animal that cannot survive a wide fluctuation in external osmolarity
- *Euryhaline animal* = Animal that can survive wide fluctuations in external osmolarity
  - Can be osmoconformers or osmoregulators

1. Maintaining water balance in the sea

Most marine invertebrates are osmoconformers.

- Body fluids are isoosmotic to the environment.

- Body fluid composition usually differs from the external medium due to internal regulation of specific ions.

Some vertebrates of the Class Agnatha (hagfishes) are also osmoconformers; however, all other marine vertebrates are osmoregulators.

Most cartilaginous fishes, including sharks, maintain internal salt concentrations lower than sea water by pumping salt out through rectal glands and through the kidneys, yet their osmolarity is slightly hyperosmotic to seawater.

- Sharks retain urea as a dissolved solute in the body fluids.
- Sharks also produce and retain trimethylamine oxide (TMAO), which protects their proteins from denaturation by urea.
- Retention of these organic solutes (urea, TMAO) in the body fluids actually makes them slightly hyperosmotic to seawater.
- Water enters the shark's body by osmosis rather than by drinking, and they balance osmotic uptake of water by excreting urine.

Marine bony fishes are hypoosmotic to seawater.

- Compensate for osmotic water loss by drinking large amounts of seawater and pumping excess salt out with their gill epithelium.
- Excrete only a small amount of urine.

2. Maintaining osmotic balance in fresh water

Freshwater animals are hyperosmotic to their environment and constantly take in water by osmosis.

- Freshwater protists compensate with contractile vacuoles that pump out excess water.
- Many freshwater animals, including fish, compensate by excreting large amounts of very dilute urine.

  Since salts are lost in this process, salt is replenished either by eating substances with a higher salt content, or in the case of some fish, by active uptake of sodium and chloride ions from the surrounding water by gill epithelium.

Anadromous fishes such as salmon are euryhaline and migrate between seawater and fresh water.

- While in the ocean, they osmoregulate like other marine fishes.
- When in fresh water, they cease drinking and their gills start taking up salt from the dilute environment, just like other freshwater fishes.

3. Special problems of living in temporary waters

Anhydrobiosis is an adaptation found in a small number of aquatic invertebrates that permits them to survive in a dormant state when their habitat dries up.

Best exemplified by the tardigrades (see Campbell, Figure 44.12)

- Hydrated animals are about 1 mm long and are about 85% water.
- They can dehydrate to less than 2% water and survive in an inactive state.
- Tardigrades can survive many years in this state and will rehydrate and become active when water returns.

Dehydrated and frozen animals face the problem of keeping their cell membranes intact.

Researchers have found that dehydrated anhydrobiotic animals contain large amounts of the disaccharide trehalose along with other sugars.

Trehalose appears to replace the water associated with membranes and proteins.

Trehalose is also found in insects that survive freezing.

4. **Maintaining osmotic balance on land**

Terrestrial animals live in a dehydrating environment and cannot survive desiccation.

- Humans die if 12% of their body water is lost.

Osmoregulatory mechanisms in terrestrial animals include protective outer layers, drinking and eating moist foods, behavioral adaptations, and excretory organ adaptations that conserve water.

- Arthropods have waxy cuticles, land snails possess shells, and vertebrates are covered by a multi-layer skin comprised of dead, keratinized cells.
- Drinking and eating moist foods replaces much of the water lost during gas exchange.
- Some desert animals are nocturnal; being active only at night reduces dehydration and some like the kangaroo rat produce large amounts of metabolic water (see Campbell, Figure 44.13).
- The excretory organs of terrestrial animals are adapted to conserve water while eliminating wastes.

III. Excretory Systems

A. Most excretory systems produce urine by refining a filtrate derived from body fluids: an overview

Although the excretory systems of animals are structurally diverse, they share functional similarities

In general, urine is produced in two steps:

1. Filtration of body fluids
2. Modification of the filtrate

Modification of the filtrate can occur by two means:

1. Selective secretion of solutes (e.g., salts, toxins, etc.) from body fluids into the filtrate
2. Selective reabsorption of solutes from the filtrate back into body fluids (e.g., glucose)

B. Diverse excretory systems are variations on a tubular theme

1. **Protonephridia: flame-bulb systems**

Flatworms, which have neither circulatory systems nor coeloms, have a simple tubular excretory system called a protonephridium (see Campbell, Figure 44.15).

- *Protonephridium* = A network of closed tubules lacking internal openings that branch throughout the body; the smallest branches are capped by a cellular flame bulb
- Interstitial fluid passes through a flame bulb and is propelled by a tuft of cilia (in the flame bulb) along the branched system of tubules.
- Urine from the system empties into the external environment through numerous openings called nephridiopores.
- Transport epithelium lining the tubules function in osmoregulation by absorbing salts before the fluid exits the body.

Some parasitic flatworms are isoosmotic to their hosts and this closed system is used mainly to excrete nitrogenous wastes.

Protonephridia are also found in rotifers, some annelids, the larvae of mollusks, and lancelets.

2. Metanephridia

Each segment of most annelids, including earthworms, contains a pair of metanephridia, excretory tubules that have internal openings to collect body fluids (see Campbell, Figure 44.16)

- Coelomic fluid enters the funnel-shaped nephrostome, which is surrounded with cilia.
- The fluid passes through the metanephridium and empties into a storage bladder that empties outside the body through the nephridiopore.
- The nephrostome collects coelomic fluid from the body segment just anterior.
- A network of capillaries envelops each metanephridium.

  These capillaries reabsorb essential salts pumped out of the collecting tubules by transport epithelium bordering the lumen.
- Excretion of hypoosmotic, dilute urine offsets the continual osmosis of water from damp soil across the skin.

3. Malpighian tubules

Malpighian tubules = Excretory organs of insects and other terrestrial arthropods that remove nitrogenous wastes from the hemolymph and function in osmoregulation (see Campbell, Figure 44.17)

They are outpocketings of the gut that open into the digestive tract at the midgut-hindgut juncture.

The tubules dead-end at the tips away from the gut and are bathed in the hemolymph.

Transport epithelium lining each tubule moves solutes (salts and nitrogenous wastes) from the hemolymph into the tubule's lumen.

Accumulates nitrogenous wastes from the hemolymph and water follows by osmosis.

The fluid in the tubule then passes through the hindgut to the rectum.

Salts and water are reabsorbed across the epithelium of the rectum and dry nitrogenous wastes are excreted with feces.

4. Vertebrate kidneys

The invertebrate chordate ancestors of vertebrates probably possessed segmentally arranged excretory structures arranged throughout the body.

- Extant hagfishes have segmentally arranged excretory tubules associated with their kidneys.

The kidneys of vertebrates (other than hagfishes) are compact organs and contain large numbers of non-segmentally arranged tubules.

- Kidney structure also includes a dense capillary network intimately associated with the tubules.
- The tubules function in both excretion and osmoregulation in vertebrates that osmoregulate.

The vertebrate excretory system is comprised of the kidneys, blood vessels serving the kidneys, and the structures that carry urine from the kidneys out of the body (see Campbell, Figure 44.18).

Variations of the basic system are found among the vertebrate classes.

C. Nephrons and associated blood vessels are the functional units of the mammalian kidney

The human kidneys are a pair of bean-shaped organs about 10 cm long (see Campbell, Figure 44.18a).

Blood enters each kidney via the *renal artery* and exits via the *renal vein.*

About 20% of the blood pumped by each heartbeat passes through the kidneys.

Urine exits each kidney through a ureter and both ureters drain into a common urinary bladder.

Urine leaves the body from the urinary bladder through the urethra.

Sphincter muscles near the junction of the urethra and bladder control urination.

1. Structure and function of the nephron and associated structures

The two distinct regions of the kidney are the outer *renal cortex* and inner *renal medulla* (see Campbell, Figure 44.18b).

- Each region contains many microscopic *nephrons* and *collecting ducts* (see Campbell, Figure 44.18c).
- Associated with each excretory tubule is a network of capillaries.

Nephron = Functional unit of the kidney, consisting of a single long tubule and its associated capillaries

The blind end of the renal tubule that receives filtrate from the blood forms a cup-shaped *Bowman's capsule*, which embraces a ball of capillaries called the *glomerulus* (see Campbell, Figure 44.18d).

The Bowman's capsules and the proximal and distal convoluted tubules are located in the cortex.

The composition of blood is regulated by transport epithelia of the nephrons and collecting ducts through three processes: filtration, secretion, and reabsorption.

a. Filtration of the blood

Blood pressure forces fluid (containing water, salts, urea and other small molecules) from the glomerulus into the lumen of the Bowman's capsule.

- Porous capillaries and *podocytes* (specialized cells of the capsule) nonselectively filter out blood cells and large molecules; any molecule small enough to be forced through the capillary wall enters the nephron tubule.
- Filtrate at this point contains a mixture of glucose, salts, vitamins, nitrogenous wastes, and small molecules in concentrations similar to that in blood plasma.

b. Pathway of the filtrate

Filtrate then passes through the *proximal tubule*, the *loop of Henle* (a long hairpin turn with a descending limb and an ascending limb) and the *distal tubule*, which empties into a *collecting duct.*

- The collecting duct receives filtrate from many nephrons.
- Filtrate, now called presumptive urine (further modification can occur in the bladder), flows from the collecting ducts into the renal pelvis. The presumptive urine then drains from the chamberlike pelvis into the ureter.

Two types of nephrons are found in mammals and birds: cortical nephrons and juxtamedullary nephrons.

- *Cortical nephrons* = Nephrons that have reduced loops of Henle and are confined to the renal cortex; 80% of the nephrons in humans are cortical nephrons
- *Juxtamedullary nephrons* = Nephrons that have long loops that extend into the renal medulla; 20% of the nephrons are juxtamedullary nephrons (see Campbell, Figure 44.18c).
- The nephrons in other vertebrates lack loops of Henle.

The nephron and collecting duct are lined by transport epithelium that processes the filtrate into urine.

- About 1100 to 1200 L of blood flow through the human kidneys each day.
- The nephrons process 180 L of filtrate per day, and the transport epithelium processes this filtrate to form the approximately 1.5 L urine excreted daily.
- The rest of the filtrate is reabsorbed into the blood.

The loops of Henle and collecting tubules extend into the medulla.

c. Blood vessels associated with the nephrons

Each nephron is closely associated with blood vessels:

- *Afferent arteriole* is a branch of the renal artery that divides to form the capillaries of the glomerulus.
- *Efferent arteriole* forms from the converging capillaries as they leave the glomerulus. This subdivides to form the *peritubular capillaries* which intermingle with the proximal and distal tubules.
- *Vasa recta* is the capillary system branching downward from the peritubular capillaries that serves the loop of Henle.

Materials are exchanged between capillaries and nephrons through interstitial fluids.

d. Secretion

Filtrate is joined by substances transported across the tubule epithelium from the surrounding interstitial fluid as it moves through the nephron tubule.

- Adds plasma solutes to the filtrate.

The proximal and distal tubules are the most common sites of secretion.

Secretion is a very selective process involving both passive and active transport.

- For example, controlled secretion of H^+ ions helps maintain constant body fluid pH.

e. Reabsorption

Reabsorption is the selective transport of filtrate substances across the excretory tubule epithelium from the filtrate back to the interstitial fluid.

- Reclaims small molecules essential to the body
- Occurs in the proximal tubule, distal tubule, loop of Henle, and collecting duct
- Nearly all sugar, vitamins, organic nutrients are reabsorbed. In mammals and birds, water is also reabsorbed.

The composition of the filtrate is modified by selective secretion and reabsorption.

- The concentration of beneficial substances in the filtrate is reduced as they are returned to the body.
- The concentration of wastes and nonuseful substances is increased and excreted from the body.

The kidneys are central to the process of homeostasis as they clear metabolic wastes from the blood and respond to body fluid imbalances by selectively secreting ions.

D. From blood to filtrate: *a closer look*

Reclamation of small molecules and water from the filtrate as it flows through the nephron and collecting duct converts the filtrate into urine (see Campbell, Figure 44.19).

1. The proximal tubule alters the volume and composition of filtrate by reabsorption and secretion.
   - In this area, ammonia, drugs, and poisons processed in the liver are secreted to join the filtrate.
   - Helps maintain a constant body fluid pH by controlled secretion of H^+ and reabsorption of bicarbonate.
   - Nutrients such as glucose and amino acids are reabsorbed (by active transport) from the filtrate and returned to the interstitial fluid from which they enter the blood.

   The reabsorption of NaCl and water is also an important function of the proximal tubule.
   - Salt diffuses into the transport epithelium cells; the membranes facing the interstitial fluid then actively pump Na^+ out of the cells, which is balanced by passive transport of Cl^-. Water follows passively by osmosis.
   - Cells facing the interstitial fluid (outside the tubule) have a small surface area to minimize leakage of salt and water back into the filtrate.
2. In the descending limb of the loop of Henle, the transport epithelium is freely permeable to water but not to salt and other small solutes.
   - Filtrate moving down the tubule from the cortex to the medulla continues to lose water by osmosis since the interstitial fluid in this region increases in osmolarity.
   - The NaCl concentration of the filtrate increases due to the water loss.
3. In the ascending limb of the loop of Henle, the transport epithelium is very permeable to salt, but not to water.
   - As the filtrate ascends through the thin segment near the loop tip, NaCl diffuses out and contributes to the high osmolarity of interstitial fluids of the medulla.
   - In the thick segment leading to the distal convoluted tubule, NaCl is actively transported out into the interstitial fluid.
   - The filtrate becomes more dilute due to the removal of salts without loss of water.
4. The distal tubule is an important site of selective secretion and absorption.
   - It regulates K^+ and NaCl concentrations of body fluids by regulating K^+ secretion into the filtrate and NaCl reabsorption from the filtrate.
   - This region also contributes to pH regulation by controlled secretion of H^+ and reabsorption of bicarbonate.
5. The collecting duct carries filtrate back through the medulla into the renal pelvis.
   - The transport epithelium here is permeable to water but not to salt.

     The filtrate loses water by osmosis to the hyperosmotic fluid outside the duct which results in a concentration of urea in the filtrate.
   - The lower portion of the duct is permeable to urea, some of which diffuses out.

This contributes to the high osmolarity of the interstitial fluid of the renal medulla, which enables the kidney to conserve water by excreting a hyperosmotic urine.

E. The mammalian kidney's ability to conserve water is a key terrestrial adaptation

Cooperative action between the loop of Henle and the collecting duct maintains the osmolarity gradient in the tissues of the kidney.

- The two solutes responsible for the gradient are NaCl (deposited by the loop of Henle) and urea which leaks across the epithelium of the collecting ducts.
- The urine formed is up to four times as concentrated as the blood (about 1200 mosm/L).

1. Conservation of water by two solute gradients

The juxtamedullary nephron, with its urine-concentrating features, is a key adaptation to terrestrial life that enables mammals to excrete nitrogenous waste without squandering water.

Filtrate passing from the Bowman's capsule to the proximal tubule has about the same osmolarity as blood (300 mosm/L) (see Campbell, Figure 44.20)

A large amount of water and salt is reabsorbed as filtrate passes through the proximal tubule, which is located in the renal cortex.

The osmolarity remains about the same during the decrease in volume.

Water moves out of the filtrate by osmosis as it flows from the cortex into the medulla through the descending loop of Henle.

The osmolarity steadily increases due to loss of water until it peaks at the apex.

As filtrate moves up the ascending loop of Henle back to the cortex, salt leaves the filtrate first by passive transport and then by active transport.

Osmolarity decreases to about 100 mosm/L at this point.

Osmolarity changes very little as filtrate flows through the distal tubule as it is hypoosmotic to the interstitial fluids of the cortex.

After entering the collecting duct, the filtrate passes back through the medulla.

The filtrate loses water which increases osmolarity.

Some urea also leaks out of the lower portion of the collecting duct.

The passage of the filtrate back through the hyperosmotic medulla causes a gradual increase in osmolarity to about 1200 mosm/L; the remaining molecules are excreted in a minimal amount of water as urine which passes to the renal pelvis to the ureter.

NOTE: The loss of salt from the filtrate passing through the ascending limb of the loop of Henle to the interstitial fluid of the medulla contributes to the high osmolarity of the medulla. This, in turn, helps conserve water.

The *vasa recta* (capillary network of the renal medulla) maintains the crucial osmolarity gradient in the kidney.

- As the descending vessel conveys blood toward the inner medulla, water is lost from the blood and NaCl diffuses into the blood.
- These fluxes are reversed as blood flows back toward the cortex in the ascending vessel.
- This countercurrent system allows the vasa recta to supply the tissues with necessary substances without interfering with the osmolarity gradient.

Urine, at its most concentrated, is isoosmotic to the interstitial fluid of the inner medulla, but is hyperosmotic to body fluids elsewhere.

F. Nervous and hormonal feedback circuits regulate kidney functions

The kidney is a versatile osmoregulatory organ subject to a combination of nervous and hormonal controls.

- It excretes hyper- or hypoosmotic urine as necessary.

Three mechanisms regulate the kidney's ability to change the osmolarity, salt concentration, volume, and blood pressure: 1) antidiuretic hormone, 2) juxtaglomerular apparatus, and 3) atrial natriuretic factor.

1. *Antidiuretic hormone (ADH)* enhances fluid retention by increasing the water permeability of epithelium of the distal tubules and the collecting duct (see Campbell, Figure 44.21a)
   - ADH is produced in the hypothalamus and stored and released from the posterior pituitary gland.
   - ADH release is triggered when osmoreceptor cells in the hypothalamus detect increased blood osmolarity due to an excessive loss of water from the body.
   - Increased water reabsorption reduces blood osmolarity and reduces stimulation of the osmoreceptor cells.
     - Results in less ADH being secreted
     - Ingestion of water returns blood osmolarity to normal
   - When a large volume of water has been ingested, little ADH is released and the kidneys produce a dilute urine since little water is absorbed.
   - Alcohol can inhibit ADH release, causing dehydration.
2. The *juxtaglomerular apparatus (JGA)* is a specialized tissue near the afferent arterioles, which carries blood to the glomeruli (see Campbell, Figure 44.21b).
   - It responds to a decrease in blood pressure or blood volume, as well as to a decrease in blood sodium ion concentration by releasing the enzyme renin into the blood.
   - Renin leads to the conversion of inactive angiotensinogen to active *angiotensin II*, which functions as a hormone.
   - Angiotensin II directly increases blood pressure by causing arteriole constriction.
   - Angiotensin II acts indirectly by:
     - Signaling adrenal glands to release *aldosterone*, which stimulates Na^+ reabsorption by the distal tubules (water follows by osmosis)
     - Stimulating thirst centers in brain to induce drinking behavior
     - Increasing blood pressure and blood volume.
   - The increased blood pressure and blood volume suppresses further release of renin.
   - The *renin-angiotensin-aldosterone system (RAAS)* is part of a complex feedback circuit that functions in homeostasis.

ADH and the RAAS cooperate in homeostasis.

- ADH is released in response to increased blood osmolarity, but this does not compensate for excessive loss of salts and body fluids if blood osmolarity does not change.
- RAAS responds to a decrease in blood volume caused by fluid loss.

- ADH alone would lower blood Na^+ concentration by increasing water reabsorption, but the RAAS maintains balance by stimulating Na^+ reabsorption.

3. The hormone *atrial natriuretic factor (ANF)* opposes the RAAS.
   - Released by the heart's atrial walls in response to increased blood volume and pressure
   - Inhibits release of renin from the JGA, inhibits NaCl absorption by the collecting ducts, and reduces aldosterone release from the adrenal glands; this decreases blood volume and lowers blood pressure

G. Diverse adaptations of the vertebrate kidney have evolved in different habitats

Nephrons vary in structure and physiology and help different vertebrates to osmoregulate in their various habitats.

- Desert mammals have very long loops of Henle to maintain steep osmotic gradients that conserve water by allowing urine to become very concentrated.
- Mammals living in aquatic environments (e.g., beavers) have nephrons with very short loops of Henle, which result in production of dilute urine.
- Birds have shorter loops of Henle and produce a more dilute urine than mammals.
- Reptiles have only cortical nephrons and produce isoosmotic urine, but the epithelium of their cloaca conserves fluid by reabsorbing water from urine and feces.

  Also, most excrete nitrogenous wastes as uric acid which conserves water.
- Freshwater fish (hyperosmotic to surroundings) nephrons use cilia to sweep the large volume of very dilute urine from the body.

  Salts are conserved by efficient ion reabsorption from filtrate.
- Amphibians excrete dilute urine and accumulate certain salts from the water by active transport across the skin. On land, body fluid is conserved by water reabsorption across urinary bladder epithelium.
- Bony marine fishes (hypoosmotic to surroundings) excrete very little concentrated urine (many lack glomeruli and capsules).

  The kidneys function mainly to rid the body of divalent ions such as Ca^{2+}, $Mg^{2+,}$ and SO_4^{2-} taken in by drinking seawater.

  Monovalent ions like Na^+ and Cl^-, and the majority of nitrogenous waste (in the form of ammonium) is excreted mainly by the gills.

H. Interacting regulatory systems maintain homeostasis

Maintaining homeostasis in the internal environment involves a number of regulatory systems within an animal's body.

- Regulation of body temperature involves mechanisms that control osmolarity, metabolic rate, blood pressure, tissue oxygenation, and body weight.

While the regulatory systems normally work in concert to maintain homeostasis, under extreme physiological stress, demands of one regulatory system may conflict with those of other systems.

- Water conservation takes precedence over evaporative heat loss in very warm, dry climates.
- Many desert animals must tolerate occasional hyperthermia (abnormally high body temperature) in order to maintain body water.

The functions of the vertebrate liver are critical to maintaining homeostasis and involve interactions with most of the body's organ systems.

1. Excretion

   Excretion by the kidneys is supported by the liver, which synthesizes ammonia, urea, or uric acid from the nitrogen of amino acids.

   The liver also detoxifies many chemical poisons.

2. Bioenergetics

   The liver plays a role in regulating basal metabolic rate, a thyroid hormone-sensitive process, by converting thyroxin to the bioactive triiodothyronine.

   The liver also plays a central role in nutrient metabolism, especially the metabolism of carbohydrates.

   - Liver cells take up glucose from the blood and store excess amounts as glycogen.
   - When glucose is needed by the body, the liver converts glycogen back to glucose and releases it into the blood.
   - Blood glucose levels are closely controlled by feedback circuits which regulate the homeostatic mechanisms.

3. Osmoregulation. The liver plays a role in osmoregulation through its production of angiotensinogen, the precursor to angiotensin II.
4. Growth. The liver plays a role in growth regulation through its production and release of the proximate regulator of growth, insulin-like growth factor.

Thus, while the liver performs the essential functions, feedback circuits are in turn controlled by the nervous and endocrine systems.

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CHAPTER 45

CHEMICAL SIGNALS IN ANIMALS

OUTLINE

I. An Introduction to Regulatory Systems
   - A. The endocrine system and the nervous system are structurally, chemically, and functionally related
   - B. Invertebrate regulatory systems clearly illustrate endocrine and nervous system interactions

II. Chemical Signals and Their Modes of Action
   - A. A variety of local regulators affect neighboring target cells
   - B. Chemical signals bind to specific receptor proteins within target cells or on their surface
   - C. Most chemical signals bind to plasma-membrane proteins, initiating signal-transduction pathways
   - D. Steroid hormones, thyroid hormones, and some local regulators enter target cells and bind with intracellular receptors

III. The Vertebrate Endocrine System
   - A. The hypothalamus and pituitary integrate many functions of the vertebrate endocrine system
   - B. The pineal gland is involved in biorhythms
   - C. Thyroid hormones function in development, bioenergetics, and homeostasis
   - D. Parathyroid hormone and calcitonin balance blood calcium
   - E. Endocrine tissues of the pancreas secrete insulin and glucagon, antagonistic hormones that regulate blood glucose
   - F. The adrenal medulla and adrenal cortex help the body manage stress
   - G. Gonadal steroids regulate growth, development, reproductive cycles, and sexual behavior.

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. Compare the response times of the two major systems of internal communication: the nervous system and the endocrine system.
2. On the basis of structure and function, distinguish among types of chemical messengers.
3. Distinguish between endocrine and exocrine glands.
4. Describe the relationships among endocrine system components: hormones, endocrine glands, target cells, and target cell receptors.
5. List the general chemical classes of hormones and give examples of each.
6. Explain how pheromone function differs from hormone function.

7. Provide indirect evidence that humans may communicate with pheromones.
8. State which of the two classes of hormones is lipid soluble, and explain how this property affects hormone function.
9. Describe the mechanism of steroid hormone action, and explain the location and role of steroid hormone receptors.
10. Explain how to account for specificity in target cell response to hormonal signals.
11. Compare and contrast the two general modes of hormone action.
12. Describe hormonal regulation of insect development including the roles of ecdysone, brain hormone, and juvenile hormone.
13. Describe the location of the hypothalamus, and explain how its hormone-releasing cells differ from both endocrine gland secretory cells and other neurons.
14. Describe the location of the pituitary, and explain the functions of the posterior and anterior lobes.
15. List the posterior pituitary hormones, and describe their effects on target organs.
16. Using antidiuretic hormone as an example, explain how a hormone contributes to homeostasis and how negative feedback can control hormone levels.
17. Define tropic hormone, and describe the functions of tropic hormones produced by the anterior pituitary.
18. Explain how the anterior pituitary is controlled.
19. List hormones of the thyroid gland, and explain their role in development and metabolism.
20. Diagram the negative feedback loop which regulates the secretion of thyroid hormones.
21. State the location of the parathyroid glands, and describe hormonal control of calcium homeostasis.
22. Distinguish between α and β cells in the pancreas and explain how their antagonistic hormones (insulin and glucagon) regulate carbohydrate metabolism.
23. List hormones of the adrenal medulla, describe their function, and explain how their secretion is controlled.
24. List hormones of the adrenal cortex, describe their function, and explain how their secretion is controlled.
25. Describe both the short-term and long-term endocrine responses to stress.
26. Identify male and female gonads, and list the three categories of gonadal steroids.
27. Define gonadotropin, and explain how estrogen and androgen synthesis is controlled.
28. Describe the location of the pineal and thymus glands, list their hormone products, and describe their functions.
29. Explain how the endocrine and nervous systems are structurally, chemically, and functionally related.

KEY TERMS

hormone
target cells
endocrine system
endocrine glands
neurosecretory cells
ecdysone
brain hormone (BH)
juvenile hormone (JH)
releasing hormones
inhibiting hormones
posterior pituitary (neurohypophysis)
growth hormone (GH)
insulinlike growth factors (IGFs)
prolactin (PRL)
endorphins
pineal gland
melatonin
thyroid gland
triiodothyronine (T_3)
thyroxine (T_4)
calcitonin
parathyroid glands
adrenal glands
adrenal cortex
adrenal medulla
epinephrine
norepinephrine
catecholamines
corticosteroids
glucocorticoids

nitric oxide	follicle-stimulating hormone (FSH)	parathyroid hormone (PTH)	mineralocorticoids
growth factors	luteinizing hormone (LH)	pancreas	androgen
prostaglandins (PGs)	thyroid-stimulating hormone (TSH)	islets of Langerhans	testosterone
signal-transduction pathways	gonadotropins	alpha (α) cells	estrogen
tropic hormones	adrenocorticotropic hormone (ACTH)	glucagon	progestins
hypothalamus	melanocyte-stimulating hormone (MSH)	beta (β) cells	
pituitary gland		insulin	
anterior pituitary (adenohypophysis)		type I diabetes mellitus	
		type II diabetes mellitus	

LECTURE NOTES

I. An Introduction to Regulatory Systems

The activities of the various specialized parts of an animal are coordinated by the two major systems of internal communication: the nervous system and the endocrine system.

- The nervous system is involved with high-speed messages.
- The endocrine system is slower and involves the production, release, and movement of chemical messages.

Endocrine glands = Ductless glands that secrete hormones into the body fluids for distribution throughout the body

Exocrine glands = Secrete chemicals, such as sweat, mucus, and digestive enzymes, into ducts which convey the products to the appropriate locations

As we learn more about the regulatory processes of animals, it becomes increasingly clear that the endocrine system and the nervous system are interrelated; homeostasis depends heavily on their overlap.

A. The endocrine system and the nervous system are structurally, chemically, and functionally related

Many endocrine organs and tissues contain specialized nerve cells called *neurosecretory cells* that secrete hormones.

Several chemicals serve both as hormones of the endocrine system and as signals in the nervous system.

- Norepinephrine functions as both an adrenal hormone and as a neurotransmitter.

The regulation of several physiological processes involves structural and functional overlap between the two systems.

Positive and negative feedback regulate mechanisms of both systems (see Campbell, Figure 45.1).

B. Invertebrate regulatory systems clearly illustrate endocrine and nervous system interactions

Invertebrates possess a diversity of hormones which function in homeostasis, reproduction, development, and behavior.

In many cases, the hormone may stimulate one activity while inhibiting another.

- In *Hydra*, one hormone stimulates growth and budding while inhibiting sexual reproduction.
- In the sea hare *Aplysia*, a peptide hormone secreted by specialized neurons stimulates egg laying while inhibiting feeding and locomotion.

All arthropods have extensive endocrine systems that regulate growth and reproduction, water balance, pigment movement in the integument and eyes, and metabolism.

Hormones may act together, such as in the case of insect development and molting.

- *Ecdysone* is secreted by a pair of prothoracic glands; it triggers molting and favors development of adult characteristics and metamorphosis (see Campbell, Figure 45.2).
    - Ecdysone stimulates transcription of specific genes, the same mechanism of action as vertebrate steroid hormones.
- *Brain hormone* promotes development by stimulating production of ecdysone.
    - Brain hormone and ecdysone are balanced by *juvenile hormone (JH)*, which actively promotes retention of larval characteristics; JH is secreted by the corpora allata.
    - When JH levels decrease, ecdysone-induced molting produces a pupa; in the pupa, adult anatomy replaces larval anatomy during metamorphosis.

II. Chemical Signals and Their Mode of Action

Chemical signals operate at virtually all levels of organization

- Intracellular (includes elements of signal transduction systems)
- Cell to cell
- Tissue to tissue
- Organ to organ (this is level that was considered the subject of classic endocrinology, with hormones acting as the chemical signals)
- Organism to organism (includes pheromones, chemical signals that function between organisms of the same species; classified according to function e.g., mate attractant, territorial marker, alarm substance).

Compounds called local regulators operate at the cell to cell and tissue to tissue levels of organization (see Campbell, Figure 11.3a).

> NOTE: It is important to note that chemical mediators may act without regard to the conceptual boundaries that we place on them. A single compound may act in one instance as a cell to cell chemical mediator and in another instance as hormones or pheromones. Prostaglandins, for example, have been shown to operate at every level of biological organization.

A. A variety of local regulators affect neighboring target cells

Examples of local regulators include the following:

- Histamine (involved with various immune and regulatory responses; see Campbell, Chapters 41 and 43)
- Interleukins (involve with various immune responses; see Campbell, Chapter 43)
- Retinoic acid (involved with vertebrate development; see Campbell, Chapter 47)
- Nitric oxide (NO)
    - NO released by endothelial cells of blood vessels makes the adjacent smooth muscle cells relax, dilating the vessel.
    - NO released by white blood cells kills certain cancer cells and bacteria in the body fluids.

Growth factors = Peptides and proteins that regulate the behavior of cells in growing and developing tissues

- Must be present in the extracellular environment for certain cell types to grow and develop normally.
  - Studied mainly in cultures of mammalian cells, but also regulate development within the animal body.
  - It is likely that the interaction of numerous growth factors regulates cell behavior in developing tissues and organs.

Prostaglandins (PGs) = Modified fatty acids released into interstitial fluid that function as local regulators

- Often derived from lipids of the plasma membrane
- Very subtle differences in their molecular structure profoundly affect how these signals affect target cells (e.g., antagonistic actions of PGE and PGF).
- PGs secreted by the placenta help induce labor during childbirth by causing chemical changes in the nearby uterine muscles.
- Other PGs help defend the body by inducing fever and inflammation.

B. Chemical signals bind to specific receptor proteins within target cells or on their surface

A chemical signal can affect different target cells within an animal differently, or it may affect different species differently (e.g., thyroxine).

The action of a particular chemical signal depends upon:

- Recognition of the signal by a specific receptor in or on the target cell (see Campbell, Figure 45.3)
- Activation of a signal-transduction pathway that leads to a specific cellular response

Binding of a chemical signal to a specific receptor protein triggers chemical events within the target cell that result in a change in its behavior.

The nature of the response to a chemical signal depends on the number and affinity of the receptor proteins (see Campbell, Figure 45.4).

C. Most chemical signals bind to plasma-membrane proteins, initiating signal-transduction pathways

Because of their chemical nature, most signal molecules (e.g., peptides, proteins, glycoproteins) are unable to diffuse through the plasma membrane.

- The biological action of these factors begins at the plasma membrane, where the signal molecule binds to a specific plasma membrane receptor.
- Binding of the signal molecule to a plasma membrane receptor initiates a *signal transduction pathway*, the series of events that converts the signal into a specific cellular response.

> A specific example is the binding on the polypeptide hormone insulin to the insulin receptor. Hormone binding initiates a chain of events that leads to the activation of glucose transporters, plasma membrane transport molecules, and the subsequent uptake of glucose that accounts for the blood sugar lowering effects of insulin. Refer to Chapter 11 for specific details of signal transduction.

D. Steroid hormones, thyroid hormone, and some local regulators enter target cells and bind with intracellular receptors

The chemical nature of some regulators allows them to pass through the plasma membrane (e.g., steroids, thyroid hormones, NO). The receptors for these factors are located within target cells (see Campbell, Figure 45.5).

The binding of the signal molecule with a specific receptor initiates the signal transduction process. In many cases, the signal-receptor complex binds to DNA to modify gene expression.

III. The Vertebrate Endocrine System

The vertebrate endocrine system, through its production of numerous hormones, coordinates various aspects of metabolism, growth, development, and reproduction.

- Campbell, Figure 45.6 shows where the major endocrine glands in humans are located.
- Campbell, Table 45.1 summarizes the functions of the major vertebrate hormones.

Some of the hormones in vertebrates have a single action while others have multiple actions.

Tropic hormones act on other endocrine glands.

A. The hypothalamus and pituitary integrate many functions of the vertebrate endocrine system

The *hypothalamus* is a region of the lower brain that receives information from nerves throughout the body and brain and initiates endocrine signals appropriate to the environmental conditions.

- Contains two sets of neurosecretory cells whose secretions are stored in or regulate activity of the pituitary gland.

The *pituitary gland* is an extension of the brain located at the base of the hypothalamus. It consists of two lobes and has numerous endocrine functions (see Campbell, Figure 45.7).

The *adenohypophysis*, or *anterior pituitary*, consists of endocrine cells that synthesize and secrete several hormones directly into the blood.

- Controlled by two kinds of hormones secreted by neurosecretory cells in the hypothalamus: releasing hormones and inhibiting hormones.
  - *Releasing hormones* stimulate the anterior pituitary to secrete its hormones.
  - *Inhibiting hormones* stop the anterior pituitary from secreting its hormones.

The *neurohypophysis*, or *posterior pituitary*, stores and secretes peptide hormones that are made by the hypothalamus (e.g., oxytocin and antidiuretic hormone).

1. Posterior pituitary hormones

The hypothalamic peptide hormones, oxytocin and antidiuretic hormone (ADH), are stored in and released from the posterior pituitary.

- They are synthesized in neurosecretory cell bodies located in the hypothalamus and are secreted from the neurosecretory cell axons located in the posterior pituitary.
- Oxytocin induces uterine muscle contraction and causes the mammary glands to eject milk during nursing.
- ADH acts on the kidneys to increase water retention, which results in a decrease in urine volume.

ADH is part of the feedback mechanism that helps regulate blood osmolarity.

- Osmoreceptors (specialized nerve cells) in the hypothalamus monitor blood osmolarity.

- When plasma osmolarity increases, the osmoreceptors shrink slightly (lose water by osmosis) and transmit nerve impulses to certain hypothalamic neurosecretory cells.
- These neurosecretory cells respond by releasing ADH into the general circulation from their tips in the posterior pituitary.
- The target cells for ADH are cells lining the collecting ducts of nephrons in the kidneys.
- ADH binds to receptors on the target cells and activates a signal-transduction pathway that increases the water permeability of the collecting duct.
- Water retention is increased as water exits the collecting ducts and enters nearby capillaries.
- The osmoreceptors also stimulate a thirst drive.

  When an individual drinks water it reduces blood osmolarity to the set point.
- As more dilute blood (lower osmolarity) arrives at the brain, the hypothalamus responds by reducing ADH secretion and lowering thirst sensations.

  This prevents overcompensation by stopping hormone secretion and quenching thirst.
- Note that this negative feedback scheme includes a hormonal action and a behavioral response (drinking).

2. Anterior pituitary hormones

The anterior pituitary produces many different hormones and is regulated by releasing factors and release-inhibiting factors from the hypothalamus.

Four of the hormones (TSH, ACTH, FSH, LH) secreted from the anterior pituitary are tropic hormones that stimulate other endocrine glands to synthesize and release their hormones.

> Keep in mind that hormones may have multiple actions. The effect of GH on the liver to secrete IGFs is a tropic action, one of many actions of GH in vertebrates.

Growth hormone (GH) is a protein hormone that affects a wide variety of tissues.

- It promotes growth directly and stimulates the production of growth factors.
- For example, GH stimulates the liver to secrete *insulinlike growth factors (IGFs,)* which stimulate bone and cartilage growth.

Prolactin (PRL) is a protein hormone similar in structure to GH, although their physiological roles are very different.

- PRL produces a diversity of effects in different vertebrates, including:
  - Stimulation of mammary gland development and milk synthesis in mammals
  - Regulation of fat metabolism and reproduction in birds
  - Delay of metamorphosis; it may also function as a larval growth hormone in amphibians
  - Regulation of salt and water balance in freshwater fish

Follicle-stimulating hormone (FSH) is a tropic hormone that affects the gonads (*gonadotropin*).

- In males, it is necessary for spermatogenesis.
- In females, it stimulates ovarian follicle growth.

Luteinizing hormone (LH) is another gonadotropin, which stimulates ovulation and corpus luteum formation in females and spermatogenesis in males.

Thyroid-stimulating hormone (TSH) is a tropic hormone that stimulates the thyroid gland to produce and secrete its own hormones.

The remaining hormones from the anterior pituitary are formed by the cleaving of a single large protein, pro-opiomelanocortin, into short fragments.

- At least three of these fragments become active peptide hormones:
  - *Adrenocorticotropin (ACTH)* stimulates the adrenal cortex to produce and secrete its steroid hormones.
  - *Melanocyte-stimulating hormone (MSH)* regulates the activity of pigment-containing skin cells in some vertebrates.
  - *Endorphins* inhibit pain perception (see Campbell, Chapter 48).

B. The pineal gland is involved in biorhythms

The *pineal gland* is a small mass of tissue near the center of the mammalian brain (it is closer to the surface in some other vertebrates).

The pineal contains light-sensitive cells or has nervous connections with the eyes.

It secretes *melatonin,* a modified amino acid.

- Melatonin modulates skin pigmentation.
- Melatonin regulates functions related to light and to seasons marked by changes in day length, such as biological rhythms associated with reproduction.
- Melatonin is secreted only at night; larger amounts are secreted during winter.
- The role of melatonin in regulating biological rhythms is not yet understood.

C. Thyroid hormones function in development, bioenergetics, and homeostasis

The *thyroid gland* consists of two lobes located on the ventral surface of the trachea in mammals, and on the two sides of the pharynx in other vertebrates.

- Produces two modified amino acid hormones, T_3 (*triiodothyronine*) and T_4 (*thyroxine* or tetraiodothyronine) derived from the amino acid tyrosine.

  These differ in structure by only one iodine atom.
- Both have the same effects on their target, although T_3 is usually more active in mammals than T_4.

The thyroid gland plays a major role in vertebrate development and maturation.

- Thyroid hormones control metamorphosis in amphibians.
- Normal function of bone-forming cells and the branching of nerve cells during embryonic brain development of nonhuman animals also requires the presence of the thyroid hormones.

The thyroid gland is critical for maintaining homeostasis in mammals.

- It helps maintain normal blood pressure, heart rate, muscle tone, digestion, and reproductive functions.
- T_3 and T_4 tend to increase the rate of oxygen consumption and cellular metabolism.
- Serious metabolic disorders can result from a deficiency or excess of thyroid hormones.

  Hyperthyroidism, excessive secretion of thyroid hormones, causes high body temperature, sweating, weight loss, irritability, and high blood pressure.

  Hypothyroidism, low secretion of thyroid hormones, can cause cretinism in infants and weight gain, lethargy, and cold-intolerance in adults.

  Goiter (enlarged thyroid) is caused by a dietary iodine deficiency.

Thyroid hormone secretion is regulated by the hypothalamus and pituitary through a negative feedback system (see Campbell, Figure 45.9).

- The hypothalamus secretes TRH (TSH-releasing hormone), which stimulates TSH (thyroid-stimulating hormone) secretion by the anterior pituitary.
- When TSH binds to receptors in the thyroid, cAMP is generated and triggers release of T_3 and T_4.
- High levels of T_3, T_4, and TSH inhibit TRH secretion.

The thyroid gland in mammals also produces and secretes *calcitonin*, a peptide hormone that lowers blood calcium levels.

D. Parathyroid hormone and calcitonin balance blood calcium

Four *parathyroid glands* are embedded in the surface of the thyroid and function in the homeostasis of calcium ions.

- They secrete *PTH (parathyroid hormone)*, which raises blood Ca^{2+} levels (antagonistic to calcitonin) and needs vitamin D to function.
- PTH stimulates Ca^{2+} reabsorption in the kidney and induces osteoclasts to decompose bone and release Ca^{2+} into the blood.

PTH and calcitonin (which have opposite affects) work in an antagonistic manner and their balance in the body maintains the proper blood calcium levels (see Campbell, Figure 45.10).

E. Endocrine tissues of the pancreas secrete insulin and glucagon, antagonistic hormones that regulate blood glucose

The pancreas of many vertebrates is a compound gland that performs both exocrine and endocrine functions.

- In addition to secreting two hormones, it produces the pancreatic enzymes associated with digestion, which are carried to the small intestine via ducts.

The endocrine cells are typically clustered together is solid balls called the *islets of Langerhans.*

- Each islet is composed of *alpha (α) cells*, which secrete the peptide hormone *glucagon*, and *beta (β) cells* which secrete the hormone *insulin*.

Glucagon and insulin work together in an antagonistic manner to regulate the concentration of glucose in the blood (see Campbell, Figure 45.11)

- Blood glucose levels must remain near 90 mg/100 mL in humans for proper body function.
- At glucose levels above the set point, insulin is secreted and lowers blood glucose concentration by stimulating body cells to take up glucose from the blood.

  It also slows glycogen breakdown in the liver and inhibits the conversion of amino acids and fatty acids to sugar.
- When blood glucose levels drop below the set point, glucagon is secreted and increases blood glucose concentrations by stimulating the liver to increase the hydrolysis of glycogen, convert amino acids and fatty acids to glucose, and slowly release glucose into the blood.

Glucose homeostasis is critical due to its function as the major fuel for cellular respiration and a key source of carbon for the synthesis of other organic compounds.

Serious conditions can result when glucose homeostasis is unbalanced. Diabetes mellitus is caused by a deficiency of insulin or a loss of response to insulin in target tissues. Diabetes occurs in two forms:

- *Type I diabetes mellitus* (insulin-dependent diabetes) is an autoimmune disorder, in which the immune system attacks the cells of the pancreas.

- Usually occurs suddenly during childhood and destroys the ability of the pancreas to produce insulin
- Treated by insulin injections several times each day.

- *Type II diabetes mellitus* (non-insulin-dependent diabetes) occurs most frequently in adults over 40.
  - May be due to an insulin deficiency but more commonly results from reduced responsiveness in target cells because of changes in insulin receptors
  - Heredity is a major factor
  - Is non-insulin-dependent and can be treated with exercise and dietary controls

Both types of diabetes mellitus will result in high blood sugar concentrations if untreated.

- Kidneys excrete glucose, resulting in higher concentrations in the urine.
- More water is excreted due to the high concentration of glucose (results in the symptoms of copious urine production accompanied by thirst).
- Fat must serve as the major fuel source for cellular respiration since glucose does not enter the cells.
- In severe cases, acidic metabolites formed during fat metabolism may lower the blood pH to a life-threatening level.

F. The adrenal medulla and adrenal cortex help the body manage stress

Adrenal glands are located adjacent to kidneys.

In mammals, each gland has an outer *adrenal cortex* and inner *adrenal medulla*, which are composed of different cell types, have different functions, and are of different embryonic origin.

- Different arrangements of these same tissues are found in other vertebrates.
- The adrenal medulla has close developmental and functional ties with the nervous system.

The adrenal medulla synthesizes and secretes catecholamines (epinephrine and norepinephrine) (see Campbell, Figure 45.13).

- *Catecholamines* are secreted in times of stress when nerve cells excited by stressful stimuli release the neurotransmitter acetylcholine in the medulla. Acetylcholine combines with cell receptors, stimulating release of epinephrine.
  - Norepinephrine is released independently of epinephrine.
- Epinephrine and norepinephrine released into the blood results in rapid and dramatic effects on several targets:
  - Glucose is mobilized in skeletal muscle and liver cells.
  - Fatty acid release from fat cells is stimulated (may serve as extra energy sources).
  - The rate and stroke volume of the heartbeat is increased.
  - Blood is shunted away from the skin, gut, and kidneys to the heart, brain, and skeletal muscles by stimulation of smooth muscle contraction in some blood vessels and relaxation in others.
  - Oxygen delivery to the body cells is increased by dilation of bronchioles in the lungs.

The adrenal cortex synthesizes and secretes corticosteroids.

- Stressful stimuli cause the hypothalamus to secrete a releasing hormone that stimulates release of ACTH from the anterior pituitary.
- ACTH stimulates release of corticosteroids from the adrenal cortex.

In humans, the two primary types are glucocorticoids (e.g., cortisol) and mineralocorticoids (e.g., aldosterone).

Glucocorticoids promote glucose synthesis from noncarbohydrate substances such as proteins.

Skeletal muscle proteins are broken down and the carbon skeletons transported to the liver and kidneys.

The liver and kidneys convert the carbon to glucose which is released into the blood to increase the fuel supply.

Also have immunosuppressive effects and are used to treat inflammation.

Mineralocorticoids affect salt and water balance.

- Aldosterone stimulates kidney cells to reabsorb sodium ions and water from the filtrate.
  - This raises blood volume and blood pressure.
- Aldosterone from the RAAS (renin-angiotensin-aldosterone system), ADH, and ANF (atrial natriuretic factor) from the heart form a regulatory complex that influences the kidneys' ability to maintain the blood's ion and water concentrations.

The RAAS regulates aldosterone secretion in response to changes in plasma ion concentrations.

Severe stress also stimulates aldosterone secretion by causing the hypothalamus to secrete releasing hormones that increase ACTH secretion from the anterior pituitary, which increases aldosterone secretion by the adrenal cortex.

Current evidence indicates glucocorticoids and mineralocorticoids are important to maintaining body homeostasis during extended periods of stress (see Campbell, Figure 45.15).

G. Gonadal steroids regulate growth, development, reproductive cycles, and sexual behavior

The testes of males and ovaries of females produce steroid hormones that affect growth and development as well as regulate reproductive cycles and behaviors.

The gonads of both males and females produce all three categories of gonadal steroids (androgens, estrogens, and progestins), although the proportions differ. (see Campbell, Figure 45.14).

Androgens generally stimulate the development and maintenance of the male reproductive system.

- They are produced in greater quantities in males than females.
- Primary androgen is *testosterone*.
- Androgens produced during early embryonic development determine whether the fetus will be male or female.
- High androgen concentrations at puberty stimulate development of male secondary sex characteristics.

Estrogens perform the same functions in females as androgens do in males.

- Estradiol is the primary estrogen produced.
- They maintain the female system and stimulate development of female secondary sex characteristics.

Progestins are primarily involved with preparing and maintaining the uterus for reproduction in mammals.

- Include progesterone

The gonadotropins from the anterior pituitary (FSH and LH) control the synthesis of both androgens and estrogens.

- FSH and LH are in turn controlled by gonadotropin-releasing hormone (GnRH) from the hypothalamus.

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CHAPTER 46
ANIMAL REPRODUCTION

OUTLINE

I. Overview of Animal Reproduction
   - A. Both asexual and sexual reproduction occur in the animal kingdom
   - B. Diverse means of asexual reproduction enable animals to produce identical offspring rapidly
   - C. Reproductive cycles and patterns vary extensively among animals

II. Mechanisms of Sexual Reproduction
   - A. Internal and external fertilization both depend on mechanisms ensuring that mature sperm encounter fertile eggs of the same species
   - B. Species with internal fertilization usually produce fewer zygotes but provide more parental protection than species with external fertilization
   - C. Complex reproductive systems have evolved in many animal phyla

III. Mammalian Reproduction
   - A. Human reproduction involves intricate anatomy and complex behavior
   - B. Spermatogenesis and oogenesis both involve meiosis but differ in three significant ways
   - C. A complex interplay of hormones regulates reproduction
   - D. Embryonic and fetal development occur during pregnancy in humans and other eutherian (placental) mammals
   - E. Modern technology offers solutions for some reproductive problems

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. Distinguish between asexual and sexual reproduction.
2. List and describe four forms of asexual reproduction.
3. Explain how asexual reproduction may be advantageous for a population of organisms living in a stable, favorable environment.
4. Explain the advantages of sexual reproduction.
5. Explain the importance of reproductive cycles.
6. Distinguish among parthenogenesis, hermaphroditism, and sequential hermaphroditism.
7. Describe three mechanisms which increase the probability of successful fertilization that are found in organisms that use external fertilization.
8. List and describe the various methods of parental care by animals.
9. Using a diagram, identify and give the function of each part of the reproductive systems of an insect and a platyhelminth.

10. Using a diagram, identify and give the function of each component of the reproductive system of the human male.
11. Using a diagram, identify and give the function of each component of the human female reproductive system.
12. Discuss the hormonal control of reproduction in male mammals.
13. Explain the differences between menstrual cycles and estrous cycles.
14. Discuss the hormonal control of reproduction in female mammals.
15. Explain how the menstrual cycle and ovarian cycle are synchronized in female mammals.
16. Describe spermatogenesis.
17. Describe oogenesis.
18. Compare and contrast oogenesis and spermatogenesis.
19. Describe the hormonal changes which occur at puberty in humans.
20. Describe the four phases of the sexual response cycle.
21. Describe the changes which occur in the developing embryo and the mother during each trimester of a human pregnancy.
22. Describe the hormonal control of a pregnancy in a human female.
23. Explain the possible mechanisms which prevent the mother's immune system from rejecting the developing embryo.
24. List the various methods of contraception and explain how they work.
25. Explain how technological advancements are used to study human reproductive problems.

KEY TERMS

asexual reproduction
sexual reproduction
gametes
zygote
ovum
spermatozoon
fission
budding
gemmules
fragmentation
regeneration
parthenogenesis
hermaphroditism
sequential hermaphroditism
protogynous
protandrous
fertilization
external fertilization
internal fertilization
pheromones
gonads
spermatheca
seminiferous tubules
Leydig cells
scrotum
epididymis
ejaculation
vas deferens
ejaculatory duct
urethra
semen
seminal vesicles
prostate gland
bulbourethral glands
penis
baculum
glans penis
prepuce
ovaries
follicles
ovulation
corpus luteum
oviduct
uterus
endometrium
hymen
vestibule
labia minora
labia majora
clitoris
Bartholin's glands
mammary glands
vasocongestion
myotonia
coitus
orgasm
spermatogenesis
acrosome
oogenesis
menstrual cycle
estrous cycles
menstruation
estrus
menstrual flow phase
proliferative phase
secretory phase
ovarian cycle
follicular phase
pregnancy (gestation)
embryos
conception
trimesters
cleavage
blastocyst
placenta
organogenesis
fetus
human chorionic gonadotropin (hCG)
parturition
labor
lactation
contraception
rhythm method
natural family planning
barrier methods
condom
tubal ligation
vasectomy
in vitro fertilization

cloaca	cervix	luteal phase
testes	vagina	menopause

LECTURE NOTES

An individual organism exists for only a length of time (lifespan).

For a species to remain viable, its members must reproduce.

Only through reproduction can extinction be avoided.

I. Overview of Animal Reproduction

A. Both asexual and sexual reproduction can occur in the animal kingdom

Two principal modes of reproduction are found in animals: asexual reproduction and sexual reproduction.

Asexual reproduction is the production of offspring whose genes come from one parent without the fusion of egg and sperm.

- Relies completely on mitotic cell division

Sexual reproduction is the production of offspring by the fusion of *gametes* to form a diploid *zygote*.

- The gametes are formed by meiosis.
- The female gamete, or *ovum*, is usually a large, nonmotile cell, while the male gamete, or *spermatozoan*, is usually a small, motile cell.
- Usually involves two parents, each contributing genes to the offspring.

In sexual reproduction, the offspring have a combination of genes inherited from both parents. This mode of reproduction increases genetic variability and is, therefore, advantageous in a fluctuating environment.

B. Diverse means of asexual reproduction enable animals to produce identical offspring rapidly

There are various types of asexual reproduction found in invertebrates: fission, budding, the release of specialized cells, and fragmentation and regeneration.

Fission involves the separation of a parent into two or more individuals of approximately equal size (see Campbell, Figure 46.1).

Budding occurs when a new individual splits off from an existing one.

In cnidarians, new individuals grow out from the parental body.

Offspring may detach from the parent or remain joined to form extensive colonies.

Some invertebrates release specialized groups of cells that grow into new adults.

Freshwater sponges produce *gemmules*, which form from aggregates of several types of cells surrounded by a protective coat.

Fragmentation is the breaking of the body into several pieces, each of which develops into a complete adult.

Must be accompanied by *regeneration*, the regrowth of lost body parts

Found in sponges, cnidarians, polychaete annelids, and tunicates

Regeneration allows many animals to replace lost parts following an injury. (When the arm of a sea star is removed, it will grow a new arm.)

Several advantages are associated with asexual reproduction:

- Allows animals living in isolation to produce offspring without finding mates (e.g., sessile animals or animals in conditions of low population density)
- Allows production of many offspring in a short time

- Most advantageous in stable, favorable environments because it perpetuates successful genotypes precisely.

C. Reproductive cycles and patterns vary extensively among animals

Most animals have reproductive cycles, often related to changing seasons.

- It allows for conservation of resources; animals reproduce when energy is above that needed for maintenance.
- It allows for reproduction when environmental conditions favor offspring survival.
- Cycles are controlled by a combination of hormonal and environmental cues.

Animals employ various patterns of reproduction and may use either sexual or asexual reproduction exclusively or alternate between the two.

- In animals that employ both mechanisms, asexual reproduction often occurs under favorable conditions and sexual reproduction during times of environmental stress.
- Environmental conditions will stimulate parthenogenesis in aphids, rotifers, some freshwater crustaceans, and other animals.
  - *Parthenogenesis* = Development of an egg without fertilization
  - *Daphnia*, a freshwater crustacean, will switch from sexual to asexual reproduction depending on the season and environmental conditions.

    Each female can produce two types of eggs, one type is fertilized, the other develops by parthenogenesis.

    Adults developing by parthenogenesis are often haploid and their cells do not undergo meiosis when forming new eggs.
  - Parthenogenesis plays a role in the social organization of some insects; male honey bees (drones) are produced parthenogenetically, females develop from fertilized eggs.
  - Some fish, amphibians and lizards reproduce via a more complex form of parthenogenesis which involves a doubling of chromosomes after meiosis to create diploid “zygotes” (see Campbell, Figure 46.2).
- *Hermaphroditism* is a solution found in many animals that may have difficulty finding a member of the opposite sex.
  - Each individual has both functional male and female reproductive parts.
  - This solves the problem of finding a mate of the opposite sex for some sessile, burrowing, or parasitic animals.
  - Some self-fertilize, but most mate with another; each donates and receives sperm, thus potentially producing twice as many offspring from one mating.
- *Sequential hermaphroditism* occurs in some species.
  - An individual reverses its sex during its lifetime.
  - Some species are *protogynous* (female first); others are *protandrous* (male first).
  - Reversal is often associated with age and size.

    In protogynous species, such as the bluehead wrasse, the largest (usually the oldest) fish in the harem becomes a male and defends the harem (see Campbell, Figure 46.3).

    Some oysters are protandrous; the largest individuals become females and can produce more egg cells.

II. Mechanisms of Sexual Reproduction

Two major mechanisms of *fertilization* (the union of sperm and egg) have evolved in animals: external fertilization (see Campbell, Figure 46.4) and internal fertilization. Each has specific environmental and behavioral requirements.

A. Internal and external fertilization both depend on mechanisms ensuring that mature sperm encounter fertile eggs of the same species

Internal fertilization occurs when sperm are deposited in or near the female reproductive tract and fertilization occurs within the female's body.

- Usually requires more sophisticated reproductive systems and cooperative mating behaviors.
- Copulatory organs for sperm delivery and receptacles for sperm storage and transport must be present.
- Mating behaviors must include specific reproductive signals for copulation to occur.

In *external fertilization*, eggs are shed by a female and fertilized by a male's sperm in the environment.

- Occurs almost exclusively in moist habitats where development can occur without desiccation or heat stress.
- Some aquatic invertebrates release their eggs and sperm into the surrounding water with no contact occurring between the parents.
- Environmental cues and pheromones trigger release of mature gametes in close proximity, which increases the probability of successful fertilization.
- In vertebrates exhibiting external fertilization (fishes and amphibians), courtship behavior increases the probability of successful fertilization and permits mate selection.

Pheromones, chemical signals between organisms of the same species, may be operative in organisms that use either internal or external fertilization.

- Pheromones are easily dispersed in the environment and are active in minute amounts.
- Sex attractants in insects may be effective at distances of up to one mile.
- The role of pheromones in social behavior is further explored in Campbell, Chapter 51.

B. Species with internal fertilization usually produce fewer zygotes but provide more parental protection than species with external fertilization

Once fertilization occurs, the zygote undergoes embryonic development. The degree to which these developing embryos are protected, varies with the mechanism of fertilization and the organisms involved.

Organisms using external fertilization do not have protective coverings for the embryos.

- Fish and amphibian eggs are covered with a gelatinous coat, which permits the free exchange of gases and water.
- The water or moist habitat into which the gametes are released prevent desiccation and temperature stress.
- Very large numbers of zygotes are usually formed although only a small proportion survive to complete development.

Many types of protection are found in those animals that use internal fertilization.

- Eggs resistant to harsh environments are produced by many reptiles, all birds, and monotremes. The amniotic egg of these animals has a protective shell of protein (reptiles and monotremes) or calcium (birds), which makes them resistant to water loss and physical damage.
- Mammals (other than monotremes) do not produce a shelled egg, but possess reproductive tracts that permit embryonic development within the female parent.
  - In marsupials, the embryo develops for a short time in the uterus, then moves to the mother's pouch to complete development.
  - Eutherian (placental) mammals retain the embryo in the uterus until development is completed.
- Internal fertilization usually produces fewer zygotes than external fertilization, but survival through development is much greater due to the protection and care of the developing offspring.

Parental protection is important to survival of the developing embryo (see Campbell, Figure 46.5).

While some organisms using external fertilization show forms of parental care (nesting fish will guard the eggs against predators), parental care is most highly developed in animals using internal fertilization.

C. Complex reproductive systems have evolved in many animal phyla

The only prerequisite for sexual reproduction is that the animal possesses the capability to produce and deliver gametes to the gametes of the opposite sex.

- The simplest systems do not contain distinct *gonads*, organs that produce gametes in most animals.
- The most complex forms involve many sets of accessory structures for the transport and protection of gametes and developing embryos.

The complexity of the reproductive system is *not* necessarily related to the phylogenetic position of the animal.

- For example, the reproductive systems of parasitic flatworms is among the most complex of all animals (see Campbell, Figure 46.6).

Most polychaetes have separate sexes without distinct gonads.

- Gametes develop from undifferentiated cells lining the coelom and fill the coelom as they mature.
- In some species they are released through excretory openings; in others, the parental body splits open to release the eggs to the environment as the parent dies.

Most insects have separate sexes and complex reproductive structures (see Campbell, Figure 46.7).

- In males, sperm develop in a pair of testes, pass through a coiled duct to seminal vesicles, where they are stored.
  - During mating, the sperm are ejaculated into the female’s system.
- In females, eggs develop in a pair of ovaries and pass through ducts to the vagina where they are fertilized.
  - May have a *spermatheca*, a blind-ended sac in which sperm may be stored for a year or more.

The reproductive systems of vertebrates are all similar, but some important differences are found.

- Most mammals have separate openings for digestive, excretory, and reproductive tracts, while many nonmammalian vertebrates have only a common opening, the *cloaca*.
- Some mammals, birds and snakes have a uterus with only one branch, while most other vertebrates have a uterus that is partly or completely divided into two chambers.
- Nonmammalian vertebrates do not have well-developed *penises* and use other mechanisms to transfer spermatozoa.

III. Mammalian Reproduction

A. Human reproduction involves intricate anatomy and complex behavior

1. Reproductive anatomy of the human male

In most mammalian species, including humans, the reproductive system includes the external genitalia and the internal reproductive organs.

- The external genitalia includes the *scrotum* and *penis*.
- The internal reproductive organs consist of the gonads (*testes*), accessory glands, and associated ducts.

The male genitalia (*scrotum* and *penis*) aid the reproductive process in different ways.

- Testes develop in the abdomen and descend into the scrotum just before birth. This is important since sperm cannot develop at normal body temperature.
- By having the testes hang outside the abdominal cavity in the scrotum, the temperature is 2°C lower and sperm production can occur.
- The penis serves as the male copulatory organ. The ejaculatory duct joins the urethra (from the excretory system) which opens at the tip of the penis.
- The movement of semen through the urethra during copulation results in the sperm being deposited directly in the female system.

Internal male reproductive organs are the gonads and associated ducts (see Campbell, Figure 46.8):

- The *testes* are comprised of highly coiled tubes surrounded by layers of connective tissue.
  - The tubules, or *seminiferous tubules*, are where sperm form.
  - *Interstitial cells*, or *Leydig cells*, are scattered between the tubules and produce testosterone and other androgens.
- Sperm pass from the seminiferous tubules into the tubules of the *epididymis*.
  - These coiled tubules are where sperm are stored and mature (gain motility and fertilizing power).
- At *ejaculation*, sperm are forced through the *vas deferens*, which is a muscular duct running from epididymis to the *ejaculatory duct*.
  - The ejaculatory duct forms by the joining of the two vas deferens ducts (one from each testis) with the duct from the seminal vesicles.
  - The ejaculatory duct opens into the *urethra*, the tube that runs through the penis and drains both the excretory and reproductive systems.

There are three sets of accessory glands associated with the male system. These glands add their secretions to the *semen*.

1. A pair of *seminal vesicles* is located below and behind the bladder and empty into the ejaculatory duct.

They secrete a fluid containing mucus, amino acids (causes semen to coagulate after deposited in female), fructose (provides energy for sperm) and prostaglandins (stimulate female uterine contractions to help move semen to the uterus).

Seminal vesicle secretions make up about 60% of the total semen volume.

2. The *prostate gland* is a large gland that surrounds the upper portion of, and empties directly into, the urethra.

    It secretes a thin, milky alkaline fluid that contains several enzymes.

    Prostatic fluid balances the acidity of residual urine in the male system and the acidity of the vagina and helps activate sperm.

3. The *bulbourethral glands* are a pair of small glands below the prostate that empty into the urethra at the base of the penis.

    Secrete a clear mucus before sperm ejaculation

    The fluid neutralizes any acidic urine remaining in the urethra.

Prostaglandins in the semen thin the mucus at the opening of the uterus and stimulate contractions of the uterine muscle to help the semen move up the uterus.

The human penis is composed of three cylinders of spongy erectile tissue that fill with blood during sexual arousal.

- Rodents, raccoons, walruses and some other mammals also possess a *baculum* (a bone that helps stiffen the penis).
- The head of the penis, the *glans penis*, is covered by *prepuce*, or foreskin.

2. Reproductive anatomy of the human female

The *human female reproductive system* is more complicated than that of the male; it possesses structures not only for the production of female gametes, but also to house the embryo and fetus (see Campbell, Figure 46.9).

- The internal reproductive organs are the gonads (*ovaries*) and associated ducts and chambers, which are involved with gamete movement and embryo development.
- The external genitalia include the *clitoris* and the two sets of *labia* that surround the clitoris and vaginal opening.

The *ovaries* are located in the abdominal cavity and enclosed in a tough protective capsule.

- A mesentery flanks and attaches each ovary to the uterus.
- Each ovary contains many *follicles* (one egg cell surrounded by follicle cells, which nourish and protect the developing egg).

    All are formed at birth.

- Follicle cells also produce estrogens.
- Starting at puberty, and continuing to menopause, one follicle matures and releases its egg cell during each menstrual cycle.

During *ovulation*, the egg is expelled from the follicle (see Campbell, Figure 46.10). The remaining follicular tissue forms the *corpus luteum*, which secretes progesterone (maintains the uterine lining) and additional estrogen.

- If the egg is not fertilized, the corpus luteum degenerates.
- The egg cell is expelled into the abdominal cavity near the opening of the *oviduct*.
- Cilia lining the oviduct draw in the egg cell and convey it to the uterus.
- The *uterus* (or womb) is a thick muscular organ that can expand to accommodate a 4-kg. fetus.

- The inner uterine lining, the *endometrium*, is richly supplied with blood vessels.

The remaining female reproductive structures are:

Cervix = The neck of the uterus which opens into the vagina

Vagina = Thin-walled chamber that is the repository for semen during copulation; also forms the birth canal

The *hymen*, a vascularized membrane, usually covers the vaginal opening from birth until ruptured by vigorous physical activity or sexual intercourse.

Vestibule = Chamberlike area formed by the two pairs of skin folds covering the vaginal orifice and urethral opening

Labia minora = The slender skin folds bordering the vestibule

Labia majora = A pair of thick, fatty ridges enclosing and protecting the labia minora and vestibule

Clitoris = Bulb of erectile tissue at the front edge of the vestibule which is covered by a prepuce (small hood of skin)

Bartholin's glands = Small glands located near the vaginal opening that secrete mucus into the vestibule during sexual arousal, which facilitates intercourse by lubricating the vagina

Mammary glands are important to mammalian reproduction, although not actually a part of the reproductive system.

- They consist of small sacs of epithelial tissue that secrete milk.
- The milk drains into a series of ducts that open at the nipple.
- In a nonlactating female mammal, the mammary glands are composed primarily of adipose tissue.

3. Human sexual response

Human sexuality includes a diversity of stimuli and responses.

- Although variable, human sexual behavior is based on a common physiological pattern, the *sexual response cycle*.
- The sexual responses of males and females show similarities and differences.

Physiological reactions that predominate in both sexes can be divided into two types: vasocongestion and myotonia.

- *Vasocongestion* is the filling of a tissue (e.g., penis, clitoris) with blood due to an increased in blood flow through the arteries of that tissue.
- *Myotonia* is increased muscle tension, and both skeletal and smooth muscles may show sustained or rhythmic contractions.

There are four phases in the sexual response cycle:

1. In the *excitement* phase, the vagina and penis are prepared for *coitus* (sexual intercourse).

   Vasocongestion of the penis and clitoris occurs along with enlargement of testes, labia, and breasts. Vaginal lubrication and myotonia also occur.

2. The *plateau* phase continues the responses of the excitement phase.

   The vagina forms a depression to receive the sperm: the outer third becomes vasocongested, the inner two-thirds slightly expand, and the uterus elevates.

   In both sexes, the heart rate rises and breathing rates increase in response to stimulation of the autonomic nervous system.

3. *Orgasm* is the third and shortest phase, it is characterized by rhythmic, involuntary contractions in the reproductive systems of both sexes.

Two stages occur in males:

◊ *Emission* is the forcing of semen into the urethra due to contraction of the glands and ducts of the reproductive system.

◊ *Expulsion* (ejaculation) expels the semen due to contraction of the urethra.

In females, the uterus and outer vagina contract but the inner two-thirds of the vagina do not.

4. The *resolution* phase reverses the responses of earlier phases and completes the cycle.

   Vasocongested organs return to normal size and color.

   Muscles relax.

B. Spermatogenesis and oogenesis both involve meiosis but differ in three significant ways

Spermatogenesis is the production of mature sperm cells in adult males.

- A continuous process in adult males, which can result in 100 to 650 million sperm cells per ejaculation on a daily basis.
- Occurs in seminiferous tubules of the testes (see Campbell, Figure 46.12).

The thick head of a sperm cell contains the haploid nucleus tipped with the *acrosome*, which contains enzymes to aid in egg penetration (see Campbell, Figure 46.11).

Behind the head, the sperm cell contains many mitochondria that provide ATP for movement of the flagellum.

Oogenesis is the development of ova (mature, unfertilized egg cells) (see Campbell, Figure 46.13).

- Begins in the embryo when primordial germ cells undergo mitotic divisions to produce diploid oogonia.
- Each oogonium will develop into a primary oocyte by the time of birth of the female, resulting in all potential ova being present in the ovaries at birth.
- Between birth and puberty, primary oocytes enlarge and their surrounding follicles grow.

  They replicate their DNA and enter prophase I and remain there until activated by hormones.
- After puberty, during each ovarian cycle, FSH stimulates a follicle to enlarge and the primary oocyte within completes meiosis I to produce a haploid secondary oocyte and the first polar body. Meiosis then stops again.
- LH triggers ovulation and the secondary oocyte is released from the follicle.
- If a sperm cell penetrates the secondary oocyte's membrane, meiosis II will occur and the second polar body will separate from the ovum; this completes oogenesis.

The three important differences between spermatogenesis and oogenesis are:

1. In spermatogenesis, all four products of meiosis I and II become mature spermatozoa. In oogenesis, the unequal cytokinesis, which occurs during meiosis I and II, results in most of the cytoplasm being in one daughter cell, which will form the single ovum—the other cells (polar bodies) will degenerate.
2. Spermatogenesis is a continuous process throughout the reproductive life of the male. All potential ova that can be produced via oogenesis will be present as primary oocytes in the ovaries at the time of the female's birth.

3. Spermatogenesis occurs as an uninterrupted sequence. In oogenesis, long "resting" periods occur between the formation of the initial steps and final production of the ovum.

C. A complex interplay of hormones regulates reproduction

1. The male pattern

In males, androgens are directly responsible for formation of primary sex characteristics (reproductive organs) and secondary sex characteristics (deepening of voice, hair growth pattern, muscle growth).

- Androgens are steroid hormones produced primarily by the Leydig cells of the testes.
- Testosterone is the most important androgen produced.
- Androgens are also potent determinants of sexual and aggressive behaviors.
- GnRH from the hypothalamus stimulates the anterior pituitary to release LH (stimulates androgen production) and FSH (acts on seminiferous tubules to increase sperm production).

2. The female pattern

Hormonal control in females is more complicated and reflects the cyclic nature of female reproduction. Female mammals display two different types of cycles: estrous cycles and menstrual cycles.

Estrous cycles occur in non-primate mammals.

- Ovulation occurs after the endometrium thickens and vascularizes.
- If pregnancy does not occur, the endometrium is reabsorbed by the uterus.
- Pronounced behavioral changes occur, and seasonal and climatic changes affect the estrous cycle more than the menstrual cycle.
- *Estrus* is the period of sexual activity surrounding ovulation and is the only time most non-primate mammals will copulate. The length and frequency varies widely among species.

Menstrual cycles occur in humans and many other primates.

- Ovulation occurs after the endometrium thickens and vascularizes (as in the estrous cycle).
- If pregnancy does not occur, the endometrium is shed from the uterus through the cervix and vagina during menstruation.

The term *menstrual cycle* refers to the changes that occur in the uterus during the reproductive cycle.

- In human females, the cycle varies from one woman to another.
- Usually ranges from 20 – 40 days with an average of 28 days.
- Some women have very regular cycles; others vary from one cycle to the next.

There are three phases of the menstrual cycle. (These refer specifically to changes in the uterus; see Campbell, Figure 46.15)

1. The *menstrual flow phase* is the time during which most of the endometrium is being lost from the uterus (menstruation).

   Persists only a few days

   The first day of this phase is usually designated day 1 of the cycle.

2. The *proliferative phase* lasts for one to two weeks and involves the regeneration and thickening of the endometrium.

   The endometrium is thin at the beginning since most of its structure was lost during the preceding phase.

3. The *secretory phase* lasts about two weeks and is a time when the endometrium continues to develop.

    The endometrium continues to thicken, becomes more vascularized, and develops glands which secrete a glycogen-rich fluid.

    If an embryo does not implant in the uterine lining by the end of this phase, a new menstrual flow phase begins.

An *ovarian cycle* parallels the menstrual (uterine) cycle.

- The *follicular phase* begins this cycle and is a time during which several follicles in the ovaries begin to grow.

    The egg cells within the follicles enlarge and the follicle cell coat becomes multilayered.

    Only one of the growing follicles will continue to mature while the others degenerate.

    A fluid-filled cavity develops in the maturing follicle and grows large enough to form a bulge on the surface of the ovary.

    The ovulatory phase ends with ovulation, an event marked by eruption of the follicle and expulsion of the egg from the ovary.

- The *luteal phase* begins after ovulation.

    Follicular tissue remaining in the ovary after ovulation forms a *corpus luteum.*

    The corpus luteum is endocrine tissue that secretes female hormones.

Five hormones work together (by positive and negative feedback mechanisms) to coordinate the menstrual and ovarian cycles. This coordination synchronizes follicle growth and ovulation with preparation of the uterine lining for embryo implantation (see Campbell, Figure 46.15).

- During the follicular phase of the ovarian cycle, *GnRH* secreted by the hypothalamus stimulates the anterior pituitary to secrete small quantities of *FSH* and *LH*. Note that GnRH is secreted in a phasic manner; this secretory pattern, linked with higher brain centers (biological clock), drives the cyclic nature of the female reproductive pattern.
- FSH stimulates the immature follicles in the ovary to grow and these follicle cells secrete small amounts of *estrogen.*
- As the follicle continues to grow, the amount of estrogen secreted increases. The mature follicle secretes a large amount of estrogen.
- The high concentration of estrogen stimulates the hypothalamus to increase secretion of GnRH, which results in a sudden increase in FSH and LH secretion.

    LH increases more than FSH because high estrogen levels increases the sensitivity of LH-releasing mechanisms (in the pituitary) to GnRH.

    The follicles have LH receptors and can respond directly to the hormone.

- The sudden surge in LH concentration stimulates final maturation of the follicle and ovulation (after about 24 hours). The high concentration of LH stimulates the ruptured follicular tissue to transform into the corpus luteum.
- The presence of LH during the luteal phase of the ovarian cycle stimulates the corpus luteum to continue to secrete estrogen, but to also secrete increasing amounts of *progesterone.*
- Increasing concentrations of estrogen and progesterone inhibits GnRH secretion by the hypothalamus resulting in a decrease in FSH and LH.

- As the LH concentration declines, the corpus luteum begins to atrophy; this results in a sudden drop in estrogen and progesterone concentrations.
- Decreasing levels of estrogen and progesterone removes the inhibition exerted on the hypothalamus, which begins to secrete small amounts of GnRH that stimulates the anterior pituitary to secrete low levels of FSH and LH.
- A new follicular phase begins at this point.

Coordination of the menstrual cycle with the ovarian cycle depends primarily on the levels of estrogen and progesterone.

- Increasing amounts of estrogen secreted by growing follicles during the follicular phase stimulate the endometrium lining the uterus to thicken in preparation for the embryo.

  Coordination of the follicular phase of ovarian cycle with proliferative phase of the menstrual cycle.
- After ovulation, the estrogen and progesterone secreted by the corpus luteum stimulate continued development and maintenance of the endometrium.

  Arteries supplying blood to the endometrium enlarge and the endometrial glands that supply the nutritional fluid to the early embryo grow and mature.

  Coordination of the luteal phase of the ovarian cycle with the secretory phase of the menstrual cycle.
- Decreasing concentrations of estrogen and progesterone due to the disintegration of the corpus luteum reduce blood flow to the endometrium.

  The endometrium breaks down and passes out of the uterus as the menstrual flow.
- A new menstrual cycle begins with a new ovarian cycle.
- Estrogens are also responsible for development of the female secondary sex characteristics.

a. Menopause

Human females stop menstruation and ovulation at *menopause*, usually between the ages of 46 to 54.

- Ovaries lose their responsiveness to LH and FSH.
- Some scientists suggest that menopause is adaptive so that females can provide better care to their children and grandchildren.

D. Embryonic and fetal development occur during pregnancy in humans and other eutherian (placental) mammals

1. From conception to birth

In placental mammals, *pregnancy (gestation)* is the condition of carrying one or more developing *embryos* in the uterus.

- It is preceded by *conception* (fertilization of an egg by a sperm cell) and ends with birth of the offspring.
- Human pregnancy averages 266 days from conception.
- Duration in other species correlates with body size and extent of development of young at birth.

Human gestation is divided into three *trimesters*, each of about 3 months duration.

The *first trimester* is when the most radical changes occur for both the mother and baby.

- Fertilization occurs in the oviduct and *cleavage* (cell division) begins in about 24 hours (see Campbell, Figure 46.16).
- As cleavage continues, the zygote develops into a ball of cells passing down the oviduct to the uterus.
- The embryo reaches the uterus in 3 to 4 days and develops into a hollow ball of cells called a *blastocyst.*
    - This stage develops about one week after fertilization.
- The blastocyst will implant into the endometrium in the next 5 days.
- During implantation, the blastocyst bores into the endometrium, which grows over the blastocyst.
    - For the first 2 to 4 weeks of development, nutrients are obtained directly from the endometrium.
- Embryonic tissues begin to mingle with the endometrium to form the *placenta*, which functions in respiratory gas exchange, nutrient transfer, and waste removal for the embryo.
    - Blood from the embryo passes through the umbilical arteries to the placenta and returns through the umbilical vein (see Campbell, Figure 46.17).
- The first trimester is also the main period of *organogenesis* (development of organs) (see Campbell, Figure 46.18).
    - After eight weeks, the embryo develops into a *fetus* and possesses all organs of the adult in rudimentary form.
    - The fetus is about 5 cm in length by the end of the first trimester.
- During this trimester, the embryo secretes hormones that signal its presence and controls the mother's reproductive system.
- *Human chorionic gonadotropin* (h*CG*) is an embryonic hormone that maintains progesterone and estrogen secretion by the corpus luteum to prevent menstruation, which would end the pregnancy.
- High progesterone levels also stimulate formation of a protective mucous plug in the cervix, growth of the maternal part of the placenta, uterus enlargement, and cessation of ovulation and menstrual cycling.

In the *second trimester*, rapid growth occurs and the fetus is very active.

- The fetus grows rapidly to about 30 cm in length.
- The mother may feel movement during the early part of this trimester.
- Hormone levels stabilize as hCG declines, the corpus luteum degenerates, and the placenta secretes its own progesterone to maintain the pregnancy.
- The uterus grows sufficiently for the pregnancy to become obvious.

In the *third trimester,* growth is rapid and fetal activity decreases.

- The fetus grows to about 50 cm in length and 3 to 3.5 kg in weight.
- The maternal abdominal organs become compressed and displaced.
- Labor is induced and regulated by interplay among estrogen, oxytocin, and prostaglandins (see Campbell, Figure 46.19).
    - High estrogen levels during the last weeks of pregnancy trigger the formation of oxytocin receptors on the uterus.
    - Oxytocin (from the fetus and maternal posterior pituitary) stimulate the smooth muscles of the uterus to contract.

  - Oxytocin also stimulates prostaglandin secretion by the placenta (the prostaglandins enhance the muscle contractions).
  - The physical and emotional stresses caused by the uterine muscle contractions stimulate secretion of additional oxytocin and prostaglandins.

Parturition (birth) occurs through a series of strong, rhythmic contractions of the uterus usually called *labor* (see Campbell, Figure 46.20).

- The first stage of labor involves the opening and thinning of the cervix until it is completely dilated.
- The second stage is the expulsion of the baby from the uterus.

  During this time there are continuous strong uterine contractions.
- The last stage is expulsion of the placenta from the uterus.

Mammals are unique among animals due to the *lactation* component of their postnatal care.

- Decreasing levels of progesterone after birth remove the inhibition from the anterior pituitary, which allows *prolactin* secretion.
- Prolactin stimulates milk production after 2 to 3 days' delay.
- Oxytocin controls the release of milk from the mammary glands.

2. Reproductive immunology

One function of the immune system is to protect the body from bodies identified as foreign (nonself).

- Although the embryo possesses many chemical markers that are "foreign" to the mother, an immune response is not mounted against the embryo.

  Foreign markers result from the half of the genome inherited from the father.
- Reasons why the mother does not reject the developing embryo are only partly known but include the presence of the trophoblast and a number of hypotheses.

The *trophoblast* is a protective layer that forms a physical barrier preventing the embryo from actually contacting maternal tissues.

- Develops from embryonic cells of the blastocyst and penetrates the endometrium.
- May not be detected as foreign due to production of a chemical signal that stimulates production of specialized type of white blood cells in the uterus.

  These special white blood cells act to suppress other white blood cells by secreting a chemical that blocks the interleukin-2 action required for normal immune responses.
- Some researchers believe this interference with localized immune responses may occur only after the trophoblast has been identified as foreign by uterine white blood cells which have begun an immune response.

  No suppressor cells are produced if the paternal cellular markers are very similar to the maternal markers.

Many women who have multiple miscarriages may be rejecting the embryo as foreign tissue.

- Some researchers have speculated that in some cases, spontaneous abortions are due to a failure to suppress the immune response in the uterus.

- The hypothesis is that the mother's immune response is too weak to trigger suppression and that the continued immune response is sufficient to reject the embryo.

3. Contraception

There are three major ways to achieve contraception: prevent fertilization by keeping sperm and eggs apart; prevent implantation of the embryo; or prevent the release of mature eggs and sperm from the gonads (see Campbell, Figure 46.21).

Preventing the egg and sperm from meeting in the female reproductive tract prevents fertilization.

- The *rhythm method* (or *natural family planning*) involves refraining from intercourse when conception is most likely (failure rate = 10-20%).
  - Temporary abstinence during the days before and after ovulation is necessary since the egg can survive for 24 to 48 hours in the oviduct and sperm up to 72 hours.
  - The time of ovulation may be hard to predict even in women with regular menstrual cycles.
- Condoms, diaphragms, cervical caps, and contraceptive sponges are physical barriers that block the sperm from meeting the egg.
  - Failure rate < 10%; most effective when used in conjunction with spermicidal foam or jelly.
- Preventing implantation of a blastocyst in the uterus can be accomplished by using an *intrauterine device* (*IUD*).
  - IUDs are small plastic devices fitted into the uterine cavity.
  - Probably works by irritating the endometrium but precise mechanism is unknown.
  - May have serious side effects such as persistent bleeding, uterine infections and other complications.
- Withdrawal is unreliable since sperm may be present in secretions preceding ejaculation.
- Chemical contraception prevents the release of mature gametes from the gonads.
  - Failure rates < 1%.
  - The commonly used birth control pills are combination of synthetic estrogen and progestin (similar to progesterone).
  - These hormones stop release of GnRH, LH and FSH through a negative feedback mechanism.
    - By blocking LH release, progestin prevents ovulation.
    - Estrogen inhibits FSH so no follicles develop.
  - The *minipill* contains only progestin and may be in the form of an oral pill or an implant.
    - Prevents sperm from entering the uterus by altering the woman's cervical mucus.
- Sterilization by *tubal ligation* (cutting the oviduct in women) or *vasectomy* (cutting the vas deferens of men) is nearly 100% effective, safe, but difficult to reverse.

If contraceptive methods are unsuccessful, a pregnancy will occur. The pregnancy may be terminated in several ways.

- A *miscarriage* (spontaneous abortion) occurs in as many as one-third of all pregnancies.

May occur so early that the woman isn't aware of the pregnancy.

- Physician assisted abortions are chosen by about 1.5 million women annually in the United States.
- A drug-induced abortion using RU-486 is a nonsurgical method, which is effective in the first few weeks of the pregnancy.

  RU-486 is a progesterone analog which blocks progesterone receptors in the uterus.

E. Modern technology offers solutions for reproductive problems

Technological advances have made it possible to detect problems in the developing fetus (see Campbell, Figure 46.22).

Ultrasound imaging is a noninvasive procedure in which a scanner emits high-frequency sound waves that are reflected back by tissues of varying densities to form an image of the fetus.

Sampling of maternal blood also provides a means of diagnosing fetal status. A few fetal blood cells (which are nucleated as compared to the non-nucleated red blood cells of adults) cross the placenta a can serve as source material for genetic screening.

Amniocentesis is an invasive procedure in which a needle is inserted into the amnion and a sample of fluid is withdrawn.

- Fluid contains fetal cells that are cultured and analyzed for chromosomal defects and genetic disorders
- Often takes weeks to obtain the results
- 1% risk of spontaneous abortion following procedure

Chorionic villus sampling is another invasive procedure where a small portion of the chorion (a fetal part of the placenta) is removed, cultured and analyzed for genetic and metabolic disorders.

- 5% to 20% risk of spontaneous abortion following procedure
- Can be performed earlier in pregnancy and results are obtained in days

Scientific discovery has solved some fertility problems.

- For cases of male infertility, sperm from anonymous donors are widely available from sperm banks.
- *In vitro fertilization* can permit women with blocked oviducts to become pregnant.
  - Ova are surgically removed from hormonally stimulated follicles, fertilized in petri dishes and the embryo placed in the uterus for implantation.
  - Difficult and costly procedure with a success rate of about 1 in every 6 attempts.
  - Embryos may be frozen for use after unsuccessful attempts.

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CHAPTER 47
ANIMAL DEVELOPMENT

OUTLINE

I. The Stages of Early Embryonic Development
   A. From egg to organism, an animal's form develops gradually: *the concept of epigenesis*
   B. Fertilization activates the egg and brings together the nuclei of sperm and egg
   C. Cleavage partitions the zygote into many smaller cells
   D. Gastrulation rearranges the blastula to form a three-layered embryo with a primitive gut
   E. In organogenesis, the organs of the animal body from the three embryonic germ layers
   F. Amniote embryos develop in a fluid-filled sac within a shell or uterus

II. The Cellular and Molecular Basis of Morphogenesis and Differentiation
   A. Morphogenesis in animals involves specific changes in cell shape, position, and adhesion
   B. The developmental fate of cells depends on cytoplasmic determinants and cell-cell induction: *a review*
   C. Fate mapping can reveal cell geneologies in chordate embryos
   D. The eggs of vertebrates contain cytoplasmic determinants that help establish the body axes and differences among cells of the early embryo
   E. Inductive signals drive differentiation and pattern formation in vertebrates

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. List the two functions of fertilization.
2. Describe the acrosomal reaction, and explain how it ensures the gametes are conspecific.
3. Describe the cortical reaction.
4. Explain how the acrosomal and cortical reactions function sequentially to prevent polyspermy.
5. Describe the changes that occur in an activated egg and explain the importance of cytoplasmic materials to egg activation.
6. Explain the importance of embryo polarity during cleavage.
7. Describe the process of gastrulation and explain its importance.
8. List adult structures derived from each of the primary tissue layers.
9. Using diagrams, identify the various stages of embryonic development of an amphibian.
10. Distinguish between meroblastic cleavage and holoblastic cleavage.
11. List and explain the functions of the extraembryonic membranes in bird and reptile eggs.

12. Compare and contrast development in birds and mammals.
13. Explain the relationships among polarity, cytoplasmic determinants, and development.
14. Describe how cell extension, contraction and adhesion are involved in shaping the embryo.
15. Explain how interactions among the three primary tissue layers influence organogenesis.
16. Explain the relationship between cytoplasmic cues and cell determination.
17. Describe the importance of cell location and orientation along the three body axes with respect to polarity in the embryo, morphogenetic movements, and pattern formation.
18. Explain how positional cues influence pattern formation.

KEY TERMS

preformation	morula	yolk plug	inner cell mass
epigenesis	blastocoel	organogenesis	trophoblast
acrosomal reaction	blastula	notochord	convergent extension
fast block to polyspermy	meroblastic cleavage	neural tube	cell adhesion molecules (CAMs)
cortical reaction	holoblastic cleavage	somites	cadherins
cortical granules	gastrulation	amniotes	fate map
fertilization membrane	gastrula	blastodisc	pattern formation
slow block to polyspermy	ectoderm	primitive streak	positional information
zona pellucida	endoderm	extraembryonic membranes	apical epidermal ridge (AER)
cleavage	mesoderm	yolk sac	zone of polarizing activity (ZPA)
blastomeres	invagination	amnion	
yolk	archenteron	chorion	
vegetal pole	blastopore	allantois	
animal pole	dorsal lip	blastocyst	
gray crescent	involution		

LECTURE NOTES

Animals develop throughout their lifetime. Development begins with the changes that form a complete animal from the zygote and continue as progressive changes in form and function.

I. The Stages of Early Embryonic Development

A. From egg to organism, an animal's form develops gradually: *the concept of epigenesis*

Two early views of how animals developed from an egg competed for supporters until modern techniques were developed. One view was termed preformation and the other epigenesis.

Preformation suggested that the embryo contained all of its descendants as a series of successively smaller embryos within embryos (see Campbell, Figure 47.1).

- Based on this idea, by dissecting an egg an individual would be able to find smaller and smaller individuals as the dissection continued.
- This was a popular idea as recently as the eighteenth century.

Epigenesis proposed that the form of an embryo gradually emerged from a formless egg.

- Originally proposed by Aristotle
- Gained support in the nineteenth century as improved microscopy permitted biologists to view embryos as they gradually developed.

Modern biology has found that an organism's development is mostly determined by the zygote's genome and the organization of the egg cell's cytoplasm.

- The heterogenous distribution of messenger RNA, proteins, and other components in the unfertilized egg greatly impacts the development of the embryo in most animals.
- After fertilization, cell division partitions the heterogenous cytoplasm in such a way that nuclei of different embryonic cells are exposed to different cytoplasmic environments.
- These different cytoplasmic environments result in the expression of different genes in different cells.
- This leads to an emergence of inherited traits that is ordered in space and time by mechanisms controlling gene expression.

B. Fertilization activates the egg and brings together the nuclei of sperm and egg

Fertilization is important because:

- It forms a diploid zygote from the haploid sets of chromosomes from two individuals.
- It triggers onset of embryonic development.

1. The acrosomal reaction

The *acrosomal reaction* is the discharge of hydrolytic enzymes from a vesicle in the acrosome of a sperm cell (based on studies with sea urchins):

- Upon contacting the egg's jelly coat, the acrosomal vesicle in the head of the sperm releases hydrolytic enzymes via exocytosis.
- These enzymes enable an acrosomal process to elongate and penetrate the jelly coat (see Campbell, Figure 47.2).
- A protein coating the tip of the process attaches to specific receptors on the egg's vitelline layer (just external to the plasma membrane).
- This provides species specificity for fertilization.
- Enzymes of the acrosomal process probably digest vitelline layer materials allowing the tip of the process to contact the egg’s plasma membrane.
- The sperm and egg's plasma membranes fuse, allowing the sperm nucleus to enter the egg and causing a depolarization of the plasma membrane that prevents other sperm cells from also uniting with the egg (*fast block to polyspermy*).

2. The cortical reaction

The fusion of the egg and sperm membranes stimulates a series of changes in the egg’s cortex known as a *cortical reaction* (see Campbell, Figure 47.2, step 6).

- The fusion of sperm and egg stimulates a signal transduction pathway that causes the release of calcium (Ca^{2+}) from the egg cell’s endoplasmic reticulum (ER) (see Campbell, Figure 47.3).
- The signaling pathway also leads to the production of IP_3, which in turn, opens ligand-gated calcium channels on the ER.
- The high Ca^{2+} concentration results in a change in the egg’s *cortical granules* (special vesicles).
- The increase in Ca^{2+} causes the cortical granules to fuse with the plasma membrane and release their contents into the perivitelline space outside the plasma membrane.

  The contents of the cortical granules include enzymes that separate the vitelline layer from the plasma membrane.

Mucopolysaccharides produce an osmotic gradient which stimulates osmosis into the perivitelline space causing the area to swell.

The swelling elevates the vitelline layer and other granule enzymes harden it to form the *fertilization* membrane.

- The fertilization membrane prevents entry of additional sperm.
- The fast block to polyspermy no longer functions and is replaced by a *slow block to polyspermy* consisting of the fertilization membrane and other changes to the egg's surface.

3. Activation of the egg

The sharp rise in cytoplasmic Ca^{2+} concentration also incites metabolic changes that *activates* the egg cell.

- Cellular respiration and protein synthesis rates increase.
- Cytoplasmic pH changes from slightly acidic to slightly alkaline due to H^+ extrusion.
- Activation can be artificially induced by injection of Ca^{2+}.
- The sperm nucleus within the egg swells and merges with the egg nucleus to form the zygote (actual fertilization).
- DNA replication begins and the first division occurs in about 90 minutes.

The events of fertilization in sea urchins are illustrated in Campbell, Figure 47.4.

4. Fertilization in mammals

The events of internal fertilization in mammals are similar to those of external fertilization discussed for sea urchins but include some important differences.

Fertilization in terrestrial animals is generally internal (see Campbell, Figure 47.5).

Capacitation (enhanced sperm function) results from secretion in the female's reproductive tract.

- Alters certain molecules on the surface of sperm cells and increases sperm motility.

The capacitated sperm cell must reach the *zona pellucida* for the process to continue.

- The secondary oocyte (egg) released at ovulation is surrounded by follicle cells released at the same time.

The sperm cell must migrate through this layer of cells.

- The zona pellucida (extracellular matrix of the egg) is a three-dimensional network of cross-linked filaments formed by three different glycoproteins.
- The glycoprotein ZP3 acts as a sperm receptor by binding to a complementary molecule on the surface of the sperm head.
- The binding of ZP3 and its complementary molecule stimulates an acrosomal reaction similar to that described earlier.
  - Protein-digesting enzymes and other hydrolases from the acrosome allow the sperm cell to penetrate the zona pellucida and reach the plasma membrane of the egg.
  - The acrosomal reaction also exposes a sperm membrane protein that binds and fuses with the egg membrane.

Binding of the sperm to the egg depolarizes the egg's plasma membrane (a fast block to polyspermy).

- A cortical reaction occurs, however, cortical granule contents stimulate a hardening of the zona pellucida (slow block to polyspermy) instead of raising a fertilization membrane.

- Microvilli from the egg pull the whole sperm cell into the egg cell.
    - The sperm cell's flagellar basal body divides and forms the zygote's centrosomes.
    - Nuclear envelopes disperse and the chromosomes from the gametes share a common spindle apparatus for the first mitotic division of the zygote.
    - The chromosomes from the two parents form a common nucleus (offspring's genome) as diploid nuclei form in the daughter cells after the first division.

C. Cleavage partitions the zygote into many smaller cells

The basic body plan of an animal is established in three successive stages following fertilization: cleavage, gastrulation, and organogenesis. The following information is based upon studies of the sea urchin, frogs, and *Drosophila*.

Cleavage is a succession of rapid mitotic cell divisions following fertilization that produce a multicellular embryo, the blastula (see Campbell, Figure 47.6).

- During cleavage, the cells undergo the S and M phases of the cell cycle but the G_1 and G_2 phases are virtually skipped.
- Very little gene transcription occurs during cleavage and the embryo does not grow.
- The cytoplasm of the zygote is simply divided into many smaller cells called *blastomeres*, each of which has a nucleus.
- The heterogenous nature of the zygote's cytoplasm results in blastomeres with differing cytoplasmic components.

A definite polarity is shown by the eggs of most animals and the planes of division during cleavage follow a specific pattern relative to the poles of the zygote.

- The polarity results from concentration gradients in the egg of such cellular components as mRNA, proteins, and yolk (stored nutrients).
- The yolk gradient is a key factor in determining polarity and influencing the cleavage pattern in frogs and other animals.
- The *vegetal pole* of the egg has the highest concentration of yolk.
- The *animal pole*, opposite the vegetal pole, has the lowest concentration of yolk and is the site where polar bodies are budded from the cell.
- The animal pole also marks the area where the most anterior part of the embryo will form in most animals.

The zygote is composed of two hemispheres named for the respective poles: vegetal and animal.

- The hemispheres in the egg of many frogs have different coloration due to the heterogeneous distribution of cytoplasmic substances (see Campbell, Figure 47.7).
    - The animal hemisphere has a gray hue due to the presence of melanin granules in the outer cytoplasm.
    - The vegetal hemisphere has a light yellow hue due to the yellow yolk.
- The cytoplasm in amphibian eggs is rearranged at fertilization.
    - The plasma membrane and the outer cytoplasm rotate toward the point of sperm entry.
    - This rotation may be due to a reorganization of the cytoskeleton around the centriole introduced by the sperm.
    - A narrow *gray crescent* is seen due to the exposure of a light-colored region of cytoplasm by the rotation.

The gray crescent is located near the equator of the egg on the side opposite of sperm entry.

The presence of the gray crescent is an early marker of the egg's polarity.

Cleavage in the animal hemisphere of a frog's zygote is more rapid than in the vegetal hemisphere.

- Large amounts of yolk impedes cell division.
- This discrepancy in the rate of cleavage divisions results in a frog embryo with different size cells.

  Animal hemisphere cells are smaller than those in the vegetal pole.
- In sea urchins and many other animals, the blastomeres are about equal in size due to small amounts of yolk.

  Animal-vegetal pole axes are present but are due to concentration gradients of cytoplasmic components other than yolk.

  The absence of yolk permits cleavage divisions to occur at about the same rate.

The first two cleavage divisions in sea urchins and frogs are vertical and divide the embryo into four cells that extend from the animal pole to the vegetal pole (see Campbell, Figures 47.7 an 47.8)

- The third cleavage plane is horizontal and produces an eight cell embryo with two tiers (animal and vegetal) of four cells each.
- In deuterostomes, which have radial cleavage, the upper tier of cells is aligned directly over the lower tier.
- In protostomes, which have spiral cleavage, the upper tier of cells align with the grooves between cells of the lower tier.

A continuation of cleavage produces a solid ball of cells called a *morula* (see Campbell, Figure 47.8b).

- The *blastocoel*, a fluid-filled cavity, develops within the morula as cleavage continues which changes the embryo from the solid morula to a hollow ball of cells, the *blastula* (see Campbell, Figure 47.8c).
- In sea urchins, the blastocoel is centrally located in the blastula due to equal cell divisions.
- Unequal cell divisions in the frog embryo produces a blastocoel in the animal hemisphere (see Campbell, Figure 47.8d).

The amount of yolk present in an egg greatly effects the cleavage.

- In eggs with little yolk (sea urchins) or moderate amounts of yolk (frogs), a complete division of the egg occurs and is called *holoblastic cleavage*.
- In eggs which contain large amounts of yolk (birds, reptiles), cleavage is incomplete and confined to a small disc of yolk-free cytoplasm at the animal pole of the egg; this is termed *meroblastic cleavage*.

A unique type of meroblastic cleavage occurs in the yolk-rich eggs of *Drosophila* and other insects.

- The zygote's nucleus is located within a mass of yolk.
- Cleavage begins with the nucleus undergoing a series of mitotic division *without* cytoplasmic divisions.
- The several hundred nuclei produced by these division migrate to the outer margin of the egg.
- Cytoskeletal proteins surround each nucleus and separate them from each other without membranes.

At this point the embryo is a syncytium, a cell containing many nuclei within a common cytoplasm.

- Several more mitotic divisions occur before plasma membranes form around the nuclei.
- The formation of the plasma membranes forms a blastula consisting of about 6000 cells in a single layer surrounding a yolk mass.

D. Gastrulation rearranges the blastula to form a three-layered embryo with a primitive gut

Gastrulation involves an extensive rearrangement of cells which transforms the blastula, a hollow ball of cells, into a three-layered embryo called the *gastrula*.

- A set of common cellular changes is involved in all animals: changes in cell motility; changes in cell shape; and changes in cellular adhesion to other cells and to molecules of the extracellular matrix.

  Some cells at or near the surface move to a more interior location.
- Specific details of processes may differ from one animal group to the next.

The three layers produced by gastrulation are embryonic tissues called embryonic germ layers. These three cell layers (the primary germ layers) will eventually develop into all parts of the adult animal.

- The *ectoderm* is the outermost layer of the gastrula. The nervous system and outer layer of skin in adult animals develop from ectoderm.
- The *endoderm* lines the archenteron. The lining of the digestive tract and associated organs (i.e. liver, pancreas) develop from endoderm.
- The *mesoderm* partly fills the space between the ectoderm and endoderm. The kidneys, heart, muscles, inner layer of the skin, and most other organs develop from mesoderm.

Gastrulation in sea urchins begins at the vegetal pole (see Campbell, Figure 47.9).

- The sea urchin blastula consists of a single layer of cells.
- Vegetal pole cells form a flattened plate that buckles inward (*invagination*).
- Cells near the plate detach and enter the blastocoel as migratory mesenchyme cells.
- The invaginated plate undergoes rearrangement to form a deep, narrow pouch, the *archenteron* or primitive gut.

  The archenteron opens to the surface through the *blastopore* which will become the anus.
- A second opening forms at the other end of the archenteron, forming the mouth end of the rudimentary digestive tube.
- At this point, gastrulation has produced an embryo with a primitive gut and three germ layers.
- The sea urchin embryo will develop into a ciliated larva that feeds on bacteria and unicellular algae while drifting near the ocean's surface as plankton.

Gastrulation during frog development also results in an embryo with the three embryonic germ layers and an archenteron that opens through a blastopore.

- The mechanics of gastrulation are more complicated than in the sea urchin because of the large, yolk-laden cells in the vegetal hemisphere and the presence of more than one cell layer in the blastula wall (see Campbell, Figure 47.10).
- A small crease forms on one side of the blastula where the blastopore will eventually form.

  Invagination is due to a cluster of cells burrowing inward.

- The invagination produces an external tuck that becomes the dorsal lip (upper edge) of the blastopore.
    - The dorsal lip forms where the gray crescent was located in the zygote.
- *Involution* then occurs. This is a process in which cells on the surface of the embryo roll over the dorsal lip and move into the embryo's interior away from the blastopore.
    - These cells continue to migrate along the dorsal wall of the blastocoel.
- As involution continues, migrating internal cells become organized into layered mesoderm and endoderm.
    - The archenteron forms within the endoderm.
- The cell movements of gastrulation produce a three-layered embryo.
- As gastrulation continues, more and more lateral cells involute with the dorsal cells resulting in a wider blastopore lip which eventually forms a complete circle.
- The circular blastopore lip surrounds a group of large, food-laden cells from the vegetal pole called the *yolk plug.*
- Gastrulation is complete with the formation of the three germ layers.
- Ectoderm is formed from those cells remaining on the surface (other than the yolk plug).
    - Surrounds the layers of mesoderm and endoderm.

E. In organogenesis, the organs of the animal body form from the three embryonic layers

The three germ layers that develop during gastrulation will give rise to rudimentary organs through the process of *organogenesis* (see Campbell, Table 47.1).

- The first evidence of organ development is morphogenetic changes (folds, splits, condensation of cells) that occur in the layered embryonic tissues.

The neural tube and notochord are the first organs to develop in frogs and other chordates.

- The dorsal mesoderm above the archenteron condenses to form the *notochord* in chordates.
- Ectoderm above the rudimentary notochord thickens to form a neural plate that sinks below the embryo's surface and rolls itself into a *neural tube*, which will become the brain and spinal cord (see Campbell, Figure 47.11).
- The notochord elongates and stretches the embryo lengthwise; it functions as the core around which mesoderm cells that form the vertebrae gather.
- Strips of mesoderm lateral to the notochord condense into blocks of mesodermal cells called *somites* from which will develop the vertebrae and muscles associated with the axial skeleton.
- As organogenesis continues, other organs and tissues develop from the embryonic germ layers.
    - Ectoderm also gives rise to epidermis, epidermal glands, inner ear, and eye lens.
    - Mesoderm also gives rise to the notochord, coelom lining, muscles, skeleton, gonads, kidneys and most of the circulatory system.
    - Endoderm forms the digestive tract linings, liver, pancreas and lungs.
- The neural crest forms from ectodermal cells which develop along the border where the neural tube breaks off from the ectoderm.

These cells migrate to other parts of the body and form pigment cells in the skin, some bones and muscles of the skull, teeth, adrenal medulla, and parts of the peripheral nervous system.

The end result of embryonic development in the frog is an aquatic, herbivorous tadpole.

- Metamorphosis will later change this larval stage into a terrestrial, carnivorous adult.

F. Amniote embryos develop in a fluid-filled sac within a shell or uterus

All vertebrate embryos require an aqueous environment for development.

- Fish and amphibians lay their eggs in water.
- Terrestrial animals live in dry environments and have evolved two solutions to this problem: the shelled egg in birds and reptiles and the *uterus* in placental mammals.
- The embryos of reptiles, birds, and mammals develop in a fluid-filled sac, the *amnion.*

These three classes of animals are referred to as *amniotes* due to the presence of the amnion around the embryo.

Important differences between cleavage and gastrulation occur in the development of birds and mammals, as well as differences between these amniotes and nonamniotes, such as the frog previously discussed.

1. Avian development

The larger yellow "yolk" of a bird egg is actually the ovum containing a large food reserve properly called yolk.

- Surrounding this large cell is a protein-rich solution (the egg white) that provides additional nutrients during development.
- After fertilization, meroblastic cleavage will be restricted to a small disc of yolk-free cytoplasm at the animal pole.
- Cell division partitions the yolk-free cytoplasm into a cap of cells called the *blastodisc* which rests on large undivided yolk mass.
- The blastomeres sort into an upper layer (epiblast) and lower layer (hypoblast) with a cavity (blastocoel) forming between them (see Campbell, Figure 47.12).
- Although different in appearance, this blastula is equivalent to the hollow ball stage in the frog.

Gastrulation begins with the movement of some epiblast cells toward the midline of the blastodisc. These cells then detach and move inward toward the yolk.

- The medial and inward movement of these cells produce a groove called the *primitive streak*, in the upper cell layer along the anterior-posterior axis.

Some cells in the epiblast migrate through the primitive streak and into the blastocoel to form mesoderm; others invade the hypoplast and contribute to endoderm.

- The ectoderm forms from cells remaining in the epiblast.
- Hypoblast cells appear to direct formation of the primitive streak and are necessary for development even though they contribute no cells to the embryo.

    Hypoblast cells segregate from the endoderm and form portions of a sac surrounding the yolk and a stalk which connects the embryo and yolk.

- Embryonic disc borders fold downward, come together below the embryo, and form a three-layered embryo attached to the yolk below by a stalk at midbody.

Subsequent organogenesis occurs as in the frog, except that primary germ layers also form four extraembryonic membranes: the *yolk sac*, *amnion*, *chorion* and *allantois* (see Campbell, Figure 47.14).

2. Mammalian development

Fertilization occurs in the oviducts of most mammals and the early development occurs while the embryo travels down the oviduct to the uterus.

- The egg of placental mammals stores little nutrients and the zygote displays holoblastic cleavage.
- Gastrulation and organogenesis follow a similar pattern to that in birds.

Cleavage is relatively slow in mammals and the zygote has no apparent polarity.

- Cleavage planes appear randomly oriented and blastomeres are of equal size.
- The process of compaction, which occurs at the 8-cell stage, produces cadherins, which help the cells to tightly adhere to one another.

The development of a human embryo can represent mammalian development (see Campbell, Figure 47.15).

- Cleavage is relatively slow with the first, second and third divisions being completed at 36, 60, and 72 hours, respectively.
- At 7 days post-fertilization the embryo consists of about 100 cells arranged around a central cavity forming the *blastocyst.*
- The *inner cell mass* protrudes into one end of the cavity and will develop into the embryo and some of its extraembryonic membranes.
- The *trophoblast* is the outer epithelium surrounding the cavity which will, along with mesodermal tissue, form the fetal part of the placenta.
- During implantation, the inner cell mass forms a flat disc with an epiblast and hypoblast similar to those in birds; the embryo develops from epiblast cells and the yolk sac from hypoblast cells.

The blastocyst stage reaches the uterus and begins to implant.

- The trophoblast layer:

    Secretes enzymes that enable blastocyst implantation in the uterus

    Thickens and extends fingerlike projections into the endometrium

- Gastrulation occurs by inward movement of mesoderm and endoderm through a primitive streak.

Four extraembryonic membranes homologous to those in birds and reptiles form in mammals.

- The chorion forms from the trophoblast and surrounds the embryo and all extraembryonic membranes.
- The amnion forms as a dome above the epiblast and encloses the embryo in a fluid-filled cavity.
- The yolk sac encloses a fluid-filled cavity but no yolk; its membrane is the site of early blood cell formation.

    These cells later migrate into the embryo.

- The allantois develops from an outpocketing of the rudimentary gut and is incorporated into the umbilical cord where it forms blood vessels that transport oxygen and nutrients from the placenta to the embryo and waste products from the embryo to the placenta.

Organogenesis begins with formation of the neural tube, notochord, and somites.

- Rudiments of all major organs have developed from the three germ layers by the end of the first trimester in humans.

II. The Cellular and Molecular Basis of Morphogenesis and Differentiation

Early in the embryonic development of an animal, a sequence of changes takes place that establishes the basic body plan of that animal.

- These include not only morphogenetic changes, which result in characteristic shapes, but also differentiation of many kinds of cells in specific locations.

A. Morphogenesis in animals involves specific changes in cell shape, position, and adhesion

The changes in cell shape and the cell migrations during cleavage, gastrulation and organogenesis are morphogenetic movements. These various morphogenetic movements help shape an embryo.

- Cell extension, contraction and adhesion are involved in these movements.
- Changes in shape usually involve reorganization of the cytoskeleton.
- Amoeboid or "cell crawling" movement based on extension and contraction is an important factor, especially during gastrulation.
    - Cell crawling is involved in *convergent extension*, a morphogenic movement in which the cells of a tissue layer rearrange themselves such that the sheet of cells becomes narrower as it lengthens.

Morphogenetic movements are partially guided by the extracellular matrix.

- The matrix contains adhesive substances and fibers that may direct migrating cells. (Laminin and fibronectins are extracellular glycoproteins that help cells adhere to their substratum as they migrate.)
- Nonmigrant cells along the pathways may promote or inhibit migration depending on the substances they secrete.
- Migrating cells receive direction cues, by way of surface receptor proteins, as they migrate along specific pathways.
    - Signals from the receptors direct the cytoskeletal elements to propel the cell in the proper direction.
- Other substances in the extracellular matrix direct cells by preventing migration along certain paths.

Cell adhesion molecules (CAMs) are substances on a cell surface that contribute to the selective association of certain cells with each other.

- CAMs vary either in amount or chemical identity from one type of cell to another which helps regulate morphogenetic movements and tissue building.
- *Cadherins* are a class of CAM that require the presence of calcium in order to function. Various cadherin genes have been found to be expressed in a tissue-specific manner as development proceeds.

B. The developmental fate of cells depends on cytoplasmic determinants and cell-cell induction: *a review*

Two general principles appear to integrate the genetic and cellular mechanisms underlying differentiation during embryonic development.

1. The heterogeneous distribution of cytoplasmic determinants in the unfertilized egg leads to regional differences in the early embryos of many animal species.
    - Different blastomeres receive different substances (mRNA, proteins, etc.) during cleavage due to the partitioning of the heterogenous cytoplasm of the ovum.
    - Gene expression in, and the developmental fate of, cells in the early embryo are influenced by these local differences in the distribution cytoplasmic determinants.

2. In induction, interactions among the embryonic cells themselves induce changes in gene expression.
   - Interactions among embryonic cells induce development of many specialized cell types.
   - Induction may be mediated by diffusible chemical signals.
   - Membrane interaction between cells that are in contact may also induce cytoplasmic changes.

C. Fate mapping can reveal cell geneologies in chordate embryos

It is often possible to develop a fate map for embryos whose axes are defined early in development.

- The *fate map* shows which parts of the embryo are derived from each region of the zygote or blastula.
- First accomplished by W. Vogt in the 1920s, using nontoxic dyes to color different regions of the amphibian blastula surface and subsequently sectioning the embryo to see where each color turned up.

Cell lineage analysis is a more detailed form of fate mapping, which is possible due to the development of new techniques.

- Modern techniques permit the marking of an individual blastomere during cleavage and following the marker as it is distributed to the mitotic descendants of that cell.
- Using such techniques, it has been possible to map the developmental fate of every cell in the nematode *Caenorhabditis elegans* (see Campbell, Figures 21.4 and 47.20)

Events crucial to the normal development and growth of *C. elegans* and other animals have been determined through cell lineage analyses combined with experimental manipulation of parts of organisms. Two conclusions have emerged:

- In most animals, certain early “founder” cells generate specific tissues of the embryo.
- The developmental potential of a cell, that is the range of structures to which it can give rise, becomes limited as development proceeds.

D. The eggs of vertebrates contain cytoplasmic determinants that help establish the body axes and differences among cells of the early embryo

1. Polarity and the basic body plan

Bilaterally symmetrical animals have an anterior-posterior axis, a dorsal-ventral axis, and left and right sides.

- The first step in morphogenesis is establishment of this body plan, which is prerequisite to tissue and organ development.
- In humans and other mammals, the basic polarities do not appear to be established until after cleavage.
- In most animals polarity of the embryo is established in the unfertilized egg or during early cleavage.

In frogs and many other animals, all three axes of the embryo are defined before cleavage begins.

- The animal-vegetal axis of the egg is due to concentrations gradients of cytoplasmic contents and marks the anterior-posterior axis.
- The dorsal-ventral and left-right axes are marked by the gray crescent which forms opposite of the sperm entry point.
- The embryo continues development along all three axes.

2. Restriction of cellular potency

Two blastomeres with equal developmental potential can develop from a zygote with asymmetrically distributed cytoplasmic determinants.

- Requires that the axis of the first cleavage equally distribute these substances.
- In amphibians, a normal first cleavage divides the gray crescent between the two blastomeres.
    - If the two blastomeres are separated, each will develop into a normal tadpole.
    - The cells are totipotent in that each cell retains the zygote's potential to form all parts of the animal.
    - Experimental manipulation of the first cleavage plane so that it bypasses the gray crescent produces one cell that will develop into a normal tadpole and one that fails to develop properly (see Campbell, Figure 47.21).

The developmental fate of different regions of the embryos of some animals are affected by the distribution of cytoplasmic determinants and the zygote's characteristic pattern of cleavage.

- Cytoplasmic determinants are substances localized within specific regions of the egg's cytoplasm, which leads them to be included in specific blastomeres.
    - May control gene expression

Only the zygote is totipotent in many species, while in others, there is a progressive restriction in potency of the cells.

- Only the zygote is totipotent in those where the first cleavage plane divides the cytoplasmic determinants in a way that each blastomere will give rise to only certain parts of the embryo.
- In mammals, cells of the embryo remain totipotent until they become arranged into the trophoblast and inner cell mass of the blastocyst.
- The cells of the early gastrula of some species can still give rise to more than one type of cell even though they have lost their totipotency.
- By the late gastrula stage, the developmental fate of all cells is fixed.

Determination is the progressive restriction of a cell's developmental potential.

- A determined cell is one whose developmental fate can not be changed by moving it to a different location in the embryo.
- Daughter cells receive a developmental commitment from the original cell.
- Involves the cytoplasmic environment's control of the genome of the cell.
- The partitioning of heterogeneous cytoplasm of an egg during cleavage exposes the nuclei of the cells to cytoplasmic determinants that will affect which genes are expressed as the cells begin to differentiate.

E. Inductive signals drive differentiation and pattern formation in vertebrates

Induction = The ability of one cell group to influence the development of another

1. The "organizer" of Spemann and Mangold

In the 1920s, Spemann and Mangold performed a series of transplantation experiments in which they discovered that the dorsal lip of the blastopore acts as a primary organizer, setting up the interaction between chordamesoderm and the overlying ectoderm.

- Transplanting the chordamesoderm, which forms the notochord, to an abnormal site in the embryo will cause the neural plate to develop in an abnormal location.
- The rudimentary notochord induces the dorsal ectoderm of a gastrula to form the neural plate.

Recent experiments provide clues to the molecular basis of induction by Spemann's organizer

- In amphibians, bone morphogenic protein 4 (BMP-4) is exclusively active on the ventral side of the gastrula.
- Organizer cells on the dorsal side release factors that inactivate BMP-4.

Morphogenetic movements are important to cellular determination and differentiation since cells move to areas with differing physical and chemical environments.

Interactions among cells and cell layers are crucial during and after gastrulation.

Many inductions appear to involve a sequence of inductive steps that progressively determine the fate of the cells, as in the development of an amphibian's eye.

2. Pattern formation in the vertebrate limb

Pattern formation is the development of an animal's spatial organization with organs and tissues in their characteristic places in the three dimensions of the animal.

- Occurs in addition to the determination and differentiation of cells.

Pattern formation is controlled by *positional information*, which is a set of molecular cues that indicate a cell's location relative to other cells in an embryonic structure and that help to determine how the cell and its descendants respond to future molecular signals.

- Vertebrate limbs all develop from undifferentiated limb buds (see Campbell, Figure 47.23).
- A specific pattern of tissues (e.g., bone, muscle) emerges as the limb develops.
- Every component has a precise location and orientation relative to three axes.
    - The proximal-distal axis (shoulder to fingertip)
    - The anterior-posterior axis (thumb to little finger)
    - The dorsal-ventral axis (knuckle to palm)
- For proper development to occur, embryonic cells in the limb bud must receive positional information indicating location along all three axes.

Experiments on the development of chick limbs have provided information about positional information.

- A region of mesoderm located beneath an *apical epidermal ridge (AER)* at the wing bud tip is believed to assign embryonic tissue position along the proximal-distal axis. Transplantation experiments reversing the position of this tissue have produced limbs with reversed orientation. The AER produces several proteins of the fibroblast growth factor (FGF) family which serve as the inducing signals.
- A *zone of polarized activity (ZPA)* has been found to be the point of reference for the anterior-posterior axis.
    - The ZPA is located where the posterior part of the bud is attached to the body.
    - ZPA cells release a protein growth factor called Sonic hedgehog.

- Cells nearest the ZPA give rise to posterior structures, while cells farthest from the ZPA give rise to anterior structures (see Campbell, Figure 47.24)

Such experiments have led to the conclusion that pattern formation requires cells to receive and interpret environmental cues that vary between locations.

- Certain polypeptides (e.g., FGF, Sonic hedgehog) are believed to be the cues which function as positional signals for vertebrate limb development.
- Regional gradients of these polypeptides along the three orientation axes would provide a cell positional information needed to determine its position in a three-dimensional organ.
    - The regional variation in production of these polypeptides result from differential gene expression in different locations of the embryo.

A hierarchy of gene expression events affects the expression of the homeobox-containing (Hox) genes (see Chapter 21 for a review of homeoboxes). These genes appear to be involved in specifying the identity of various regions of the limb as well as of the entire body.

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CHAPTER 48
NERVOUS SYSTEMS

OUTLINE

I. An Overview of Nervous Systems
   A. Nervous systems perform the three overlapping functions of sensory input, integration, and motor output
   B. The nervous system is composed of neurons and supporting cells

II. The Nature of Neural Signals
   A. Membrane potentials arise from differences in ion concentration between a cell's contents and the extracellular fluid
   B. An action potential is an all-or-none change in the membrane potential
   C. Action potentials "travel" along an axon because they are self-propagating
   D. Chemical or electrical communication between cells occurs at synapses
   E. Neural integration occurs at the cellular level
   F. The same neurotransmitter can produce different effects on different types of cells

III. Organization of Nervous Systems
   A. Nervous system organization tends to correlate with body symmetry
   B. Vertebrate nervous systems are highly centralized and cephalized
   C. The vertebrate PNS has several components differing in organization and function

IV. Structure and Function of the Vertebrate Brain
   A. The vertebrate brain develops from three anterior bulges of the spinal cord
   B. The brain stem conducts data and controls automatic activities essential for survival
   C. The cerebellum controls movement and balance
   D. The thalamus and hypothalamus are prominent integrating centers of the diencephalon
   E. The cerebrum contains the most sophisticated integrating centers
   F. The human brain is a major research frontier

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. Compare the two coordinating systems in animals.
2. Describe the three major functions of the nervous system.
3. List and describe the three major parts of a neuron, and explain the function of each.
4. Explain how neurons can be classified by function.
5. Describe the function and location of each type of supporting cell.
6. Explain what a resting potential is, and list four factors that contribute to the maintenance of the resting potential.

7. Define equilibrium potential, and explain why the K^+ equilibrium potential is more negative than the resting potential.
8. Define graded potential, and explain how it is different from a resting potential or action potential.
9. Describe the characteristics of an action potential, and explain the role membrane permeability changes and ion gates play in the generation of an action potential.
10. Explain how the action potential is propagated along a neuron.
11. Describe two ways to increase the effectiveness of nerve transmission.
12. Describe synaptic transmission across an electrical synapse and a chemical synapse.
13. Describe the role of cholinesterase, and explain what would happen if acetylcholine was not destroyed.
14. List some other possible neurotransmitters.
15. Define neuromodulator, and describe how it may affect nerve transmission.
16. Explain how excitatory postsynaptic potentials (EPSP) and inhibitory postsynaptic potentials (IPSP) affect the postsynaptic membrane potential.
17. Explain how a neuron integrates incoming information, including a description of summation.
18. List three criteria for a compound to be considered a neurotransmitter.
19. List two classes of neuropeptides, and explain how they illustrate overlap between endocrine and nervous control.
20. Describe two mechanisms by which a neurotransmitter affects the postsynaptic cell.
21. Diagram or describe the three major patterns of neural circuits.
22. Compare and contrast the nervous systems of the following invertebrates and explain how variation in design and complexity correlate with phylogeny, natural history, and habitat:
    a. *Hydra*
    b. Jellyfish, ctenophores, and echinoderms
    c. Flatworms
    d. Annelids and arthropods
    e. Mollusks
23. Outline the divisions of the vertebrate nervous system.
24. Distinguish between sensory (afferent) nerves and motor (efferent) nerves.
25. Define reflex and describe the pathway of a simple spinal reflex.
26. Distinguish between the functions of the autonomic nervous system and the somatic nervous system.
27. List the major components of the central nervous system.
28. Distinguish between white matter and gray matter.
29. Describe three major trends in the evolution of the vertebrate brain.
30. From a diagram, identify and describe the functions of the major structures of the human brain:
    a. Medulla oblongata
    b. Pons
    c. Cerebellum
    d. Superior and inferior colliculi
    e. Telencephalon
    f. Diencephalon
    g. Thalamus
    h. Hypothalamus
    I. Cerebral cortex
    j. Corpus callosum
31. Explain how electrical activity of the brain can be measured, and distinguish among alpha, beta, theta, and delta waves.
32. Describe the sleep-wakefulness cycle, the associated EEG changes, and the parts of the brain that control sleep and arousal.

33. Define lateralization and describe the role of the corpus callosum.
34. Distinguish between short-term and long-term memory.
35. Using a flowchart, outline a possible memory pathway in the brain.

KEY TERMS

central nervous system (CNS)
effector cells
nerves
peripheral nervous system (PNS)
neurons
cell body
dendrites
axons
myelin sheath
Schwann cells
oligodendrocytes
synaptic terminals
synapse
sensory neurons
interneurons
motor neurons
reflex
ganglion (pl., ganglia)
nuclei
supporting cells (glia)
blood-brain barrier
membrane potential
excitable cells
resting potential
gated ion channels
hyperpolarization
depolarization
graded potentials
threshold potential
action potential
voltage-gated ion channels
refractory period
saltatory conduction
presynaptic cell
postsynaptic cell
synaptic cleft
synaptic vesicles
neurotransmitter
white matter
presynaptic membrane
postsynaptic membrane
excitatory postsynaptic potential (EPSP)
inhibitory postsynaptic potential (IPSP)
summation
biogenic amines
epinephrine
norepinephrine
dopamine
serotonin
gamma aminobutyric acid (GABA)
glycine
glutamate
aspartate
neuropeptides
substance P
endorphins
cephalization
nerve cord
metencephalon
gray matter
central canal
ventricles
cerebrospinal fluid
meninges
cranial nerves
spinal nerves
sensory division
motor division
somatic nervous system
autonomic nervous system
parasympathetic division
sympathetic division
forebrain
midbrain
hindbrain
telencephalon
diencephalon
mesencephalon
myencephalon
brain stem
medulla oblongata
pons
inferior colliculi
superior colliculi
cerebellum
epithalamus
choroid plexus
thalamus
hypothalamus
suprachiasmatic nuclei
cerebral hemispheres
basal nuclei
cerebral cortex
corpus callosum
electroencephalogram (EEG)
reticular formation
limbic system
amygdala
short-term memory
long-term memory
hippocampus
long-term depression
long-term-potentiation
consciousness
nerve net

LECTURE NOTES

The *endocrine* and *nervous* systems of animals often cooperate and interact to maintain homeostasis and control behavior. Though structurally and functionally linked, these two systems play different roles.

	Nervous System	Endocrine System
Complexity	More structurally complex; can integrate vast amounts of information and stimulate a wide range of responses	Less structurally complex
Structure	System of *neurons* that branch throughout the body	*Endocrine glands* secrete *hormones* into the bloodstream where they are carried to the *target organ*
Communication	Neurons conduct electrical signals directly to and from specific targets; allows fine pin-point control.	Hormones circulate as chemical messengers throughout the body via the bloodstream; most body cells are exposed to the hormone and only target cells with receptors respond
Response Time	Fast transmission of nerve impulses up to 100m/sec	May take minutes, hours or days for hormones to be produced, carried by blood to target organ, and for response to occur

I. An Overview of Nervous Systems

A. Nervous systems perform the three overlapping functions of sensory input, integration, and motor output

The nervous system has three overlapping functions (see Campbell, Figure 48.1):

1. Sensory input is the conduction of signals from sensory receptors to integration centers of the nervous system.
2. Integration is a process by which information from sensory receptors is interpreted and associated with appropriate responses of the body.
3. Motor output is the conduction of signals from the processing center to *effector cells* (muscle cells, gland cells) that actually carry out the body's response to stimuli.

The signals are conducted by *nerves*, threadlike extensions of nerve cells wrapped in connective tissue.

These functions involve both parts of the nervous system:

1. *Central nervous system (CNS)* = Comprised of the brain and spinal cord; responsible for integration of sensory input and associating stimuli with appropriate motor output
2. *Peripheral nervous system (PNS)* = Consists of the network of nerves extending into different parts of the body that carry sensory input to the CNS and motor output away from the CNS

B. The nervous system is composed of neurons and supporting cells

The nervous system includes two main types of cells: neurons, which actually conduct messages; and supporting cells (glia), which provide structural reinforcement as well as protect, insulate, and assist the neuron.

1. Neurons

Neurons = Cells specialized for transmitting chemical and electrical signals from one location in the body to another

They have a large *cell body*.

Contains most of the cytoplasm, the nucleus, and other organelles (see Campbell, Figure 48.2)

The cell bodies of most neurons are located in the CNS, although certain types of neurons have their cell bodies located in ganglia outside of the CNS.

Have *two* types of fiberlike extensions (processes) that increase the distance over which the cells can conduct messages:

- *Dendrites* convey signals to the cell body. They are short, numerous, and extensively branched to increase the surface area where the cell is most likely to be stimulated.
- *Axons* conduct impulses away from the cell body. They are long, single processes.
  - Vertebrate axons in PNS are wrapped in concentric layers of *Schwann cells*, which form an insulating *myelin sheath.* In the CNS, the myelin sheath is formed by *oligodendrocytes.*
  - Axons extend from the axon hillock (where impulses are generated) to many branches, which are tipped with *synaptic terminals* that release neurotransmitters.
    - *Synapse* = Gap between a synaptic terminal and a target cell—either dendrites of another neuron or an effector cell
    - *Neurotransmitters* = Chemicals that cross the synapse to relay the impulse

2. Functional organization of neurons

There are three major classes of neurons (see Campbell, Figure 48.3):

1. *Sensory neurons* convey information about the external and internal environments from sensory receptors to the central nervous system. Most sensory neurons synapse with interneurons.
2. *Interneurons* integrate sensory input and motor output; located within the CNS, they synapse only with other neurons..
3. *Motor neurons* convey impulses from the CNS to effector cells.

Neurons are arranged in groups, or circuits, of two or more kinds of neurons

- The simplest circuits involve synapses between sensory neurons and motor neurons, resulting in a simple *reflex* arc (e.g., knee-jerk reflex) (see Campbell, Figure 48.4).
- Complex circuits, such as those associated with most behaviors, involve integration by interneurons in the central nervous system.

  Convergent circuits = Neural circuit in which information from several presynaptic neurons come together at a single postsynaptic neuron; permits integration of information from several sources.

  Divergent circuits = Neural circuit in which information from a single neuron spreads out to several postsynaptic neurons; permits transmission of information from a single source to several parts of the brain.

  Reverberating circuits = Circular circuits in which the signal returns to its source; believed to play a role in memory storage.

Nerve cell bodies are often arranged into clusters; these clusters allow coordination of activities by only part of the nervous system.

- A *nucleus* is a cluster of nerve cell bodies within the brain.

- A *ganglion* is a cluster of nerve cell bodies in the peripheral nervous system.

3. Supporting cells

Supporting cells, or *glia*, structurally reinforce, protect, insulate, and generally assist neurons.

- Do not conduct impulses
- Outnumber neurons 10- to 50-fold

Several types of glia are present.

- Astrocytes encircle capillaries in the brain.

  Contribute to the *blood-brain barrier*, which restricts passage of most substances into the CNS.

  Probably communicate with one another and with neurons via chemical signals.
- Oligodendrocytes form myelin sheaths that insulate CNS nerve processes.
- Schwann cells form the insulating myelin sheath around axons in the PNS.

Myelination of neurons in a developing nervous system occurs when Schwann cells or oligodendrocytes grow around an axon so their plasma membranes form concentric layers.

- Provides electrical insulation since membranes are mostly lipid, which is a poor current conductor.
- Insulating myelin sheath increases the speed of nerve impulse propagation.
- In multiple sclerosis, myelin sheaths deteriorate causing a disruption of nerve impulse transmission and consequent loss of coordination.

II. The Nature of Neural Signals

Signal transmission along the length of a neuron depends on voltages created by ionic fluxes *across* neuron plasma membranes.

A. Membrane potentials arise from differences in ion concentrations between a cell's contents and the extracellular fluid

All cells have an electrical *membrane potential* or voltage across their plasma membranes.

- Ranges from -50 to -100 mV in animal cells
- The charge outside the cell is designated as zero, so the minus sign indicates that the cytoplasm inside is negatively charged compared to the extracellular fluid.
- Is about -70mV in a resting neuron

The membrane potential arises from differences in the ionic composition of the intracellular and extracellular fluids (see Campbell, Figure 48.5). For example, the approximate concentrations in millimoles per liter (mM) are listed below for ions in mammalian cells:

Ion	Inside Cell	Outside Cell
$[Na^+]$	15 mM	150mM
$[K^+]$	150mM	5mM
$[Cl^-]$	10mM	120mM
[A-]	100mM	---------------

Note: [A-] symbolizes all anions within the cell including negatively charged proteins, amino acids, sulfate and phosphate.

- Principal cation inside the cell is K^+, while the principal cation outside the cell is Na^+.
- Principal anions inside the cell are proteins, amino acids, sulfate, phosphate, and other negatively charged ions (A-); principal anion outside the cell is Cl^-.
- Because internal anions (A-) are primarily large organic molecules, they cannot cross the membrane and remain in the cell as a reservoir of internal negative charge.

The selective permeability of the plasma membrane maintains ionic differences.

- As charged molecules, ions cannot readily diffuse through the hydrophobic core of the plasma membrane's phospholipid bilayer.
- Ions can only cross membranes by carrier-mediated transport or by passing through ion channels.

Ion channel = Integral transmembrane protein that allows a specific ion to cross the membrane

- May be passive and open all the time; or may be gated, requiring a stimulus to change into an open conformation
- Are selective for a specific ion, such as Na^+, K^+ and Cl^-
- Membrane permeability to each ion is a function of the type and number of ion channels. For example, membranes are usually more permeable to K^+ than to Na^+, suggesting that there are more potassium channels than sodium channels.

How does the cell create and maintain the membrane potential?

- K^+ diffuses out of the cell down its concentration gradient, since the K^+ concentration is greater inside cell and the membrane has a high permeability to potassium.
- K^+ diffusion out of the cell transfers positive charges from inside of the cell to outside.
- The cell's interior becomes progressively more negative as K^+ leaves because the molecules of the anion pool (A^-) are too large to cross the membrane.
- As the electrical gradient increases, the negatively charged interior attracts K^+ back into the cell.
- If K^+ was the only ion to cross the membrane, an *equilibrium potential* for potassium ions (= -85 mV) would be reached; this is the potential at which no net movement of K^+ would occur since the electrical gradient attraction of K^+ would balance the K^+ loss due to the concentration gradient.

- However, K^+ is not the only ion to cross the membrane; although the membrane is less permeable to Na^+ than K^+, some Na^+ diffuses into the cell down both its concentration gradient and the electrical gradient.
- The Na^+ trickle into the cell transfers positive charge to the inside resulting in a slightly more positive charge (-70 mV) than if the membrane were permeable only to K^+ (-85 mV).
- If left unchecked, the Na^+ trickle into the cell would cause a progressive increase in Na^+ concentration and a decrease in K^+ concentration (the electrical gradient would be weakened by the positive sodium ions and the potassium ions would diffuse down its concentration gradient).
- This shift in ionic gradients is prevented by sodium-potassium pumps, special transmembrane proteins which use energy from ATP to:

  Pump sodium back out of the cell against concentration and electrical gradients.

  Pump potassium into the cell, restoring its concentration gradient.

B. An action potential is an all-or-none change in the membrane potential

All cells in the body exhibit the properties of membrane potential described above. However, only neurons and muscle cells can change their membrane potentials in response to stimuli.

- Such cells are called *excitable cells*.
- The membrane potential of an excitable cell at rest (unexcited state) is called a *resting potential*.

The presence of *gated ion channels* in neurons permits these cells to change the plasma membrane's permeability and alter the membrane potential in response to stimuli received by the cell.

- Sensory neurons are stimulated by receptors that are triggered by environmental stimuli.
- Interneurons normally receive stimuli produced by activation of other neurons.

The effect on the neuron depends on the type of gated ion channel the stimulus opens (see Campbell, Figure 48.6).

- Stimuli that open potassium channels *hyperpolarize* the neuron. K^+ effluxes from the cell; this increases the electrical gradient making the interior of the cell more negative.
- Stimuli that open sodium channels *depolarize* the neuron. Na^+ influxes into the cell; this reduces the electrical gradient and membrane potential because the inside of the cell becomes more positive.

Voltage changes caused by stimulation are called *graded potentials* because the magnitude of the change depends on the strength of the stimulus.

- Each excitable cell has a *threshold* to which depolarizing stimuli are graded. This threshold potential is usually slightly more positive (−50 to −55 mV) than the resting potential.
- If depolarization reaches the threshold, the cell responds differently by triggering an action potential.
- Hyperpolarizing stimuli do not produce action potentials since they cause the potential to become more negative; actually reduces the probability an action potential will occur by making it more difficult for depolarizing stimuli to reach the threshold.

An *action potential* is the rapid change in the membrane potential of an excitable cell, caused by stimulus-triggered selective opening and closing of *voltage-gated ion channels*.

- Voltage-gated ion channels open and close in response to changes in membrane potential.
- Voltage-gated sodium channels have two gates: the activation gate opens *rapidly* at depolarization, the inactivation gate closes slowly at depolarization.
- The voltage-gated potassium channel has one gate that opens *slowly* in response to depolarization.

An action potential has four phases (see Campbell, Figure 48.7):

1. Resting state; no channels are open.
2. Large depolarizing phase during which the membrane briefly reverses polarity (cell interior becomes positive to the exterior). The Na^+ activation gates open, allowing an influx of Na^+, while potassium gates remain closed.
3. The steep repolarizing p*hase* follows quickly and returns the membrane potential to its resting level; inactivation gates close the sodium channels and the potassium channels open.
4. The undershoot phase is a time when the membrane potential is temporarily more negative than the resting state (hyperpolarized); sodium channels remain closed but potassium channels remain open since the inactivation gates have not had time to respond to repolarization of the membrane.

   A *refractory period* occurs during the undershoot phase; during this period, the neuron is insensitive to depolarizing stimuli. The refractory period limits the maximum rate at which action potentials can be stimulated in a neuron.

Action potentials are all-or-none events and their amplitudes are not affected by stimulus intensity. The nervous system distinguishes between strong and weak stimuli based on the frequency of action potentials generated.

- Strong stimuli produce action potentials more rapidly than weak stimuli.
- Maximum frequency is limited by the refractory period of the neuron.

C. Action potentials "travel" along an axon because they are self-propagating

A neuron is stimulated at its dendrites or cell body, and the action potential travels along the axon to the other end of the neuron.

- Action potentials in the axon are usually generated at the axon hillock.
- Strong depolarization in one area results in depolarization above the threshold in neighboring areas.
- The action potential does not travel down the axon, but is regenerated at each position along the membrane.

The signal travels in a perpendicular direction along the axon regenerating the action potential (see Campbell, Figure 48.8).

- Na^+ influx in the area of the action potential results in depolarization of the membrane just ahead of the impulse, surpassing the threshold.
- The voltage-sensitive channels in the new location will go through the same sequence previously described regenerating the action potential.
- Subsequent portions of the axons are depolarized in the same manner.
- The action potential moves in only one direction (down the axon) since each action potential is followed by a refractory period when sodium channel inactivation gates are closed and no action potential can be generated.

Factors affecting the speed of action potential propagation include:

1. The larger the diameter of the axon, the faster the rate of transmission since resistance to the flow of electrical current is inversely proportional to the cross-sectional area of the "wire" conducting the current.

2. *Saltatory conduction.* The action potential "jumps" from one node of Ranvier to the next, skipping the myelinated regions of membrane (see Campbell, Figure 48.9)
   - *Nodes of Ranvier* are gaps in the myelin sheath between successive glial cells.
   - Voltage-sensitive ion channels are concentrated in node regions of the axon.
   - Extracellular fluid only contacts the axon membranes at the nodes; restricts the area for ion exchange to these regions.
   - This results in faster transmission of the nerve impulse.

D. Chemical or electrical communication between cells occurs at synapses

Synapse = Tiny gap between a synaptic terminal of an axon and a signal-receiving portion of another neuron or effector cell.

- Also found between sensory receptors and sensory neurons, and between motor neurons and muscle cells.
- *Presynaptic cell* is the transmitting cell; *postsynaptic cell* is the receiving cell.
- There are two types of synapses: electrical and chemical.

1. Electrical synapses

Electrical synapses allow action potentials to spread directly from pre- to postsynaptic cells via gap junctions (intercellular channels).

- Allows impulses to travel from one cell to the next without delay or loss of signal strength
- Much less common than chemical synapses
- Example: the giant neuron processes of crustaceans

2. Chemical synapses

At a chemical synapse a *synaptic cleft* separates the pre- and postsynaptic cells so they are not electrically coupled (see Campbell, Figure 48.10).

- Within the cytoplasm of the synaptic terminal of a presynaptic cell are numerous *synaptic vesicles* containing thousands of neurotransmitter molecules.
- An action potential arriving at the synaptic terminal depolarizes the *presynaptic membrane* causing Ca^{2+} to rush through voltage-sensitive channels.
- The sudden rise in Ca^{2+} concentration stimulates synaptic vesicles to fuse with the presynaptic membrane and release *neurotransmitter* into the synaptic cleft by exocytosis.
- The neurotransmitter diffuses to the *postsynaptic membrane* where it binds to specific receptors, causing ion gates to open.
- Depending on the type of receptors and the ion gates they control, the neurotransmitter may either excite the membrane by depolarization or inhibit the postsynaptic cell by hyperpolarization.
- The neurotransmitter molecules are quickly degraded by enzymes and the components recycled to the presynaptic cell.

Chemical synapses allow transmission of nerve impulses in only one direction.

- Synaptic vesicles and their neurotransmitter molecules are found only in the synaptic terminals at the tip of axons.
- Receptors for neurotransmitters are located only on postsynaptic membranes.

E. Neural integration occurs at the cellular level

One neuron may receive information from thousands of synapses. Some synapses are excitatory, others are inhibitory (see Campbell, Figure 48.11).

- *Excitatory postsynaptic potentials (EPSP)* occur when excitatory synapses release a neurotransmitter that opens gated channels allowing Na^+ to enter the cell and K^+ to leave (depolarization).
- *Inhibitory postsynaptic potentials (IPSP)* occur when neurotransmitters released from inhibitory synapses bind to receptors that open ion gates, which make the membrane more permeable to K^+ (which leaves the cell) and/or to Cl^- (which enters the cell) causing hyperpolarization.

EPSPs and IPSPs are graded potentials; they vary in magnitude with the number of neurotransmitter molecules binding to postsynaptic receptors.

- Change in voltage lasts only a few milliseconds since neurotransmitters are inactivated by enzymes soon after release.
- The electrical impact on the postsynaptic cell also decreases with distance from the synapse.

A single EPSP is rarely strong enough to trigger an action potential, although an additive effect (*summation*) from several terminals or repeated firing of terminals can change membrane potential (see Campbell, Figure 48.12).

- Temporal summation is when chemical transmissions from one or more synaptic terminals occur so close in time that each affects the membrane while it is partially depolarized and before it has returned to resting potential.
- Spatial summation is when several different synaptic terminals, usually from different presynaptic neurons, stimulate the postsynaptic cell at the same time and have an additive effect on membrane potential.
- EPSPs and IPSPs can summate, each countering the effects of the other.

At any instant, the axon hillock's membrane potential is an average of the summated depolarization due to all EPSPs and the summated hyperpolarization due to all IPSPs.

- An action potential is generated when the EPSP summation exceeds the IPSP summation to the point where the membrane potential of the axon hillock reaches threshold voltage.

F. The same neurotransmitter can produce different effects on different types of cells

Dozens of different molecules are known to be neurotransmitters and many others are suspected to function as such.

Criteria for neurotransmitters include:

- Must be present in and discharged from synaptic vesicles in the presynaptic cell when stimulated and affect the postsynaptic cell's membrane potential
- Must cause an IPSP or EPSP when experimentally injected into the synapse
- Must be rapidly removed from the synapse by an enzyme or uptake by a cell permitting the postsynaptic membrane to return to resting potential

Types of neurotransmitters (see Campbell, Table 48.2):

1. *Acetylcholine* may be excitatory or inhibitory depending on the receptor; functions in the vertebrate neuromuscular junction (between a motor neuron and muscle cell) and in the central nervous system.
    - This is the most common neurotransmitter in both vertebrates and invertebrates.
2. *Biogenic amines* are derived from amino acids.

- *Epinephrine*, *norepinephrine*, and *dopamine* are produced from tyrosine; *serotonin* is synthesized from tryptophan.
- Commonly function in the central nervous system. Norepinephrine also functions in the peripheral nervous system.
- Imbalances in dopamine and serotonin are associated with mental illness.

3. Amino acids *glycine*, *glutamate*, *aspartate*, and *gamma aminobutyric acid (GABA)* function as neurotransmitters in the central nervous system.
   - GABA is the most abundant inhibitory transmitter in the brain.
4. *Neuropeptides* are short chains of amino acids.
   - *Substance P* is an excitatory signal that mediates pain perception.
   - *Endorphins* (or enkephalins) function as natural analgesics in the brain.

Neurotransmitters may affect the postsynaptic cell by:

- Altering the permeability of the postsynaptic membrane to specific ions (e.g., acetylcholine, amino acid transmitters)
- Affecting postsynaptic cell metabolism (e.g., biogenic amines, neuropeptides) by triggering a signal transduction pathway

A single neurotransmitter can elicit different responses in different postsynaptic cells by

- Binding to different receptor (e.g., acetylcholine)
- Binding to the same receptor, but the receptor is linked to different signal-transduction pathways

1. Gaseous signals of the nervous system

Some neurons of the vertebrate PNS and CNS release gas molecules, such as nitric oxide (NO) and carbon monoxide (CO), as local regulators. For example,

- During sexual arousal, neurons release NO into erectile tissue of the penis, which causes blood vessels to dilate and fill with blood, producing an erection.
- Acetylcholine released by neurons into blood vessel walls stimulates their endothelial cells to produce and release NO. In response, neighboring smooth muscle cells relax, dilating the vessels.
- Similarly, nitroglycerin is effective in treating angina because it is converted to NO, which dilates the heart's blood vessels.

Cells do not store gaseous messengers, so they must be produced on demand.

- Within a few seconds, they diffuse into target cells, produce a change, and are broken down.
- NO often works by a signal-transduction pathway; it stimulates a membrane-bound enzyme to synthesize a second messenger that directly affects cellular metabolism.

III. Organization of Nervous Systems

There is great diversity in nervous system organization among animals; some even lack nervous systems (e.g., sponges).

A. Nervous system organization tends to correlate with body symmetry

The *Hydra*, a cnidarian, has a *nerve net*—a loosely organized system of nerves with no central control.

- Impulses are conducted in both directions causing movements of the entire body.

- Some cnidarians, ctenophores, and echinoderms have modified nerve nets with rudimentary centralization (see Campbell, Figure 48.13).

Cephalization = Evolutionary trend for concentration of sensory and feeding organs on the anterior end of a moving animal; gave rise to the first brains

- Found in bilaterally symmetrical animals

Most bilaterally symmetrical animals have a peripheral nervous system and a central nervous system. In most cases, the central nervous systems consists of a brain in the head end and one or more *nerve cords*.

- Flatworms have a simple "brain" containing many large interneurons that coordinate most nervous functions. Two or more nerve trunks travel posteriorly in a ladderlike system with transverse nerves connecting the main trunks.
- Annelids and arthropods have a well-defined ventral nerve cord and a prominent brain. Often contain ganglia in each body segment to coordinate actions of that segment.
- Cephalopods have the most sophisticated invertebrate nervous system containing a large brain and giant axons.

Nervous system complexity often correlates with phylogeny, habitat, and natural history. For example, sessile animals such as clams show little or no cephalization.

B. Vertebrate nervous systems are highly centralized and cephalized

Vertebrate nervous systems are structurally and functionally diverse, however, they all have distinct central and peripheral elements and a high degree of cephalization (see Campbell, Figure 48.14).

Because vertebrate nervous systems are so complex, it is useful to group them into functional components: the peripheral nervous system and the central nervous system.

The CNS provide the basis for the complex behaviors of vertebrates by bridging the sensory and motor functions of the peripheral nervous system.

- Consists of the *spinal cord*, which is located inside the vertebral column and receives information from skin and muscles and sends out motor commands for movement; and the *brain*, which carries out complex integration for homeostasis, perception, movement, intellect and emotions.
- Both are covered with *meninges*, protective layers of connective tissue.
- In the brain, *white matter* is in the inner region and *gray matter* is in the outer region. This orientation is reversed in the spinal cord.
- *Cerebrospinal fluid* fills the *ventricles* in the brain and the *central canal* of the spinal cord; it functions in circulation of hormones, nutrients, and white blood cells and in absorption of shock, which cushions the brain.

The spinal cord integrates simple responses to certain stimuli (reflexes) and carries information to and from the brain.

- The patellar (knee-jerk) reflex is one of the simplest and involves only two neurons. A stretch receptor in the quadriceps muscle is stimulated by stretching of the patellar tendon; this activates a sensory neuron that carries the information to the spinal cord where it synapses with a motor neuron; if an action potential is generated in the motor neuron, it travels back to the quadriceps, which contracts and causes the forward knee jerk.
- Larger-scale, more complex responses result when branches of a reflex pathway carry signals to other parts of the spinal cord or to the brain.

The peripheral nervous system of mammals consists of 12 pairs of cranial nerves and 31 pairs of spinal nerves.

- Cranial nerves originate from the brain and innervate organs of the head and upper body; most contain both sensory and motor neurons, although some are sensory only (e.g., optic nerve).
- Spinal nerves innervate the entire body and contain both sensory and motor neurons.

C. The vertebrate PNS has several components differing in organization and function

The PNS consists of:

- *Sensory division*, which brings information from sensory receptors to the CNS
- *Motor division*, which carries signals from the CNS to effector cells

The two basic functions of a nervous system are to:

- Control responses to external environment
- Maintain homeostasis by coordinating internal organ functions

The sensory nervous system contributes to both functions by carrying stimuli from the external environment and monitoring the status of the internal environment.

The motor nervous system has two separate divisions associated with these functions.

1. The *somatic nervous system's* neurons carry signals to skeletal muscles in response to external stimuli; includes reflexes (automatic responses to stimuli) and is often considered "voluntary" because it is subject to conscious control.
2. The *autonomic nervous system* controls primarily "involuntary," automatic, visceral functions of smooth and cardiac muscles and organs of the gastrointestinal, excretory, cardiovascular, and endocrine systems.
   - Divided into a *parasympathetic division* that enhances activities that gain and conserve energy, and a usually antagonistic *sympathetic division* that increases energy expenditures.

IV. Structure and Function of the Vertebrate Brain

A. The vertebrate brain develops from three anterior bulges of the spinal cord

In all vertebrates, the brain develops from the anterior region of the neural tube. The following three bilaterally symmetrical regions arise as the neural tube differentiates:

- Forebrain
- Midbrain
- Hindbrain

As vertebrates evolved, the structure of their brains became more complex. The complexity is evident in the latter stages of brain development of higher vertebrates. In 6-week old human fetuses, for example, five brain regions have formed from the three primary bulges (see Campbell, Figure 48.17b).

- Telencephalon (from forebrain)
- Diencephalon (from forebrain)
- Mesencephalon (from midbrain)
- Metencephalon (from hindbrain)
- Myelencephalon (from hindbrain)

B. The brain stem conducts data and controls automatic activities essential for life

The mesencephalon, metencephalon, and myelencephalon form the *brain stem.*

The brain stem consists of three parts: the *medulla oblongata*, the *pons*, and the midbrain.

- The *medulla oblongata* and *pons* control visceral functions including breathing, heart and blood vessel activity, swallowing, vomiting,and digestion. They also coordinate large-scale body movements such as walking.

The *superior* and *inferior colliculi* are areas of the midbrain that function in the visual and auditory systems.

C. The cerebellum controls movement and balance

The *cerebellum*, derived from part of the metencephalon, functions in balance and coordination of movement (see Campbell, Figure 48.17).

D. The thalamus and hypothalamus are prominent integrating centers of the diencephalon

The embryonic diencephalon gives rise to the *epithalamus,* the *thalamus*, and the *hypothalamus.*

The *epithalamus* includes the pineal gland (site of melatonin synthesis) and a *choroid plexus,* a cluster of capillaries that produces cerebrospinal fluid.

The *thalamus*, a prominent integrating center in the diencephalon, relays sensory information to and from the cerebrum.

- Contains many different nuclei, each one dedicated to one type of sensory information
- Sorts incoming sensory information and sends it to appropriate higher brain centers for further interpretation and integration
- Receives input from the cerebrum and from parts of the brain that regulate emotion and arousal

The *hypothalamus* is one of the most important regulators of homeostasis.

- Is the source of posterior pituitary hormones (e.g., ADH) and releasing hormones of the anterior pituitary
- Contains the body's thermostat and centers for regulating hunger and thirst
- Plays a role in sexual response and mating behavior, the fight-or-flight response, and pleasure.

1. The hypothalamus and circadian rhythms

The hypothalamus of mammals contains a pair of *suprachiasmiatic nuclei (SCN)* that function as a biological clock.

The SCN use visual information to synchronize certain bodily functions with the natural cycles of day length and darkness. This biological clock maintains daily biorhythms such as when:

- Sleep occurs
- Blood pressure is highest
- Sex drive peaks

E. The cerebrum contains the most sophisticated integrating centers

The *cerebrum*, which is derived from embryonic telencephalon, is divided into the right and left *cerebral hemispheres* (see Campbell, Figure 48.19a). Each hemisphere consists of:

- Outer covering of gray matter, the *cerebral cortex*
- Internal white matter
- Cluster of nuclei deep within the white matter, the *basal nuclei*

    They are centers for motor coordination, relaying impulses from other motor systems.

    They send motor impulses to the muscles.

If damaged, passivity and immobility result, because they no longer allow motor impulses to be sent to the muscles. Degeneration of cells entering the basal ganglia occurs in Parkinson's disease.

The largest, most complex part of the human brain is the cerebral cortex.

- Its highly folded convolutions result in a surface area of about 0.5 m^2.
- Bilaterally symmetrical with two hemispheres connected by a thick band of fibers (white matter) known as the *corpus callosum*.
- Each hemisphere is divided into four lobes; some functional areas within each lobe have been identified (see Campbell, Figure 48.19b).

Two functional cortical areas, the primary motor cortex and the primary somatosensory cortex, form the boundary between the frontal lobe and the parietal lobe (see Campbell, Figure 48.20).

- In response to sensory stimuli, the motor cortex sends appropriate commands to skeletal muscles.
- The somatosensory cortex receives and partially integrates signals from the body's touch, pain, pressure, and temperature receptors.
- The proportion of somatosensory or motor cortex devoted to a particular body region depends upon how important sensory or motor information is for that part.
    - For example, more brain surface is committed to sensory and motor communication with the hands than with the entire torso.
    - Impulses transmitted from receptors to specific areas of somatosensory cortex enable us to associate pain, touch, pressure, heat, or cold with specific parts of the body receiving those stimuli.

A complicated interchange of signals among receiving centers and association centers produces our sensory perceptions.

- The special senses—vision, hearing, smell and taste—are integrated by cortical regions other than the somatosensory cortex.
- Each of these functional regions, as well as, the somatosensory cortex, cooperate with an adjacent association area.

F. The human brain is a major research frontier

1. Arousal and sleep

Electrical potential between areas of the cortex can be measured and recorded with an *electroencephalogram* or *EEG* (see Campbell, Figure 48.21). Different states of sleep and arousal produce different patterns of electrical activity or brain waves, which can be classified into four types:

1. Alpha waves – Slow synchronous waves; produced in the relaxed closed-eye state of wakefulness
2. Beta waves – Faster and less synchronous than alpha waves; produced during mental alertness such as occurs during problem solving.
3. Theta waves – More irregular than beta waves; predominate in the early stages of sleep
4. Delta waves – Slow, high amplitude, highly synchronized waves; occur during deep sleep

Sleep is a dynamic process during which a person alternates between two types of sleep: nonrapid eye movement sleep (NREM) and rapid eye movement sleep (REM*)*.

- NREM sleep - In the early stages of sleep, the brain produces slow, regular theta waves; during deeper sleep, it produces high amplitude delta waves.

- REM sleep - Characterized by rapid eye movement and desynchronized EEG similar to that of wakefulness. Most dreaming occurs during REM sleep.

Sleep and arousal are controlled by several centers in the cerebrum and brain stem; the most important is the *reticular formation* (see Campbell, Figure 48.22).

- Part of the reticular formation, the reticular activating system (RAS), regulates sleep and arousal.
- RAS serves as a filter that selects what sensory information reaches the cortex.

2. Lateralization, language, and speech

Lateralization (right brain/left brain) refers to the fact that the association areas of the cerebral cortex are not bilaterally symmetrical; each side of the brain controls different functions.

- The left hemisphere controls speech, language, calculation, and the rapid serial processing of detailed information.
- The right hemisphere controls overall context, creative abilities, and spatial perception.
    - The corpus callosum transfers information between the left and right hemispheres. Severing the corpus callosum will not alter perception, but will dissociate sensory input from spoken response.

Understanding and generating language are controlled by several association areas in the left hemisphere, while the emotional content of language is processed by the right hemisphere.

- Damage to parts of the left hemisphere can cause some form of aphasia, the inability to speak coherently.
- See the Methods box to see PET scans of the different "areas" in action.

3. Emotions

Emotions depend on interactions between the cerebral cortex and the *limbic system*, a group of giant nuclei and interconnecting axon tracts in the forebrain (see Campbell, Figure 48.23).

- Includes parts of the thalamus, hypothalamus, and inner portions of the cerebral cortex, including two nuclei called the *amygdala* and *hippocampus*.
- Cerebral components of the limbic system are linked to areas of the cerebral cortex involved in complex learning, reasoning, and personality, so there is a close relationship between emotion and thought.
- Frontal lobotomies, the surgical destruction of the limbic cortex or its connection with the cerebral cortex, were once used to treat severe emotional disorders. Drug therapy is now the treatment of choice.

4. Memory and learning

Memory is the ability to store and retrieve information related to previous experiences.

Memory occurs in two stages: short-term memory and long-term memory.

- *Short-term memory* reflects immediate sensory perceptions of an object or idea and occurs before the image is stored.
- *Long-term memory* is stored information that can be recalled at a later time.
- Transfer of information from short-term to long-term memory is enhanced by rehearsal, favorable emotional state, and association of new information with previously learned and stored information.

Fact memory differs from skill memory.

- Fact memory involves conscious and specific retrieval of data from long-term memory.
- Skill memory usually involves motor activities learned by repetition, which are recalled without consciously remembering specific details.

There is no highly localized memory trace in the nervous system; instead, memories are stored in certain association areas of the cortex.

Fact memory involves a pathway in which sensory information is transmitted from the cerebral cortex to the hippocampus and amygdala, which are two parts of the limbic system.

- The amygdala may filter memory, labeling information to be saved by tying it to an event or emotion.
- In the hippocampus, certain synapses functionally change as a result of altered responsiveness by postsynaptic cells.
  - In *long-term depression (LTD)*, the postsynaptic cell displays decreased responsiveness to action potentials.
  - In *long-term potentiation (LTP),* the postsynaptic cell displays increased responsiveness to action potentials.
    - Results from brief, repeated action potentials that strongly depolarize the postsynaptic membrane, so an action potential from the presynaptic cell has a much greater effect at the synapse than before.
    - Lasts for hours, days or weeks and may occur when a memory is stored or learning takes place.
  - LTP mechanism involves presynaptic release of glutamate, an excitatory neurotransmitter.
    - Glutamate binds with postsynaptic receptors and opens gated channels highly permeable to calcium ions.
    - Ca^{2+} influx triggers intracellular changes that induce LTP.
  - Postsynaptic neurons may also change to enhance LTP.
    - In a positive feedback loop, the affected postsynaptic cell may signal the presynaptic cell to release more glutamate, enhancing LTP.
    - A likely messenger for this backward signaling is the local mediator nitric oxide.

5. Consciousness

The study of consciousness has drawn considerable attention; however, its neurological basis remains a mystery.

A number of hypothesis concerning consciousness have been put forth:

- Involves simultaneous cooperation of extensive areas of the cerebral cortex.
- Cerebral neurons and functional groups of neurons are generating conscious thoughts while engaged in more specific, less complex tasks.

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CHAPTER 49
SENSORY AND MOTOR MECHANISMS

OUTLINE

I. Introduction to Sensory Reception
   A. Sensory receptors transduce stimulus energy and transmit signals to the nervous system
   B. Sensory receptors are categorized by the type of energy they transduce

II. Photoreceptors
   A. A broad array of photoreceptors has evolved among invertebrates
   B. Vertebrates have single-lens eyes
   C. The light absorbing pigment rhodopsin operates via signal transduction
   D. The retina assists the cerebral cortex in processing visual information

III. Hearing and Equilibrium
   A. The mammalian hearing organ is within the inner ear
   B. The inner ear also contains the organs of equilibrium
   C. A lateral line system and inner ear detect pressure waves in most fishes and aquatic amphibians
   D. Many invertebrates have gravity sensors and are sound-sensitive

IV. Chemoreception – Taste and Smell
   A. Perceptions of taste and smell are usually interrelated

V. Movement and Locomotion
   A. Locomotion requires energy to overcome friction and gravity
   B. Skeletons support and protect the animal body and are essential to movement
   C. Muscles move skeletal parts by contracting
   D. Interactions between myosin and actin underlie muscle contractions
   E. Calcium ions and regulatory proteins control muscle contraction
   F. Diverse body movements require variation in muscle activity

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. Differentiate between sensation and perception.
2. Give the general function of a receptor cell, and explain the five processes involved in this function.
3. Explain the difference between exteroreceptors and interoreceptors.
4. List and describe the energy stimulus of the five types of receptors.

5. Using a cross-sectional diagram of human skin, identify the various receptors present, and explain the importance of having near-surface and deep-layer receptors for such stimuli as pressure.
6. Compare and contrast the structure and processing of light in eye cups of *Planaria*, compound eyes of insects, and single-lens eyes of mollusks.
7. Using a diagram of the vertebrate eye, identify and give the function of each structure.
8. Describe how the rod cells and cone cells found in the vertebrate eye function.
9. Explain how retinal signals following a horizontal pathway can enhance visual integration.
10. Using a diagram of the human ear, identify and give the function of each structure.
11. Explain how the mammalian ear functions as a hearing organ.
12. Explain how the mammalian ear functions to maintain body balance and equilibrium.
13. Compare the hearing and equilibrium systems found in non-mammalian vertebrates.
14. Describe the structure and function of statocysts.
15. Explain how the chemoreceptors involved with taste and smell function.
16. List any advantages or disadvantages associated with moving through a(n):
    a. Aquatic environment
    b. Terrestrial environment
17. Give the three functions of a skeleton.
18. Describe how hydrostatic skeletons function, and explain why they are not found in large terrestrial organisms.
19. Explain how the structure of the arthropod exoskeleton provides both strength and flexibility.
20. Explain the adaptive advantage of having different types of joints in different locations in the vertebrate skeleton.
21. Explain how the skeleton combines with an antagonistic muscle arrangement to provide a mechanism for movement.
22. Using a diagram, identify the basic components of skeletal muscle.
23. Explain how muscles contract according to the sliding filament model of contraction.
24. Describe the processes involved in excitation-contraction coupling.
25. List and explain the two mechanisms responsible for graded contraction of muscles.
26. Explain the adaptive advantage of possessing both slow and fast muscle fibers.
27. Distinguish among skeletal muscle, cardiac muscle, and smooth muscle.

KEY TERMS

sensation	sclera	outer ear	endoskeleton
perception	choroid	tympanic membrane	skeletal muscle
sensory reception	conjunctiva	middle ear	myofibrils
sensory receptor	cornea	malleus	myofilaments
exteroreceptors	iris	incus	thin filaments
interoreceptors	pupil	stapes	thick filaments
sensory transduction	retina	oval window	sarcomere
receptor potential	lens	Eustachian tube	Z lines
amplification	ciliary body	inner ear	I band
transmission	aqueous humor	cochlea	A band
integration	vitreous humor	organ of Corti	H zone
sensory adaptation	accommodation	round window	sliding-filament model

mechanoreceptors	rod cells	pitch	cross-bridge
muscle spindle	cone cells	utricle	phosphagens
hair cell	fovea	saccule	creatine phosphate
pain receptor	retinal	semicircular canals	tropomyosin
nociceptor	opsin	lateral line system	troponin complex
thermoreceptor	rhodopsin	neuromast	sarcoplasmic reticulum
chemoreceptor	photopsins	statocysts	T (transverse) tubules
gustatory receptor	bipolar cells	statoliths	tetanus
olfactory receptor	ganglion cells	taste buds	motor unit
electromagnetic receptor	horizontal cells	locomotion	recruitment
photoreceptor	amacrine cells	hydrostatic skeleton	fast muscle fiber
eye cup	lateral inhibition	peristalsis	slow muscle fiber
compound eyes	optic chiasm	exoskeleton	cardiac muscle
ommatidia	lateral geniculate nuclei	cuticle	intercalated discs
single-lens eye	primary visual cortex	chitin	smooth muscle

LECTURE NOTES

I. Introduction to Sensory Reception

An animal's interaction with its environment depends on the processing of sensory information and the generation of motor output.

Sensory receptors receive information from the environment.

- Action potentials that reach the brain via sensory neurons are termed *sensations*.
- Interpretation of a sensation leads to the *perception* of the stimulus (e.g., smells, sounds)

Motor effectors carry out the movement in response to the sensory information.

A. Sensory receptors transduce stimulus energy and transmit signals to the nervous system

Sensory reception = Ability of a cell to detect the energy of a stimulus

Sensory receptors = Structures that transmit information about changes in an animal's internal and external environment

- They are usually modified neurons or epithelial cells occurring singly or within groups in sensory organs.
  - *Exteroreceptors* detect external stimuli, such as heat, pressure, light, and chemicals.
  - *Interoreceptors* detect internal stimuli, such as blood pressure and body position.
- Specialized to convert stimuli energy into changes in membrane potentials and then transmit signals to the nervous system
- All receptor cells have the same four functions: transduction, amplification, transmission, and integration.

1. Sensory transduction

Sensory transduction is the conversion of stimulus energy into a change in the membrane potential of a receptor cell.

Stimulus energy changes membrane permeability of the receptor cell (via opening or closing ion channel gates, or increasing ion flow by stretching the receptor cell membrane) and results in a graded change in the membrane potential called *receptor potential.*

2. **Amplification**

   Amplification of stimulus energy that is too weak to be carried into the nervous system often occurs.

   May take place in accessory structures or be a part of the transduction process.

3. **Transmission**

   Transmission of a sensation to the CNS occurs in two ways:

   1. The receptor cell doubles as a sensory neuron (e.g., pain cells). In this case, the intensity of the receptor potential will affect the frequency of action potentials that convey sensations to the CNS.
   2. The receptor cell transmits chemical signals (neurotransmitters) across a synapse to a second sensory neuron. In this case the receptor potential affects the amount of neurotransmitter that is released, which in turn influences the frequency of action potential generated by the sensory neuron.

4. **Integration**

   Receptor signals are integrated through summation of graded potentials.

   Sensory adaptation is a decrease in sensitivity during continued stimulation; a type of integration that results in selective information being sent to the CNS.

   The threshold for transduction by receptor cells varies with conditions resulting in a change in receptor sensitivity.

   Sensory information integration occurs at all levels in the nervous system.

B. Sensory receptors are categorized by the type of energy they transduce

Receptors can be grouped into five types depending on the type of energy they detect.

1. *Mechanoreceptors* are stimulated by physical deformation caused by pressure, touch, stretch, motion, sound—all forms of mechanical energy (see Campbell, Figure 49.1).
   - Bending of the plasma membrane increases its permeability to Na^+ and K^+ resulting in a receptor potential.
   - In human skin, Pacinian corpuscles deep in the skin respond to strong pressure, while Meissner's corpuscles and Merkel's discs, closer to the surface, detect light touch.
   - *Muscle spindles* are stretch receptors (a type of interoreceptor) that monitor the length of skeletal muscles, as in the reflex arc.
   - Hair cells detect motion.
2. *Nociceptors* are a class of naked dendrites that function as *pain receptors*
   - Different groups respond to excess heat, pressure, or specific chemicals released from damaged or inflamed tissue.
   - Prostaglandins increase pain by lowering receptor thresholds; aspirin and ibuprofen reduce pain by inhibiting prostaglandin synthesis.
3. *Thermoreceptors* respond to heat or cold and help regulate body temperature.
   - There is still debate about the identity of thermoreceptors in the mammalian skin. May be two receptors consisting of encapsulated, branched dendrites or the naked dendrites of certain sensory neurons.
   - The interothermoreceptors in the hypothalamus function as the primary temperature control of the mammalian body.

4. *Chemoreceptors* include general receptors that sense total solute concentration (e.g., osmoreceptors of the mammalian brain), receptors that respond to individual molecules, and those that respond to categories of related chemicals (e.g., *gustatory* and *olfactory receptors*).
5. *Electromagnetic receptors* respond to electromagnetic radiation such as light (*photoreceptors*), electricity, and magnetic fields (magnetoreceptors).
    - A great variety of light detectors has evolved in animals, from simple clusters of cells to complex organs.
    - Molecular evidence indicates that most, if not all, photoreceptors in animals may be homologous.

II. Photoreceptors

A. A broad array of photoreceptors has evolved among invertebrates

The *eye cup* of planarians is a simple light receptor that responds to light intensity and direction without forming an image (see Campbell, Figure 49.4).

- An opening on one side of the cup permits light to enter; the opening to one cup faces left and slightly forward, the other cup opens right and slightly forward.
- Light enters the opening and stimulates photoreceptors that contain light-absorbing pigments.
- Planaria move away from light sources to avoid predators.
- The proper direction is determined by the brain, which compares the rate of nerve impulses coming from the two cups; the animal turns until the impulses from each cup are equal and minimal.

Two types of image-forming eyes have evolved in invertebrates:

1. A *compound eye* contains thousands of light detectors called *ommatidia,* each with its own cornea and lens (see Campbell, Figure 49.5).
    - Found in insects, crustaceans, and some polychaete worms
    - Results in a mosaic image
    - More acute at detecting movement partly due to rapid recovery of photoreceptors
    - Superimposition eyes have ommatidia with lens that work like prisms and parabolic mirrors, focusing light entering several ommatidia onto photoreceptor (increases sensitivity to light)
2. In a *single-lens eye,* one lens focuses light onto the retina, which consists of a bilayer of photosensitive receptor cells.
    - Found in some jellies, polychaetes, spiders and many mollusks

B. Vertebrates have single-lens eyes

The parts of the vertebrate eye are structurally and functionally diverse (see Campbell, Figure 49.6)

- The vertebrate eye consists of a tough outer layer of connective tissue, the *sclera*, and a thin inner pigmented layer, the *choroid.* A thin layer of cells, known as the *conjunctiva*, covers the sclera and keeps the eye moist.
- The *cornea* is located in front and is a transparent area of the sclera; it allows light to enter the eye and acts as a fixed lens.
- The anterior choroid forms the *iris*, which regulates the amount of light entering the *pupil.* The iris is pigmented and gives the eye color; the pupil is the hole in the center of the iris.

- The *retina* is the innermost layer of the eyeball; it contains photoreceptor cells which transmit signals from the optic disc, where the optic nerve attaches to the eye.
  - The *lens* and *ciliary body* divide the eye into two chambers: a small chamber between the lens and cornea and a large chamber within the eyeball.
  - The ciliary body produces *aqueous humor* that fills the cavity between the lens and cornea.
  - *Vitreous humor* fills the cavity behind the lens and comprises most of the eye's volume.
  - Both aqueous humor and vitreous humor help to focus light onto the retina.

The lens is a transparent, protein disc that focuses an image onto the retina by changing shape (*accommodation*) (see Campbell, Figure 49.7).

- Is nearly spherical when focusing on near objects and flat when focusing at a distance
- Controlled by the ciliary muscle

The photoreceptors of the eye are *rod cells* and *cone cells* (see Campbell, Figure 45.8).

- Their relative numbers in the retina are partly correlated with whether an animal is diurnal or nocturnal.

Rod cells are sensitive to light but do not distinguish colors.

- Found in greatest density at peripheral regions of the retina; completely absent from the *fovea* (center of visual field) (see Campbell, Figure 49.6).

Cone cells are responsible for daytime color vision.

- Most dense at the fovea.

C. The light absorbing pigment rhodopsin operates via signal transduction

Cells in the retina transduce stimuli (caused by the lens focusing a light image onto the retina) into action potentials.

Each rod cell or cone cell has an outer segment with a stack of folded membranes in which visual pigments are embedded (see Campbell, Figure 49.8a).

- The visual pigments consists of light-absorbing *retinal*, which is synthesized from vitamin A, bonded to a membrane protein *opsin*.

Rods contain their own type of opsin, and when combined with retinal, makes up *rhodopsin*.

- When rhodopsin absorbs light, its retinal component changes shape. This triggers a chain of metabolic events that hyperpolarizes the photoreceptor cell membrane; thus, a decrease in chemical signal to the cells with which photoreceptors synapse serves as the message (see Campbell, Figure 49.9).
- Light-induced change in retinal is referred to as "bleaching" of rhodopsin; in bright light, rods become unresponsive and the cones take over.
- In the dark, enzymes convert retinal back to its original form.

Color vision involves more complex signal processing than the rhodopsin mechanism in rods.

- Color vision results from the presence of three subclasses of cones: red cones, green cones and blue cones, each with its own type of opsin associated with retinal for form visual pigments (*photopsins*).

D. The retina assists the cerebral cortex in processing visual information

Integration of visual information begins at the retina.

Rod and cone cell axons synapse with neurons called *bipolar cells*, which in turn synapse with *ganglion cells*.

Horizontal cells and *amacrine cells* are neurons in the retina that help integrate the information, after which ganglion cell axons convey action potentials along the optic nerve to the brain.

Rod and cone cell signals may follow vertical or lateral pathways.

- Vertical pathways involve information passing directly from receptor cells to bipolar cells to ganglion cells.
- Lateral pathways involve: horizontal cells carrying signals from one rod or cone to other receptor cells and several bipolar cells; amacrine cells spread the signals from one bipolar cell to several ganglion cells.

Horizontal cells, stimulated by rod or cone cells, stimulate nearby receptors but inhibit more distant receptors and non-illuminated bipolar cells, thus sharpening image edges and enhancing contrast (*lateral inhibition*) (see Campbell, Figure 49.10)

- Occurs at all levels of visual processing.

Optic nerves from each eye meet at the *optic chiasm* (see Campbell, Figure 49.11).

- The optic chiasm has nerve tracts arranged so that what is viewed in the left field of view is transmitted to the right side of the brain and vice versa.
- Ganglion axons usually continue through the *lateral geniculate nuclei* of the thalamus, and these neurons continue back to the *primary visual cortex* in the occipital lobe of the cerebrum.
- Additional neurons carry information to more sophisticated visual processing centers in the cortex.

III. Hearing and equilibrium

Hearing and equilibrium are related in most animals and involve mechanoreceptors.

A. The mammalian hearing organ is within the inner ear

Sound waves are collected by the outer ear (the external pinna and the auditory canal) and are channeled to the *tympanic membrane* of the *middle ear* (see Campbell, Figure 49.12).

The sound waves cause the tympanic membrane to vibrate at the same frequency; the tympanic membrane transmits the waves to three small bones—the *malleus, incus*, and *stapes*—which amplify and transmit the mechanical movements of the membrane to the *oval window,* a membrane of the *cochlea* surface.

- The middle ear opens into the *Eustachian tube*, a channel to the pharynx to aid in pressure equalization on both sides of the tympanic membrane.
- Oval window vibrations produce pressure waves in the fluid (endolymph) in the coiled cochlea of the *inner ear*.

The pressure waves vibrate the basilar membrane (forms the floor of the cochlear duct) and the attached *organ of Corti,* which contains receptor hair cells.

- The bending of the hair cells against the tectorial membrane depolarizes the hair cells and causes them to release a neurotransmitter that triggers an action potential in a sensory neuron, which then carries sensations to the brain through the auditory nerve.
- The pressure wave continues through the tympanic canal and is dissipated as it strikes the *round window*.

Volume is determined by the amplitude of the sound wave; *pitch* is a function of sound wave frequency.

- The greater the amplitude of a sound, the more vigorous the vibrations; this results in more bending of the hair cells and more action potentials.
- Different sound frequencies affect different areas of the basilar membrane, thus some receptors send more action potentials than others.

B. The inner ear also contains the organs of equilibrium

Several organs in the inner ear detect body position and balance.

- Behind the oval window is a vestibule that contains two chambers, the *utricle* and the *saccule*.
- The utricle opens into three *semicircular canals* (see Campbell, Figure 49.14a).

Hair cells in the utricle and saccule respond to changes in head position with respect to gravity and movement in one direction.

- Hair cells are arranged in clusters with their hairs projecting into a gelatinous material containing numerous otoliths (small calcium carbonate particles).
- The otoliths are heavier than endolymph in the saccule and utricle; gravity pulls them down on the hairs of receptor cells, thus causing a constant series of action potentials indicating position of the head.

Semicircular canals detect rotation of the head due to endolymph movement against the hair cells (see Campbell, Figure 49.14b and c).

C. A lateral line system and inner ear detect pressure waves in most fishes and aquatic amphibians

The inner ear of a fish has no eardrum, does not open to the outside of the body, and has no cochlea, but a saccule, utricle, and semicircular canals are present.

- Sound waves are conducted through the skeleton of the head to the inner ear. This sets otoliths in motion, stimulating the hair cells.
- Some fish have a Weberian apparatus, a series of three bones which conducts vibrations from the swim bladder to the inner ear.
- Fish can hear higher frequencies due to their inner ears.

In terrestrial amphibians, reptiles and birds, sound is conducted from the tympanic membrane to the inner ear by a single bone, the stapes.

Fishes and aquatic amphibians have a *lateral line system* running along both sides of the body (see Campbell, Figure 49.15)

- Mechanoreceptors called *neuromasts* contain hair cell clusters whose hairs are embedded in a gelatinous cap, the cupula.
- Water enters the system through numerous pores on the animal's surface and flows along the tube past the neuromasts.
- Pressure of moving water bends the cupula causing an action potential in the hair cells.
  - This provides information about the body's movement direction and velocity of water currents, and movements or vibrations caused by predators and prey.

D. Many invertebrates have gravity sensors and are sound-sensitive

Most invertebrates have mechanoreceptors called *statocysts* that function in their sense of equilibrium (see Campbell, Figure 46.16).

- Gravity causes *statoliths* (dense granules) to settle to the low point in a chamber, stimulating hair cells in that location.
- Statocysts are located along the bell fringe of many jellies and at the antennule bases in lobsters and crayfish.

Many invertebrates demonstrate a general sensitivity to sound, although specialized structures for hearing seem to be less widespread than gravity sensors.

The body hairs of many insects vibrate in response to sound waves of specific frequencies.

- Fine hairs on the antennae of male mosquitoes detect the hum produced by a female's wings.

- Vibrating body hairs of some caterpillars detect predatory wasps.

Many insects also have "ears," commonly located on their legs, consisting of a tympanic membrane stretched over an internal air chamber containing receptor cells that send nerve impulses to the brain (see Campbell, Figure 49.17).

IV. Chemoreception—Taste and Smell

Animals rely on chemoreception for many purposes, including locating food and mates, recognizing territories, and to assist with navigation (see Campbell, Figure 49.18).

A. Perceptions of taste and smell are usually interrelated

The perceptions of taste and smell depend on chemoreceptors that detect specific chemicals in the environment.

Insects have taste receptors within sensory hairs called sensillae on the feet and mouthparts; olfactory sensillae are usually located on antennae.

- Several chemoreceptor cells, each responding to a particular chemical, are located on each tasting hair; integrating impulses from the different receptors permits distinguishing many tastes (see Campbell, Figure 49.19).

In humans and other mammals, receptor cells for taste are organized into *taste buds* scattered in several areas of the tongue and mouth.

- Sweet, sour, salty and bitter are detected in distinct regions of the tongue.
- These tastes are associated with specific molecular shapes and charges that bind to separate receptor molecules.

In humans, olfactory receptor cells line the upper nasal cavity and send impulses along their axons directly to the olfactory bulb of the brain (see Campbell, Figure 49.20).

- Receptive ends of the cells contain cilia that extend into the coating layer of mucus lining the nasal cavity.
- Specific receptors respond to certain odorous molecules by depolarizing.
- The olfactory sense responds to airborne chemicals.
- Taste and olfaction have different receptors but interact.

V. Movement and Locomotion

Movement is a hallmark of animals. To catch food, an animal must move through the environment or move the surrounding medium (water or air) past itself. While some animals are sessile, most are mobile and rely on *locomotion* to acquire food or to escape from becoming food and to locate mates.

A. Locomotion requires energy to overcome friction and gravity

Different modes of transportation (running, flying, swimming) have evolved along with adaptations of animals to overcome the difficulties associated with each type of locomotion.

At the cellular level, all movements are based on the contractile systems of microfilaments and microtubules.

1. Swimming

Swimming animals must overcome resistance; thus, many are fusiform in body shape.

Animals swim in diverse ways.

2. Locomotion on land

A walking or running land animal must support itself and move against gravity,

- Inertia must be overcome with each step; leg muscles accelerate a leg from a standing start.

Animals that hop generate a lot of power in their hind legs by momentarily storing energy in their tendons.

Maintaining balance is also essential for running, walking, or hopping.

- Bipedal animals keep part of at least on e foot on the ground when walking.
- When running, momentum more than foot contact keeps the body upright.

Crawling animals must exert considerable effort to overcome friction.

3. Flying

Flying animals do not use a skeleton for support during motion, and must almost completely overcome gravity to become airborne.

Wings must provide enough lift to overcome gravity; the key is in the shape of the wings.

B. Skeletons support and protect the animal body and are essential to movement

Skeletons function in support, protection, and movement.

- Help maintain shape of aquatic animals.
- Hard skeletons protect soft body tissues.
- Skeletons provide a firm attachment against which muscles can work during movement.

1. Hydrostatic skeletons

Hydrostatic skeletons consist of fluid held under pressure in a closed body compartment.

Found in most cnidarians, flatworms, nematodes, and annelids

Control form and movement by using muscles to change the shape of fluid-filled compartments

Provide no protection and could not support a large land animal

The hydrostatic skeleton of earthworms and other annelids allows for the rhythmic locomotion (*peristalsis*) these animals are known for (see Campbell, Figure 49.23).

2. Exoskeletons

Exoskeleton = Hard encasement deposited on the surface of an animal

Mollusks are shed (molted) as the animals grow.

3. Endoskeletons

Endoskeleton = Hard supporting elements buried within the soft tissues of an animal

Sponges possess hard spicules of inorganic material or softer protein fibers.

Echinoderms have ossicles composed of magnesium carbonate and calcium carbonate forming hard plates beneath the skin.

Chordates have cartilage and/or bone skeletons divided into several areas.

The vertebrate frame is divided into an axial skeleton (the skull, vertebral column, and rib cage) and an appendicular skeleton (limb bones, pectoral and pelvic girdles) (see Campbell, Figure 49.24).

Bones of the vertebrate act in support and as levers when their attached muscles contract.

C. Muscles move skeletal parts by contracting

Animal movement is based on contraction of muscles working against some kind of skeleton.

- Muscles always contract actively; they can extend only passively.
- Ability to move a body part in opposite directions requires that muscles be attached to the skeleton in antagonistic pairs (see Campbell, Figure 49.25).

1. Structure and function of vertebrate skeletal muscle

Skeletal muscle = Bundle of long fibers running the length of the muscle; attached to bones and responsible for their movement (see Campbell, Figure 49.26)

- Each fiber is a single cell with many nuclei; consists of bundles of smaller *myofibrils* arranged longitudinally.
- Two kinds of *myofilaments* are found in each myofibril.
  1. *Thin filaments* consist of two strands of actin and one strand of regulatory protein coiled together.
  2. *Thick filaments* are staggered arrays of myosin molecules.

The unit of organization of skeletal muscle is the *sarcomere.*

- *Z lines* are the borders of the sarcomere; aligned in adjacent myofibrils.
- *I bands* are areas near the edge of the sarcomere containing only thin filaments.
- *A bands* are regions where thick and thin filaments overlap and correspond to the length of the thick filaments.
- *H zones* are areas in the center of the A bands containing only thick filaments.

D. Interactions between myosin and actin underlie muscle contractions

Muscle contraction reduces the length of each sarcomere.

This behavior is explained by the *sliding filament model* (see Campbell, Figure 49.27)

- Thin filaments ratchet across thick filaments to pull the Z lines together and shorten the sarcomere; the myofilaments themselves do not contract.
- Myosin molecules on thick filaments attach to actin on the thin filament to form a *cross-bridge*. It then bends inward, pulling the thin filament toward the center of the sarcomere, breaks the cross-bridge, and forms a new cross-bridge further down.
- Energy for cross-bridge formation comes from the hydrolysis of ATP by the head region of myosin (see Campbell, Figure 49.28).
  - Muscles store only a enough ATP for a few contractions. Most of the energy is stores as *phosphagens*.
  - Creatine phosphate, the phosphagen of vertebrates, can provide a phosphate group to ADP to make the ATP as needed.

E. Calcium ions and regulatory proteins control muscle contraction

Skeletal muscles contract when stimulated by motor neurons.

- An action potential in the motor neuron innervating the muscle cell causes the axon to release a neurotransmitter (e.g., acetylcholine).
- Binding on the neurotransmitter to the muscle cell triggers an action potential in the muscle cell
- The action potential of the muscle cell causes contraction.

In a muscle at rest, myosin-binding sites on the actin are blocked by the regulatory protein strand (*tropomyosin*) in the thin filament and by the *troponin complex* located at each binding site. A contraction cycle is as follows:

- The wave of depolarization spreads rapidly in the muscle via infoldings in the muscle cell plasma membrane (*transverse* or *T tubules*).
- The *sarcoplasmic reticulum* (the specialized endoplasmic reticulum of muscle cells) membrane becomes depolarized and releases its store of Ca^{2+}.
- The calcium ions bind to troponin, causing the thin filament to change shape and expose the myosin-binding sites; the muscle can then contract.

- The contraction is terminated as calcium is pumped out of the cytoplasm by the sarcoplasmic reticulum; as the calcium concentration falls, the tropomyosin-troponin complex again blocks the myosin-binding sites.

F. Diverse body movements require variation in muscle activity

Graded contractions of skeletal muscles are due to summation of multiple motor unit activity (*recruitment*) and wave summation.

- Motor neurons usually deliver their stimuli rapidly, resulting in smooth contraction typical of *tetanus* (sustained contraction) rather than the jerky actions of muscle twitches.
- A *motor unit* consists of a single motor neuron and all the muscle fibers it controls; all fibers in the motor unit contract as a group when the motor neuron fires.
- As more motor neurons are recruited by the brain, tension in the muscle progressively increases.

1. Fast and slow muscle fibers

Duration of muscle contraction is controlled by how long the Ca^{2+} concentration in the cytoplasm remains elevated.

Slow muscle fibers have longer-lasting twitches because they have less sarcoplasmic reticulum; thus, Ca^{2+} remains in the cytoplasm longer.

- Have many mitochondria, a rich blood supply, and the oxygen-storing protein myoglobin
- Used to maintain posture since they can sustain long contractions

Fast muscle fibers have short duration twitches and are used in fast muscles for rapid, powerful contractions.

- Some are able to sustain long periods of repeated contractions without fatiguing.

2. Other types of muscles

Vertebrate *cardiac muscle* is found only in the heart.

- Is striated
- Muscle cells are branched, and the junction between cells contain *intercalated discs* that electrically couple all heart muscle cells, allowing coordinated action.
- Cells can also generate their own action potentials.
- Rhythmic depolarizations due to pacemaker channels in the plasma membrane trigger action potentials which last up to 20 times longer than those for skeletal muscle and have long refractory periods.

Smooth muscles lack striations and contain less myosin; the myosin is not associated with specific actin strands.

- They generate less tension, but can contract over a greater range of lengths.
- Do not have a transverse tubule system or a well developed sarcoplasmic reticulum; calcium ions must enter the cytoplasm through the plasma membrane during an action potential.
- Contractions are relatively slow but there is greater range of control.
- They are found mainly in the walls of blood vessels and digestive tract organs.

Invertebrates have muscles similar to the skeletal and smooth muscles of vertebrates, but with some interesting adaptations.

- Arthropod skeletal muscles are very similar to vertebrate skeletal muscle.

- Insect wings actually beat faster than action potentials arrive from the CNS since the flight muscles are capable of independent, rhythmic contractions.
- The thick filaments of muscles in clams which hold the shell closed contain paramyosin; this unique protein allows the muscles to stay in a fixed state of contraction for up to a month.

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CHAPTER 50

AN INTRODUCTION TO ECOLOGY AND THE BIOSPHERE

OUTLINE

I. The Scope of Ecology
   A. Ecology is the scientific study of the interactions between organisms and their environment
   B. Ecological research ranges from the adaptations of organisms to the dynamics of ecosystems
   C. Ecology provides a scientific context for evaluating environmental issues

II. Abiotic Factors of the Biosphere
   A. Climate and other abiotic factors are important determinants of the biosphere's distribution of organisms

III. Aquatic and Terrestrial Biomes
   A. Aquatic biomes occupy the largest part of the biosphere
   B. The geographical distribution of terrestrial biomes is based mainly on regional variations in climate

IV. Concepts of Organismal Ecology
   A. The costs and benefits of homeostasis affect an organism's responses to environmental variation
   B. An organism's short-term responses to environmental variations operate within a long-term evolutionary framework

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. Explain why the field of ecology is a multidisciplinary science.
2. Distinguish among physiology, ecology, community ecology, and ecosystem ecology.
3. Describe the relationship between ecology and evolution.
4. Explain the importance of temperature, water, light, soil, and wind to living organisms.
5. Explain the principle of allocation.
6. Describe how environmental changes may produce behavioral, physiological, morphological, or adaptive responses in organisms.
7. Explain the concept of environmental grain and under what situation(s) a single environment may be both coarse-grained and fine-grained.
8. Describe the characteristics of the major biomes: tropical forest, savanna, desert, chaparral, temperate grassland, temperate forest, taiga, tundra.
9. Compare and contrast the types of freshwater communities.
10. Using a diagram, identify the various zones found in the marine environment.

KEY TERMS

ecology	turnover	eutrophic	benthos
abiotic components	photic zone	mesotrophic	abyssal zone
biotic components	aphotic zone	wetlands	canopy
organismal ecology	thermocline	estuary	permafrost
population	benthic zone	intertidal zone	regulator
community	benthos	neritic zone	conformer
ecosystem	detritus	oceanic zone	principle of allocation
biosphere	littoral zone	pelagic zone	acclimation
climate	limnetic zone	benthic zone	
biome	profundal zone	coral reef	
tropics	oligotrophic	oceanic pelagic biome	

LECTURE NOTES

Ecology is the scientific study of the interactions of organisms and their environments.

- A complex and critical area of biology.
- There are three key words in the definition: scientific, environment, and interactions.

I. The Scope of Ecology

A. Ecology is the scientific study of the interactions between organisms and their environments

The scientific nature of ecology involves using observations and experiments to test hypothetical explanations of ecological phenomena.

- Ecology has a long history of being a descriptive science but is young as an experimental science.
  - Very difficult to conduct experiments and control variables
  - Some scientists test hypotheses in lab experiments and by manipulating populations and communities in field experiments
  - Some scientists devise mathematical models that include important variables and hypothetical relationships; usually studied with the aid of a computer.
  - Mathematical models are also used to simulate large-scale experiments that are impossible to conduct in the field; however, the basic information on which the models are based still must be obtained through fieldwork.
- It is a multidisciplinary field examining questions from all areas of biology as well as many physical sciences.

The environment of an organism includes both biotic and abiotic components.

- *Biotic components* include all other organisms that are a part of any individual organism's environment.
- *Abiotic components* are the nonliving chemical and physical factors (e.g., temperature, light, water, nutrients) to which an organism is exposed.

The interactions between organisms and their environments include how the environment affects an organism and how an organism can change the environment.

- Photosynthetic bacteria began to use sunlight for energy about three billion years ago.
  - Oxygen, a by-product of photosynthesis, accumulated and resulted in an aerobic atmosphere.

- The shading of the forest floor by trees sometimes makes the floor unsuitable (due to reduced light) for their offspring to grow.

Short-term (ecological time) interactions of organisms with their environments could have long-term (evolutionary time) effects through natural selection.

- For example, predator-prey interactions may affect gene pools where individuals with protective coloration would become more prevalent.
- The current distribution and abundance of organisms are products of long-term evolutionary changes and ongoing interactions.

B. Ecological research ranges from the adaptations of organisms to the dynamics of ecosystems

Ecology can be divided into four increasingly comprehensive levels of inquiry:

1. *Organismal ecology* studies the behavioral, physiological, and morphological ways individuals meet abiotic environmental challenges.

   The distribution of organisms is limited by their tolerance of abiotic conditions.

2. *Population ecology* studies groups of individuals of the same species living in a particular geographic area.

   Questions in population ecology concern factors that affect population size and composition

3. *Community ecology* studies all organisms that inhabit a particular area.

   Questions concern predation, competition, disease, and other ways in which interactions among organisms affect community structure and organization

4. *Ecosystem ecology* studies all abiotic factors as well as communities of organisms in an area.

   Questions concern energy flow and chemical cycling among the abiotic and biotic components

Ecological study is multidisciplinary in nature, encompassing genetics, evolution, physiology, behavior, chemistry, physics, geology, and meteorology.

C. Ecology provides a scientific context for evaluating environmental issues

Although distinct, basic ecology and environmental issues have many connections.

- To properly address environmental problems, it is necessary to understand the relationships between organisms and their environments.
- Current environmental awareness began with Rachel Carson's 1962 book *Silent Spring*, which exposed the fact that widespread use of pesticides often affects nontarget organisms.
- The realization that Earth is a finite resource and that pollution, overpopulation, and habitat destruction are threatening that resource is a concern of most people.

II. Abiotic Factors of the Biosphere

The *biosphere* is the global ecosystem—the sum of all Earth's ecosystems.

- It is a thin layer consisting of the atmosphere to an altitude of a few kilometers; the land down to and including water-bearing rocks at least 1500 meters below ground, lakes and streams, caves; and the oceans to a depth of several kilometers.

A. Climate and other abiotic factors are important determinants of the biosphere's distribution of organisms

Global and regional patterns reflect differences in climate and other abiotic factors.

- Abiotic factors such as temperature, humidity, salinity, and light influence the distribution of organisms.
- The patchiness of the global biosphere illustrates how different physical environments produce a mosaic of habitats.

1. Major abiotic factors

Some of the important abiotic factors that affect distribution of species include: temperature, water, sunlight, wind, rocks and soil, and periodic disturbances.

a. Temperature

Environmental temperature affects biological processes and body temperature.

- Most organisms are unable to regulate their body temperature precisely
- Temperature greatly affects metabolism: few organisms have active metabolisms at temperatures close to 0°C, and temperatures above 45°C denature most essential enzymes.
- The actual body temperature of ectotherms is affected by heat exchange with the environment.
- Most animals maintain a body temperature only a few degrees above or below ambient temperature.
- Even endotherms function best within the environmental temperature range to which they are adapted.

b. Water

Water is essential for life and adaptations for water balance and conservation help determine a species' habitat range.

- Marine and freshwater animals face the problems of regulating intracellular osmolarity; terrestrial animals face the problem of desiccation.

c. Sunlight

Sunlight provides the energy that drives nearly all ecosystems although only photosynthetic organisms use it directly as an energy source.

Light is not the most important limiting factor in terrestrial environments but may play a role as in the reduction of competition due to shading in a forest.

In aquatic environments, the distribution of photosynthetic organisms is limited by the intensity and quality of light.

- Water selectively reflects and absorbs certain wavelengths; therefore, most photosynthesis occurs near the water surface.

The physiology, development, and behavior of many animals and plants are often sensitive to photoperiod.

d. Wind

Wind amplifies the effects of temperature by increasing heat loss by evaporation and convection.

- Wind also increases the evaporation rate of animals and transpiration rate of plants, resulting in more rapid water loss.

Mechanical pressure of wind can affect plant morphology (for example, inhibiting growth of limbs on windward side of trees).

e. Rocks and soil

The physical structure, pH, and mineral composition of soil limit distribution of plants and hence animals that feed on those plants.

- The composition of the substrate in a stream or river greatly influences the water chemistry, which in turn influences the plants and animals.

- The type of substrate influences what animals can attach or burrow in intertidal zones.

f. Periodic disturbances

Catastrophic disturbances such as fire, hurricanes, typhoons, and volcanic eruptions can devastate biological communities.

- After the disturbance, the area is recolonized by organisms or repopulated by survivors., but the structure of the community undergoes a succession of changes.
- Those disturbances that are infrequent (volcanic eruptions) do not elicit adaptations. Adaptations do evolve to periodically recurring disturbances such as fires.

2. Climate and the distribution of organisms

Climate is the prevailing weather conditions at a locality.

- The major components of climate are temperature, water, light, and wind.
- Climate has a major impact on the distribution of organisms.

A climatograph plots temperature and rainfall in a particular region (see Campbell, Figure 50.3).

- Usually plotted in terms of annual means
- Must be careful to distinguish a correlation between climate variables and biomes from causation.
  - *Biomes* are the major types of ecosystems typical of broad geographic areas.
- Only a detailed study of a species' tolerances to water and temperature ranges could establish the direct effects of these variables.
- The fact that biomes overlap on climatographs indicate that factors other than mean temperature and rainfall play roles in determining biome location (e.g., soil composition).

3. Global climate patterns

Solar energy input and the Earth's movement in space determine the planet's global climate patterns.

About 50% of the solar energy that reaches the atmosphere's upper layers is absorbed before it reaches the surface.

- Ultraviolet and certain other wavelengths are more readily absorbed by oxygen and ozone than other wavelengths.
- Some of the solar energy that reaches the Earth's surface is reflected back into the atmosphere; large amounts are absorbed by land, water, and organisms.

The atmosphere, land, and water are heated when they absorb solar energy. This heating establishes the temperature variations, air movement cycles, and evaporation of water responsible for the latitudinal variations in climate.

- Latitudinal variation in the intensity of sunlight results from the Earth's spherical shape; seasonal variation in solar radiation in the Northern and Southern Hemispheres are due to the Earth's tilt of 23.5° relative to its plane of orbit (see Campbell, Figures 50.4 and 50.5). The tilt causes solar radiation to change daily as the Earth rotates around the sun.
- Only the *tropics* (23.5°N to 23.5°S) receive sunlight from directly overhead year round. The tropics receive the greatest annual input of solar radiation and show the least seasonal variation; only small variations in daylength and temperature occur.

- Seasonal variation in light and temperature increases steadily toward the poles; polar regions have long, cold winters with periods of continual darkness and short summers with periods of continual light.

A global circulation of air which creates precipitation and winds results from the intense solar radiation near the equator (see Campbell, Figure 50.6).

- Evaporation of surface water due to high tropical temperatures causes warm, wet air masses to rise near the equator; this rising air creates an area of light, shifting winds (doldrums) along the equator.
- As these warm air masses rise, they expand and cool; cool air can hold less water vapor so the rising air masses drop large amounts of rain in the tropics.
- The cool, dry air masses flow toward the poles at high altitudes; they continue to cool as they move farther from the equator.
- Air mass density increases as they become cooler; they begin to descend toward the surface as cool, dry air masses at about 30° latitude.
- The air masses absorb water as they descend, thus creating arid climates around 30°N and 30°S.
- Some of the descending air masses flows toward the poles at low altitudes, the rest flows toward the equator.
- The air masses flowing toward the poles are warmed and rise again at about 60°N and 60°S; as these masses of air begin to cool with increased altitude, the water vapor is lost as precipitation.
- As air from this third cell reaches the higher altitude and cools, it flows toward the poles where it descends and flows back toward the equator.

4. Local and seasonal effects on climate

Although global climate patterns explain the geographic distribution of major biomes, local variations due to bodies of water and topographical features create a regional patchiness in climatic conditions.

- The regional and local variations in climate and soil have a major influence on less widely distributed communities and individual species.

Proximity of large bodies of water affect local climates.

- Ocean currents are generated by the Earth's rotation and may heat or cool (depending on whether they are tropical or polar currents) air masses passing over them toward land; evaporation is also greater over the ocean than over land.
- Coastal areas are more moist than inland areas at the same latitude; the California current flows from southward along the western U.S. and helps form a cool, moist climate in this area.
- During warm summer days, air over land heats faster than that over the ocean or large inland lakes; this warmer air rises, drawing a cool breeze from the water across the land.

Topographical variations, such as mountains, also exert an influence on solar radiation, local temperature and rainfall.

- In the Northern Hemisphere, south-facing slopes receive more sunlight and are therefore warmer and drier than north-facing slopes.

  The vegetation differs with south-facing slopes being covered by shrubby, drought resistant plants while the north-facing slopes have forests.

- Air temperature declines 6° C for each 1000m increase in elevation.

This parallels the decline in temperature associated with increasing latitude.

For this reason, mountain communities are similar to those at lower elevations farther from the equator.

- When warm, moist air moves over a mountain, its altitude is increased and it cools; cooling causes the air to release its moisture as rain on the windward side.
- The cooler, drier air then flows down the leeward side of the mountain; the cool dry air is warmed and absorbs moisture, producing the rainshadow (see Campbell, Figure 50.7).
- Deserts commonly occur on leeward sides of mountains.

The Earth's orbit around the sun causes seasonal changes in local conditions.

- The changing angle of the sun causes slight shifts in the wet and dry air masses on either side of the equator.

  These shifts result in the wet and dry seasons at 20° latitude where tropical deciduous forests grow.

- Seasonal changes in wind patterns produce variations in ocean currents, sometimes causing upwellings that bring nutrient-rich, cold water from the deep ocean layer to the surface.
- Seasonal temperature changes also cause the temperature profiles that develop during the summer in temperate zone ponds and lakes.

  These profiles reverse in the autumn and spring resulting in biannual mixing that brings nutrient-rich water from the bottom to the top (*turnover*; see Campbell, Figure 50.8)

Climate also varies on a smaller scale, the microclimate. Microclimate refers to small areas within a habitat that may have very different conditions than the overall area (e.g., under a rock, a forest floor).

- Cleared areas in a forest generally show greater temperature extremes than the shaded forest floor due to greater solar radiation and wind currents.
- Low-lying areas are usually moister than high ground and support different forms of vegetation.
- The area under a large stone or log is protected from extremes of temperature and moisture; a large number of small organisms usually live in such sheltered areas.

III. Aquatic and Terrestrial Biomes

The worldwide distribution of aquatic and terrestrial biomes is shown in Campbell, Figures 50.9 and 50.15.

A. Aquatic biomes occupy the largest part of the biosphere

Life arose in water and evolved there for almost three billion years before moving into terrestrial habitats.

- Aquatic biomes still account for the largest part of the biosphere.

Freshwater and marine biomes are distinguished on the basis of physical and chemical differences.

- Freshwater biomes have a salt concentration less than 1%; marine biomes average 3% salt concentration.

The oceans cover 75% of Earth’s surface and contain the marine biomes.

- Evaporation from the oceans provides most of the rainfall.
- Ocean temperatures greatly effect world climate and wind patterns.

- Marine algae ad photosynthetic bacteria consume large amounts of the atmospheric carbon dioxide and produce a major portion of the world's oxygen.

Freshwater biomes are closely linked to the soils and biotic components of the terrestrial biomes in which they are located or through which they flow.

- Runoff from terrestrial habitats creates streams and rivers.
- Accumulated runoff creates ponds and lakes.
- Freshwater biomes are also influenced by the patterns and speed of water flow and the climate to which they are exposed.

1. Vertical stratification of aquatic biomes

Aquatic biomes often exhibit pronounced vertical stratification

- There is a decrease in light intensity with increasing depth as light is absorbed by the water and suspended microorganisms. This divides bodies of water into two layers:

  The *photic zone* is the upper layer where light is sufficient for photosynthesis.

  The lower *aphotic zone* receives little light and no photosynthesis occurs.
- Water temperature tends to be stratified, especially during winter and summer.
- Heat energy from sunlight warms the upper layers of water as far as it penetrates; the deeper waters remain cold.
  - The *thermocline* is a narrow vertical zone between the warmer and colder waters where a rapid temperature change occurs.
- At the bottom of all aquatic biomes is the *benthic zone*, which is occupied by communities of benthos organisms that consume dead organic matter.

2. Freshwater biomes

Standing bodies of water vary greatly in size, from ponds to large lakes.

Ponds and lakes usually exhibit a significant vertical stratification in light penetration and water temperature.

The distribution of plants and animals within a pond or lake also shows a stratification based on water depth and distance from the shore (see Campbell, Figure 50.10).

- The *littoral zone* is shallow, well-lit waters close to shore.

  Characterized by the presence of rooted and floating vegetation, and a diverse attached algal community (especially diatoms)

  There is a diverse animal fauna including suspension feeders (clams); herbivorous grazers (snails); and herbivorous and carnivorous insects, crustaceans, fishes, and amphibians.

  Some reptiles, water fowl, and mammals also frequent this zone.
- The *limnetic zone* is the open, well-lit waters away from shore.

  Occupants include photosynthetic phytoplankton (algae and cyanobacteria), zooplankton (rotifers and small crustaceans) that graze on phytoplankton, and small fish which feed on the zooplankton.

  Occasional visitors to this zone are large fish, turtles, snakes, and piscivorous birds.
- The *profundal zone* is the deep, aphotic zone lying beneath the limnetic zone.
  - This is an area of decomposition where detritus (dead organic matter that drifts in from above) is broken down.

    - Water temperature is usually cold and oxygen is low due to cellular respiration of decomposers.
    - Mineral nutrients are usually plentiful due to decomposition of detritus.
    - Waters of the profundal zone usually do not mix with surface waters due to density differences related to temperature.
- Mixing of these layers usually occurs twice each year in temperate lakes and ponds; thus, oxygen enters the profundal zone and nutrients are cycled into the limnetic zone.

Lakes are often classified as oligotrophic or eutrophic, depending on the amount of organic matter produced.

- *Oligotrophic* lakes are deep, nutrient-poor lakes in which the phytoplankton are not very productive (see Campbell, Figure 50.11a).

    The water is usually clear and the profundal zone has a high oxygen concentration since little detritus is produced in the limnetic zone to be decomposed.

- *Eutrophic* lakes are usually shallow, nutrient-rich lakes with very productive phytoplankton (see Campbell, Figure 50.11b).

    The waters are usually murky due to large phytoplankton populations and the large amounts of detritus being decomposed may result in oxygen depletion in the profundal zone during the summer.

- *Mesotrophic* lakes have moderate amounts of nutrients and phytoplankton productivity.

Oligotrophic lakes may develop into mesotrophic and then eutrophic lakes over a long period of time.

- Runoff from surrounding terrestrial habitats brings in mineral nutrients and sediments.
- Human activities increase the nutrient content of runoff due to lawn and agricultural fertilizers; municipal wastes dumped into lakes dramatically enriches the nitrogen and phosphorus concentrations, which increases phytoplankton and plant growth.
- Algal blooms and increased plant growth results in more detritus and can lead to oxygen depletion due to increased decomposition.

    This cultural eutrophication usually makes the water unusable.

Streams and rivers are bodies of water that move continuously in one direction (see Campbell, Figure 50.11c).

- There is a change in structure of these bodies of water from their headwaters (point of origin) to their mouths (where they empty into a larger body of water).
- At the headwaters, the water is cold and clear, carries little sediment, and has few mineral nutrients.
- The channel is narrow with a rocky substrate and the water flows swiftly.
- Near the mouth, water moves slowly and is more turbid due to sediment entering from other streams and erosion; the nutrient content is also higher.
- The channel is usually wider with a silty substrate that has resulted from deposition of silt.

Human activities have greatly affected many streams and rivers.

- Channelization (increases flow rate) and damming (slows flow rate) often change associated ecosystems.

- Pollutants may be taken up by the natural flora and fauna.

3. Wetlands

A *wetland* is an area covered by water that supports aquatic vegetation (see Campbell, Figure 50.12).

- Includes a broad range of habitats from periodically flooded regions to soil that is permanently saturated during growing season
- Conditions favor hydrophytes, which are plants specially adapted to grow in water or soil that is periodically anaerobic due to being saturated with water.
    - Cattails, pond lilies, and sedges are examples of hydrophytes.
- Both the hydrology and the vegetation are important determinants in wetland classification.

A wide variety of wetlands has been recognized although they form in one of only three topographic situations:

1. Basin wetlands develop in shallow basins ranging from upland depressions to lakes and ponds that have filled in.
2. Riverine wetlands develop along shallow and periodically flooded banks of streams and rivers.
3. Fringe wetlands are found along coasts of large lakes and seas where rising lake levels or tides cause water to flow back and forth.
    - Fringe wetlands include both freshwater and marine habitats.
    - Marine coastal wetlands are closely linked to estuaries.

Wetlands are among the richest and valuable of biomes.

- A diverse invertebrate community is present which supports a wide variety of birds.
- A variety of herbivorous species consume the algae, detritus, and plants.
- They provide water storage basins that reduce the intensity of flooding.
- They improve water quality by filtering pollutants.

Although many wetlands have been destroyed for agriculture and development, a move to protect the remaining wetlands is underway.

4. Estuaries

An *estuary* is the area where a freshwater stream or river merges with the ocean.

- They are often bordered by salt marshes or intertidal mudflats
- Their salinity varies spatially within the estuary from nearly fresh water to ocean water; varies daily in these areas due to rise and fall of tides
- Estuaries are very productive due to nutrients brought in by rivers.

Because of their productivity, estuaries have a diverse flora and fauna.

- Salt marsh grasses, algae, and phytoplankton are the major producers.
- Many species of annelids, oysters, crabs, and fish are also present.
- Many marine invertebrates and fish breed in estuaries or migrate through them to freshwater habitats upstream.
- A large number of water fowl and other semiaquatic vertebrates use estuaries as feeding areas.

Human activities have had a large impact on estuaries.

- Estuaries receive the pollutants dumped into the streams and rivers that feed them.
- Residential and commercial development not only adds to pollution but eliminates some estuaries due to land filling.

- Very little undisturbed estuary habitat remains.

5. **Zonation in marine communities: *an introduction***

Similar to freshwater communities, marine communities are distributed according to depth of the water, distance from shore, degree of light penetration, and open water versus bottom (see Campbell, Figure 50.13).

- A photic zone is present and extends to the depth at which light penetration supports photosynthesis; occupied by phytoplankton, zooplankton, and many fish species.
- The aphotic zone is below the level of effective light penetration and represents a majority of the ocean's volume.
- The *intertidal zone* is the shallow zone where terrestrial habitat meets the ocean's water.
- The *neritic zone* extends from the intertidal zone, across the shallow regions, to the edge of the continental shelf.
- The *oceanic zone* extends over deep water from one continental shelf to another; reaches great depth.
- *Pelagic zone* refers to open waters of any depth.
- *Benthic zone* refers to the seafloor.

6. **The intertidal zones**

Intertidal zones, where land and sea meet, are alternately submerged and exposed by daily tide cycles.

- Organisms in this zone are exposed to variations in temperature and availability of sea water.
- These organisms are also subjected to the mechanical forces of wave action.

Rocky intertidal zones are vertically stratified and inhabited by organisms that possess structural adaptations that allow them to remain attached in this harsh environment (see Campbell, Figure 50.14)

- The uppermost zone is submerged only by the highest tides and is occupied by relatively few species of algae, grazing mollusks, and suspension-feeding barnacles.

    These organisms have various adaptations to prevent dehydration.

- The middle zone is exposed at low tide and submerged at high tide.

    Many species of algae, sponges, sea anemones, barnacles, mussels, and other invertebrates are found in this area.

    The diversity is greater here due to the longer time spans this area is submerged.

- Tide pools are often found in the middle zone.

    These are depressions which are covered during high tide and remain as pools during low tide.

    Tidepool organisms face dramatic salinity increases as water evaporates at low tide.

- The low intertidal zone is exposed only during the lowest tides and shows the greatest diversity of invertebrates, fishes, and seaweeds.

Sandy intertidal zones and mudflats do not show a clear stratification.

- Wave action continually shifts sand or mud particles; few algae or plants are present.
- Predatory crustaceans and many suspension-feeding worms and clams burrow into the sand or mud and feed when the tide submerges the area.

- Predatory or scavenging crabs and shorebirds often feed on burrowing organisms in these areas.

The diversity of intertidal zones is being reduced by human impact.

- Oil pollution destroys many species.
- Polluted water, old fishing lines, and plastic debris is harmful to most species.
- Recreational use of these areas has greatly reduced the number of beach-nesting birds and turtles.

7. Coral reefs

Coral reefs are found in the neritic zone of warm tropical waters where sunlight penetrates to the ocean floor.

- Sunlight penetration permits photosynthesis and a constant supply of nutrients is provided by currents and waves.

Coral reefs are dominated by the structure of the coral. It is formed by a diverse group of cnidarians that secrete a hard, calcium carbonate external skeleton, which provides a substrate on which other corals, sponges, and algae grow (see Campbell, Figure 50.14)

- Multicellular algae that are encrusted with calcium carbonate add large amounts of limestone to the reefs, as do bryozoans.

The cnidarian coral animals feed on microscopic organisms and organic debris, and they obtain some organic molecules from the photosynthetic products of their symbiotic dinoflagellate algae.

- Coral animals can survive without the dinoflagellates, but their rate of calcium carbon deposition is much slower without them; thus, reef formation by corals depends on this symbiotic association.

Reef communities are very old and grow very slowly.

Although many coral reefs are very large, they are delicate and can be severely damaged or destroyed by pollution, human induced damage, or introduced predators (e.g., crown-of-thorns sea star).

8. The oceanic pelagic biome

The *oceanic pelagic biome* consists of the open waters far from shore.

The area is constantly mixed by circulating ocean currents.

Nutrient content is generally lower than in coastal areas because the remains of organisms sink out of the zone to the lower benthic regions.

In tropical waters, nutrient content of surface waters is lower than surface waters of temperate oceans because a permanent thermal stratification prevents nutrient exchange with the deep waters.

Temperate oceans experience periodic upwellings which carry nutrients from the bottom to the surface.

Plankton is prevalent in this zone.

- Photosynthetic phytoplankton grow and reproduce in the photic region (top 100m) of this biome.
- Zooplankton (which graze on the phytoplankton) includes protozoans, copepods, krill, jellies, and larvae of many invertebrates and fishes.
- Most species stay afloat in this zone through the aid of morphological structures like bubble-trapping spines, lipid droplets, gelatinous capsules, and air bladders.

Nekton (free-swimming animals) are also found in the oceanic pelagic biome.

Large squid, fishes, sea turtles, and marine mammals feed in this area.

Many fish are adapted to and live in the aphotic region of the pelagic zone.

Some have large eyes allowing them to see in dim light, while others have luminescent organs used to attract mates and prey.

Many pelagic bird species also feed on fish in this region.

9. Benthos

Benthos refers to those organisms which inhabit the benthic zone, the ocean bottom below both the neritic and pelagic zones.

- The benthic zone receives nutrients in the form of detritus, which settles into the area from the waters above.
- Light and temperature decline rapidly from shallow, near-shore benthic areas to the ocean's depths.
- The benthic zone substrate may be sand or very fine sediment composed of silt and shells of dead microscopic organisms.

Neritic benthic communities are diverse and productive.

- Many bacteria, fungi, seaweeds, filamentous algae, numerous invertebrates, and fishes are found here.
- Many of the species present are burrowing forms.
- The composition of the community varies with distance from shore, water depth, and bottom composition.

Deep benthic communities living in the *abyssal zone* are exposed to very different conditions than those under the neritic and pelagic zones.

- Water temperature is continuously cold (3°C), water pressure is extremely high, there is very little (if any) light, and low nutrient concentrations are typical.
- Oxygen is usually present and a fairly diverse community of invertebrates and fishes can be found.
- The deep-sea hydrothermal vent communities are found along midocean ridges in this region (see Campbell, Figure 50.4).

  These vent communities include chemoautotrophic bacteria as the primary producers in place of photosynthesizing organisms.

  These bacteria obtain energy by oxidizing H_2S which forms by a reaction of the hot vent water with dissolved sulfate.

  The bacteria are consumed by a variety of giant polychaete worms, arthropods, echinoderms, and fishes.

B. The geographical distribution of terrestrial biomes is based mainly on regional variations in climate

The climate and other abiotic factors are important in determining why a particular terrestrial biome is found in an area.

- There are latitudinal patterns of biome distribution over the Earth’s surface due to the latitudinal patterns in climate.

Terrestrial biomes are often named for major physical or climatic features and for the predominant vegetation, but each is also characterized by microorganisms, fungi, and animals adapted to that particular environment.

Vertical stratification is an important feature of terrestrial biomes and the shape and sizes of plants largely defines the layering.

- In many forests, the layers are the canopy.
- Vertical stratification of a biome’s vegetation provides many different habitats for animals

Biomes grade into each other without sharp boundaries and may form ecotones, transitional areas between two communities.

Species composition may vary from one location to another within a biome.

Biomes are dynamic, and disturbance rather than stability is the rule.

- Disturbance may result in patchy biomes, with several communities represented in one biome.
- Human activities have radically altered the natural patterns of periodic disturbances.

Campbell, Figure 50.16 surveys the major terrestrial biomes.

IV. Concepts of Organismal Ecology

A. The costs and benefits of homeostasis affect an organism's responses to environmental variation

Organisms survive and reproduce in areas where environmental conditions to which they are adapted are found.

- The ability to tolerate one factor may be dependent on another factor; for example, many aquatic ectotherms can tolerate reduced oxygen at low temperatures, but not at high temperatures which cause higher metabolic rates.

1. Regulators and conformers

Organisms faced with a fluctuation in an environmental variable may maintain the homeostasis of their bodies through behavioral and physiological mechanisms (regulators) or by allowing their internal conditions to vary with external conditions (conformers).

- Some species are conformers under certain conditions and become regulators under others (see Campbell, Figure 50.17)

Energy expenditure by the animal is necessary if behavioral or physiological mechanisms are used to maintain homeostasis.

- For organisms to survive and reproduce, the energy "cost" of regulation cannot exceed the benefits of homeostasis.
- Since few organisms are perfect regulators or perfect conformers, a majority of organisms represent a group of evolved strategies which permits them to live in their specific environment.

2. The principle of allocation

The *principle of allocation* is an important concept for assessing the responses of organisms to a complex environment.

- This principle holds that each organism has a limited amount of energy that can be allocated for obtaining nutrients, escaping predators, coping with environmental fluctuations, growth, and reproduction.
- Energy expended for one function reduces the amount of energy available for other functions.
- If an organism expends a large amount of energy to maintain homeostasis, less is available for growth, reproduction, and other functions.

The distribution of organisms and the homeostatic mechanisms they possess establish different priorities for energy allocation.

- Conformers living in a stable environment may have more energy available for growth and reproduction; however, their geographic distribution is restricted due to intolerance to environmental change.

- Regulators that allocate a large amount of energy to survive environmental changes have less available for other functions so they grow and reproduce less efficiently; however, they can survive and reproduce over a wider range because they can cope with changing environmental conditions.

B. An organism's short-term responses to environmental variations operate within a long-term framework

It is important to remember that behavioral, physiological, and morphological responses to environmental change have evolved over evolutionary time to their current levels through natural selection.

- What appear to be short-term adjustments are actually evolutionary adaptations to maintain homeostasis.
- Natural selection also places constraints on the distribution of populations by adapting them to localized environments.
- Organisms adapted to one type of environment may not survive if dispersed to a foreign environment or may become extinct if the local environment changes to beyond their tolerance limits.
- The existence of a species in a particular location depends on the species reaching that location and being able to survive and reproduce after getting there.

Since environments vary over space and time, the impact of the variations on a particular species depends on the scale of the variation in relation to the species' overall life history.

1. Physiological responses

Physiological responses to environmental change are generally slower than behavioral responses although some may occur very rapidly.

- An example of a slow change is when a human moves to an area of less oxygen such as at higher altitudes.

  After several days to a few weeks the person responds with an increased number of red blood cells being produced.

- An example of a faster change would be when blood vessels in the skin constrict within seconds to reduce loss of body heat when the skin is exposed to very cold air.

Physiological adaptation is centered around regulation and homeostasis.

- Both regulators and conformers function most efficiently under certain environmental conditions which are optimal for the organism.
- Efficiency declines both above and below optimal values.
- Physiological responses to changing environments can shift tolerance limits of organisms (*acclimation*).
- Acclimation is a gradual process and is related to the range of environmental conditions experienced under natural conditions.

2. Morphological responses

Organisms can react to environmental change with responses that alter body form or internal anatomy.

May develop over the lifetime of an individual or across generations.

May be forms of acclimation since they are reversible.

Increase in coat fur or feather density in winter

Change in coat color between winter and summer

Other morphological changes are irreversible over an individual's lifespan since the environmental variation may have affected growth and differentiation patterns.

- Plants are more morphologically plastic than animals.
  - The arrowleaf plant lacks a waxy leaf cuticle when growing in water with submerged leaves (allows absorption of materials directly from the water).
  - Arrowleaf plants growing on land have a thick cuticle (reduces water loss) and an extensive root system.

3. Behavioral responses

Behavioral responses to unfavorable environmental changes can be almost instantaneous in their effects and are easily reversed.

- The quickest response of animals is to move to a new, more favorable location.
  - Desert animals return to burrows or move into the shade during the day when heat is most intense.
  - Migratory birds migrate to warmer climates to over winter.
- Some animals can modify their immediate environment by cooperative social behavior.
  - Honeybees seal the hive during cold periods to conserve heat and cool the hive on hot days by the collective beating of their wings.
  - Small mammals may huddle in burrows in cold weather which minimizes the total surface area exposed to cold air, thus reducing heat loss.

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CHAPTER 51
BEHAVIORAL BIOLOGY

OUTLINE

I. Introduction to Behavior and Behavioral Ecology
   A. Behavior results from both genes and environmental factors
   B. Innate behavior is developmentally fixed
   C. Classical ethology presaged and evolutionary approach to behavioral biology
   D. Behavioral ecology emphasizes evolutionary hypotheses: s*cience as a process*

II. Learning
   A. Learning is experience-based modification of behavior
   B. Imprinting is learning limited to a critical time period
   C. Many animals can learn to associate one stimulus with another
   D. Practice and exercise may explain the ultimate bases of play

III. Animal Cognition
   A. The study of cognition connects nervous system function with behavior
   B. Movement from place to place often depends on internal coding of spatial relationships
   C. The study of consciousness poses a unique challenge for scientists

IV. Social Behavior and Sociobiology
   A. Sociobiology places social behavior in an evolutionary context
   B. Competitive social behaviors often represent contests for resources
   C. Mating behavior relates directly to an animal's fitness
   D. Social interactions depend on diverse modes of communication
   E. The concept of inclusive fitness can account for most altruistic behavior
   F. Sociobiology connects evolutionary theory to human culture

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. Explain the difference between innate and learned behaviors.
2. Describe the evolutionary basis for behavioral ecology.
3. Explain the difference between ultimate and proximate causations of behavior.
4. Describe a fixed-action pattern and a sign stimulus.
5. Explain the nature versus nurture controversy.
6. Explain the effect of maturation on behavioral improvement.
7. Define habituation.
8. Discuss imprinting, imprinting stimulus, and critical period.

9. Define associative learning.
10. Distinguish among classical conditioning, operant conditioning, and observational learning.
11. Describe two hypotheses for the evolution of play behavior.
12. Discuss the ultimate bases of learning.
13. Describe and define kinesis, taxis, and migration.
14. Explain the differences among piloting, orientation, and navigation.
15. Compare generalist and specialist foraging strategies.
16. Explain how a search image is adaptive.
17. Describe optimal foraging strategies in terms of energetics and prey densities.
18. Describe agonistic behavior.
19. Explain what is meant by a ritual behavior, and describe the evolutionary advantage of ritual behavior.
20. Describe a dominance hierarchy, and explain the advantages to individuals in the hierarchy.
21. Explain how dominance hierarchies and territories may stabilize population densities.
22. Describe the advantages of courtship.
23. Explain how ritualized courtships may have evolved.
24. Define parental investment.
25. Discuss the ultimate bases for mate selection.
26. Compare and contrast the three main mating systems.
27. Describe the differences between polygyny and polyandry.
28. Discuss how the needs of the young influence the development of mating systems.
29. Describe how the certainty of paternity influences the development of mating systems.
30. Describe the various modes of communication.
31. Relate an animal's mode of communication with its lifestyle.
32. Discuss why altruistic behavior might evolve.33. Define inclusive fitness and kin selection.
34. Define reciprocal altruism.
35. Define cognitive ethology.
36. Describe the premise of sociobiology.

KEY TERMS

behavior	critical period	migration	monogamous
ethology	associative learning	social behavior	polygamous
fixed-action pattern	classical conditioning	sociobiology	polygyny
sign stimulus	operant conditioning	agonistic behavior	polyandry
foraging	play	ritual	pheromones
search image	cognition	dominance hierarchy	inclusive fitness
learning	cognitive ethology	territory	coeff'icient of
maturation	cognitive maps	parental investment	relatedness
kin selection	habituation	kinesis	lek
imprinting	reciprocal altruism	taxis	promiscuous

LECTURE NOTES

I. Introduction to Behavior and Behavioral Ecology

Behavior **= What an animal does and how it does it**

Because behavior is assumed to increase fitness, questions about *ultimate* causation, or the reasons why behaviors exist are evolutionary questions.

Ultimate causation = The evolutionary reason for the existence of a behavior

Proximate causation = The immediate cause and/or mechanism underlying a behavior

- The immediate mechanism or how a behavior is expressed is the proximate cause. Proximate causes may be internal processes or environmental stimuli
- Proximate causation limits the range of behaviors upon which natural selection can act.
- Proximate mechanisms produce behaviors that ultimately evolved because they increase fitness.

Behavioral example 1: Bluegill sunfish breeding in spring and early summer

Proximate cause: Breeding is triggered by the effect of increased day length on a fish's pineal gland.

Ultimate cause: Breeding is most successful when water temperatures and food supplies are optimal.

Behavioral example 2: Human "sweet tooth"

Proximate cause: Sweet taste buds are a proximate mechanism that increase the chances of eating high-energy foods.

Ultimate cause: Sweet, high-energy, foods were rare prior to mechanized agriculture. Increased fitness associated with consuming these foods is the ultimate reason for the natural selection of a "sweet tooth."

A. Behavior results from both genes and environmental factors

Behavioral biologists agree that behaviors result from both genetic (nature) and environmental influences (nurture).

- The debate is about the degree to which genes and environment influence phenotypic traits, including behavior.

Like all traits, behaviors display a range of phenotypic variation depending on the environment in which the genotype is expressed (see Campbell, Figure 51.1). The environmental factors that can affect behavior are numerous, and include the chemical environment within the cell, the hormonal and physical conditions experienced by the developing organism, and interactions with other organisms.

B. Innate behavior is developmentally fixed

All behaviors, including those that are present at birth (innate behaviors), require an environment to be expressed.

Innate behaviors do not appear to be influenced by the vast range of environmental differences that exists among individuals.

A behavior that remains essentially the same among organisms despite environmental differences within or outside their bodies is said to be developmentally fixed.

The ultimate cause for innate behavior may be that being capable of performing some behaviors automatically, without having any specific experience, may have maximized fitness to the point that genes for variant behavior were lost.

C. Classical ethology presaged an evolutionary approach to behavioral biology

Ethology pre-dates behavioral ecology. Relying on descriptive studies, ethologists discovered many behaviors were innate.

Ethology = Descriptive science based on studies of animals in the natural environment

Konrad Lorenz, Niko Tinbergen, and Karl von Frisch shared the 1973 Nobel Prize for their work in ethology.

The most fundamental concept in classical ethology is the *fixed-action pattern (FAP),* a highly stereotyped, innate behavior.

- A fixed-action pattern is triggered by an external *sign stimulus.*
- Once a fixed-action pattern is triggered, the behavior continues until completion even in the presence of other stimuli or if the behavior is inappropriate.
- Fixed-action patterns are adaptive responses to natural stimuli. Strange responses can be initiated by presenting unnatural situations to animals with fixed-actio patterns.

Examples of sign stimuli and FAPs include:

Example 1: Niko Tinbergen noticed male three-spined stickleback fish responded aggressively to red trucks passing by their tank.

Fixed-action pattern: Male sticklebacks attack other males that enter their territories.

Sign stimulus: The red belly of the invading male; sticklebacks will attack nonfish-like models with red on the ventral surface.

Example 2: Parent/young feeding behavior in birds

Fixed-action pattern: The begging behavior of newly hatched chicks (raised heads, open mouths, loud cheeps)

Sign stimulus: Parent landing at the nest

Example 3: Greylag goose egg retrieval behavior

Fixed-action pattern: Rolls the egg back to the nest using side-to-side head motions

Sign stimulus: The appearance of an object near the nest

If the goose loses the egg during the retrieval process, it stops the head motion, but continues the "pulling" motion of retrieval. It must sit down before it notices the egg at which time nother retrieval FAP is initiated.

If an inappropriate object (toy dog, doorknob) is placed near the nest, the goose retrieves it but may not keep or incubate it.

Example 4: Protective behavior in hen turkeys

Fixed-action pattern: Mothering behavior

Sign stimulus: Cheeping sound of chicks

A deaf turkey cannot hear the sign stimulus releasing mothering behavior and kills her chicks.

Example 5: The human infant grasping response is a fixed-action pattern released by a tactile stimulus. Human babies smile when they hear certain sounds, or see a figure consisting of two dark spots on a circle (rudimentary representation of a face).

Example 6: Female digger wasps place a paralyzed cricket in the nest as food for the young wasp after it hatches.

Fixed-action pattern: She places the cricket 2.5 cm from the nest

Sign stimulus: Nest site

Fixed-action pattern: She enters the nest and inspects it

Sign stimulus: Presence of cricket 2.5 cm from nest

Fixed-action pattern: She exits the nest and retrieves the cricket

Sign stimulus: Presence of cricket 2.5 cm from nest

If the cricket is moved during the nest inspection stage, the wasp will retrieve the cricket and repeat the FAP from the first step. She cannot get past the "inspect the nest" step if the cricket is not where she left it when she tries to retrieve it.

Sign stimuli are usually simple characteristics (e.g., ultrasonic bat sounds trigger avoidance behavior in moths).

Sign stimuli may be specific choices from an array of possibilities.

Natural selection favors cues associated with the relevant behavior or object. Some randomness is probable in fixing upon one of many possible sign stimuli for an FAP.

A *supernormal stimulus is* an artificial stimulus that may elicit stronger responses than natural stimuli.

- For example, when given a choice between an egg and a volleyball, a greylag goose ignores the egg and tries to retrieve the volleyball.

Most researchers now consider the concept of FAPs as overly simplistic because animal will often display variable responses to stimuli, depending on particular circumstances.

Modern behavioral biology is more concerned with understanding the adaptive function of behavior than with defining the precise nature of behavioral sequences.

An animal's sensitivity to general stimuli and its behavior are correlated.

- For example, frogs' retinal cells are sensitive to movement. Movement is the sign stimulus that releases the tongue-shooting FAP in frogs.
- A frog starves if surrounded by motionless flies.

D. Behavioral ecology emphasizes evolutionary hypotheses: *science as a process*

Fitness is a central concept in animal behavior. Since natural selection works on genetic variation
caused by mutation and recombination, organisms should have features that maximize fitness overtime. Animals are expected to engage in optimal behaviors.

Optimal behavior = A behavior that maximizes individual fitness

- Optimal behavior is a valid concept because behavior is genetically influenced and subject to natural selection.
- *Behavioral ecology is* a field of study that assumes animals increase fitness through optimal behavior.

Learned behaviors are typically based upon gene created neural systems that are receptive to learning.

1. Songbird repertoires

Bird songs can be analyzed with a sound spectrograph (see Campbell, Figure 51.4).

Why has natural section favored multisong behavior? From the perspective of behavioral ecology, several hypotheses could be formulated.

Example hypothesis: A repertoire increases fitness because it makes an older, more experienced male attractive to females. To determine if the hypothesis is correct, design testable predictions.

Prediction 1: Males learn more song types as they get older, so that repertoire

size is a reliable indicator of age.

Experiment 1: Determine whether there is a correlation between male age and size of song repertoire.

(As it turns out, some species of birds display this correlation and others do not.)

Prediction 2: Females prefer to mate with males having large repertoires.

Experiment 2: Determine whether females are more sexually stimulated by a large song repertoire or a small one (see Campbell, Figure 51.5).

Such an examination may lead to an evolutionary explanation: bird song repertoires result in females mating more often or earlier in the season with experienced males, which will give their offspring a greater chance of survival.

2. Cost/benefit analysis of foraging behavior

Animals feed in many ways, using various foraging behaviors that are closely linked morphological traits.

Food habits are fundamental to an animal's niche and may be shaped by interspecies competition and evolutionary factors.

Generalists feed on many items.

- They are not efficient collectors of any single food, but take advantage of multiple options when foods are scarce.
- Generalists concentrate on abundant prey.
- Generalists develop a *search image* for a favored item. If the item becomes scarce, a new search image is developed. Search images let generalists combine efficient short-term specialization with generalist flexibility.
- *Search image* = The ability of a generalist feeder to learn the key visual characteristics of a prey item

Specialists feed on specific items and usually have highly specific morphological and behavioral adaptations. They are extremely efficient foragers.

Natural selection should favor foraging strategies that maximize gains and minimize costs in terms of calories gained and expended. Other criteria such as nutrient gain may be equally important.

- Foraging costs include the energy needed to locate, catch and eat food; the risk of being caught by a predator while feeding; time taken from other activities such as courtship and breeding.
- Behavioral ecologists analyze tradeoffs to predict optimal foraging strategies.
- Tradeoffs include density and size of prey versus foraging distances or prey catchability.
- For example, small mouth bass eat minnows and crayfish. Since no preference is shown, each may be optimal under different conditions. Minnows have more useable energy per unit weight than crayfish, but are harder to catch. Crayfish are easier to catch, but more difficult to subdue.

Animals modify behavior to keep the ratio of energy gain to loss high.

- This ability is probably innate, although learning may be involved.

Experiment: Bluegill sunfish eat small crustaceans (see Campbell, Figure 51.6)

Optimal foraging theory predicts the proportion of small to large prey will vary with the density of the prey population. At low densities, sunfish should not be selective but at high densities, they should concentrate on larger prey.

Results: Sunfish were more selective at higher prey densities, but not to the extent predicted. Young fish were less efficient than adults. Younger fish may be less able to judge size and distance due to incompletely developed neural systems.

Conclusion: Maturation and learning may result in increased foraging efficiency in adults.

II. Learning

A. Learning is experience-based modification of behavior

Analyzing the genetic and environmental underpinning of behavior can help scientists understand the extent to which behavior can vary among individuals of a species.

Learning = The modification of behavior by experience

1. Learning versus maturation

Individuals may improve behaviors over time. This is often attributed to learning, but in some cases, may be due to developmental changes in neuromuscular systems as animals mature.

Maturation = Development of neuromuscular systems that allows behavioral improvement

The distinction between learning and maturation may not be obvious.

Example: Herring gull chick feeding behavior. The adult lowers its head and moves its beak. The chick pecks the red spot on the beak, causing the adult to regurgitate.

Fixed-action pattern: Pecking the red spot on the beak

Sign stimulus: Red spot swung horizontally at the end of a long, vertical object

Newly hatched chicks will indiscriminately peck at a variety of objects, but chick that are 1 to 2 weeks old show a strong response to their parents' beaks (or models).

2. Habituation

Habituation = Learning to ignore irrelevant stimuli or stimuli that convey little or no information

Animals stop responding to stimuli that do not provide appropriate feedback.

- Gray squirrels respond to the alarm calls of other squirrels. They stop responding if the calls are not followed by an attack ("cry-wolf" effect).

B. Imprinting is learning limited to a critical to period

Imprinting is a form of learning that is limited to a specific time period in an animal's life and that is generally irreversible.

Konrad Lorenz conducted an experiment with greylag geese to see how offspring know whom or what to follow (see Campbell, Figure 51.7).

Experiment: A clutch of goose eggs was divided between the mother and an incubator.

Results: Goslings reared by the mother behaved normally and mated with other geese. The incubator goslings spent their first hours of life with Lorenz and preferred humans for the rest of their lives. They even tried to mate with humans.

Conclusions: Greylags have no innate sense of "mother" or "gooseness". They identify with and respond to the first object with certain characteristics they encounter. The ability or tendency to respond is innate.

The object to which the response is directed is the imprinting stimulus. For Lorenz's geese, the imprinting stimulus was movement of an object away from the young.

Imprinting stimulus = An object in the environment to which the response is directed

- For example, salmon return to the stream they were hatched in to spawn. The imprinting stimulus is the unique chemical composition (odor) of the hatching stream.

1. Critical period

Critical period = A limited time during which imprinting can occur

Imprinting is usually thought to involve very young animals and short critical periods, but imprinting may occur at different ages with critical periods of varying durations.

- Adults require a critical period to "know" their young. Prior to imprinting on their young, adult herring gulls defend strange chicks. After the imprinting period, they kill and eat strange chicks.

Sexual imprinting (or species identity) occurs later than parental imprinting and has a longer critical period.

- In one study, male finches reared by two different finch species imprinted on the other species when they developed a sexual identity. As a result, when exposed to females of their own species, they mated reluctantly.

While irreversibility and critical period characterize imprinting, they are not always fixed.

- The cross-fostered finches eventually mated with females of their own species.

2. Song development in birds: a study of imprinting

In most songbird species, males sing complex vocalizations that have a variety of adaptive functions.

Bird songs are a complex interplay of learned and innate behaviors.

- Some species have rigid song repertoires, while others have repertoires that are more fluid, have regional dialects, and change throughout an individual bird's life.

Many studies of song development have focused on common North American species. Early experiments with male white-crowned sparrows showed:

- Birds raised in soundproof chambers developed abnormal songs.
- Birds exposed to normal song recordings at 10 to 50 days old developed normal songs.
- Birds deafened after they were exposed to the recordings, but before they began to sing, developed songs more abnormal than birds reared in isolation (see Campbell, Figure 51.8).
- White-crowned sparrows learn to sing by hearing adults and matching those songs while listening to themselves.
- 10 to 50 days was the critical period for hearing adult song. Birds who heard a recording at 50+ days never sang properly.
- Birds exposed to other species' recordings did not learn those songs. There was an innate, genetic predisposition, for their own song.
- The innate predisposition was overcome by social interaction. Sparrows 50+ days old, when in social contact with another species, learned that species' song.
- The critical period may be flexible. It was longer for a live stimulus than for a recording.

Humans also have a critical period for learning vocalizations (easier while still teens than as adults).

Song development may be more or less fixed in other species:

- Song sparrows reared in isolation develop normal songs although males have larger repertoires if they hear other birds.
- Mockingbirds have repertoires of 150+ songs. The fitness value of a large repertoire is very high for them.

There are important exceptions to the song-learning scenario based on the white-crowned sparrows.

- Males canaries sing variable numbers of songs and develop new ones eachyear.
- They have a region in their forebrain that varies greatly in size according to the season and number of songs in an individual's repertoire.
- The fitness value of learning new songs more than once in their lifetime must be critically important.

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

Associative learning = The ability of many animals to associate one stimulus with another

Classical conditioning is a type of associative learning in which an arbitrary stimulus is associated with a reward or punishment.

- Russian physiologist Ivan Pavlov induced dogs to salivate when they heard a bell by associating it with powdered meat.

Operant conditioning, or trial-and-error learning, is another type of associative learning, in which an animal learns to associate one of its own behaviors with a reward or punishment and then tends to repeat or avoid that behavior.

- Psychologist B.F. Skinner put lab animals in a box with a variety of levers. Test animals learned to choose only those levers which yielded food.
- English tits learned to open milk bottles left on doorsteps and drink the cream when one or more of the birds discovered its probing behavior was rewarded when directed at the bottles.

Operant conditioning is common in nature.

- Predators learn to associate certain kinds of prey with painful experiences and modify their behavior accordingly (see Campbell, Figure 51.9).
- Genes influence the outcome of operant conditioning.

D. Practice and exercise may explain the ultimate basis of play

Play has no apparent goal but uses movements closely associated with goal-directed behaviors (see Campbell, Figure 51.10).

- Young predators playfully stalk and attack each other using motions similar to those used to capture and kill prey.
- Play occurs in the absence of distracting external stimuli.

Play is potentially dangerous or costly.

- Young vervet monkeys are at higher risk of being caught and eaten by baboons when they are at play.
- In a study of young goats, 1/3 sustained play injuries that resulted in limps.

What is the selective advantage of play?

- Practice hypothesis. Play is a type of learning that allows the perfection ofsurvival behaviors. However, play movements rarely improve after the first few practices.
- Exercise hypothesis. Play keeps the cardiovascular and muscular systems in condition and is common in young animals because they do not exert themselves in other ways while they are under parental care. (However, recent studies of beluga whales and several species of dolphins indicate that play is also common in adults in captivity.)

III. Animal Cognition

Research efforts on animal cognition seek to understand information processing at all levels, from the nervous system activities that underlie sophisticated behavior, such as problem solving, to the internal representations animals have about physical objects in their surroundings.

A. The study of cognition connects nervous system function with behavior

Cognition ;s the ability of an animal's nervous system to perceive, store, process, and use information gathered by sensory receptors.

The study of animal cognition is called *cognitive ethology*. *Its* scientists attempt to illustrate the connection between data processing by nervous systems and animal behavior.

On area of research in cognitive ethology investigates how animal brains represent physical stimuli from the environment (this is separate and distinct from questions about consciousness).

B. Movement from place to place often depends on internal coding of spatial relationships

A central hypothesis of cognitive ethology is that animals make use of *cognitive maps,* internal representations of the spatial relationships among objects in the animal's environment.

Two kinds of movement that may occur without any internal representation are kineses and taxes.

Kinesis involves a change in activity rate in response to a stimulus.

- Sowbugs are more active in dry areas and less active in humid regions. This behavior tends to keep them in moist areas.

Taxis is a semiautomatic, directed movement toward or away from a stimulus.

- Housefly larvae are negatively phototactic after feeding. Presumably this makes them less visible to predators.
- Trout are positively rheotactic. Swimming against the current keeps them from being swept downstream.

1. Migration behavior

Migration is the most commonly known type of oriented animal movement.

- Migrants generally make an annual round trip between two regions (e.g., birds, whales, some butterflies, some pelagic fish) (see Campbell, Figures 51.12).
- *Migration* = Regular movement of animals over relatively long distances Migrating animals use one of three mechanisms or a combination of these mechanisms to find their way.

1. *Piloting* = Movement of animals from one landmark to another
   - Is used over short distances
2. *0rientation* = Movement of animals along a compass line
   - Animals that use orientation can detect compass directions and travel in a straight-line path to a destination.
3. *Navigation* = The ability of animals who can orient along compass lines to determine their location in relation to their destination
   - Migrant starlings captured in the Netherlands were released in Switzerland. Juvenile birds oriented in a straight-line to Spain. Adults navigated a new route to their wintering grounds in northern Europe.

- Many birds use celestial points for orientation and navigation. These animals need an internal clock to compensate for the movement of the sun and stars. The indigo bunting avoids the need for an internal clock by fixing on the North star.
- Some birds, bees and bacteria orient to the Earth's magnetic field. The mechanisms are poorly known, but magnetite, an iron-containing ore, has been found in animals that orient to the magnetic field.

Campbell, Figure 51.13 distinguishes between orientation and navigation.

C. The study of consciousness poses a unique challenge for scientists

The extent to which nonhuman animals are consciously aware of the themselves or their environment is difficult to determine.

- Consciousness is known only to the individual that experiences it and it is not associated with any observable behavioral or physiological change.

Donald Griffin of Princeton University believes that:

- Conscious thinking is an inherent part of animal behavior.
- Cognitive ability arises through natural selection and forms a phylogenetic continuum stretching into evolutionary history.

IV. Social Behavior and Sociobiology

A. Sociobiology places social behavior in an evolutionary context

Most sexually reproducing species must be social for part of their life cycle in order to reproduce; some species spend most of their lives in close association with conspecifics.
Social behavior = Any interaction between two or more animals, usually of the same species.

- Includes aggression, courtship, cooperation, and even deception
- Has both costs and benefits to members of species that interact extensively

Sociobiology = Study of social behavior that has evolutionary theory as its conceptual framework

- Much of the evolutionary theory underlying sociobiology stems from the work of British biologist William Hamilton. He used the concepts of fitness and the genetic basis behavior in analyzing the evolution and maintenance of social behavior in animals.
- In 1975, E.O. Wilson's *Sociobiology: The New Synthesis* was published, which helped form sociobiology into a coherent method of analysis and interpretation.

Because members of a population share a common niche, there is potential for conflict, especially among members of species that maintain densities near what the environment can sustain.

- Sometimes social behavior involves cooperative effort, as when a group accomplishes something more efficiently than a single individual (see Campbell, Figure 51.1 5).
- Even when cooperation seems to be mutually beneficial, each participant usually acts to maximize its fitness, even at a cost to the other participant.

B. Competitive social behaviors often represent contests for resources

1. Agonistic behavior

Agonistic behavior = A contest of threatening and submissive behavior that determines which competitor gains access to a resource (e.g., mate, food, territory)

- Canines show agonistic behavior by trying to look larger. They bare teeth; erect ears, tail and fur; stand upright; and make eye contact. The loser submits by sleeking its fur, tucking its tail and looking away.

Ritual behaviors are prevalent, so it is rare that participants are seriously injured (see Campbell, Figure 51.16)

Natural selection favors ending a contest as soon as a winner is established because further conflict could injure the victor as well as the vanquished. Future interactions between the same animals is usually settled more quickly in favor of the original victor.

2. Dominance hierarchies

Within a *dominance hierarchy,* the top-ranked member of a social group controls the behavior of the members of the group. The second-ranked animal controls everyone except the top individual and so on down the line to the lowest-ranked animal.

- Top ranked animals are assured access to resources. Low ranked animals do not waste energy or risk harm in combat.

Wolf packs typically have a female dominance hierarchy. The top female controls mating in the pack based on food availability.

3. Territoriality

Territories are defended areas used for feeding, mating, or rearing young.

- Territory size varies with the species, territory function, and the amount of resources available (see Campbell, Figure 51.17).
- Some species defend territories during the breeding season and form social groups at other times of the year (e.g., chickadees).

Territories are not home ranges. Home ranges are areas which animals inhabit but do not defend. Territories and home ranges may overlap.

Territories are usually successfully defended by their owners.

- Owners usually win because a territory is more valuable to the owner since he is familiar with it.
- Established territory owners are likely to be older and more experienced at agonistic interactions.
- Ownership is continually proclaimed—a primary function of bird song, red squirrel chattering and the bellowing of sea lions. Others use scent marks or patrols to announce their presence (see Campbell, Figure 51.18).

Defense is usually directed only at conspecifics who are most likely to compete directly for the same resources.

Dominance hierarchies and territoriality tend to stabilize population densities by assuring enough individuals reproduce to result in relatively stable populations from year to year.

C. Mating behavior relates directly to an animal's fitness

The correlation between mating behavior and reproductive fitness is vital to behavioral ecology.

1. Courtship

Species often have a complex courtship ritual unique to that species that must occur before mating.

Courtship assures each partner that the potential mate is not a threat, is the proper species, the proper sex and in the correct physiological condition.

In some species, courtship allows one or both sexes to choose a mate form a number of candidates.

- Females are usually more discriminating than males because they normally have a greater parental investment.

- *Parental investment* = The time and resources an individual expends to produce offspring
- Eggs are usually larger and more costly to produce than sperm.
- Gametes of placental mammals are closer in size, but females invest considerable time and energy carrying young before birth.

Competition among individuals of the same sex (usually males) may determine which individuals of that sex will mate.

- Most males mate with as many females as possible. They compete with other males for mates and may try to impress females.
- Males perform more intense courtship displays than females.
- Secondary sex characteristics may be highly developed in males (e.g., deer antlers, bird colors).

There are two ultimate bases for mate selection.

1. If the other sex gives parental care, it is best to choose the most competent mate.
    - For example, male common terns bring fish to potential mates as part of the courtship ritual. This behavior may be a proximate indicator of his ability to feed the chicks.
    - Some females prefer males with the most extreme and energetic courtship displays or secondary sex characteristics. These characteristics may be proximate indicators of the male's health.
2. Genetic quality is important when males provide no parental care and sperm are their only contribution to offspring.
    - *Lek* species have a communal area where males display. Females visit the lek and choose a mate. The proximate basis for her choice is a preference for males that court the most vigorously and have the most extreme secondary sex characteristics.

It may be difficult to determine if differential mating success among males is due to male-male competition, female choice, or both.

- Three-spined stickleback courtship is based on stereotyped releasers and FAPs (see Campbell, Figure 51.19) Despite this, the female can back out of the courtship anytime.
- Female choice is probably ultimately based on the quality of the male's parental care, because only male sticklebacks give parental care.

Ritualized acts probably evolved from actions whose meaning was more direct at one time. This is evident in insects called dance flies.

- The male of some species of dance flies spin oval silk balloons which they carry while flying in a swarm. The swarm is approached by females seeking mates. A female accepts a male's balloon and then they fly off to copulate.
- In a related species, the male brings a dead insect for the female to eat while they mate.
- In another species, the insect is presented inside a silk balloon, possibly because silk helps subdue the insect or makes it look larger.
- Males of some species eat mainly nectar, so the rituals may have evolved into bringing the female something associated with food.
- It is as if, over evolutionary time, a suitor wooed a lady with diamonds, then with a box containing diamonds, and finally with an empty box.

2. Mating systems

Mating relationships between males and females varies greatly among species.

- *Promiscuous* = A mating system with no strong pair-bonds or lasting relationships
- *Monogamous* = A mating system in which one male mates with one female
- *Polygamous = A* mating system in which an individual of one sex mates with several of the other
  - *Polygyny is* a polygamous relationship in which one male mates with multiple females.
  - *Polyandry is* a polygamous relationship in which one female mates with multiple males.

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

- Most birds are monogamous. Young birds often require significant parental care. A male may ultimately increase his reproductive fitness by helping a single mate rear a brood than by seeking additional mates.
- Polygyny is common in birds where the young are able to care for themselve soon after hatching. Males can maximize their fitness by seeking additional mates.

Another factor influencing mating systems and parental care is the certainty of paternity (see Campbell, Methods box on red-winged blackbirds).

- Young born or eggs laid by a female definitely contain the female's genes, but even in monogamous species, the young could have been fathered by a male other than the female's normal mate.
- The certainty of paternity is relatively low in species with internal fertilization because mating and birth (or egg laying) are separated over time. Exclusive male parental care is rare in birds or mammals.
- Certainty of paternity is higher when egg laying and mating occur together, as in external fertilization. Parental care, when present, in fishes and amphibians is as likely to be by males as by females.
- When parental care is given by males, the mating system may be polygynous with multiple females laying eggs in a nest tended by a male.

D. Social interactions depend on diverse modes of communication

Communication = The intentional transmission of information between individuals

Behavioral ecologists assume communication has occurred when an act by a "sender" produces a change in the behavior of another individual, the "receiver".

Ethologists assumed communication evolved to maximize the quantity and accuracy of information. Behavioral ecologists argue that communication evolved to maximize the fitness of communicators.

Animals lie. Mimicry often is adaptive to the sender and maladaptive for the receiver.

- Male and female *Photinus* fireflies communicate by a characteristic pattern of flashes. Females of the predatory firefly genus *Photurus* mimic the female *Photinus* flash pattern, attracting male *Photinus* fireflies which they kill and eat.
- In some mammals, a new dominant male kills young born too soon to be his offspring. Without dependent young, females ovulate sooner, allowing the new male to father their young.
- Hanuman langur females in the early stages of pregnancy solicit copulations from new dominant males. When they give birth shortly before young fathered by these males would appear, they may deceive the male into treating their young as his own.

An evolutionary consideration is the mode used to transmit information. Animals use visual, uditory, chemical, tactile and electrical signals.

The mode used to transmit information is related to an animal's lifestyle.

- Most mammals are nocturnal and use olfactory and auditory signals.
- Animals that communicate by odors emit chemical signals called *pheromones*. Pheromones are important releasers for specific courtship behaviors. They are also used by ant scouts to guide other ants to food.
- Birds are mostly diurnal and use visual and auditory signals. Diurnal humans also use visual and auditory signals. If we could detect the chemical signals of mammals, then mammal sniffing might be as popular as bird watching.

A complex communication system is found in honeybees (see Campbell, Figure 5 1.21).

- Pheromones maintain the social order of the hive.
- To maximize foraging efficiency, worker bees communicate the location of food sources, which change as flowers bloom and new patches are found.
- In the 1940s, Karl von Frisch studied honeybee communication. He found individual bees communicated to other bees when they returned to the hive.
- Returning bees "dance" to indicate the location of food.
- If the source is < 50m, the bee does the "round dance", moving rapidly sideways in tight circles and regurgitating nectar. Workers leave the hive and forage nearby.
- If the food is farther away, the bee does a "waggle dance", a half-circle swing in one direction, followed by a straight run and then a half-circle swing in the other direction. This dance seems to indicate both direction and distance.

1. The angle of the run in relation to the vertical surface of the hive is the same as the horizontal angle of the food in relation to the sun.
2. Distance to the food is indicated by variations in the speed at which a bee wags its abdomen during the straight run.

E The concept of inclusive fitness can account for most altruistic behavior

Behavior that maximizes individual reproductive success will be favored by selection, regardless of how much damage such behavior does to another individual, local population, or species.

Animals occasionally exhibit apparently unselfish or altruistic behavior.

- *Altruism* = A behavior that reduces an individual's fitness and increases the fitness of the recipient of the behavior

Natural selection favors anatomical, physiological, and behavioral traits that increase reproductive success, which in turn propagates the genes responsible for those traits.

- When parents sacrifice their well-being to produce and aid offspring, they increase their fitness because it maximizes their genetic representation in the population.
- Like parents and offspring, siblings share half their genes, so selection might favor helping one's parents produce more siblings, or even helping siblings directly.
- Selection might result in animals increasing their genetic representation in the next generation by "altruistically" helping close relatives.

Inclusive fitness is the concept which describes the total effect an individual has on proliferating its genes by producing its own offspring and by providing assistance to the reproductive efforts of close relatives

- *Coefficient of relatedness is* the proportion of genes that are identical in two individuals because of common ancestry. The higher the coefficient of relatedness, the more likely an individual is to aid a relative.
- *Kin selection is* the mechanism of increasing inclusive fitness. The contribution of kin selection to inclusive fitness varies among species. It may be rare or nonexistent in species that are not social or disperse widely.

In predicting if an individual will aid relatives, behavioral ecologists have derived a formula that combines coefficients of relatedness, costs to the altruist, and benefits to the recipient.

If kin selection explains altruism, then examples of unselfish behavior should involve close relatives.

- Belding ground squirrels give alarm calls when danger appears. These calls alert other squirrels but increase the risk to the alarm givers. Females remain near their birth sites and are usually related to other members of the group. Only females give alarm calls (see Campbell, Figure 51.22)
- Sterile worker bees labor on behalf of a single fertile queen. They sting intruders, a behavior that defends the hive, but results in the death of the worker. The queen is the mother of all the bees in the hive.
- Nesting red-cockaded woodpeckers are aided by two to four nonbreeders that assist in all aspects including incubation and feeding young. Nest helpers are older offspring of the breeding pair or siblings of one parent that have been unable to establish a breeding territory. Helpers may eventually inherit the territory.
- In naked mole rats, DNA analysis has shown that all members of a colony are closely related. The queen is a sibling, daughter, or mother of the kings and the nonreproductive rats are the queens siblings or direct descendants. By enhancing the chances of a queen or king reproducing, a nonreproductive individual increases the chaidentical to its own to the next generation.

Altruistic behavior toward nonrelatives sometimes occurs. This behavior is adaptive if there is a reasonable chance of the aid being returned in the future.

- *Reciprocal altruism* only occurs in stable social groups where individuals have many opportunities to exchange aid (rare outside of humans).

F. Sociobiology connects evolutionary theory to human culture

Wilson's *Sociobiology* presented the thesis that social behavior has an evolutionary basis.

- Behavioral characteristics are expressions of genes favored by natural selection.
- This has sparked debate about the connection between biological evolution and human culture
  - An example of the debate involves cultural taboos on incest.
    - Incest avoidance is adaptive because inbreeding may increase the frequency of genetic disorders.
    - Many species avoid incest.
    - Most human cultures have taboos forbidding incest.
    - Is there an innate aversion to incest or is this an acquired behavior?
      - The argument in favor of the "nurture" or learned behavior position says that cultural taboos are unnecessary if the behavior is innate, therefore, incest avoidance is a learned behavior and the social stigma attached to incest is based on experience.

- The argument in favor of the "nature" or genetic behavior position says that the occurrence of incest taboos in many cultures is evidence for an innate component and taboos are simply proximate mechanisms that reinforce a behavior mat ultimately evolved because of its effect on fitness.

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CHAPTER 52

POPULATION ECOLOGY

OUTLINE

I. Characteristics of Populations
   A. Two important characteristics of any population are density and the spacing of individuals
   B. Demography is the study of factors that affect the growth and decline of populations

II. Life History Traits
   A. Life histories are highly diverse but exhibit patterns in their variability
   B. Limited resources mandate trade-offs between investments in reproduction and in survival

III. Population Growth Models
   A. An experimental model of population growth describes an idealized population in an unlimited environment
   B. A logistic model of population growth incorporates the concept of carrying capacity

IV. Regulation of Population Growth
   A. Density-dependent factors regulate population growth by varying with the density
   B. The occurrence and severity of density-independent factors are unrelated to population density
   C. A mix of density-dependent and density-independent factors probably limits the growth of most populations
   D. Some populations have regular boom and bust cycles

V. Human Population Growth
   A. The human population has been growing almost exponentially for centuries but will not be able to do so indefinitely

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. Define the scope of population ecology.
2. Distinguish between density and dispersion.
3. Explain how ecologists measure density of a species.
4. Describe conditions which may result in clumped dispersion, random dispersion, and uniform dispersion of populations.
5. Explain how age structure, generation time, and sex structure of populations can affect population growth.

6. Describe the characteristics of populations which exhibit Type I, Type II, and Type III survivorship curves.
   Explain how carrying capacity of the environment affects the intrinsic rate of increase of a population.
8. Explain how density-dependent factors affect population growth.
9. Describe how weather and climate can function as density-independent factors in controlling population growth.
10. Explain how density-dependent and density-independent factors may work together to control a population's growth.
11. List the three major characteristics of a life history and explain how each affects the:
    a. Number of offspring produced by an individual
    b. Population's growth
12. Explain how predation can affect life history through natural selection.
13. Distinguish between r-selected populations and K-selected populations.
14. Explain how a "stressful" environment may alter the standard r-selection and K-selection characteristics.

KEY TERMS

population	birth rate	zero population growth	opportunistic
density	fecundity	intrinsic rate of increase	populations
dispersion	death rate	exponential population	intraspecifc
mark-recapture method	generation time	growth	competition
clumped	sex ratio	carrying capacity	density-dependent
grain	life table	logistic population	factor
uniform	survivorship curve	growth	density-independent
biogeography	life history	*K*-selected populations	factor
demography	semelparity	equilibrial populations	cohort
age structure	iteroparity	*r*-selected populations	

LECTURE NOTES

Population ecology is concerned with measuring changes in population size and composition and identifying the factors that cause these changes.

No population can continue to grow indefinitely.

- Many populations remain relatively stable over time with only minor increases and decreases.
- Other populations show dramatic increases followed by equally dramatic decreases.

I. Characteristics of Populations

Population = Individuals of one species simultaneously occupying the same general area, utilizing the same resources, and influenced by similar environmental factors

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

Every population has geographical boundaries and a population size. Two important characteristics of populations are *density* and *dispersion.*

Population density = The number of individuals per unit area or volume

Population dispersion = The pattern of spacing among individuals within the geographical boundaries of the population

1. Measuring density

It is usually impractical or impossible to count all individuals in a population, so ecologists use a variety of sampling techniques to estimate densities and total population size.

- May count all individuals in a sample of representative plots; estimates become more accurate as sample plots increase in size or number
- May estimate by indirect indicators such as number of nests or burrows, or by droppings or tracks
- May use the mark-recapture method (see Campbell, Methods box)
- In the *mark-recapture method,* animals are trapped within boundaries, marked in some way, and after time, retrapped.

  The number of individuals in a population (N) is estimated by the formula:

$$N = \frac{\text{(number marked) x (total catch the second time)}}{\text{number of marked recaptures}}$$

  Assumes marked individuals have same probability of being trapped as unmarked individuals. This assumption is not always valid.

2. Patterns of dispersion

A population's geographical range is the geographic limits within which a population lives.

Local densities may vary substantially because not all areas of a range provide equally suitable habitat.

Individuals exhibit a continuum of three general patterns of dispersion in relation to other individuals: clumped, uniform, and random.

1. A *clumped* pattern is when individuals are aggregated in patches.

   May result from the environment being heterogeneous, with resources concentrated in patches; the ecological concept of *grain* relates to spatial or environmental patchiness.

   - A coarse-grained environment has large environmental patches that organisms can distinguish and choose among.
   - A fined-grained environment has small patches relative to the size and activity of an organism and they organisms may behave as though patches do not exist.
   - Temporal variation in the environment can also be coarse or fine-grained.

     Clumping may be associated with mating or other social behavior in animals.

     May also be associated with defense against predators.

2. A *uniform* pattern is when the spacing of individuals is even.

   May result from direct, antagonistic interactions between individuals of the population. For example, competition for some resource or social interactions that set up individual territories for feeding, breeding or nesting.

3. A *random* pattern is when individual spacing varies in an unpredictable way. Occurs in the absence of strong attractions or repulsions among individuals.

   Not very common in nature.

While the above applies to local dispersion patterns within populations, it is important to remember that populations within a species also show dispersion patterns.

- Such populations often concentrate in clusters within the species' range.
- *Biogeography is* the study of factors that influence the distribution of a species over its range.

B. Demography is the study of factors that affect birth and death rates in a population

Demography is the study of the vital statistics affecting population size.

- Reflects relative rates of processes that add individuals to a population (birth, immigration) versus processes that eliminate individuals (death, migration).
- Birth and death rates vary among population subgroups depending on age and sex.
- A population's age structure and sex ratio are two of its most important demographic features.

1. Age structure and sex ratio

Many populations have overlapping generations where individuals of more than one generation coexist.

- Exceptions include species in which all of the adults reproduce at the same time and then die (e.g., annual plants, many insects).
- The coexistence of generations produces an age structure in most populations.
- *Age structure* = Relative numbers of individuals of each age in a population
- Generations overlap when average life span is greater than the time it takes to mature and reproduce.

Every age group has a characteristic birth and death rate.

- *Birth rate, or fecundity, is* greatest for those of intermediate age.
- *Death rate is* often greatest for the very young and very old.
- In general, a population with more older, nonreproductive individuals will grow more slowly than a population with a larger percentage of young, reproductive age individuals.

Generation time is an important demographic feature related to age structure.

- *Generation time* = The average span of time between the birth of individuals and the birth of their offspring
- Strongly related to body size (see Campbell, Figure 52.3)
- A shorter generation time usually results in faster population growth, assuming birth rate is greater than death rate and all other factors being equal.

Another important demographic factor affecting population growth is the sex ratio.

- *Sex ratio* = The proportion of individuals of each sex found in a population
- The number of females is usually directly related to the expected number of births.
- The number of males may be less significant since one male may mate with several females.
- In strictly monogamous species, the number of males is more significant in affecting the birth rate than in nonmonogamous species.

2. Life tables and survivorship curves

Life tables describe how birth rates and death rates vary with age over a time period corresponding to maximum life span.

- Constructed by following the fate of a *cohort,* a group of individuals of the same age, from birth until all are dead or by using the age specific birth and death rates in a population during a specified time.

Various information about change in population size can be obtained from life tables (see Campbell, Table 52.1).

Survivorship curves plot the numbers in a cohort still alive at each age. Organisms may exhibit one of three general types of survivorship curves (see Campbell, Figure 52.4):

1. Type I curves are flat during early and middle life and drops suddenly as death rates increase among the older individuals.
   - Associated with species such as humans and other large mammals that produce few offspring that are well cared for
2. Type II curves are intermediate with mortality being more constant over the life span.
   - Seen in *Hydra,* gray squirrels, and some lizards
3. Type III curves show very high death rates for the young followed by lower death rates after individuals have survived to a certain critical age.
   - Associated with organisms, such as oysters, that produce very large numbers of offspring but provide little or no care

Many species exhibit curves between the basic types of survivorship curves and some have more complex curves.

- Great tits show a high mortality rate in young birds (Type III) but a fairly constant mortality (Type II) in adults.
- Some invertebrates show a "stair-stepped" curve with brief periods of high mortality during molts, followed by periods of lower mortality when the exoskeleton is hard (e.g., crabs).

II. Life History Traits

Natural selection, working over evolutionary time, results in traits that affect an organism's life history.

- *Life history* = An organism's schedule of reproduction and death

In many cases there are trade-offs between survival and traits such as frequency of reproduction, investment in parental care, and the number of offspring per reproductive episode.

Life histories are important in population ecology because these traits affect population growth over time.

A. Life histories are highly diverse but exhibit patterns in their variability

There is a diversity in life histories due to the varying pressures of natural selection.

- Some animal species hatch in one type of biome, migrate to another where they mature for several years, then return to the initial biome for a single massive reproductive effort, then die (e.g., salmon).
- Other animal species hatch and mature rapidly in a single habitat, then have small reproductive efforts each year for several years (e.g., lizards).
- Life history characteristics may vary significantly among populations of the same species or even among individuals within a population.

Even though life history traits vary widely, there are some basic patterns:

- Life histories often vary in parallel with environmental factors. For example, clutch sizes increase with latitude.
    - Tropical birds lay fewer eggs than those in higher latitudes, which reflects the of offspring that can be successfully fed.
    - Since daylengths are longer at higher latitudes than the tropics during offspring-rearing season, parent birds can gather more food and feed more offspring.
    - The number of offspring per reproductive event has been found to vary in many mammals, lizards, and insects.
- Life history traits often vary in relation to one another. For example, fecundity and mortality tend to vary in close association among birds.
    - Albatrosses only average one surviving offspring every five years but adult birds have only a 5% chance of dying from one breeding season to the next.
    - Tree sparrows average six surviving offspring each year but have over a 50% chance of dying between breeding seasons.
    - Delayed maturation and high parental investment in offspring tend to be correlated with low fecundity and low mortality (see Campbell, Figure 52.5).

B. Limited resources mandate trade-offs between investments in reproduction and survival

A life history based on heritable traits that result in producing the most reproductively successful descendants will become more prevalent in a population.

A successful life history resolves the conflict between limited resources and competing functions.

- Time, energy, and nutrients used for one function are not available for other functions (see Campbell, Figure 52.6).
- The integrated life histories seen in natural populations balance the investment in the number of offspring produced against the prospects of future reproductions.
    - In general, organisms that produce fewer offspring during a reproductive effort survive longer and have more reproductive episodes.
- The life history traits exhibited by an organism are evolutionary outcomes reflected in the development and physiology of that organism

1. Number of reproductive episodes per lifetime

Two extremes are found in life history strategies where there is a trade-off between fecundity and survival probability.

1. *Semelparity is* a type of life history in which organisms invest most of their energy in growth and development, then expend that energy in a single reproductive effort before dying.
2. *Iteroparity is* a type of life history in which organisms produce fewer offspring at a time over many reproductive seasons.

Semelparity is expected when there is a high cost to parents to stay alive between broods or if there is a trade-off between fecundity and survival.

- Seen in annual plants, salmon, and some perennial plants such as bamboo and the century plant.
- In the harsh desert climates, most plants live only a single season and put all their energy into one reproductive effort.

- Rarely found in animals or plants that live more than one or two years, although some (e.g., century plants) live for several seasons before investing all their energy into a single reproduction (see Campbell, Figure 52.7).
- Century plants live in arid climates with unpredictable rainfall. They grow vegetatively and store nutrients for several years.
- The stored nutrients are used to produce seeds when an unusually wet year occurs that favors offspring survival.

Iteroparity is expected when established individuals are likely to survive but mortality is high in immature individuals.

- Iteroparous plants are more common in the tropics where competition and predation hinder seedling establishment, but mature plants survive for many seasons.
- More resources are invested in survival (e.g., root system, resistant buds) to prepare for multiple breeding episodes than is allocated by single season plants.

2. Number of offspring per reproductive episode

Organisms with a low probability of surviving to the next reproductive season usually invest more energy into producing a large number of offspring.

Organisms with a high probability of survival invest less energy and produce fewer offspring.

Clutch, litter, or seed crop size may vary seasonally within a single population in some species (see Campbell, Figure 52.8).

There is usually a trade-off between the number and quality of offspring produced.

- In general, organisms that produce many offspring produce small ones (see Campbell, Figure 52.9).
  - Each offspring thus starts with a limited amount of energy.
  - A large number of offspring and small young are typical of organisms with a Type III survivorship curve.
    - Typical of organisms that colonize disturbed or harsh environments or are subject to high levels of predation.
  - Organisms that produce small clutches, litters, or seed crops generally have larger offspring.
    - Offspring have a longer initial amount of energy which improves their chance of survival.
    - This is typical of organisms with Type I and II survivorship curves.
    - Parental investment is higher but is offset by increased survival of offspring.

a. Age at first reproduction

The timing of the first reproduction greatly influences the female's lifetime reproductive output in organisms that have several reproductive episodes during their lifespan.

- Balances the cost between current reproduction and survival plus future reproduction.
- Reproduction at a younger-than-average age may reduce a female's reproductive potential by reducing the amount of energy available for growth and maintenance.

- Female's that delay reproduction tend to be larger due to energy used for growth and maintenance; older (larger) females produce larger clutches and appear to maximize their reproductive output by delaying.

III. Population Growth Models

Indefinite increases in population size do not occur.

- A population may increase rapidly from a low level under favorable environmental conditions, but this increase in numbers will eventually approach the level where resources cannot support continued increases.
- The combination of limited resources and other factors will stop the growth of the population.

A. An exponential model of population growth describes an idealized population in an unlimited environment

A combination of observation, experimentation, and mathematical modeling is used to determine answers to many ecological questions.

- Birth rates and death rates can be quantified, by measurement or observation, in many populations and used to predict changes in the population size.
- Laboratory studies on small animals can determine how various factors affect population growth rates and a few natural populations can be manipulated experimentally to answer a range of questions.
- Mathematical models can test hypotheses about the effects of various factors on population growth in organisms that are difficult or impossible to study experimentally.
- A population consisting of a few individuals that live in an environment without limiting factors (no restrictions on available energy, growth, or reproduction) will increase over time in proportion to the birth and death rates:

$$\text{Change in population size during time interval} = \text{Births during time interval} - \text{Deaths during time interval}$$

In a mathematical form, this equation becomes:

$$\Delta N/\Delta t = B - D$$

where N = population size, t = time, B = absolute number of births during the time interval, and D = absolute number of deaths during the time interval, ΔN= change in population size, Δt = the time interval (lifespan or generation time).

Since populations differ in size, the basic model must be altered in order to apply it to *any* population. This alteration involves a conversion from absolute birth and death rates to average numbers of births and deaths per individual during the specified time interval.

- If b = the annual per capita birth rate, its value would equal 0.034 in a population of 1000 individuals where 34 births occurred (34/1000 = 0.034) in a year.
- If d = per capita death rate, its value would equal 0.016 in a population of 1000 individuals where 16 deaths occurred (16/1000 = 0.016) in a year.

Including average (or per capita) birth and death rates alters the previous equation so that expected numbers of births and deaths can be predicted for a population of any size:

$$\Delta N/\Delta t = bN - dN$$

- The change in size of our 1000 individual population would be:
  $\Delta N/\Delta t = (0.034)(1000) - (0.016)(1000)$

$\Delta N/\Delta t = 34 - 16$

$\Delta N/\Delta t = 18$

- If another population of the same species (same b and *d* values) contained 1500 individuals, then:

  $\Delta N/\Delta t = (0.034)(1500) - (0.016)(1500)$

  $\Delta N/\Delta t = 51 - 24$

  $\Delta N/\Delta t = 27$

Population ecologists study overall changes in population sizes and use r to represent the difference between per capita birth rates and per capita death rates:

$r = b - d$ thus $\Delta N/\Delta t = rN$

- The value *r is* thus the per capita population growth rate and can be used to determine if a population is growing or declining.
- *Zero population growth (ZPG)* occurs where per capita birth and death rates are equal, thus $r = 0$. (Note that births and deaths still occur, but are equal in number.)
- A population is increasing in size if $r > 0$ (more births than deaths); it is decreasing in size if $r < 0$ (fewer births than deaths).

Many population ecologists use a slightly different equation based on differential calculus to express population growth in terms of instantaneous growth rates:

$dN/dt = rN$

- This expresses the population growth over very short time intervals.

A population living under ideal conditions will increase at the fastest rate possible; nutrients are abundant and only the physiological capacity of the individuals limits reproduction.

- The maximum population growth rate is called the *intrinsic rate of increase* and is symbolized by r_{max}.

Exponential population growth is the population increase under ideal conditions due to intrinsic rate of increase. It is expressed as:

$dN/dt = r_{max}N$

- The size of the population increases rapidly due to ideal conditions of unlimited resources.
- Produces a J-shaped growth curve (see Campbell, Figure 52.11)
- Although the intrinsic rate of increase is constant, more new individuals accumulate when the population is large than when it is small; this is due to the fact that *N* gets larger.

A population with a higher intrinsic rate of increase will grow faster than one with a lower rate of increase (see Campbell, Figure 52.11).

- A population's r_{max} value is influenced by its life history features (age of first reproduction, clutch size, offspring survival rate).
- Generation time and r_{max} are usually inversely related over a range of species (see Campbell, Figure 52.12).
- Exponential growth is characteristic of populations introduced into a new or unfilled environment or whose numbers have been decimated by a catastrophe and are rebounding.

B. A logistic model of population growth incorporates the concept of carrying capacity

No population can grow exponentially for an indefinite period of time. As a population increases in size, the higher density may influence the ability of individuals to obtain resources necessary for maintenance, growth and reproduction.

- Populations inhabiting environments which contain a finite amount of available resources available to each individual.

The *carrying capacity (K)* of a habitat is the maximum stable population size that the particular environment can support over a relatively long time period.

- Carrying capacity is an environmental property that varies over space and time with the abundance of limiting resources.
- Carrying capacities can be determined by many factors:
  - Energy limitations (food resources) are the most common determinant of *K.*
  - Other factors include the availability of specialized nesting sites required by some birds; roosting sites as for some bats; shelters and refuges from potential predators.

Crowding and resource limitation can greatly effect the population growth rate.

- Insufficient resources may reduce per capita birth rates in a population (lower *b).*
- If enough energy cannot be obtained for maintenance, per capita death rates increase (higher *d).*
- A decrease in *b* and/or an increase in d results in a lower overall population growth rate (smaller *r).*

1. The logistic growth equation

A logistic population growth model assumes the rate of population growth *(r)* slows as the population size *(N)* approaches the carry capacity *(K)* of the environment.

A mathematical model for logistic population growth incorporates the effect of population density on *r,* allowing it to vary from r_{max} when resources are plentiful to zero when the carrying capacity is reached.

The equation for logistic population growth is:

$$dN/dt = r_{max}N\ (K\ \left(\frac{K-N}{K}\right)$$

- K= carrying capacity; the maximum sustainable population.
- K- N= the number of new individuals the environment can accommodate.
- $(K - N)/K$ = percentage of K available for population growth.
- Multiplying r_{max} by $(K - N)/K$ reduces the value of r as N increases (see Campbell, Table 52.2)
- The actual growth rate of a population of any size is $r_{max}\,N(K - N)/K$

The implications of the logistic growth equation at varying population sizes for a growing population are:

- When *N is* low, *(K - N)/K is* large and r is only slightly changed from r_{max}.
- When N is large and resources are limiting, (K - N)/K is small; this reduces *r* substantially from r_{max}.
- When *N= K, (K - N)/N is O* and *r* = 0; this means the number of births is equal to the number of deaths and zero population growth occurs.

The logistic model of population growth produces a sigmoid (S-shaped) growth curve (see Campbell, Figure 52.14).

- Intermediate population sizes add new individuals most rapidly since the breeding population is of a substantial size and the habitat contains plentiful amounts of resources and available space.
- *As N* approaches *K,* the population growth rate slows due to limitations in available resources.
- The logistic model is density-dependent since the rate at which a population grows changes as the density of the population changes.

2. How well does the logistic model fit the growth of real populations?

Laboratory populations of paramecia and *Daphnia,* as well as other animals, show population growth rates which fit the predicted S-shaped curve fairly well (see Campbell, Figure 52.15).

- These represent relatively unnatural situations of idealized conditions without predators and other species.
  - Even under these conditions, some populations show deviations from smooth, sigmoid curves and do not stabilize at a clear carrying capacity.
- Studies of wild populations that have been introduced into new habitats and populations rebounding after near elimination by disease or hunting, provide general support for logistic population growth (see Campbell, Figure 52.15c).

Some assumptions of the logistic model do not hold true for all populations. For example, the logistic model assumes that:

1. Even at low levels, each individual added may have the same negative effect on population growth rate; any increase in *N* reduces *(K - NJ/N.*
   - The Allee effect points out that individuals may benefit by population increase which improves the chances for survival or reproduction.
     - For example, a plant standing alone would suffer from excessive wind, but be protected from the wind in a clump of individuals.
     - Solitary animals like rhinoceros have a greater chance of locating a mate during breeding season if populations are higher.
   - When a population is at low levels, there is a greater possibility that chance events will eliminate all individuals or inbreeding will lead to reduction in fitness.
2. Populations approach carrying capacity smoothly.
   - Often see a lag time before the negative effects of an increasing population are realized, this causes the population to overshoot carrying capacity.
     - Eventually, deaths exceed births and population size drops below carrying capacity.
     - Many populations thus appear to oscillate about a general carrying capacity.

Populations do not necessarily remain at, or even reach, levels where population density is an important factor. In these cases, the idea of carrying capacity does not really apply.

- Seen in short-lived, quickly reproducing insects and other small organisms sensitive to environmental fluctuations

Although the logistic model fits few if any real populations, it incorporates ideas that apply to many.

3. Population growth models and life histories

The logistic population growth model predicts that there will be different growth rates for populations with high and low densities in relation to the environmental carrying capacity.

- Each individual has fewer resources available at high densities and the population is growing slowly.
- Abundant resources are available to individuals at low densities and the population is growing rapidly.

The concept that different life history adaptations would be favored under high densities and low densities was introduced by ecologist Martin Cody in the late 1960s. For example,

- Under high population densities, selection would favor adaptations that enhanced survival and reproduction with few resources.
  - Competitive ability and maximum efficiency of resource utilization would be favored in a population that was maintained at or near the carrying capacity.
- Under low population densities, selection would favor adaptations that enhanced rapid and high rates of reproduction regardless of efficiency.
  - Increased fecundity and reaching maturity quickly would be favored.

The development of Cody's concept lead to designations of *K-selected* (also called *equilibrium populations)* and *r-selected* (also called *opportunistic populations)* traits of life history strategies.

- The designations *r* and *K* refer to variables in the logistic growth model equation. *K*-selected populations are those living at a density near the limits of their resources (*K*).
- *r*-selected populations are more likely to be found in variable environments where population densities fluctuate or in open or disturbed habitats where individuals have little competition.
- Most populations show a mixture of *r*-selected and K-selected traits since life history evolves in a natural setting of complex factors (see Campbell, Table 52.3).

IV. Population Limiting Factors

Populations are regulated by density-dependent factors and density-independent factors, either separately or in combination.

- The relative importance of these factors differs among species and their specific circumstances.

A. Density-dependent factors regulate population growth by varying with the density

The prime implication of the logistic growth model is that increasing population density reduces resource availability and resource limitations ultimately limits population growth.

- This model can thus be applied to *intraspecific competition:* the reliance of two or more individuals of the same species on the same limited resource.
- Competition becomes more intense as population size increases, and r is reduced in proportion to the intensity of competition.

In restricting population growth, a *density-dependent factor* intensifies as the population size increases, affecting each individual more strongly. They also affect a greater percentage of individuals in a population as the number of individuals increases.

- Population growth declines because death rate increases, birth rate decreases or both.
- Resource limitation is one such factor.
  - A reduction in available food often limits reproductive output as each individual produces fewer eggs or seeds (see Campbell, Figure 52.16).
- Resources other than nutrients may also limit populations.
  - Territoriality (the defense of a well- bounded physical space) is a behavioral mechanism to reduce intraspecific competition since each individual protects resources only within their own territory.
  - Competition still occurs when individuals compete for space to establish their territories.
- Health and survivorship also decrease as crowding results in smaller, less robust individuals (see Campbell, Figure 52.17).
- Many predators concentrate on a particular prey when its population density is high, taking a greater percentage than usual.
  - Predators may switch to other more dense prey populations if energy expenditure to capture prey increases.
- The accumulation of toxic metabolic wastes may also limit a population. Intrinsic factors may also play a role in regulating population size.
- Population growth rate decreases may occur even when food and shelter are abundant. High densities may cause stress syndromes resulting in hormonal changes that delay sexual maturation or otherwise inhibit reproduction.
- High densities have also been shown to produce a stress syndrome which suppresses the immune system.
- High densities can thus reduce birth rates and increase death rates.

B. The occurrence and severity of density-independent factors are unrelated to population density

Density-independent factors are unrelated to population size and affect me same percentage of individuals regardless of the size of the population.

- Weather, climate and natural disasters such as freezes, seasonal changes, hurricanes and fires are examples.
  - The severity and time of occurrence is the determining factor on what proportion of the population is affected.
  - In some natural populations, these effects routinely control population size before density- dependent factors become important.

C. A mix of density-dependent and density-independent factors probably limits the growth of most populations

Over the long term, species' populations exhibit varied dynamics.

Many populations remain fairly stable in size, close to the carrying capacity determined by density- dependent factors.

- Although exhibiting stability, they often display short-term fluctuations due to density-independent factors.
- Long-term population size may remain the same, masking short-term effects of some factor such as an extremely cold winter.

Density-dependent and density-independent factors sometimes work together to regulate a population, although the relative importance of each may vary seasonally.

- A severe winter may greatly reduce a population due to cold temperatures (density-independent) and intraspecific competition for limited food (density-dependent).
- This reduction in population size may benefit the surviving adults by reducing competition for food in the following spring.

D. Some populations have regular boom and bust cycles

Some bird, mammal and insect populations show a regular fluctuation in density. Among mammals:

- Small herbivores (e.g., lemmings) show 3- to 5- year cycles.
- Larger herbivores (e.g., snowshoe hares) show 9- to 11-year cycles.

Several hypotheses have been proposed to explain population cycles:

Crowding may regulate cyclical population by affecting the organisms endocrine systems.

- Stress from high density may alter hormone balance and reduce fertility, increase aggressiveness, and induce mass emigrations.

Population cycles may result from a time lag in the response to density-dependent factors. This lag causes the population to overshoot and undershoot the carrying capacity.

- A high density of snowshoe hares may cause a deterioration of food quality which makes it unfit for consumption.
- Predation may also play a role if predators take enough prey to cause a decrease in prey population density.

Much longer cycles are also known. The periodical cicadas have population cycles of 13 or 17 years.

- This may be an adaptation to reduce predation.
- Cicada populations are controlled in some local regions by a fungus whose spores can survive in soil for the years between cicada outbreaks.

V. Human Population Growth

A. The human population has been growing almost exponentially for centuries but will not be able to do so indefinitely

The exponential growth of the human population has caused severe environmental degradation.

- Until 1650, the human population increased slowly.
- The population doubled by 1850 (200 years), doubled again by 1920 (80 years), and doubled yet again by 1975 (45 years) (see Campbell, Figure S2.21).

Human population growth is affected by the same parameters (birth and death rates) that affect other plant and animal populations.

- The advent of agriculture 10,000 years ago increased birth rates and decreased death rates.
- Since the Industrial Revolution, virtually exponential growth has resulted mainly from a drop in deaths, especially infant mortality.
  - The decrease was due to improved nutrition, better medical care, and improved sanitation.
- The population growth rates in most developing countries are actually increasing due to relatively high birth rates coupled with decreasing mortality.

Population ecologists cannot agree on Earth's carrying capacity for the human population or what factor will eventually limit the population.

- Limited nutrients is the usual factor in restraining populations of other animals, but agricultural technology has advanced to the point that food supplies have maintained an equivalent pace to population increases. Malnutrition and famine result from unequal distribution as opposed to inadequate production.
- Space limitations may play a role. As the human population continues to increase, conflicts over land use will intensify.
- Resources other than nutrients and space may play a role.
    - How will the disappearance of nonrenewable fossil fuels and metals affect the human population?
    - Will the accumulation of pollutants and other forms of wastes eventually reach toxic levels?

Because of the interrelatedness of food production, land use, and energy consumed in producing food, it is likely that the carrying capacity for humans will be determined by several interacting factors.

Worldwide population growth is a mosaic with some countries having near zero population growth while others have relatively high growth rates.

- Although variation in growth rates is found, the human population as a whole continues to grow.

Age structure within each country appears to be a major factor in the variation of population growth rates (see Campbell, Figure 52.23)

- A relatively uniform age distribution, where individuals of reproductive age or younger are not disproportionately represented, lends itself to a stable population size.
- A population which contains a large proportion of reproductive age or younger individuals will face a sudden increase in the rate of population growth in the future.

A unique feature of human reproduction is the ability to be consciously controlled by voluntary contraception or government-sponsored family planning.

- Social change, such as women delaying reproduction in favor of employment and advanced education, can also result in decreases in population growth rates.

Human cultural evolution has had an impact on Earth's carrying capacity.

- The development of agriculture and industrial technology has twice increased the Earth's carrying capacity for humans.
- What Earth's carrying capacity is and how we approach it are questions generating concern and debate.

The human population will eventually stop growing due to social changes, individual choice, government intervention, or increased mortality due to environmental limitations.

- Hopefully, if the human population reaches K, it will approach it smoothly and level off.
- This will occur when birth rates and death rates are equal.
- If the population fluctuates around K, periods of increase will be followed by times of mass death due to famine, disease, or conflict.

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CHAPTER 53

COMMUNITY ECOLOGY

OUTLINE

I. Early Hypotheses of Community Structure
   A. The interactive and individualistic hypotheses pose alternative explanations of community structure: *science as a process*

II. Interactions between Populations of Different Species
   A. Intraspecific interactions can be strong selection factors in evolution
   B. Interspecific interactions may have positive, negative, or neutral effects on a population's density: *an overview*
   C. Predation and parasitism are (+ /-) interactions: *a closer look*
   D. Interspecific competitions are (- / -) interactions: *a closer look*
   E. Commensalism and mutualism are (+ / 0) and (+ / +) interactions, respectively: *a closer look*

III. Interspecific Interactions and Community Structure
   A. Predators can alter community structure by moderating competition among prey species
   B. Mutualism and parasitism can have community-wide effects
   C. Interspecific competition influences populations of many species and can affect community structure
   D. A complex interplay of interspecific interactions and environmental variability characterizes community structure

IV. Disturbance and Nonequilibrium
   A. Nonequilibrium resulting from disturbance is a prominent feature of most communities
   B. Humans are the most widespread agents of disturbance
   C. Succession is a process of change that results from disturbance in communities
   D. The nonequilibrial model views communities as mosaics of patches at different stages of succession

V. Community Ecology and Biogeography
   A. Dispersal and survivability in ecological and evolutionary time account for the geographical ranges of species
   B. Species diversity on some islands tends to reach a dynamic equilibrium in ecological time

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. Compare and contrast the individualistic hypothesis of H.A. Gleason and the interactive hypothesis of F.E. Clements with respect to communities.
2. Explain the relationship between species richness, relative abundance, and diversity.

3. List four properties of a community, and explain the importance of each.
4. Explain how interspecific competition may affect community structure.
5. Describe the competitive exclusion principle, and explain how competitive exclusion may affect community structure.
6. Distinguish between an organism's fundamental niche and realized niche.
7. Explain how resource partitioning can affect species diversity.
8. Describe the defense mechanisms evolved by plants to reduce predation by herbivores.
9. Explain how cryptic coloration and aposematic coloration aid an animal in avoiding predators.
10. Distinguish between Batesian mimicry and Mullerian mimicry.
11. Describe how predators use mimicry to obtain prey.
12. Explain the role of predators in community structure.
13. Distinguish among parasitism, mutualism, and commensalism.
14. Explain why it is difficult to determine what factor is most important in structuring a community.
15. Distinguish between primary succession and secondary succession.
16. Explain how inhibition and facilitation may be involved in succession.
17. Describe how natural and human disturbances can affect community succession.
18. Explain how the intensity of disturbances can affect equilibrium and species diversity.
19. List the factors involved in limiting a species to a particular range.
20. Describe the mechanisms which contribute to the global clines in diversity.
21. Explain the factors which determine what species eventually inhabit islands.

KEY TERMS

species richness	cryptic coloration	principle	stability
relative abundance	aposematic coloration	ecological niche	disturbances
species diversity	mimicry	fundamental niche	ecological
predation	predator	prey	succession
individualistic hypothesis	Batesian mimicry	realized niche	primary
interactive hypothesis	Mullerian mimicry	resource partitioning	succession
secondary succession	parasite	character displacement	recruitment
interspecific interactions	host	symbiosis	dynamic
coevolution	endoparasites	symbiont	equilibrium
parasitism	ectoparasites	parasitism	hypothesis
parasitoidism	interspecific competition	commensalism	intermediate
herbivory	interference competition	mutualism	disturbance
community	exploitative competition	keystone species	hypothesis
biogeography	competitive exclusion	exotic species	

LECTURE NOTES

A community consists of all the organisms inhabiting a particular area; an assemblage of populations of different species living close enough together for potential interaction.

I. Early Hypotheses of Community Structure

Communities, even those that appear similar, vary with regard to their species diversity.

- *Species diversity* = The number and relative abundance of species in a biological community
  - Based on both species richness and relative abundance
    - *Species richness is* the number of species in a community.
    - *Relative abundance is* a measure of the proportion of a species in the community as a whole.

A community with a certain species richness with equal relative abundance of each species would have a greater diversity than a second community with the same species richness with a few common species and many rare ones.

A. The interactive and individualistic hypotheses pose alternative explanations of community structure: *science as a process*

Among the pioneers of community ecology, there were two divergent views on why certain combinations of species are found together as members of a community: the individualistic hypothesis and the interactive hypothesis.

The *individualistic hypothesis* was proposed by H.A. Gleason. This hypothesis depicted a community as a chance assemblage of species found in an area because they have similar abiotic requirements.

- Emphasizes studying single species
- Predicts each species will have an independent distribution along an environmental gradient and there are no discrete geographical boundaries between communities (see Campbell, Figure 53.1)
- In most cases, the composition of communities would change continuously along some environmental gradient due to addition or loss of particular species

The *interactive hypothesis* proposed by F.E. Clements saw each community as an assemblage of closely linked species having mandatory biotic interactions that cause the community to function as an integrated unit.

- Based on the observation that certain plant species are consistently found together
- Emphasizes entire assemblages of species as the essential units for understanding the interrelationships and distributions of organisms
- Predicts species should be clustered, with discrete boundaries between communities. The presence or absence of one species is governed by the presence or absence of other species with which it interacts (see Campbell, Figure 53.2).

Animals in a community are often linked more rigidly to other organisms.

- Some animals feed primarily on certain food items so their distribution is linked to distribution of their prey.
- Other animals feed on a variety of food items and tend to be distributed in a variety of communities.

Distribution of almost all organisms is affected by both abiotic gradients and interactions with other species.

- Among the most significant abiotic factors are disturbances (e.g,. floods, fire, storms) that destabilize existing relationships among organisms.

II. Interactions between Populations of Different Species

Interspecific interaction are those that occur between populations of different species living together within a community.

A. Interspecific interactions can be strong selection factors in evolution

Interactions between species are as important to adaptation by natural selection as the physical and chemical features of the environment.

Coevolution is a change in one species that acts as a selective force on another species.

Counteradaptation of the second species, in turn, affects selection of individuals in the first species.

- Studied most extensively in predator-prey relationships, in mutualism, and in parasite-host relationships

The association between passionflower vines *(Passiflora)* and the butterfly *Heliconius is* believed to be an example of coevolution.

- The vines produce toxic chemicals to reduce damage to young shoots and leaves by herbivorous insects.
- Butterfly larvae of *Heliconius* can tolerate these chemicals due to digestive enzymes that break down the toxic chemicals (a counteradaptation) (see Campbell, Figure 53.3).
- Females of some *Heliconius* species avoid laying eggs (which are bright yellow) on leaves where other yellow egg clusters have been laid.
  - This may reduce intraspecific competition on individual leaves.
- Some species of passionflowers develop large, yellow nectaries which resemble *Heliconius* eggs; an adaptation that may divert egg-laying butterflies to other plants.
- These nectaries, as well as smaller ones, also attract ants and wasps which prey on butterfly eggs 'end larvae.
- Thus, what appears to be coevolution may actually result from interactions with many species (not just the obvious two).

Biologists agree that adaptation of organisms to other species in a community is a fundamental characteristic of life.

B. Interspecific interactions may have positive, negative, or neutral effects on a population's density: *an overview*

While adaptations to abiotic factors largely determine the geographic distributions of many species, all organisms are influenced by biotic interactions with other individuals.

Interspecific interactions may take a variety of forms (see Campbell, Table 53.2).

The two species involved in the interaction may have a positive (+), negative (-), or neutral (0) effect on their population densities.

Both population densities may increase (+ / +), one may increase while the other decreases (+ /–), one may increase while the other is not affected (+ / 0), or both may decrease
(– / –).

C. Predation and parasitism are (+/–) interactions: a *closer look*

There are several (+ / –) interactions, some are obvious, some are not.

- *Predation* involves a *predator* that eats its *prey.*
- *Parasitism* involves predators that live in or on their *hosts* and seldom involves outright host death.
- *Parasitoidism* involves insects, such as small wasps, who lay their eggs on living hosts. After hatching, the larvae feed within the host's body and eventually cause its death.
- *Herbivory* occurs when animals eat plants. May only cause damage to a portion of the plant (grazing) or may kill an entire plant (seed eating).

1. Predation

Predation = *A* community interaction where one species, the predator, eats another, the prey.

Includes both animal-animal interactions and animal-plant interactions.

Adaptations of predators to this interaction are obvious and familiar. Predators have:

- Acute senses that are used to locate and identify prey items (e.g., heat-sensing pits of rattlesnakes, chemical sensors of herbivorous insects)
- Structures such as claws, teeth, fangs, stingers, and poisons that function to catch, subdue, or chew the prey item
- Speed and agility to pursue prey or camouflage that permits them to ambush prey

Various defensive adaptations have evolved in prey species as a result of repeated encounters with predators over evolutionary time.

a. Plant defenses against herbivores

Since plants cannot escape herbivores, they have evolved several ways to protect themselves from predation.

Plants have mechanical and chemical defenses against herbivores.

- Thorns or microscopic hooks, spines, and crystals may be present to discourage herbivores.
- Plants may produce chemicals (formed as byproducts of major metabolic pathways) that make vegetation distasteful or harmful.
- Plants may produce analogues of insect hormones that cause abnormal development in insects that prey on them.

Plant defenses may act as selective factors leading to counteradaptations in herbivores that can then nullify those defenses and consume the plant.

b. Animal defenses against predators

Animal defenses against predators may be passive (hiding), active (escaping and physical defense), mechanical, or chemical (toxins).

Active defenses include fleeing, active self-defense, alarm calls, mobbing (see Campbell, Figure 53.4), direct attack, and distraction.

Passive forms of defense involving adaptive coloration have evolved repeatedly among animals.

- *Cryptic coloration* (coloration making prey difficult to spot against its surroundings) is common and only requires the animal to remain still to avoid detection (see Campbell, Figure 53.5).
- The shape of an animal can also help camouflage it.
- Deceptive marking such as large, fake eyes can startle predators, allowing prey to escape, or cause predators to strike a nonvital area (see Campbell, Figure 53.6).
- *Aposematic coloration* (bright coloration that acts as a warning of effective physical or chemical defense) appears to be adaptive since predators quickly learn to avoid prey with this coloration (see Campbell, Figure 53.7).

Some mechanical and chemical defenses actively discourage predators (e.g., porcupine quills and skunk spray).

- Some insects acquire chemical defense passively by accumulating toxins from plants they eat; these make them distasteful to predators.

c. Mimicry

Mimicry is a phenomenon in which a mimic bears a superficial resemblance to another species, the model.

- Occurs in both predatory and prey species
- Defensive mimicry in prey usually involves aposematic models

Batesian mimicry = A palatable species mimics an unpalatable or harmful model (see Campbell, Figure 53.8)

- Mimic must be much less abundant than the model to be effective since predators must learn the coloration indicates a bad or harmful food item.

Mullerian mimicry = Two or more unpalatable, aposematically colored species resemble each other

- Each gains additional advantage since predators learn more quickly to avoid prey with this coloration.

Predators also use mimicry to lure prey.

- The tongue of snapping turtles resembles a wriggling worm which attracts small fish into capture range.

2. Parasitism

Parasitism is a (+ / –) interaction in which one organism, the *parasite,* derives its nourishment from another organism, the *host,* which is harmed in some way.

- *Endoparasites* live within the host tissues or body cavities.
- *Ectoparasites* attach to or briefly feed on the external surface of the host.

Natural selection favors parasites that are best able to locate and feed on a host.

- Infection by a parasite (locating a host) may be passive as when an endoparasite's egg is swallowed by a host.
- Active location of a host may involve thermal or chemical cues that help the parasite identify the host.

Natural selection has also favored the evolution of defensive capabilities in potential hosts.

- Secondary plant products toxic to herbivores may also be toxic to parasitic fungi and bacteria.
- The vertebrate immune system provides defense against endoparasites (see Campbell, Figure 53.9).
- Many parasites are adapted to specific hosts, often a single species.
- Coevolution generally results in stable relationships in which the host is not killed (host death would also kill the parasite).

Some forms of parasitism do not involve the consumption of the host, but are the exploitation of the host's behavior by the parasite.

- Some species of birds (cowbirds, European cuckoos) lay their eggs in the nests of other species. Often a newly hatched brood parasite will move other eggs out of the nest. Host parents invest their energy in feeding the brood parasite instead of their own offspring – a (+ / –) interaction.
- An evolutionary adaptation in many host species is the ability to detect parasite eggs which are removed or the nest is abandoned.
- A counteradaptation to this host defense is egg mimicry in some brood parasites.

D. Interspecific competitions are (– / –) interactions: a *closer look*

Interspecific competition occurs when two or more species in a community rely on similar limiting resources.

- May take the form of *interference competition* (actual fighting) or *exploitative competition* (consumption or use).
- As the population density of one species increases, it may limit the density of the competing species as well as its own.

1. The competitive exclusion principle

The *competitive exclusion principle* predicts that two species competing for the same limiting resources cannot coexist in the same community. One will use resources more efficiently, thus reproducing more rapidly and eliminating the inferior competitor.

- Derived independently by A.J. Lotka and V. Volterra, each of whom modified the logistic model of population growth to interspecific competition.
- Experiments by G.F. Gause confirmed competitive exclusion among species *of Paramecium* (see Campbell, Figure 53.10).
- Laboratory experiments have confirmed the principle *for* other organisms; however, natural communities are much more complex and require field experiments and observations to determine the importance *of* competition.

2. Ecological niches

An *ecological niche is* the sum total *of* an organism's use *of* biotic *and* abiotic resources *in* its environment; how it "fits into" an ecosystem.

A *fundamental niche is* the resources a population is theoretically capable *of* using under ideal circumstances.

Biological constraints (competition, predation, resource limitations) restrict organisms to their *realized niche:* the resources a population actually uses.

Two species cannot coexist in a community *if* their niches are identical.

Ecologically similar species can coexist in a community *if* there are one or more significant differences in their niches.

3. Evidence for competition in nature

If competition is as important as indicated by the competitive exclusion principle, it should be rare in natural communities, since only two outcomes are possible:

- The weaker competitor will become extinct.
- One of the species will evolve to the point *of* using a different set of resources.

Several lines of evidence, including resource partitioning and character displacement, indicate that competition in the past has had a major role in shaping current ecological relationships.

Resource partitioning is well documented among animals.

- Sympatric species consume slightly different foods or use other resources in different ways.
  - For example, in the Dominican Republic, several species of *Anolis,* small arboreal lizards, are sympatric. They feed on small arthropods that land within their territories. Each species uses a characteristic perching site, which presumably reduces competition (see Campbell, Figure 53.11).

- Natural selection appears to have favored perch site selection since each species has morphological characteristics (body size, leg length) which are adaptive to their microhabitats.

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.

- Often occurs in areas where populations of closely related species which are normally allopatric become sympatric.
- Allopatric populations of such species are similar in structure and use similar resources.
- Sympatric populations show morphological differences and use different resources.
- Two closely related species of Galapagos finches *(Geospiza fuliginosa* and *G. fortis)* have beaks of similar size when the populations are allopatric; however, on an island where they are sympatric, a significant difference in beak depth has evolved (see Campbell, Figure 53.12).
  - Indicates they feed on seeds of different sizes when sympatric.

Controlled field experiments also provide evidence for the influence of one species on the density and distribution of another species. J. H. Connell manipulated the densities of two species of barnacles that compete for attachment space in the rocky intertidal zone (see Campbell, Figure 53.13).

- *Balanus balanoides is* usually concentrated in the lower portions of the rocky intertidal zone due to a lower tolerance to desiccation.
- *Chthamalus stellatus is* usually found in the upper portions of the zone.
- After Connell removed *Balanus* from the lower strata, *Chthamalus* was able to grow there.
- This showed that one species is able to exclude another from the area where their fundamental niches overlap. That is, in the lower part of the zone, *Balanus* outcompeted *Chthamalus* for attachment sites, thus limiting it to the upper part of the rocks.

E. Commensalism and mutualism are (+ / 0) and (+ / +) interactions, respectively: a *closer look*

Symbiosis is a form of interspecific interaction in which a *host species* and a *symbiont* maintain a close association.

- May be parasitism, commensalism, or mutualism
- All are important determinants of community structure

1. Commensalism

Commensalism is a (+ / 0) interaction in which the symbiont benefits and the host is unaffected.

- Few absolute examples exist since it is unusual for one species not to be affected in some way by a close association with another species.
- Since only one species in a commensalistic association benefits, any evolutionary change in the relationship will likely occur in the baneficiary.

Cowbirds and cattle egrets and grazing herbivores appear to have a commensal association (see Campbell, Figure 53.14).

- Cattle egrets feed on insects and other small animals.

- The birds concentrate their feeding activity near grazing herbivores whose movements flush prey items from the vegetation.
- The egrets benefit by an increase in feeding rates by following the herbivores.
- Most of the time, the herbivores are not affected by the activity of the egrets. In fact, they may derive some benefit when the birds remove and eat ticks or other ectoparasites from the herbivores. However, a possible negative effect may occur if the birds somehow make an herbivore more susceptible to predators.

Commensalism, parasitism, or mutualism are best described as when two associating populations are together, they exhibit a particular symbiotic relationship most of the time.

2. Mutualism

Mutualism is a (+ / +) interaction requiring the evolution of adaptations in both species.

- A change in either species is likely to affect the survival and reproduction of the other.

Examples:
- Nitrogen fixation by bacteria in the root nodules of legumes
- Cellulose digestion by microorganisms in the alimentary canals of termites and ruminant mammals
- Photosynthesis by algae in the tissues of corals

Mutualistic relationships may have evolved from predator-prey or host-parasite relationships.

- Some angiosperms have adaptations that attract animals for pollination or seed dispersal.
  - May represent counteradaptations to herbivores feeding on seeds or pollen.
  - Pollen is spared when the pollinator can feed on nectar and seeds are dispersed when animals eat fruits.
- Plants that could derive a benefit from sacrificing tissues other than pollen or seeds would increase their reproductive success.

III. Interspeciffc Interactions and Community Structure

The relationships of organisms within a community are tied together in a complex web of community structure and processes.

One way to examine the community's web of interspecific interactions is to study the various feeding (trophic) relationships, or what eats what.

- The functional groupings approach involves placing species in groups with similar trophic positions.
  - All plants are grouped together as producers; herbivores, regardless of size, are primary consumers; organisms that feed on primary consumers are secondary consumers, and so on.
  - This method provides a broad overview of the community, but it may mask some important aspects of the population interactions.
  - Food web analysis emphasizes the trophic connections among community members.
    - Includes species-level information about the community and emphasizes species-species connections

- Can be very complex
- Presents a detailed knowledge of feeding relationships within the community structure

A. Predators can alter community structure by moderating competition among prey species

Predation plays a complex role in helping shape community structure and may actually help maintain diversity.

Predators do not always reduce diversity.

The most important effect of a predator on a community structure is to moderate competition among its prey species.

- In a predator-free environment, it has been shown that the species richness of the community declines markedly (see Campbell, Figure 53.16).
- A *keystone species* has an impact on a community that is disproportionately large relative to its own abundance.
- A *keystone* predator may maintain a higher community species diversity by reducing the densities of strong competitors, thus preventing competitive exclusion of poorer competitors.

B. Mutualism and parasitism can have community-wide effects

The interactions that characterize mutualistic and parasitic relationships play important roles in communities.

- Keystone mutualists (e.g., mycorrhizal fungi) help maintain processes that impact all other species in communities.
- Parasitic diseases that reduce populations of one species also impact other species
- Parasites also can modify host behavior (the trypanosome/tsetse relationship)

C. Interspecific competition influences populations of many species and can affect community structure

Competition is recognized as an important factor in determining community structure but whether it is the major factor is open to debate.

- Many studies have documented interspecific competition, but it does not always result in competitive exclusion: competing species sometimes coexist at reduced densities.
  - *Exotic species* (species introduced into new communities by humans) often outcompete native species and alter the community structure.
  - The competition for space between barnacles discussed earlier resulted in exclusion of *Chthamalus* from the lower intertidal zone but it remained in the upper zone.
- It is difficult to demonstrate that two species are currently competing and even more diff'icult to assess what has happened in their evolutionary past.
- It is generally recognized that competition becomes more important as population sizes approach carrying capacities and resources are limiting.

Determining the effects of interspecific factors on species diversity and structure in communities is an important goal in ecological research, as is determining the relative significance of environmental patchiness in community structure.

D. A complex interplay of interspecific interactions and environmental variability characterizes community structure

The more heterogeneous the habitat, the more ecological niches available to organisms, and the more diverse the community.

Vegetation greatly influences the types of animals found in a community. Animal populations can more easily partition a structurally complex system than one of less complexity.

Environmental patchiness is a spatial and temporal characteristic of all ecosystems.

- For example, the chemical composition of rocks influences the mineral content of the soil derived from their erosion. Soil moisture varies with topography.
- Environmental patchiness can increase community diversity by facilitating resource partitioning among potential competitors adapted to different local conditions.

Community diversity is also affected by the temporal use of habitats.

- Nocturnal animals utilize a habitat at night and are replaced by diurnal animals when it becomes daytime.
- A community will contain a variety of plants which bloom during different seasons.

Evaluating which factors are important in developing the characteristics of a community is diff'icult since interspecific interactions and abiotic factors that cause patchiness all have significant impact.

- Communities are structured by multiple interactions of organisms with the biotic and abiotic factors in their environment.
- Which types of interactions are most important varies from one type of community to another, and even among different components of the same community.

IV. Disturbance and Nonequilibrium

Communities vary in their responses to both natural and human-induced disturbances.

- The *stability* of a community is its tendency to reach and maintain equilibrium (or relatively constant condition) in response to disturbance.
- Responses depend on the type of community and nature of the disturbance.

A. Nonequilibrium resulting from disturbance is a prominent feature of most communities

Disturbances are events that disrupt communities.

- They change resource availability and create opportunities for new species to become established.
- The magnitude of the disturbance's impact depends on the size, frequency, and severity of the disturbance.
- Natural disturbances include storms, fire, floods, freezes, and drought.
- Animals, including humans, can also cause disturbances by overgrazing, damaging communities, removing organisms within them, or altering resource availability.

Increasing evidence indicates that some amount of disturbance and nonequilibrium is normal for communities. Some ecologists suggest that a given community is usually in some state of recovery from a disturbance.

B. Humans are the most widespread agents of disturbance

Human disturbances have the greatest impact on communities.

- Logging and clearing for farmland have reduced and disconnected forests.
- Agricultural development has disrupted grasslands.
- After a community disturbance, the early stages of succession, characterized by weedy and shrubby vegetation, may persist for many years.

- Centuries of overgrazing and agricultural disturbance have contributed to current famine in parts of Africa by turning grasslands into barren areas.
- Human disturbances usually reduce species diversity in communities.

It is possible for disturbances to have *positive* impact on a community.

- Small-scale natural disturbances may help maintain species diversity in a community (see Campbell, Figure 53.18).
    - When patches are formed during different successional stages, habitat heterogeneity is increased.
- Frequent small-scale disturbances can prevent large-scale disturbances of greater negative impact.
    - Small fires prevent the accumulation of flammable materials that would feed a larger, more damaging fire.
- Decades-long fire suppression efforts in Yellowstone NP provided a great accumulation of fuel that fed a large-scale fire in 1988 (see Campbell, Figure 53.19).

C. Succession is a process of change that results from disturbance in communities

Ecological succession is the transition in species composition over ecological time.

- Called primary *succession* if it begins in areas essentially barren of life due to lack of formed soil (e.g., volcanic formations) or on rubble (e.g., retreat of glaciers)
- Called *secondary succession* if an existing community has been cleared by some disturbance that leaves the soil intact (e.g., abandoned agricultural fields)

A variety of interrelated factors determines the course of succession.

Individual species compete for available resources and replace each other.

- Different species compete better at different successional stages since resource availability changes over the course of succession.
- Early stages are typically characterized by *r*-selected species that are good colonizers.
    - They have a high fecundity and excellent dispersal mechanisms.
    - Others may be fugitive species that do not compete well except in newly disturbed areas.

The species composition during early successional stages is affected by the abiotic conditions in a barren area.

- *K*-selected species may colonize an area but fail to become abundant because of environmental conditions that are outside of the* tolerance limits.
- Variation in growth rates and maturation times of colonizers impact the community.
    - For example, herbaceous species are more prevalent in early successional stages than trees because they grow faster and mature quicker.

Changes in community structure during succession may be induced by the organisms themselves.

- Direct biotic interactions include *inhibition* of some species by others through exploitative competition, interference competition, or both.
- Organisms also affect the abiotic environment by modifying local conditions.

- In facilitation, the group of organisms representing one successional stage "paves the way" for species typical of the next stage (e.g., alder leaves lower soil pH as they decompose, and lower soil pH facilitates the movement of spruce and hemlock into the area).
- Sometimes facilitation for other species makes the environment unsuitable for the very species responsible for the changes.

- Inhibition and facilitation may be involved throughout the stages of succession.

D. The nonequilibrial model views communities as mosaics of patches at different stages of succession

A traditional view of ecological succession held that the community passed through a series of predictable transitional stages to reach a relatively stable state, the *climax community*.

- The climax was reached when the web of interactions was so intricate that the community was saturated.
- No new species could enter unless a localized extinction occurred.

Ecologists now consider the concept of stable communities flawed and overly simplistic.

- Many communities are also routinely disturbed by outside factors during the course of succession.
- Communities that appear stable actually change over long periods of time.

The prevailing view is the nonequilibrial model, which sees communities as being in continual flux.

- It emphasizes the importance of less predictable factors (dispersal, disturbance) in shaping community composition and structure.
- The succession pathway depends on the size, frequency, and severity of disturbance.
- The course of succession may vary with the identity of colonizing species.
- Disturbances may prevent the community from ever reaching equilibrium.
- A mature community is an unpredictable mosaic of patches at different successional stages.
- Local environmental heterogeneity contributes to the mosaic structure as different species inhabit different patches.

What are the effects of disturbance in a community?

Disturbances result in minor changes, such as regrowth and migration from adjacent areas; usually, species originally in the area refill it.

Disturbances may also trigger major changes in community structure that result in colonization of disturbed patches by *recruitment.*

- *Recruitment* = Colonization by species from distant areas not directly associated with the disturbed patch or its immediate vicinity

Several hypotheses have been offered to explain why some communities are more diverse than others.

1. The *dynamic equilibrium hypothesis* holds that diversity depends mainly on the effect of disturbance on the competitive interactions of populations.
2. The *intermediate disturbance hypothesis* states that species diversity is greatest where disturbances are moderate in frequency and severity because organisms typical of several successional stages will be present.
   - Supported by studies of clearings formed by trees falling in tropical rain forests

- In these disturbed areas, immigrations and extinctions occur rapidly and species from different successional stages coexist.

3. The nonequilibrial model places interspecific interactions in secondary roles and suggests that high species diversity results mainly from abiotic disturbance-induced environmental patchiness.

V. Community Ecology and Biogeography

Biogeography is the study of the past and present distribution of individual species and entire communities.

- Provides a different approach to understanding community properties by analyzing global and local phenomena, mostly from a historical perspective.
- Traditionally concerned with the identities of species comprising particular communities.
- Currently also applies the principles of community ecology to the analysis of geographical distribution.

Terrestrial life can be divided into biogeographical realms having boundaries associated with continental drift patterns (see Campbell, Figure 53.20).

- Thus species distribution reflects past history as well as present interactions of organisms with their environment.

A. Dispersal and survivability in ecological and evolutionary time account for the geographical ranges of species

Limitation of a species to a particular range may be due to:

1. Failure of the species to disperse beyond its current range
2. Failure to survive of pioneer individuals that spread beyond the observed range
3. The species having retracted from a once larger range to its current boundaries

The first two limitations can be distinguished by transplant experiments in which specimens of a species are moved to similar environments outside of their range.

- If the transplants survive, they probably have not dispersed to suitable locations outside the existing range. If they die, it indicates an intolerance to different abiotic conditions or an inability to compete with resident species.
- Most species fail to survive outside their range, but there are notable exceptions.

The third limitation is well supported by data from paleontology and historical biogeography.

- The fossil record includes evidence that close relatives of some living animals with limited ranges once had much wider ranges.
- For example, fossils of close relatives of elephants and camels have been found in North America.

B. Species diversity on some islands tends to reach a dynamic equilibrium in ecological time

Islands provide opportunities to study factors affecting species diversity of communities due to their isolation and limited size.

- An island is any area surrounded by an environment not suitable for the "island" species.
- Islands can be oceanic islands or habitat islands on land (lakes or mountain peaks separated by lowlands).

Ecologists Robert MacArthur and E.O. Wilson developed a general hypothesis of island biogeography that predicts species diversity on an island will reach an equilibrium directly proportional to island size and inversely proportional to the island's distance from a mainland.

- The number of species to inhabit islands is determined by immigration and extinction rates, which are themselves affected by island size and distance from the mainland.
- Smaller islands also have higher extinction rates since they have fewer resources and less diverse habitat to be partitioned; these factors increase the probability of competitive exclusion.
- Immigration and extinction rates also are affected by the number of species already present.
    - As species numbers increase, immigration rate of new species decreases since new arrivals are less likely to represent a new species.
    - Extinction rate increases due to increased chance of competitive exclusion.
- Eventually, an equilibrium will be reached where immigration rates match extinction rates.
    - The number of species present at the equilibrium point is correlated to island size and distance from the mainland (see Campbell, Figure 53.21).
- The species composition may change since equilibrium is dynamic with immigrations and extinctions continuing.
- Experimental research by E.O. Wilson and D. Simberloff, in the late 1960s, on the small mangrove islands off the tip of South Florida, supported the hypothesis.

Over the past decades, the island biogeography hypothesis has come under considerable fire.

- May only apply in a limited number of cases and over short time periods, where colonization is the most important process determining species composition.
- Over longer periods, the species composition and community structure will be affected by speciation and evolutionary change in the island species.

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CHAPTER 54

ECOSYSTEMS

OUTLINE

I. Trophic Relationships in Ecosystems
   A. Trophic relationships determine an ecosystem's routes of energy flow and chemical cycling
   B. Primary producers include plants, algae, and many species of bacteria
   C. Many primary and higher-order consumers are opportunistic feeders
   D. Decomposition interconnects all trophic levels
II. Energy Flow in Ecosystems
   A. An ecosystem's energy budget depends on primary productivity
   B. As energy flows through an ecosystem, much is lost at each trophic level
III. Cycling of Chemical Elements in Ecosystems
   A. Biological and geological processes move nutrients among organic and inorganic compartments
   B. Decomposition rtes largely determine the rates of nutrient cycling
   C. Field experiments reveal how vegetation regulates chemical cycling: *science as a process*
IV. Human Impacts on Ecosystems
   A. The human population is disrupting chemical cycles throughout the biosphere
   B. Toxins can become concentrated in successive trophic levels of food webs
   C. Human activities are causing fundamental changes in the composition of the atmosphere
   D. The exploding human population is altering habitats and reducing biodiversity worldwide

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. Explain the importance of autotrophic organisms with respect to energy flow and nutrient cycling in ecosystems.
2. List and describe the importance of the four consumer levels found in an ecosystem.
3. Explain how gross primary productivity is allocated by the plants in an ecosystem.
4. List the factors that can limit productivity of an ecosystem.
5. Explain why productivity declines at each trophic level.
6. Distinguish between energy pyramids and biomass pyramids.

7. Describe the hydrologic (water) cycle.
8. Describe the carbon cycle, and explain why it is said to result from the reciprocal processes of photosynthesis and cellular respiration.
9. Describe the nitrogen cycle, and explain the importance of nitrogen fixation to all living organisms.
10. Explain how phosphorus is recycled locally in most ecosystems.
11. Explain why the soil in tropical forests contains lower levels of nutrients than soil in temperate forests.
12. Describe how agricultural practices can interfere with nitrogen cycling.
13. Describe how deforestation can affect nutrient cycling within an ecosystem.
14. Describe how the carbon cycle differs in terrestrial and aquatic systems.
15. Explain how "cultural eutrophication" can alter freshwater ecosystems.
16. Explain why toxic compounds usually have the greatest effect on top-level carnivores.
17. Describe how increased atmospheric concentrations of carbon dioxide could affect the Earth.
18. Describe how human interference might alter the biosphere.

KEY TERMS

ecosystem	food chain	biomass	biogeochemical cycle
trophic structure	food web	standing crop biomass	nitrogen fixation
trophic level	production	limiting nutrient	limiting nutrient
primary producers	consumption	secondary productivity	ammonification
primary consumers	decomposition	ecological efficiency	long-term ecological
secondary consumers	primary productivity	pyramid of productivity	research (LTER)
tertiary consumers	gross primary	biomass pyramid	biological
detritivores	productivity	turnover time	magnification
detritus	net primary productivity	pyramid of numbers	greenhouse effect
denitrification			

LECTURE NOTES

Ecosystem = All organisms living in a given area along with the abiotic factors with which they interact

The boundaries of ecosystems are not usually discrete.

This is the most inclusive level of biological organization.

Ecosystems involve two processes that cannot be described at lower levels: energy flow and chemical cycling.

- Energy flows through ecosystems and matter cycles within them.

I. Trophic Relationships in Ecosystems

Each ecosystem has a *trophic structure* of feeding relationships that determine the paths of energy flow and chemical cycling.

- Ecologists divide the species in a community or ecosystem into different *trophic levels* based on their main source of nutrition.

A. Trophic relationships determine an ecosystem's routes of energy flow and chemical cycling

The five trophic levels typically recognized include:

1. *Primary producers* = Autotrophs (usually photosynthetic) that support all other trophic levels either directly or indirectly by synthesizing sugars and other organic molecules using light or chemical energy
2. *Primary consumers* = Herbivores that consume primary producers (plants and algae)
3. *Secondary consumers* = Carnivores that eat herbivores
4. *Tertiary consumers* = Carnivores that eat other carnivores
5. *Detritivores (decomposers)* = Consumers that derive energy from *detritus* (organic wastes) and dead organisms from other trophic levels. Detritivore often form a major link between primary producers and the consumers in an ecosystem.

An ecosystem's trophic structure determines the routes of energy flow and chemical cycling.

Food chain is the pathway along which food is transferred from trophic level to trophic level, beginning with primary producers (see Campbell, Figure *54.1)*.

- Rarely are unbranched since several different primary consumers may feed on the same plant species and a primary consumer may eat several species of plants
- Feeding relationships are usually woven into elaborate *food webs* within an ecosystem (see Campbell, Figure *54.2)*

It is important to distinguish between ecosystem structure (trophic levels) and ecosystem processes (production, consumption, decomposition). All organisms carry out each of the ecosystem processes to some extent.

- *Production* refers to the rate of incorporation of energy and materials into the bodies of organisms.
  - In this sense, all organisms are producers; however, primary producers are often referred to as "producers" because their production supports all other organisms.
- *Consumption* refers to the metabolic use of assimilated organic molecules for organismal growth and reproduction.
- *Decomposition is* the breakdown of organic molecules into inorganic molecules.

B. Primary producers include plants, algae, and many species of bacteria

The main primary producers will vary depending on the ecosystem.

Plants are the main producers in most terrestrial ecosystems.

- Debris falling from terrestrial plants that reaches streams (directly or through runoff) is a major source of organic material.
- Phytoplankton (algae and bacteria) are the most important autotrophs in the limnetic zone of lakes and in the open ocean.
- Multicellular algae and aquatic plants are often more important primary producers in the shallow, near-shore areas of freshwater and marine ecosystems.
- The aphotic zone of the deep sea receives energy and nutrients (dead plankton, detritus) from the overlying photic zone.

Organisms in communities surrounding the hot water vents on the deep-sea floor depend more on chemical energy than solar energy.

- The main producers are chemoautotrophic bacteria that derive energy from the oxidation of hydrogen sulfide.

C. Many primary and higher-order consumers are opportunistic feeders

Consumers also vary with the type of ecosystem.

Primary consumers in terrestrial ecosystems are mostly insects, snails, plant parasites, grazing mammals, and seed-eating and fruit-eating birds and mammals.

- Primary consumers are considered opportunistic because they supplement their diet of autotrophs with heterotrophic material if it is available. Many consumers that mainly eat live organisms also scavenge dead organic material.

In aquatic ecosystems, the primary consumers are the zooplankton (heterotrophic protists, small invertebrates, numerous larval stages) and some fish. As with their terrestrial counterparts, aquatic consumers also are opportunistic

Secondary consumers in terrestrial ecosystems are spiders, frogs, insect-eating birds, carnivorous mammals, and animal parasites.

Secondary consumers in aquatic ecosystems are fish and benthic forms such as sea stars and other carnivorous invertebrates.

D. Decomposition interconnects all trophic levels

Organic matter in that composes living organisms in ecosystems is eventually recycled, decomposed, and returned to the abiotic environment in a form that can be used by autotrophs.

The most important decomposers are bacteria and fungi, which digest materials externally and then absorb the products.

Decomposition links all trophic levels.

II. Energy Flow in Ecosystems

Energy for growth, maintenance, and reproduction is required by all organisms; some species also require energy for locomotion.

A. An ecosystem's energy budget depends on primary productivity

Light energy is used by most primary producers to synthesize organic molecules (photosynthesis), which are later broken down to produce ATP (cellular respiration).

- Since only primary producers can directly utilize solar energy, an ecosystem's entire energy budget is determined by the photosynthetic activity of the system.

Consumers obtain energy in the form of organic molecules that were produced at the previous trophic level. Thus, energy flows to higher trophic levels through food webs.

1. The global energy budget

Earth receives an estimated 10^{22} joules (J) of solar radiation each day.

The amount of solar radiation striking the Earth's surface shows dramatic regional variation that limits the photosynthetic output of ecosystems in different places.

- The intensity of solar radiation also varies with latitude resulting in the tropics receiving the most input.
- Most of the solar radiation is reflected, absorbed, or scattered by the atmosphere, clouds, and dust particles in the air; this amount varies over different regions.

Only a fraction of the solar radiation which reaches the biosphere strikes plants, photosynthetic bacteria, and algae (much hits bare ground or is absorbed or reflected by water) and these primary producers can only use some wavelengths for photosynthesis.

- Only about 1% to 2% of the visible light reaching photosynthetic organisms is converted to chemical energy by photosynthesis.
  - The photosynthetic eff'iciency also varies with the type of plant, light levels, and other factors.

Even with all the variations mentioned above, primary production of Earth collectively creates about 170 billion tons of organic material each year.

2. Primary productivity

Primary productivity is the amount of light energy converted to chemical energy by autotrophs of an ecosystem.

- The total is known as *gross primary productivity (GPP),* which may be determined by measuring the total oxygen produced by photosynthesis.

Net primary productivity (NPP) = GPP - Rs (energy used by producers for respiration)

- NPP accounts for the organic mass of plants (growth) and represents storage of chemical energy available to consumers.
- The NPP:GPP ratio is generally smaller for large producers with elaborate nonphotosynthetic structures (such as trees) which support large metabolically active stem and root systems.

Primary productivity can be expressed as *biomass* (expressed as dry weight since water contains no usable energy) added to an ecosystem per unit area per unit time ($g/m^2/yr$) or as energy per unit time ($J/m^2/yr$).

- Primary productivity should not be confused with standing crop biomass.
- Primary productivity is the rate at which new biomass is synthesized by photosynthetic organisms.

- *Standing crop biomass is* the total biomass of photosynthetic autotrophs present at a given time, which may have accumulated over several growing seasons.

Primary productivity varies among ecosystems, and an ecosystem's size affects its contribution to the Earth's total productivity (see Campbell, Figure 54.3).

- Tropical rain forests are very productive and contribute a large proportion to the planet's overall productivity since they cover a large portion of the Earth's surface.
- Estuaries and coral reefs are also very productive but make only a small contribution to planetary productivity since they do not cover an extensive area.
- The open ocean has a relatively low productivity but makes the largest contribution to overall productivity of any ecosystem due to its very large size.
- Deserts and tundra also have low productivity.

Factors important in limiting productivity depend on the type of ecosystem and temporal changes such as seasons.

Generally, precipitation, temperature, and light intensity are factors limiting productivity in terrestrial ecosystems.

- Productivity increases as latitudes approach the equator because availability of water, heat, and light increases in the tropics.
- Productivity in terrestrial ecosystems may also be limited by availability of inorganic nutrients.
    - Plants require a variety of nutrients, some in large quantities and some in small quantities.
    - Primary productivity sometimes removes nutrients from the system faster than they can be replenished.
    - If a nutrient is removed in such quantities that sufficient amounts are no longer available, it becomes the *limiting nutrient.*

   - Adding the limiting nutrient will stimulate the system to resume growth until another nutrient or it becomes limiting (usually nitrogen or phosphorus).
   - Carbon dioxide availability sometimes limits productivity.

An aquatic ecosystem's productivity is usually determined by light intensity, water temperature, and availability of inorganic nutrients.

- Productivity is greatest in shallow waters near continents and along coral reefs due to abundant nutrients and sunlight.
- Light intensity and temperature affect primary productivity of phytoplankton in the open oceans; productivity is highest near the surface and decreases with depth.
- Inorganic nutrients are limiting at the surface of open ocean waters with nitrogen and phosphorus in especially short supply.
   - This is a primary reason for the relatively low productivity of open oceans.
- Marine phytoplankton is most productive where upwellings bring nutrient-rich waters to the surface.
   - These areas (usually in Antarctic seas) are more productive than tropical seas.
   - Thermal vent communities are also very productive though they are not very widespread and contribute little to marine productivity.
- Freshwater ecosystem productivity also varies from the surface to the depths in relation to light intensity.
   - Availability of inorganic nutrients is sometimes limiting, but biannual turnovers bring nutrients to the surface waters.

B. As energy flows through an ecosystem, much is lost at each trophic level

The transfer of energy from one trophic level to another is not 100%.

The amount of energy available to each trophic level is determined by NPP and the efficiencies with which food energy is converted to biomass in each link of the food chain.

1. Secondary productivity

Secondary productivity is the rate at which consumers convert the chemical energy in the food they eat into their own biomass.

Consider that herbivores consume only a small fraction of available plant material and they cannot digest all of the organic compounds in what they do ingest (see Campbell, Figure 54.4)

- About 1/6 of the calories is used for growth which adds biomass to the trophic level.
- The remaining organic material consumed is used for cellular respiration or is passed out of the body as feces.
- The energy in the feces stays in the system and is consumed by decomposers.
- The energy used in cellular respiration is lost from the system.
- Carnivores are more efficient at converting food into biomass but more is used for cellular respiration, further decreasing energy available to the next trophic level.

Consequently, energy flows through an ecosystem, it does not cycle within the ecosystem.

2. Ecological efficiency and ecological pyramids

Ecological efficiency is the ratio of net productivity at one trophic level compared to net productivity at the level below, or the percentage of energy transferred from one trophic level to the next.

- Efficiencies can vary greatly depending on the organisms involved, but usually range from 5% to 20%.
- This means that 80% to 95% of the energy available at one trophic level never transfers to the next.

Loss of energy in a food chain can be represented diagrammatically in several ways:

1. A *pyramid of productivity* has trophic levels stacked in blocks proportional in size to the productivity of each level.
   - Usually bottom heavy since ecological efficiencies are low (see Campbell, Figure 54.5)
2. A *biomass pyramid* has tiers that each symbolize the total dry weight of all organisms (standing crop biomass) in a trophic level (see Campbell, Figure
   - Most narrow sharply from producers at the base to top-level carnivores at the apex because of energy transfers between trophic levels are so inefficient.
   - Some aquatic ecosystems are inverted because producers have a short *turnover time.* They grow rapidly but are consumed rapidly, leaving little standing crop biomass.
3. A *pyramid of numbers is* comprised of blocks which are proportional in size to the numbers of individuals present at each trophic level (see Campbell, Figure 54.7).
   - Biomass of top-level carnivores is usually small compared to the total biomass of producers and lower-level consumers.
   - Only about 1/1000 of the chemical energy fixed by photosynthesis flows through a food web to a tertiary consumer.
   - Only 3 to 5 trophic levels can be supported since the energy in the webs is insufficient to support another trophic level.
   - Predators (top-level consumers) are highly susceptible to extinction when their ecosystem is disturbed due to their small population and wide spacing within the habitat.

For humans, eating meat is a relatively ineffcient way of tapping photosynthetic productivity—eating grains directly as a primary consumer provides far more calories.

III. Cycling of Chemical Elements in Ecosystems

Despite an inexhaustible influx of energy in the form of sunlight, continuation of life depends on recycling of essential chemical elements.

- These elements are continually cycled between the environment and living organisms as nutrients are absorbed and wastes released.
- Decomposition of wastes and the remains of dead organisms replenishes the pool of inorganic nutrients available to autotrophs.

Biogeochemical cycles = Nutrient circuits involving both biotic and abiotic components of ecosystems

A. Biological and geological processes move nutrients among organic and inorganic compartments

There are two general categories of biogeochemical cycles:

1. Elements such as carbon, oxygen, sulfur, and nitrogen have gaseous forms, thus, their cycles are global in character and the atmosphere serves as a reservoir.
2. Elements less mobile in the environment like phosphorus, potassium, calcium and trace elements generally cycle on a more localized scale over the short term. The soil serves as the main reservoir for these elements.

A general scheme of nutrient cycling includes the four main reservoirs of elements and the processes that transfer elements between reservoirs (see Campbell, Figure 54.8).

Reservoirs are defined by two characteristics: whether they contain organic or inorganic materials; and whether or not the materials are directly available for use by organisms.

- The available organic reservoir contains the living organisms and detritus.
  - The nutrients are readily available when consumers feed on one another and when detritivores eat nonliving organic matter..
- The unavailable organic reservoir is comprised of coal, oil, and peat which formed from organisms that died and were buried millions of years ago.
  - These nutrients cannot be directly assimilated.
- The available inorganic reservoir includes all matter (elements and compounds) present in the soil or air and those dissolved in water.
  - Organisms can directly assimilate these nutrients from the soil, air, or water.
- The unavailable inorganic reservoir contains nutrients tied up in limestone and minerals of other rocks.
  - These nutrients cannot be assimilated until released by weathering or erosion.

Various processes are involved in the transfer of nutrients between the four reservoirs which form the basis for biogeochemical cycling. The general schemes were determined by adding small amounts of radioactive tracers to systems in order to follow the movement of elements.

- Weathering and erosion are the primary processes which move nutrients from the unavailable inorganic reservoir to the available inorganic reservoir.
- Erosion is also important, along with the burning of fossil fuels, in moving nutrients from the unavailable organic reservoir to the available inorganic reservoir.
- Nutrients are transferred from the available organic reservoir to the unavailable organic reservoir only by the covering of detritus by sediments and its eventual fossilization to oil, coal, or peat.
- Sedimentary rock formation is the process which moves nutrients from the available inorganic reservoir to the unavailable inorganic reservoir.
- Nutrients enter the available organic reservoir from the available inorganic reservoir through photosynthesis and assimilation by living organisms.
- Nutrients are transferred from the available organic reservoir to the available inorganic reservoir by respiration, decomposition, excretion, and leaching.

The cycling of materials through an ecosystem depends on both biological and geological processes.

1. The water cycle

The essential nature of water to living organisms has many facets:

- It is essential to maintaining homeostasis in every organism.
- It contributes to the fitness of the environment.
- Its movement within and between ecosystems transfers other materials in several biogeochemical cycles.

Most of the water cycle occurs between the oceans and the atmosphere (see Campbell, Figure 54.9).

- Solar energy results in evaporation from the oceans.
- Water vapor rises, cools, and falls as precipitation.
- Over the oceans, evaporation exceeds precipitation; the excess water vapor is moved onto land by winds.
- Precipitation exceeds evaporation and transpiration over land; runoff and ground water balance the net flow of water vapor to land.

The water cycle differs from other cycles in that it occurs primarily due to physical processes, not chemical processes.

2. The carbon cycle

In the carbon cycle, photosynthesis and cellular respiration form a link between the atmosphere and terrestrial environments (see Campbell, Figure 54.10).

- During the carbon cycle, autotrophs acquire carbon dioxide (CO_2) from the atmosphere by diffusion through leaf stomata, incorporating it into their biomass. Some of this becomes a carbon source for consumers, and respiration returns CO_2 to the atmosphere.

Carbon recycles relatively quickly. Plants have a high demand for CO_2, yet CO_2 is present in the atmosphere at a low concentration (0.03%).

- Carbon loss by photosynthesis is balanced by carbon release during respiration.

Some carbon is diverted from cycling for longer periods of time, as when it accumulates in wood or other durable organic material.

- Decomposition eventually recycles this carbon to the atmosphere.
- Can be diverted for millions of years, such as in the formation of coal and petroleum.

The amount of atmospheric CO_2 decreases in the Northern Hemisphere in summer due to increased photosynthetic activity.

- Amounts increase in the winter when respiration exceeds photosynthesis.

Atmospheric CO_2 is increased by combustion of fossil fuels by humans, disturbing the balance.

In aquatic environments photosynthesis and respiration are also important but carbon cycling is more complex due to interaction of CO_2 with water and limestone.

- Dissolved CO_2 reacts with water to form carbonic acid, which reacts with limestone to form bicarbonates and carbonate ions.
- As CO_2 is used in photosynthesis, bicarbonates convert back to CO_2; thus bicarbonates serve as a CO_2 reservoir and some aquatic autotrophs can use dissolved bicarbonates directly as a carbon source.
- The ocean contains about 50 times the amount of carbon (in various inorganic forms) as is available in the atmosphere. The ocean may act as a buffer to absorb excess CO_2.

3. The nitrogen cycle

Nitrogen is a key chemical in ecosystems as it is found in all amino acids which comprise the proteins of organisms.

Although the Earth's atmosphere is almost 80% N_2, it is unavailable to plants since they cannot assimilate this form.

- Nitrogen is available to plants in only two forms: ammonium (NH_4^+) and nitrate (NO_3)

Nitrogen enters ecosystems by either atmospheric deposition or nitrogen fixation.

Atmospheric deposition accounts for only 5 to 10% of the usable nitrogen that enters an ecosystem.

- NH_4^+ and NO_3 are added to the soil by being dissolved in rain or by settling as part of fine dust or other particulates.
- Some plants (epiphytic bromeliads) in the canopy of tropical rain forests have aerial roots that can take up NH_4^+ and NO_3^- from the atmosphere.

Nitrogen fixation is the reduction of atmospheric nitrogen (N_2) to ammonia (NH_3), which can be used to synthesize nitrogenous organic compounds such as amino acids.

- Only certain prokaryotes can fix nitrogen (see Campbell, Figure 54.11).
  - In terrestrial ecosystems some nonsymbiotic soil bacteria and some symbiotic *(Rhizobium)* bacteria fix nitrogen.
  - Cyanobacteria fix nitrogen in aquatic ecosystems.
  - Nitrogen fixing prokaryotes are fulfilling their own metabolic needs, but other organisms benefit since excess ammonia is released into the soil or water.
  - Industrial fixation in the form of fertilizer makes significant contributions to the nitrogen pool in agricultural regions.
- The slightly acidic nature of soil results in NH_3 being protonated to ammonium (NH_4^+).
  - NH_3 is a gas and can evaporate quickly to the atmosphere.
  - NH_4^+ can be used directly by plants.

The nitrogen cycle involves three processes in addition to nitrogen fixation: nitrification, denitrification, and ammonification (see Campbell, Figure 54.11).

1. *Nitrification is* a metabolic process by which certain aerobic soil bacteria use ammonium (NH_4^+) as an energy source by first oxidizing it to nitrite (NO_2^-) and then to nitrate (NO_3^-).
   - While plants can use NH_4^+ directly, the nitrifying bacteria use most of the available NH_4^+ as an energy source.
   - Plants assimilate the NO_3^- released from these bacteria and convert it to organic forms, such as amino acids and proteins.
   - Animals can only assimilate organic nitrogen which they obtain by eating plants and other animals.
2. *Denitrification* occurs when bacteria obtain the oxygen necessary for their metabolism from NO_3^- rather than O_2 under anaerobic conditions. This process returns nitrogen to the atmosphere by converting NO_3^- to N_2.
3. *Ammonification is* the decomposition of organic nitrogen back into ammonium.
   - Carried out mainly by decomposer bacteria and fungi
   - Process is especially important because it recycles large amounts of nitrogen to the soil

Some important aspects of the nitrogen cycle to remember include

- Prokaryotes serve as vital links at several points in the cycle.
- Most of the nitrogen cycling involves nitrogenous compounds in the soil and water.

- While atmospheric nitrogen is plentiful, nitrogen fixation contributes only a small fraction of the nitrogen assimilated by plants; however, many species of plants depend on symbiotic, nitrogen-fixing bacteria in their root nodules as a source of nitrogen in a form that can be assimilated.
- Denitrification returns only a small amount of N_2 to the atmosphere.
- Most assimilated nitrogen comes from nitrate, which is efficiently recycled from organic forms by ammonification and nitrification.
- The majority of nitrogen in most ecosystems is recycled locally by decomposition and reassimilation, although nitrogen exchange between the soil and atmosphere are of long-term importance.

4. The phosphorus cycle

Phosphorus is a major component of nucleic acids, phospholipids, ATP, and a mineral in bones and teeth.

The phosphorus cycle is relatively simple since it does not have a gaseous form and it occurs in only one important inorganic form, phosphate.

Phosphorus cycles locally as follows (see Campbell, Figure 54.12):

- Weathering of rock adds phosphate to the soil.
- Producers absorb the soil phosphate and incorporate it into molecules. Phosphorus is transferred to consumers in organic form.
- Phosphorus is added back to the soil by excretion by animals and by decomposition of detritus by decomposers.
- Phosphorus cycling is localized since humus and soil particles bind phosphate.
    - Some leaching does occur and phosphate is lost to the oceans through the water table.
    - Weathering of rocks keeps pace so terrestrial systems are not depleted.
    - Phosphate that reaches the oceans accumulates in sediments and becomes incorporated into rocks which may eventually be exposed to weathering.

Phosphorus may limit algal productivity in aquatic habitats.

- Production in these habitats is stimulated by the introduction of phosphorus in the form of sewage or runoff from fertilized agricultural areas.

B. Decomposition rates largely determine the rates of nutrient cycling

The rate of decomposition has a great impact on the timetable for nutrient cycling.

- The rate of decomposition (and thus nutrient cycling) is affected by water availability, oxygen, and temperature.
- Decomposition of organic material in the tropical forests usually occurs in a few months to a few years.
- It takes an average of four to six years for decomposition to occur in temperate forests.
- Decomposition in the tundra may take 50 years.
- In aquatic ecosystems, where most decomposition occurs in anaerobic bottom muds, decomposition may occur even more slowly than in the tundra.

Soil chemistry and the frequency of fires also influence nutrient cycling times.

Some key nutrients are present in the soil of tropical rain forests in levels much lower than those found in temperate forests. Several conditions influence this paradox:

- There is rapid decomposition in tropical areas due to warm temperature and abundant water.

- The large biomass of tropical rain forests creates a high demand for nutrients, which are absorbed as soon as they become available through the action of decomposers.
  - About 10% of the nutrients are in the soil; 75% are present in the woody parts of trees.
- Relatively little organic material accumulates as litter due to the rapid decomposition.
- The low nutrient content of the soil results from the rapid cycling time.

The soil in temperate forests may contain 50% of all organic material in the ecosystem.

- The rate of decomposition is slow.
- The nutrients present in detritus and soil may stay there for long periods before being assimilated.

The sediments of aquatic systems form a nutrient sink and there must be an interchange between the bottom layers of water and the surface for the ecosystem to be productive.

- The rate of decomposition in the sediments is very slow.
- Algae and aquatic plants usually assimilate their nutrients directly from the water.

C. Field experiments reveal how vegetation regulates chemical cycling: *science as a process*

Long-term ecological research (LTER) is being used to examine the dynamics of many natural ecosystems over relatively long periods of time.

Since 1963, scientists have been studying nutrient cycling in a forest ecosystem under natural conditions and after vegetation is removed. The study site is the Hubbard Brook Experiment Forest in New Hampshire.

- The team first determined mineral budgets of six valleys by measuring inflow and outflow of several key nutrients.
- Rainwater was collected to measure amounts of water and dissolved minerals added to the ecosystem.
- Water and mineral loss were monitored by using small concrete dams with a V-shaped spillway across the creek at the bottom of each valley (see Campbell, Figure 54.14).
- Scientists found that 60% of the water added by rainfall exits through streams and 40% | is lost by plant transpiration and evaporation from soil.
- They also found that mineral inflow and outflow were nearly balanced and were small compared to minerals being recycled within the forest ecosystem.
  - Only about 0.3% more Ca^{++} exited a valley through its creek than was added by rainwater. Net mineral losses were probably replaced by chemical decomposition of bedrock.
  - During most years, some net gains of a few mineral nutrients occurred.

In 1966, after logging an experimental area and preventing reforestation, comparisons were made over a three-year period.

- Water runoff increased by 30 to 40% (no plants were left to absorb and transpire water).
- Net losses of minerals were very large:
  - Nitrate loss increased 60-fold (water nitrate levels made the water unsafe for drinking).
  - Calcium loss increased 400%
  - Potassium loss increased 1500%.

The study demonstrated the importance of plants in retaining nutrients within an ecosystem and the effects of human intrusion into a system.

- None of the watersheds was undisturbed by human activity even when the study began. Acid precipitation has leached most of the Ca^{2+} from forest soil, resulting in increased levels of Ca^{2+} in stream water. By the 1990s, the forest plants stopped adding new growth, apparently due to the lack of Ca^{2+}.

IV. Human Impacts on Ecosystems

The ever increasing human population has intruded into the dynamics of most ecosystems through human activities or technology.

- Some natural systems are totally destroyed while others have had major components (trophic structure, energy flow, chemical cycling) disrupted.
- Most effects are local or regional, while others are global in scale (e.g., acid rain).

A.The human population is disrupting chemical cycles throughout the biosphere

Human activity often removes nutrients from one part of the biosphere and adds them to another.

- May deplete one area of key nutrients while creating an excess in another area
- These occurrences disrupt the natural equilibrium of chemical cycles in both areas.

Farming exhausts the natural store of nutrients as crop biomass is removed from an area, this greatly reduces the amount of nutrients recycled. Supplements must then be added in the form of fertilizer.

- Nutrients in crops soon appear in human and livestock wastes, and then turn up in lakes and streams through sewage discharge and field run-off.
- Once in aquatic systems, these nutrients may stimulate excessive algal growth which degrades the system.
- Consequently, disruptions can flow from one system to another.

1. Agricultural effects on nutrient cycling

As the human population has continued to grow, greater demands for production of food has resulted in natural habitats being converted to agricultural use. This has resulted in:

- Intrusions into the cycling of nutrients
- Overharvesting of natural populations of food species
- Introductions of toxic compounds into ecosystems in the form of pesticides.

After natural vegetation is cleared from an area, the time period during which no additional nutrients need to be added to new agricultural ecosystems varies greatly.

- Nutrient reserves in the soil will support crops for some time after the natural vegetation has been removed.
- These nutrients are not recycled locally since they system as crop biomass.
- Some new farmlands in the tropics can be farmed for only one or two years.
  - Remember, in the tropical rain forests only about 10% of the nutrients are in the soil.
- In temperate areas, crops may be grown for many years due to the nutrients present in the soil.
- When nutrients are added, it is normally in the form of industrially synthesized fertilizers.

The nitrogen cycle of an area is greatly impacted by agriculture.

- Breaking up and mixing the soil increase the rate of decomposition of organic matter.
- This releases usable nitrogen, which is taken up by the crop and exported from the system at harvest.
- Nitrates remaining in the soil are quickly leached out of the system.
- Fertilizers are applied to replace the lost nitrogen.
    - Human activities have approximately doubled the Earth's supply of fixed nitrogen.
    - Excess nitrogen in fertilizers leaches into the water table.
    - Increased nitrogen fixation is also associated with a greater release of nitrogen compounds into the air by denitrifiers.
        - Nitrogen oxides can contribute to atmospheric warming, to the depletion of atmospheric ozone, or to acid precipitation.
        - Excess algal and bacterial growth typically results from an overabundance of nitrogen entering surface waters.

2. Accelerated eutrophication of lakes

Lakes are classified on a scale of increasing nutrient availability as oligotrophic, mesotrophic, or eutrophic.

- Oligotrophic lakes have low primary productivity because mineral nutrient levels will not support large phytoplankton populations.
- In other lakes, basic and watershed characteristics cause the addition of more nutrients that are captured by the primary producers and continuously recycled through the lake's food webs.
- Overall productivity is higher in mesotrophic lakes and highest in eutrophic ones.

Sewage, factory wastes, livestock runoff, and fertilizer leaching increases inorganic nutrient levels in waters and results in cultural eutrophication.

- This enrichment often results in explosive growth of photosynthetic organisms.
    - Large algal blooms occur; shallow areas become choked with weeds.
- As these producers die, metabolism of detritivores consumes all the oxygen in the water and many species die.

B. Toxins can become concentrated in successive levels of food webs

A variety of toxic chemicals, including unnatural synthetics, are dumped into ecosystems.

- Many cannot be degraded by microbes and persist for years or decades.
- Some are harmless when released but are converted to toxic poisons by reactions with other substances or by the metabolism of microbes (e.g., conversion of mercury to methyl mercury).

Organisms acquire toxic substances along with nutrients or water, some are metabolized and excreted wile others accumulate in their tissues (e.g., DDT, PCBs).

Biological magnification = Process by toxins become more concentrated with each successive trophic level of a food web; results from biomass at each trophic level being produced from a much larger biomass ingested from the level below.

- Top level carnivores are usually most severely affected by toxic compounds released into the environment.

The pesticide DDT is a well known example of biological magnification (see Campbell, Figure 54.1 6).

- It is used to control mosquitoes and agricultural pests.
- DDT persists in the environment and is transported by water to areas away from the point of application.
- It is lipid-soluble and collects in fatty tissues of animals.
- One of the first signs that DDT was a serious environmental problem was the decline in bird populations that feed at the top of food chains.
  - Reproductive rates declined dramatically because DDT interfered with the deposition of calcium in eggshells and the weight of nesting birds broke the weakened shells.
- DDT use was banned in the United States in 1971 and the affected bird populations have recovered.
- The use of DDT still continues in other parts of the world.

C. Human activities are causing fundamental changes in the composition of the atmosphere

Human activities have resulted in the release of many gaseous waste products into the atmosphere.

One problem directly related to nutrient cycling is the rising levels of carbon dioxide.

1. Carbon dioxide emissions and the greenhouse effect

Carbon dioxide emissions have caused atmospheric CO_2 concentrations to increase 14% since 1958. This increase is due to combustion of fossil fuels and burning of wood removed by deforestation.

Some effects of increased carbon dioxide levels might appear to be beneficial while others are definitely detrimental.

- Increased productivity by vegetation would occur with increased CO_2.
  - C_3 plants are more limited than C_4 plants by CO_2, so spread of C_3 species into habitats previously favoring C_4 species may have important natural and agricultural implications.
- Temperature increases with increased CO_2 concentration since CO_2 and water vapor absorb infrared radiation and slows its escape from Earth.
  - Called the greenhouse effect
  - A number of studies predict a doubling of CO_2 by the end of the 21st century and an associated average temperature increase of about 2°C above that in 1990.
  - Scientists are predicting a variety of scenarios based on the global warming trend.
    - Some predict warming near the poles will result in melting of polar ice and flooding of current coastal areas.
    - A warming trend would probably alter geographical distribution of precipitation, which could have major agricultural implications.
  - Ecologists are studying the records of pollen cores to determine how past temperature changes have affected vegetation.

2. Depletion of atmospheric ozone

Depletion of atmospheric ozone weakens a protective layer in the stratosphere that absorbs ultraviolet radiation.

- Much of the ultraviolet radiation is absorbed by an ozone layer 17 to 25 km above the Earth's surface.

- Destruction of the ozone layer is largely due to accumulation of chlorofluorocarbons used as aerosol propellants and in refrigeration.
- Breakdown products of chlorofluorocarbons include chlorine which rises to the stratosphere where it reacts with ozone (O_3) and reduces it to atmospheric oxygen (O_2).
    - The chlorine is released in other reactions and reacts with additional ozone molecules.
- Ozone depletion is best documented over Antarctica but levels in the middle latitudes have decreased 2% – 10% in the last 20 years.

Ozone depletion could have serious consequences.

- Increases are expected in lethal and nonlethal forms of skin cancer and cataracts among humans.
- Unpredictable effects on crops and natural communities (especially phytoplankton) are expected.

D. The exploding human population is altering habitats and reducing biodiversity worldwide

The growth of human populations, human activities, and our technological capabilities have disrupted the trophic structure, energy flow, and chemical cycling of ecosystems in most areas of the world.

Some effects are local while others affect the biosphere's distribution and diversity of organisms.

The destruction of natural systems due to human encroachment has resulted in only a small proportion of natural, undisturbed habitat remaining in existence.

- Only 15% of the original primary forest and just 1% of original tallgrass prairie remain in the United States.
- Tropical rainforests are being cut at a rate of 500,000 km^2 per year and will be eliminated in a couple of decades.
- Human activities that disrupt entire systems include development, logging, war, and oil spills.

One result of the destruction of natural habitat will be the loss of biodiversity.

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CHAPTER 55

CONSERVATION BIOLOGY

OUTLINE

I. The Biodiversity Crisis: An Overview
   - A. Numerous examples indicate that estimates of extinction rates are on track
   - B. The major threats to biodiversity are habitat destruction, over-exploitation, and competition by exotic species
   - C. Biodiversity is vital to human welfare
   - D. Change in ecological and evolutionary time is the focus of conservation biology

II. The Geographic Distribution of Biodiversity
   - A. Gradual variation in biodiversity correlates with geographical gradients
   - B. Biodiversity hot spots have high concentrations of endemic species
   - C. Migratory species present special problems in conservation

III. Conservation at the Population and Species Levels
   - A. Sustaining genetic diversity and the environmental arena for evolution is an ultimate goal
   - B. The dynamics of subdivided populations apply to problems caused by habitat fragmentation
   - C. Population viability analyses examine the chances of a species persisting or becoming extinct in the habitats available to it
   - D. Analyzing the viability of selected species may help sustain other species: *science as a process*
   - E. Conserving species involves weighing conflicting demands

IV. Conservation at the Community, Ecosystem and Landscape Levels
   - A. Edges and corridors can strongly influence landscape biodiversity
   - B. Nature reserves must be functional parts of landscapes
   - C. Restoring degraded areas is an increasingly important conservation effort
   - D. Sustaining development goals are reorienting ecological research and will require changing some human values

OBJECTIVES

After reading the text and attending lecture, the student should be able to do the following:

1. List the major threats to biodiversity and give example of each.
2. Describe why biodiversity is important to humans.
3. Describe the three concepts upon which the field of biodiverstiy emerged.
4. Describe the goal of conservation biology.
5. Describe how biodiversity is distributed.
6. Define the term, "biodiversity hot spot."

7. Describe the problems presented to conservation by migratory species
8. Describe how the biodiversity crisis extends throughout the hierarchy of biological organization.
9. Describe how habitat fragmentation affects population dynamics.
10. Define "source habitat" and "sink habitat" and discuss how these terms relation to conservation efforts.
11. Describe how population viability analysis as well as estimates of minimum viability size and effective population size are used to evaluate the chances of a species persisting or becoming extinct.
12. Give examples of how predictive models are being used in conservation efforts.
13. Describe the conflicting demands that arise in conservation management plans.
14. Describe how edges and corridors influence landscape biodiversity.
15. Discuss why nature reserves are important to preserving biodiversity and why conservation efforts will involve working in landscapes dominated by humans.
16. Describe why restoring degraded areas is an important part of conservation biology an how bioremediation and augmentation play a role in restoration efforts.
17. Describe how sustainable development goals are reorienting ecological research and will require changes some human values.

KEY TERMS

conservation biology	endangered species	population size	restoration ecology
biodiversity crisis	threatened species	minimum dynamic area	bioremediation
source habitat	metapopulation	effective population size	sustainable development
sink habitat	population viability	landscape ecology	Sustainable Biosphere
biodiversity hot spot	analysis	movement corridor	Initiative
endemic species	minimum viable	zoned reserve systems	

LECTURE NOTES

The planet is populated with a vast richness of living organism—so vast that we have only cataloged a minority of the species that exist. Unfortunately, we are altering ecosystems and ecosystem process to an extent that we are accelerating the extinction of species, creating a *biodiversity crisis. Conservation biology*, a recently conceived subdiscipline of biology, is dedicated to countering the biodiversity crisis.

I. The Biodiversity Crisis: An Overview

Extinction is a natural phenomenon, but it is the current *rate* of extinction that underlies the biodiversity crisis.

The high rate of ecosystem degradation is being causes by one species—*Homo sapiens*.

A. Numerous examples indicate that estimates of extinction rates are on track

Extinction rates are usually expressed as the number or percentage of species expected to become extinct in an area in a unit of time.

Estimates are difficult at best.

Since birds are among the most studied animals, the extinction rates for less well-known, nonavian taxa are sometimes based on the rate of loss of bird species.

Most often, extinction rates are estimated from the concept of species-area relations in which the number of species in an area is directly related to the size of the area.

- This rule predicts that, on average, about 50% of the total number of species will be lost in an area where 90% of the habitat is lost.

The absence of clear documentation of the rate of extinction has led some to argue that there is no reason to worry at this time. Population census data, however, indicate that extinction of known organisms is occurring at an alarming rate..

- 11% of the 9040 known species of bird are endangered
- 680 of the ca. 20,000 known plant species are in danger of becoming extinct by the year 2000
- Approximately 20% of the known species of freshwater fish have become extinct or have become threatened during recorded history.

In order to know for certain that a given species is extinct, we must know its exact distribution and habits. However, we do not have a complete catalogue of biodiversity and knowledge of the geographic distribution and ecological roles of Earth's species, thus, our understanding remains incomplete.

B. The major threats to biodiversity are habitat destruction, over-exploitation, and competition by exotic species

The most significant threat to biodiversity is human alteration of habitat. Human activities which disrupt entire systems include development, logging, war, and oil spills

- 73% of the IUCN's designations of extinct, endangered, vulnerable, and rare species are related to destruction of natural habitats.
- Marine biodiversity also is threatened by human activity. About 93 % of the coral reefs (reefs are estimated to support about 1/3 of the known species of fish) have been damaged, if the current rate of destruction continues, 40% to 50 % of the reefs could be lost within 30 to 40 years.

Overexploitation of wildlife by humans is another source of threat.

- Species threatened by excessive commercial harvest or sport hunting include whales, American bison, Galapagos tortoises, and numerous fishes.
- The often illegal trade of rare animals and animal products also jeopardizes many species.

The introduction of exotic species can cause a variety of problems. Although most transplanted species fail to survive, there are notable exceptions.

- The introduction of Nile perch into Lake Victoria in east Africa has resulted in the loss of 200 of 300 species of chichlids (see Campbell, Figure 55.1).
- Fire ants, which were accidentally introduced into the southern United States from Brazil in 1918, have continued to spread northward (see Campbell, Figure 55.2).
- Displacement by introduced species is considered at least partially responsible for 68% of the IUCN's listings of extinct, endangered, vulnerable, and rare species.

C. Biodiversity is vital to human welfare

Why should we care about the loss of biodiversity?

Answers to this question range from general to specific:

- *Biophilia,* the human sense of connection to nature and other forms of life, is centered around aesthetics and ethics.
- Biodiversity is a crucial natural resource and threatened species could provide crops, fibers, and medicines.
    - 25% of the prescriptions dispensed from pharmacies in the United States contain substances derived from plants.

   - In the 1970s, alkaloids isolated from the rose periwinkle of Madagascar were found to inhibit cancer cell growth and result in remission of childhood leukemia and Hodgkin's disease.
- The loss of species results in the loss of genes and all the genetic potential.
- Humans are dependent on ecosystems and other species. By allowing the extinction of species and degradation of habitats to continue, we are taking a risk with our own species survival.

In an effort to influence policy-making, ecologists and economists have estimated the cost of replacing ecosystem "services" as a measure of the services' value at US$33 trillion.

D. Change in ecological and evolutionary time is the focus of conservation biology

Globally, an area half the size of the U.S. has been protected as natural areas (about 3% of the plant's land surface).

Three concepts form the roots of conservation biology

1. *Preservation is* the practice of setting aside select areas to remain natural and undeveloped.
2. *Resource conservation is* a management scheme aimed at balancing "multiple uses" of natural resources (e.g., agricultural, industrial, preservation, recreation)
3. *Evolutionary/ecological view* recognizes that natural systems are the result of millions of years of evolution and that ecosystems processes are critical for the maintenance and proper function of the biosphere.

The goal of conservation biology is preserve individuals species *and* to sustain ecosystems, where natural selection can continue to function and to maintain the genetic variability upon which it acts.

- Conservation biology follows the ecological tenets of nonequilibrium discussed in Chapter 53 and recognizes that disturbance is a natural force.
- Consideration of human presence is vital in conservation biology because no ecosystems are unaffected by humans. Conservation biology seeks to foster human activities that sustain ecosystems and reduce the current rate of environmental degradation.

II. The Geographic Distribution of Biodiversity

Biodiversity is not evenly distributed and there are recognizable patterns of distribution, including clines (gradual variation), hot spots, concentrations of diversity, and ranges of migratory species.

A. A gradual variation in biodiversity correlates with geographical gradients

Biogeographers have long recognized the existence of clines in species diversity in the form of major geographical gradients.

- The number of terrestrial bird species in North and Central America increases steadily from the Arctic to the tropics (see Campbell, Figure 55.4).
- The number of marine benthic species increases with depth.

Four hypotheses have been developed to explain clines, and more generally, the factors that influence patterns of diversity in all communities.

1. *Energy availability.* Holds that because solar radiation is greatest in the tropics, the resource base is greatest there.
2. *Habitat heterogeneity.* Holds that tropical regions experience more local disturbances that contribute to greater environmental patchiness; the greater patchiness allows a greater diversity of plants species to form a resource base for diverse communities of animals.

3. *Niche specialization.* Holds that the stability and predictability of tropical climate may allow organisms to specialize on a narrower range of resources; smaller niches would reduce competition and contribute to greater species diversity.
4. *Population interactions.* Holds that diversity is self-propagating because population interactions coevolve, and the resulting predator-prey and symbiotic interactions in a diverse community prevent any populations from becoming dominant.

Many ecologist believe that a complex combination of factors is responsible for clines.

B. Biodiversity hot spots have high concentrations of endemic species

Biodiversity hot spot = Relatively small areas with exceptional concentrations of species

Endemic species = A species found nowhere else

Biogeographers have identified 18 vascular plant hot spots (see Campbell, Figure 55.5).

- These hot spots contain about 20% of the known vascular plant species and 7% of all land vertebrate species.
- Six of the 18 hot spots have lost close to 90% of their original habitats to human development; as a result, the biodiversity hot spots also are hot spots of extinction.

Islands are hot spots of bird extinction.

- 30% of all bird species are endemic.
- Approximately 90% of the 104 species of birds lost in the last 400 years were endemic on islands
- Today, all of the areas where over 10% of the bird species are threatened with extinction are islands (e.g., Hawaii, Philippines, New Zealand).
- It seems likely that most of the non-avian threatened species also are endemic on islands.

In the U.S., most of the endangered species are found in the areas with the most endemic species: Hawaii, southern California, southern Appalachians, southeastern coastal states. Most of these species are threatened because of loss of habitat due to human population growth and agriculture.

Studies of biodiversity and recent extinctions show that many threatened, endangered, and potentially endangered species are concentrated in biodiversity hot spots.

- This pattern suggests that with appropriate measures, many species could be saved in relatively small areas.
- The biodiversity crisis is a global problem and focus on hot spots should not detract form efforts to preserve biodiversity in other areas.

C. Migratory species present special problems in conservation

The preservation of migratory species is complicated by a life history that involves residence in multiple jurisdictions.

- Monarch butterflies, for example, migrate from Canada to Mexico (see Campbell, Figure 55.6). Human intrusion is making the migration an "endangered phenomenon."
- Similar situations exist for migratory songbirds, sea turtles, and marine mammals.

Successful conservation efforts for such species require international cooperation and the careful preservation of habitat in both parts of the species' range.

III. Conservation at the Population and Species Level

Much of the attention of the biodiversity crisis has focused on species.

Endangered species are species that are in danger of extinction in all or a significant portion of its range

Threatened species are species that are likely to become endangered in the foreseeable future throughout all or a significant portion of its range.

A. Sustaining genetic diversity and the environmental arena for evolution is an ultimate goal

Species are only one component of earth's biodiversity. Other components include:

- Genetic variability within populations of species
- Myriad biotic and abiotic factors that provide the arena for evolution

Modern conservation science attempts to concentrate more on sustaining ecosystem processes and the evolutionary lineages that species represent than on conserving individual species.

Alteration of ecosystems by human activities already makes it impractical to conserve all the genetic diversity within most species.

Conservation biology has focused on understanding the dynamics of small populations, diagnosing declines, assessing the factors responsible for a population's decline, and determining how to revise declines and sustain small, often fragmented populations.

- Currently, conservation efforts lag far behind the rate of decline and loss of species.
- Many species are at critically low numbers and the strategy has mainly been to reverse the trend.
- Conservation biologists also use some features of crisis management and apply some untested hypotheses and concepts.

B. The dynamics of subdivided populations apply to problems caused by habitat fragmentation

Degradation of habitats often leads reduction in the area of suitable habitat as well as to fragmentation of the remaining area (see Campbell, Figure 55.7).

- Some ecologists have likened fragmentation to islands surrounded by areas of human activity (see Campbell, Figure 53.21).
- The island model may be overly simplistic, and concepts developed by studying subdivided populations may prove to be more useful to conservation efforts.

Metapopulation = A subdivided population or a network of subpopulations of a species

- Vary greatly, depending on size, quality, spatial arrangement, and persistence of habitat patches

The subpopulations of a metpopulation are separated into habitat patches that vary in quality.

- Patches with abundant, high-quality resources tend to have persistent subpopulations that produce more offspring.
- Low-quality patches may be populated only when new individuals reared in high-quality patches disperse to them.
- Dispersal is essential to maintaining genetic variability within subpopulations; a subpopulation that is cut off from others may eventually become genetically extinct.

Human activity may impact population structure.

- Fragmentation may result in the conversion a population to a metapopulation with reduced genetic variability.

- Human encroachment on a metapopulation (e.g., loss or reduction of habitat patches; restriction of dispersal) may decrease the number, size, and or genetic variability of subpopulations.

1. The source and sink dynamics in metapopulations

Reproductive rates of metapopulations vary widely among habitat patches

- *A source habitat is* one where a population's reproductive success exceeds mortality.
- A *sink habitat is* one where a population's mortality exceeds reproductive success.

Distinguishing sources from sinks requires:

- Detailed analysis of birth rates and death rates
- Identification of factors that affect dispersal
- Identification of habitat factors that are critical to a species

Sustaining metapopulations created or altered by human habitat fragmentation requires the identification and protection of source habitats.

- For example, efforts to sustain the peregrine falcon population in California focused on stocking the wild subpopulation in southern California with captive-reared birds until it was discovered that southern California was a sink habitat. Efforts are now directed at the source habitat in northern California.

Understanding source and sink dynamics is also essential to designing the most effective nature reserves.

C. Population viability analyses examine the chances of a species persisting or becoming extinct in the habitats available to it

Population viability analysis (P VA) is a method of predicting whether or not a particular given will persist in a specific environment.

- It is generated by computer simulation.
- It integrates information about a population's genetic variability and life history (e.g., sex ratio, fecundity)
- It considers information of a population's response to environmental factors (e.g., predation, competition)
- It also considers potential effects of planned human activities (e.g., logging, mining

A PVA usually predicts long-term viability.

- Periodic natural disasters are factored in
- However, because threatened populations are small, their survival may depend on chance events.

The development of PVAs may be a multistep process

- An initial PVA may be developed to predict the viability of a population for a specific number of generations.
- More extensive PVAs may be developed following the initial prediction by further modeling and additional research.

1. Estimating minimum viable population size (MVP)

Most PVAs are designed to predict a species' *minimum viable population size (MVP),* the smallest number of individuals needed to propagate a population, subpopulation, or species.

- Prediction usually indicates a percent chance of survival and time span.
- MVP size varies widely.

    - Some populations of rare birds have remained viable with only 10 breeding pairs.
  - Estimates of MVP aid in predictions about the *minimum dynamic area,* the amount of suitable habitat needed to sustain a viable population.

2. Estimating effective population size

Meaningful MVP estimates require the determination of the *effective population size* (N_e).

  - N_e *is* based on the number of adults that successfully breed (contribute gametes to the next generation).
  - N_e *is* calculated by the following formula:
  - $N_e = (4N_m \times N_f) / (N_m + N_f)$

    where N_m and N_f are the numbers of males and female, respectively, that successfully breed.
  - Numerous life history traits can affect N_e; other formulas factor in family size, age at maturation, genetic relatedness among population members, the effects of gene flow between geographically separated populations, and population fluctuations.

3. The effect of genetic diversity on survivability

The management goal of sustaining effective population sizes, N_e, is based on the concern that populations should possess sufficient genetic diversity to be evolutionarily adaptable.

  - Populations with low N_e are prone to inbreeding, reduced heterozygosity, and the random effects of genetic drift and bottlenecking.
  - For many species (e.g., especially those that reproduce slowly, such as the cheetah and grizzly bear), however, low genetic variability appear normal.

Low genetic variability does not always lead to permanently small populations.

  - After intense hunting reduced the number of northern elephant seals to about 20 individuals, the population has rebounded to about 30,000.

Reduced genetic variability by itself may not be critical the survival of wild populations.

D. Analyzing the viability of selected species may help sustain other species: *science as a process*

Modeling requires extensive background research and time, thus only populations of relatively few threatened or endangered species will be systematically analyzed.

What we learn from the viability studies of one species may help us develop strategies to sustain other species.

Patrick Nantel's PVA of two species of edible herbaceous plants, American ginseng and wild leek, in Canada, exemplifies how predictive models can be used in planning conservation strategy (see Campbell, Figure 55.11).

- His data included trends in the numbers of individuals capable of reproducing in several populations for two-, three-, and four-year periods.
- Computer simulations projected the likely effect of environmental influences on these populations.
- The PVA indicated that most populations of these two species in Canada are too small to persist if harvested.

One of the first PVAs was part of a long-term study of grizzly bears in Yellowstone National Park (see Campbell, Figure 55.12).

- Grizzly bears require very large habitat sizes (e.g., in western Canada, a population of 50 individual requires 5 million hectares)

- In the U.S., the grizzly bear population is fragmented into 6 isolated subpopulations; most of the subpopulations have fewer than 100 individuals (the Yellowstone subpopulation numbers about 200).
- PVA models predicted that a grizzly bear population of 70 to 90 individuals in a suitable habitat have about a 95% chance of surviving for 100 years.
- The N_e of grizzly bear populations was estimated to be 25% of the total subpopulation size (e.g., 50 for the Yellowstone subpopulation).

E. Conserving species involves weighing conflicting demands

The determination of viable population numbers and habitat needs make up only part of the effort to save species.

Often, it is necessary to weight a species' needs against other conflicting demands.

- In the Pacific Northwest, for example, an ongoing debate exists over saving habitat for populations of spotted owl, timber wolf, grizzly bear, and bull trout versus demands for jobs in timber, mining, and other resource extraction industries.
- Habitat use is almost always at issue.

The magnitude of the biodiversity crisis raises practical considerations. Since we will not be able to save every endangered species, which ones are most important?

- Keystone species have disproportionately large impacts relative to their numbers. Identifying them and finding ways to sustain their populations can ensure the continuance of numerous other species and can be central to the survival of whole communities.

IV. Conservation at the Community, Ecosystem, and Landscape Levels

Today, conservation efforts are aimed at sustaining the biodiversity of entire communities and ecosystems. Some efforts are even directed at the broader level of landscapes, regional assemblages of interacting ecosystems (e.g., forest or forest patches, adjacent open fields, wetlands, streams)

Landscape ecology is the application of ecological principles to the study of land use patterns.

A. Edges and corridors can strongly influence landscape biodiversity

The boundaries or edges between and within ecosystems are the defining features of landscapes (see Campbell, Figure 55.13).

Edges have their own communities of organisms in association with their physical features; some organisms thrive in edge communities because they need resources from each of the adjacent ecosystems.

The proliferation of edge species can have either positive or negative effects on the biodiversity of the community.

- In the tropical rain forest of Cameroon, edge areas are important regions of speciation.
- In communities in which edges have expanded because of human alteration, however, there is often a reduction of biodiversity as a result of abundance of edge-adapted species (e.g., brown-headed cowbird takes over the nests of other birds).

Another important feature of landscapes, particularly in habitats that have been severely fragmented is a *movement corridor*, a strip or series of clumps of quality habitat that connect patches (e.g., streamside habitats often function as corridors, and in some areas where human alteration is significant, artificial corridors have been constructed).

- Corridors promote dispersal and help sustain metapopulations.

- In some instances, corridors can be detrimental (e.g., avenues for the spread of disease).

B. Nature reserves must be functional parts of landscapes

Terrestrial and aquatic parks as well as other wilderness and protected areas are important to the efforts of conservation biology.

- In some regions, protected sites are the sole habitat of endangered or threatened species.
- Protected reserves are subject to outside influences.

A preserve should be planned so as to be self-regulating and to allow natural disruption; policies to the contrary are counterproductive (e.g., preventing the spread of wildfires).

Consideration of patch dynamics, metapopulation dynamics, edges, and corridor effects in the design of management plans for protected areas is necessary because of ever increasing human-induced disturbance and fragmentation. Still, there are questions:

- *Is one large habitat better than a group of smaller ones?* The ultimate answers may be governed more by human land use patterns than on ecological considerations.
- Some countries use a *zoned reserve system* for landscape management (see Campbell, Figure 55.14). In such a system, the core preserve is surrounded by successive layers that increase in human alteration as distances increase from the core.

Projections estimate that less than 10% of the biosphere will ever be protected as nature reserves.

- Conservation measures must, therefore, be put to work in landscapes dominated by humans.

C. Restoring degraded areas is an increasingly important conservation effort

Some areas are damaged so badly by human activity that they are abandoned.

- Soils of tropical lands become unproductive quickly and are often abandoned with five years of being cleared for farming.
- Mining is a protracted human activity that can render an area unusable by wildlife for many years, even following cessation of the activity.
- Many ecosystems are damaged accidentally (e.g., oil spills).
- Because the natural rates of recovery are slower than the rate of human- induced degradation, the area of degraded habitats and ecosystems is increasing.

Restoration ecology applies ecological principles to find ways to restore degraded ecosystems as close to their original state as possible.

Two key approaches to restoration ecology are bioremediation and augmentation of ecosystem processes.

1. *Bioremediation* makes use of living organisms (e.g., prokaryotes, fungi) to detoxify a polluted ecosystem. For example, the bacterium *Pseudomonas* has been used to clean up oil spills on beaches.
2. Augmenting ecosystem processes is accomplished by supplying the critical components (e.g., nutrients) that have been identified to restrict the rate of recovery. For example, encouraging the growth of plants that perform well in nutrient-deficient soils can speed up succession and ultimately lead to the recovery of a damaged habitat.

D. Sustainable development goals are reorienting ecological research and will require changing some human values

In order to make informed decisions about how best to conserve the Earth's resources, it is necessary to understand the complex interactions of the biosphere.

Many countries have adopted the concept of *sustainable development*, a plan than provides for the long-term prosperity of human societies and the ecosystems that support them.

The goal of the *Sustainable Biosphere Initiative is* to acquire the basic ecological information needed for intelligent development, management, and conservation of the Earth's resources. This will include studies on:

- Global change, including interactions between climate and ecological processes
- Biological diversity and its role in maintaining ecological processes
- The ways in which productivity of natural and artificial ecosystems can be sustained

The nature of ecological research will have to be reoriented but the importance cannot be overstated due to the current state of the biosphere.

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