animal sciences

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VOLUME 2
Cret–Hab

Allan B. Cobb, Editor in Chief

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Preface

Six hundred million years of animal evolution and adaptation have produced a stunning range and variety of life on Earth. From the oldest, single-celled creatures to the most complex mammalian forms, animal diversity defies easy categorization or explanation. The Macmillan *Animal Sciences* encyclopedia provides a clear and comprehensive resource for better understanding this vast domain. By the nature of its interdisciplinary scope, the subject of animal sciences demands an approach that is both specific and general, detailed and thematic. *Animal Sciences* achieves this end in the course of nearly three hundred well-researched, clearly presented entries that explore the wide ranging diversity that exists within the animal kingdom.

Students will learn how animals develop throughout their lives, how they adapt to their changing environments, and how they develop specialized structures over time. Entries in this category explain how animals develop from fertilized eggs to adults. While some forms of development are straightforward—like a puppy maturing to become a dog—other changes are more dramatic—like a caterpillar changing its body forms over the course of its metamorphosis into a butterfly. Other entries study the various forms of animals and how body parts function.

The encyclopedia gives significant attention to animal ecology and behavior. Entries show how animals are part of the world environment while exhibiting unique behaviors within their own particular environments. Animal ecology addresses how animals are a part of ecosystems and how they interact with plants and other animals, both within and beyond their individual species. Given the close relationship of animal behavior and ecology, a number of entries discuss how animals select mates, whether they live alone or as members of groups, or how they share resources within an ecosystem, to give just a few examples.

Finally, *Animal Sciences* surveys the connection between animals and humans. Humans are unique in the animal kingdom because of their ability to alter environments significantly. Agriculture, which includes the domestication of animals and farming, serves as the chief example of such human-inspired environmental change and its impact on animal life worldwide. In addition, humans are the most social of animals and have developed complex social interactions. As human populations grow, habitat once occupied

by other animals is converted to human use. One consequence of such socialization is the pollution generated from an expanding human population and its deleterious effect on animal environments.

Animal Sciences also presents biographies of selected scientists who have made significant contributions to the many related fields, and introduces readers to the myriad career opportunities in the discipline.

The authors who contributed entries to *Animal Sciences* represent diverse backgrounds, and include members of academic and research institutions, as well as practicing scientists. The editorial board sought informative, up-to-date, and engaging articles, most of which include cross references, photographs or illustrations that prove helpful in understanding challenging concepts. A generous collection of sidebars accent related subjects. Every attempt has been made to avoid overly technical terms or scientific jargon, and whenever necessary such terms are highlighted and defined in the margin. Selected bibliographies guide readers to additional up-to-date resources, including those found on the Internet. Each of the four volumes also includes a geologic time scale, with particular emphasis on animals, as well as a phylogenetic tree and an alternative table of contents that groups articles under more general topic headings.

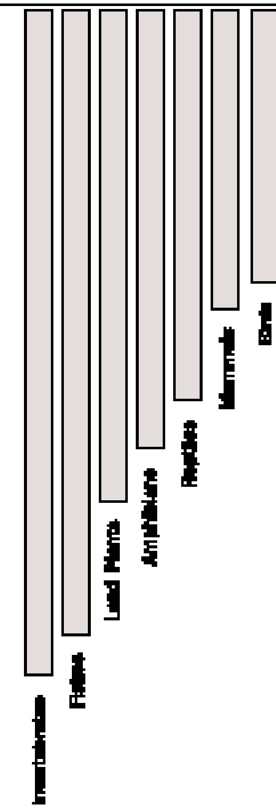
I wish to thank the staff at Macmillan Reference USA and the Gale Group for their hard work and attention to detail. In particular, I would like to thank Hélène Potter, Elly Dickason, Linda Hubbard, and Christa Brelin. I want to offer special thanks to Kate Millson for all her efforts and long hours in helping guide this project to fruition. I wish to thank the editorial board members—Amy Bryan, Andrew Gluesenkamp, and Marvin Elliot Richmond—for their vast knowledge and hard work. Finally, it is my hope that *Animal Sciences* can spark the interest of the next generation of committed scholars, researchers, and laypersons.

Allan B. Cobb
Editor in Chief

Geological Time Scale

Eon	Era	Period	Epoch	Significant Events	Million Years Before Present
Phanerozoic	Cenozoic	Quaternary	Holocene	recorded human history, rise and fall of civilizations, global warming, habitat destruction, pollution mass extinction	0.01
			Pleistocene	Homo sapiens, ice ages	1.6
		Tertiary	Pliocene	global cooling, savannahs, grazing mammals	5.3
			Miocene	global warming, grasslands, Chalicotherium	24
			Oligocene		37
			Eocene	modern mammals flourish, ungulates	58
			Paleocene		66
	Mesozoic	Cretaceous		last of age of dinosaurs, modern mammals appear, flowering plants, insects	144
		Jurassic		large plant-eating dinosaurs, carnivorous dinosaurs, first birds, breakup of Pangea	208
		Triassic		lycophytes, glossopterids, and dicynodonts, and the dinosaurs	245
	Paleozoic	Permian		Permian ends with largest mass extinction in history of Earth, most marine invertebrates extinct	286
		Pennsylvanian		vast coal swamps, evolution of amniote egg allowing exploitation of land	320
		Mississippian		shallow seas cover most of Earth	360
		Devonian		vascular plants, the first tetrapods, wingless insects, arachnids, brachiopods, corals, and ammonite were also common, many new kinds of fish appeared	408
		Silurian		Coral reefs, rapid spread of jawless fish, first freshwater fish, first fish with jaws, first good evidence of life on land, including relatives of spiders and centipedes	438
		Ordovician		most dry land collected into Gondwana, many marine invertebrates, including graptolites, trilobites, brachiopods, and the conodonts (early vertebrates), red and green algae, primitive fish, cephalopods, corals, crinoids, and gastropods, possibly first land plants	505
		Cambrian		most major groups of animals first appear, Cambrian explosion	570
Precambrian	Proterozoic			stable continents first appear, first abundant fossils of living organisms, mostly bacteria and archaeobacteria, first eukaryotes, first evidence of oxygen build-up	2500
	Archean			atmosphere of methane, ammonia, rocks and continental plates begin to form, oldest fossils consist of bacteria microfossils stromatolites, colonies of photosynthetic bacteria	3800
	Hadean			pre-geologic time, Earth in formation	4600

Time Range of Several Groups of Plants & Animals



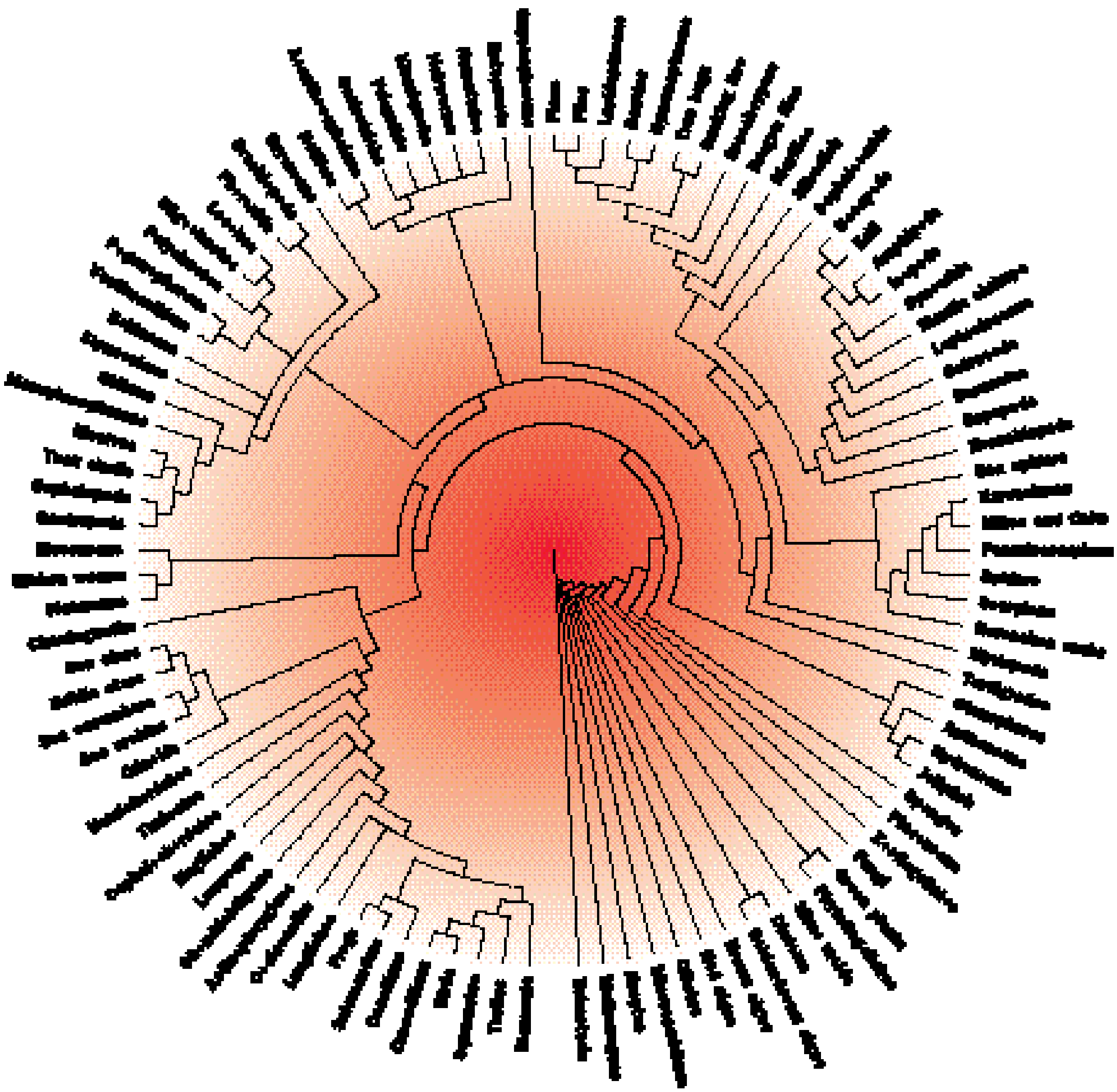
COMPARISON OF THE FIVE-KINGDOM AND SIX-KINGDOM CLASSIFICATION OF ORGANISMS

Five Kingdom	Six Kingdom
Kingdom: Monera Phylum: Bacteria Phylum: Blue-green algae (cyanobacteria)	Kingdom: Archaebacteria Kingdom: Eubacteria

- Kingdom: Protista
  - Phylum: Protozoans
    - Class: Ciliophora
    - Class: Mastigophora
    - Class: Sarcodina
    - Class: Sporozoa
  - Phylum: Euglenas
  - Phylum: Golden algae and diatoms
  - Phylum: Fire or golden brown algae
  - Phylum: Green algae
  - Phylum: Brown algae
  - Phylum: Red algae
  - Phylum: Slime molds
- Kingdom: Fungi
  - Phylum: Zygomycetes
  - Phylum: Ascomycetes
  - Phylum: Basidiomycetes
- Kingdom: Plants
  - Phylum: Mosses and liverworms
  - Phylum: Club mosses
  - Phylum: Horsetails
  - Phylum: Ferns
  - Phylum: Conifers
  - Phylum: Cone-bearing desert plants
  - Phylum: Cycads
  - Phylum: Ginko
  - Phylum: Flowering plants
    - Subphylum: Dicots (two seed leaves)
    - Subphylum: Monocots (single seed leaves)
- Kingdom: Animals
  - Phylum: Porifera
  - Phylum: Cnidaria
  - Phylum: Platyhelminthes
  - Phylum: Nematodes
  - Phylum: Rotifers
  - Phylum: Bryozoa
  - Phylum: Brachiopods
  - Phylum: Phoronida
  - Phylum: Annelids
  - Phylum: Mollusks
    - Class: Chitons
    - Class: Bivalves
    - Class: Scaphopoda
    - Class: Gastropods
    - Class: Cephalopods
  - Phylum: Arthropods
    - Class: Horseshoe crabs
    - Class: Crustaceans
    - Class: Arachnids
    - Class: Insects
    - Class: Millipedes and centipedes
  - Phylum: Echinoderms
  - Phylum: Hemichordata
  - Phylum: Cordates
    - Subphylum: Tunicates
    - Subphylum: Lancelets
    - Subphylum: Vertebrates
      - Class: Agnatha (lampreys)
      - Class: Sharks and rays
      - Class: Bony fishes
      - Class: Amphibians
      - Class: Reptiles
      - Class: Birds
      - Class: Mammals
        - Order: Monotremes
        - Order: Marsupials
        - Subclass: Placentals
          - Order: Insectivores
          - Order: Flying lemurs
          - Order: Bats
          - Order: Primates (including humans)
          - Order: Edentates
          - Order: Pangolins
          - Order: Lagomorphs
          - Order: Rodents
          - Order: Cetaceans
          - Order: Carnivores
          - Order: Seals and walruses
          - Order: Aardvark
          - Order: Elephants
          - Order: Hyraxes
          - Order: Sirenians
          - Order: Odd-toed ungulates
          - Order: Even-toed ungulates

PHYLOGENETIC TREE OF LIFE

This diagram represents the phylogenetic relationship of living organisms, and is sometimes called a "tree of life." Often, these diagrams are drawn as a traditional "tree" with "branches" that represent significant changes in the development of a line of organisms. This phylogenetic tree, however, is arranged in a circle to conserve space. The center of the circle represents the earliest form of life. The fewer the branches between the organism's name and the center of the diagram indicate that it is a "lower" or "simpler" organism. Likewise, an organism with more branches between its name and the center of the diagram indicates a "higher" or "more complex" organism. All of the organism names are written on the outside of the circle to reinforce the idea that all organisms are highly evolved forms of life.



SI BASE AND SUPPLEMENTARY UNIT NAMES AND SYMBOLS

Physical Quality	Name	Symbol
Length	meter	m
Mass	kilogram	kg
Time	second	s
Electric current	ampere	A
Thermodynamic temperature	kelvin	K
Amount of substance	mole	mol
Luminous intensity	candela	cd
Plane angle	radian	rad
Solid angle	steradian	sr

Temperature

Scientists commonly use the Celsius system. Although not recommended for scientific and technical use, earth scientists also use the familiar Fahrenheit temperature scale (°F). 1°F = 1.8°C or K. The triple point of H_2O, where gas, liquid, and solid water coexist, is 32°F.

- To change from Fahrenheit (F) to Celsius (C):
  °C = (°F-32)/(1.8)
- To change from Celsius (C) to Fahrenheit (F):
  °F = (°C x 1.8) + 32
- To change from Celsius (C) to Kelvin (K):
  K = °C + 273.15
- To change from Fahrenheit (F) to Kelvin (K):
  K = (°F-32)/(1.8) + 273.15

UNITS DERIVED FROM SI, WITH SPECIAL NAMES AND SYMBOLS

Derived Quantity	Name of SI Unit	Symbol for SI Unit	Expression in Terms of SI Base Units
Frequency	hertz	Hz	s-1
Force	newton	N	m kg s-2
Pressure, stress	Pascal	Pa	N m-2 =m-1 kg s-2
Energy, work, heat	Joule	J	N m =m2 kg s-2
Power, radiant flux	watt	W	J s-1 =m2 kg s-3
Electric charge	coulomb	C	A s
Electric potential, electromotive force	volt	V	J C-1 =m-2 kg s-3 A-1
Electric resistance	ohm	_	V A-1 =m2 kg s-3 A-2
Celsius temperature	degree Celsius	C	K
Luminous flux	lumen	lm	cd sr
Illuminance	lux	lx	cd sr m-2

UNITS USED WITH SI, WITH NAME, SYMBOL, AND VALUES IN SI UNITS

The following units, not part of the SI, will continue to be used in appropriate contexts (e.g., angtsrom):

Physical Quantity	Name of Unit	Symbol for Unit	Value in SI Units
Time	minute	min	60 s
	hour	h	3,600 s
	day	d	86,400 s
Plane angle	degree	°	(π/180) rad
	minute	'	(π/10,800) rad
	second	"	(π/648,000) rad
Length	angstrom	Å	10^{-10} m
Volume	liter	l, L	1 dm^3 = 10^{-3} m^3
Mass	ton	t	1 mg = 10^3 kg
	unified atomic mass unit	u (=m_a(^{12}C)/12)	≈1.66054 x 10^{-27} kg
Pressure	bar	bar	10^5 Pa = 10^5 N m^{-2}
Energy	electronvolt	eV (= e X V)	≈1.60218 x 10^{-19} J

CONVERSIONS FOR STANDARD, DERIVED, AND CUSTOMARY MEASUREMENTS

Length

1 angstrom (Å)	0.1 nanometer (exactly) 0.000000004 inch
1 centimeter (cm)	0.3937 inches
1 foot (ft)	0.3048 meter (exactly)
1 inch (in)	2.54 centimeters (exactly)
1 kilometer (km)	0.621 mile
1 meter (m)	39.37 inches 1.094 yards
1 mile (mi)	5,280 feet (exactly) 1.609 kilometers
1 astronomical unit (AU)	1.495979 x 10^{13} cm
1 parsec (pc)	206,264.806 AU 3.085678 x 10^{18} cm 3.261633 light-years
1 light-year	9.460530 x 10^{17} cm

Area

1 acre	43,560 square feet (exactly) 0.405 hectare
1 hectare	2.471 acres
1 square centimeter (cm^2)	0.155 square inch
1 square foot (ft^2)	929.030 square centimeters
1 square inch (in^2)	6.4516 square centimeters (exactly)
1 square kilometer (km^2)	247.104 acres 0.386 square mile
1 square meter (m^2)	1.196 square yards 10.764 square feet
1 square mile (mi^2)	258.999 hectares

MEASUREMENTS AND ABBREVIATIONS

Volume

1 barrel (bbl)*, liquid	31 to 42 gallons
1 cubic centimeter (cm^3)	0.061 cubic inch
1 cubic foot (ft^3)	7.481 gallons 28.316 cubic decimeters
1 cubic inch (in^3)	0.554 fluid ounce
1 dram, fluid (or liquid)	⅛ fluid ounce (exactly) 0.226 cubic inch 3.697 milliliters
1 gallon (gal) (U.S.)	231 cubic inches (exactly) 3.785 liters 128 U.S. fluid ounces (exactly)
1 gallon (gal) (British Imperial)	277.42 cubic inches 1.201 U.S. gallons 4.546 liters
1 liter	1 cubic decimeter (exactly) 1.057 liquid quarts 0.908 dry quart 61.025 cubic inches
1 ounce, fluid (or liquid)	1.805 cubic inches 29.573 milliliters
1 ounce, fluid (fl oz) (British)	0.961 U.S. fluid ounce 1.734 cubic inches 28.412 milliliters
1 quart (qt), dry (U.S.)	67.201 cubic inches 1.101 liters
1 quart (qt), liquid (U.S.)	57.75 cubic inches (exactly) 0.946 liter

Units of mass

1 carat (ct)	200 milligrams (exactly) 3.086 grains
1 grain	64.79891 milligrams (exactly)
1 gram (g)	15.432 grains 0.035 ounce
1 kilogram (kg)	2.205 pounds
1 microgram (μg)	0.000001 gram (exactly)
1 milligram (mg)	0.015 grain
1 ounce (oz)	437.5 grains (exactly) 28.350 grams
1 pound (lb)	7,000 grains (exactly) 453.59237 grams (exactly)
1 ton, gross or long	2,240 pounds (exactly) 1.12 net tons (exactly) 1.016 metric tons
1 ton, metric (t)	2,204.623 pounds 0.984 gross ton 1.102 net tons
1 ton, net or short	2,000 pounds (exactly) 0.893 gross ton 0.907 metric ton

Pressure

1 kilogram/square centimeter (kg/cm^2)	0.96784 atmosphere (atm) 14.22334 pounds/square inch (lb/in^2) 0.98067 bar
1 bar	0.98692 atmosphere (atm) 1.02 kilograms/square centimeter (kg/cm^2)

* There are a variety of "barrels" established by law or usage. For example, U.S. federal taxes on fermented liquors are based on a barrel of 31 gallons (141 liters); many state laws fix the "barrel for liquids" at 31½ gallons (119.2 liters); one state fixes a 36-gallon (160.5 liters) barrel for cistern measurement; federal law recognizes a 40-gallon (178 liters) barrel for "proof spirits"; by custom, 42 gallons (159 liters) comprise a barrel of crude oil or petroleum products for statistical purposes, and this equivalent is recognized "for liquids" by four states.

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Cretaceous Period

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The Cretaceous period is the third of the three divisions of the Mesozoic era of the geologic time scale. The period lasted 79 million years, from 144 million to 65 million years ago. The Cretaceous is named for chalk beds found in England.

Era	Period	Epoch	Million Years Before Present
Mesozoic	Cretaceous		144
	Jurassic		208
	Triassic		245

Cretaceous and surrounding time periods.

Laurasia and Gondwanaland, the northern and southern landmasses that resulted from the initial breakup of the supercontinent Pangea, continued to separate from each other during the Cretaceous period. These landmasses also began to fragment within themselves to form our modern continents. Throughout most of the Cretaceous, North America was divided by a vast inland sea that extended from the Gulf of Mexico to Canada.

Early in the Cretaceous, the **climate** was warm and semitropical, very much like at the end of the Jurassic period (144 million years ago). However, during the second forty million years the climate became colder at the polar regions and warmer at the equator, setting in motion ecological changes that affected the evolution of plants and animals.

climate long-term weather patterns for a particular region

Shallow oceans supported abundant marine life, including new forms of oysters, diatoms, and algae as well as fish and sharks, corals, **echinoderms**, ammonoids, and mollusks. The edges of these shallow seas provided important **habitat** for mammals, turtles, crocodiles, fish, lizards, and many **invertebrates**.

echinoderms sea animals with radial symmetry such as starfish, sea urchins, and sea cucumbers

habitat the physical location where an organism lives in an ecosystem

invertebrates animals without a backbone

Dramatic changes occurred in plant life during the Cretaceous. Pollinating insects such as bees and butterflies allowed the emerging flowering plants—the **angiosperms**—an advantage over seed-bearing plants that relied on the wind or a chance encounter with an animal to disperse their seeds. Today, nearly 90 percent of plants on Earth are angiosperms, signifying a remarkable evolutionary success story. Forests of oak and willow, cypress, magnolia, palms, and sycamore slowly replaced the cycad forests—palm-like

angiosperms a flowering plant that produces seeds within an ovary

These dinosaur eggs dating from the Cretaceous Period are part of the Smithsonian collection in Washington, D.C.

plants with a barrel shaped trunk and many long leaves growing from the top. These new plant communities provided new sources of food and habitat for many kinds of animals.

During the Cretaceous, the dinosaurs reached the height of their evolutionary success. Fossil bones found in Africa, the Gobi Desert, South America, China, Mongolia, and North America suggest that many new species emerged while earlier dinosaurs went extinct. The **carnivorous** animals such as *Albertasaurus* and *Tyrannosaurus* remained the top predators as they roamed and hunted their prey. Hadrosaurs, (duck-billed dinosaurs), Ankylosaurs (armored dinosaurs), and Ceratopsians (horned dinosaurs) replaced the giant Jurassic sauropods as the main **herbivores**. *Triceratops* fossils by the hundreds have been found, suggesting that these cows of the Cretaceous traveled in huge herds across the plains. Both herbivore and carnivore nests found in Montana, Mongolia, China, and South America suggest that many Cretaceous dinosaurs nested in colonies and possibly even cared for their young after they hatched.

carnivorous describes animals that eat other animals

herbivores animals who eat plants only

Mammals became more abundant during the Cretaceous. One group, the multituberculates, were a successful group of early mammals. By the end of the Cretaceous, when the dinosaurs were becoming extinct, the mammals survived and became a very successful group of animals.

A worldwide mass extinction occurred at the end of the Cretaceous period. This extinction killed off nearly 50 percent of Earth's existing species, including all of the remaining **terrestrial** dinosaurs other than birds, all marine and flying reptiles, and the ammonoids and other invertebrate and microscopic marine organisms. Many groups, however, including most plant species, birds, lizards and snakes, crocodiles and turtles, fish and sharks, many invertebrates, and the mammals survived into modern times.

terrestrial living on land

The causes of this mass extinction are still not completely understood and have led to many lively debates among scientists. One theory suggests that massive volcanic eruptions ejected enormous amounts of ash and harmful gases into the atmosphere, creating dark and cold conditions inhospitable to some plants and animals. One hypothesis suggests that a large asteroid hit the Earth, contributing to devastating climate changes. Still others, however, counter with the argument that the global climate was already in the process of cooling off, perhaps in part because of the drying up of North America's inland sea, and that this slow cooling may have led to more gradual changes in plant and animal life. Another proposition is that multiple factors, rather than one single catastrophic event, was responsible for the mass extinction. SEE ALSO Geological Time Scale; K/T Boundary.

Leslie Hutchinson

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Cultures and Animals

There have been many attempts to determine what it means to be human. At one time, biologists suggested that humans were the only tool users. However, many different animals use tools. Some scientists thought humans were the only animals that had language. But we now know that many animals use sophisticated communication systems similar to language. It would be an ironic twist if the thing that makes us most distinctly human is our relation to other animals, but as far as we know, humans are the only animals that keep other animals as pets.

Humans have had relationships with animals for as long as there have been humans. The human record, from prehistoric through the classical and modern periods and in every culture, is filled with examples of animals helping to shape our understanding of ourselves. Animals figure in our traditions, in our religions, in the stories we tell each other, and in our literature, such as the animal fables and parables of Aesop or Orwell.

hominid belonging to the family of primates

In West African and Caribbean cultures, animals play central roles in the native folklore. Asanti folk literature tells of the clever spider, Anancy, who frequently outwits the other creatures in his animal world. In the Caribbean, Anancy and monkey stories are known and narrated by most Afro-Caribbean children and adults. Throughout the African diaspora, these and other anthropomorphic folk tales frequently convey information about expected human behavior, good or bad.

Animals as a Natural Resource

Current debate on environmental issues is dominated by discussion of the dwindling supply of certain renewable and nonrenewable natural resources. However, one obvious renewable natural resource is often overlooked in this discussion: humans depend heavily on other animals.

As far back as our **hominid** beginnings, humans have exploited other animal species to meet our fundamental requirements for food and shelter. Animals have also served to meet other less tangible needs. The exploitation of animals as natural resources began at least 10,000 years ago as humans made the transition from a hunting and gathering lifestyle to the sedentary lifestyles of agriculture and pastoralism (herding of domestic animals). The domestication of animals brought about a fundamental change in the nature of human-animal relations. Instead of human as hunter and

The relationships of animals to each other and to their environment give us something to compare ourselves to, and thus form a basis for describing our relations to each other. Many of the phrases we use to describe human characteristics are drawn from the animals we live with, such as "eats like a pig," "stubborn as a mule," or "fierce as a lion." These phrases anthropomorphize animal behavior and then use the imagined behavior as a description of human behavior.

animals as prey, the relation became one of humans as master and animals as servant. Instead of thinking only of the dead animal as a source of food for the present, humans began to consider the living animal as a source of food for the future. With human protection, domesticated animal species have flourished, multiplied, and been transformed in many ways, so that they bear little resemblance to their wild ancestors.

We usually do not think of domesticated animals as a natural resource because they have become so much a part of our industrialized society. We tend to think of domestic animals as a sort of organic machinery for producing food. To some extent this is true. Selective breeding for desired characteristics in domestic animals has substantially reduced the genetic diversity of domestic animals in addition to making them into cultural objects. The size, shape, behavior, color, and fur of domestic animals has been transformed to make them more attractive or useful.

However, placing domesticated animals on the side of culture, rather than nature, is misleading. The natural world and the human environment do not stand separate and apart from each other. Domestication, even with human manipulation, is a product of evolution. Natural selection still operates on domestic animals.

The Human–Animal Relationship

While domestic animals constitute a crucial resource to human culture and have been given special human protection so that they now live almost exclusively within the bounds of human culture, regarding domestic animals as a product of human culture separate and apart from wild animals is an artificial distinction. Even those animals we think of as the wildest of wild animals—such as lions, tigers, elephants, rhinoceroses, and gorillas—live almost exclusively within culturally constructed environments. National parks and nature reserves set up to preserve endangered species and their natural habitats are just as much cultural artifacts as are zoos and wild animal parks.

Even when the environmental debate does consider domestic animals, the discussion is usually not about the animals themselves, but is about the pollution caused by animal waste, the plight of wild animals being threatened by human activity, or about the rights of animals involved in medical research. The discussion rarely considers human-animal relations.

The human-animal relationship has changed significantly since animals were first domesticated. Early pastoralists lived with their flocks, aiding in birth and protecting the flocks from predators. Modern human society has become increasingly more dependent on animal products while the separation between most humans and the agricultural animals we depend on has become more dramatic. We are more dependent, but less aware. The domestic animals that provide us with the wide variety of valuable products we depend on have become essentially invisible to most people.

As the divide between domestic animals and us grows ever wider, we have seemingly become more dependent on a special class of animals kept as pets. We keep pets to satisfy emotional needs rather than material needs. We enjoy stroking and cuddling our pets and seem to receive substantial emotional benefit from doing so. Thus the human-animal relation has profoundly shifted from a relation with domestic animals to a very different sort of relation with our pets.

Humans and Their Pets

Humans keep a variety of animals as pets—snakes, lizards, roaches, spiders, fish, gerbils, rats, mice, birds—but the two most common are cats and dogs, with cat-owning households slightly outnumbering dog-owning households in the United States. Most pets serve no utilitarian purpose (although some dogs contribute to household security by barking at intruders). Pets are kept because they evoke affection or curiosity and often are given a special status as companions for members of the family. Cattle, horses, and other large domestic animals usually serve a more utilitarian purpose and are not ordinarily considered pets. However, elderly horses that can no longer serve a specific purpose are often kept as pets out of respect for the long years of service and companionship they provide.

Cats. Modern domesticated cats (*Felis sylvestris catus*) are generally considered to be the descendants of the European wild cat, *Felis silvestris silvestris*, and the African wild cat, *Felis silvestris libyca*. Domestic cats probably evolved from African and European wild cats around 6,000 years ago.

The cat seems to have domesticated itself. In northern Africa, several cultures had developed well-established agricultural societies. Agriculture meant grain, and stored grain invited rodents. Out of the population of wild cats in the area, some had a higher tolerance for the presence of humans and a willingness to be near other cats (most cats are solitary creatures). Cats with these characteristics were able to move into the cities and onto the farms, where they found abundant prey. Keeping the rodents in check benefited the humans, so the cats were adopted and gradually increased in status. By 1600 B.C.E., cats were accepted as pets and by 1500 B.C.E. were regarded by the Egyptians as personal representatives of a deity, Bastet.

> Cats have not always been honored. During the Middle Ages, cats were associated with witchcraft and were slaughtered in large numbers. This slaughter may have led to an explosion in the rodent population. As fleas carried by rodents can transmit bubonic plague, the destruction of cats may have contributed to the spread of the plague epidemic known as Black Death.

Dogs. The dog was probably the first animal to be domesticated by humans. This apparently occurred about 12,000 to 10,000 years ago. Domesticated dogs are classified as *Canis familiaris.* Some experts think that dogs are descendants of wolves (*Canis lupus*) and even go so far as to assign them to the subspecies *Canis lupus familiaris*. Dogs certainly freely interbreed with wolves and produce fertile off-spring. Others suggest they are descendants of a now extinct wild dog similar to the pariah dog of India.

How dogs were domesticated is still being debated. One suggestion is that dogs began to follow humans around, living off of discarded scraps of food. Through a gradual process of acclimation, both dogs and humans become more accepting of each other. Because dogs are natural **scavengers**, village trash heaps would be perfect places to find food. The wild dogs would scavenge through the scraps removing all the meat that would attract more dangerous scavengers. In this way, the dogs provided a substantial benefit to the humans.

Another suggestion is that humans deliberately domesticated dogs to aid in hunting. Dogs that had begun to hang around human settlements but were still interbreeding with wild dogs were first captured and kept in pens. Selective breeding gradually eliminated the wild characteristics. Subsequently, specialized dogs were bred by selective breeding. Also, to prevent cross-breeding, the remaining wild dog population was systematically exterminated.

Dogs often are put to work. This work includes sheep herding, rescue work, drug sniffing, pulling a sled, sentry duty, and serving as guide dogs for hearing- or vision-impaired persons. During World War I, the Red Cross used dogs to help search for wounded men on the battlefield. The U.S. Army started officially using dogs around the time of World War II.

Domesticated dogs have been trained to help humans with a variety of tasks. Here, a team of dogs pulls a sled in the Beargrease Sled Dog Marathon in Duluth, Minnesota.

scavengers animals that feed on the remains of animals that they did not kill

Problems in the Human–Pet Relationship. Abandoned pets are an enormous problem in most cities. In some cities, hundreds of cats and dogs are euthanized each day. Those euthanized may be the lucky ones, because house pets abandoned or released back to the wild almost always suffer a short, miserable existence, inevitably resulting in the animal's death.

The number of feral cats and dogs is a significant problem in most countries in the world. Feral animals are domestic animal breeds that live wild. One strategy that has been attempted to reduce the number of feral cats is to capture the cats, neuter them, and then return them to their original territory. The theory is that the cats will remain in the same approximate area, thus keeping new cats out in addition to their not being able to reproduce to replace the population. Results of this experiment are still being debated. This technique will not work for feral dogs because their behavior is different. They run in packs and defend a territory as a pack. Feral cats and dogs are a major concern in many countries because they can act as disease vectors (rabies) or carry the parasites (fleas and ticks) that act as disease vectors (plague and Lyme disease).

The relationship between humans and domesticated animals is loaded with contradictions. Dogs are often kept as cherished, pampered pets, but may also be severely maltreated and abandoned by their owners. An animal destined for the dinner plate may nevertheless receive a great deal of respect, care, and affection during its lifetime, demonstrating that the boundary between pets and livestock is blurred.

Both the manner in which we perceive animals and the way in which we treat them is evidence of the contradictory nature of the human-animal relationship imbedded within our cultures. For example, humans (who are not prohibited by religious belief) regularly consume the flesh of pigs. On the other hand, most Westerners are repelled by the idea of eating dog meat. Yet we keep both pigs and dogs as pets. In other parts of the world dog meat is regularly consumed, even by people who also keep dogs as pets. People from Western European culture are disgusted at the thought of eating insects, but readily consume many other arthropods with apparent gusto. In other parts of the world, insects form a significant portion of human diet. Although the relationship between humans and other animals has received increasingly more attention within the social sciences, only a few authors have explicitly drawn attention to the ambiguities that pervade everyday human-animal interactions.

Animals as Entertainment

Since 1958, the World's Largest Rattlesnake Round-Up, an event that benefits local charities, has been held in Sweetwater, Texas. It takes place annually around the first of March. The project was begun by local farmers and ranchers in an attempt to rid the area of an abundance of rattlesnakes that were endangering people and livestock. Over the years, more than 100,000 kilograms of rattlesnakes have been collected in the region.

The rattlesnakes are displayed for entertainment and most are "milked" to obtain venom to be used in the manufacture of antivenom vaccine. Events include a parade, the Miss Snake Charmer Pageant, snake-handling shows, brisket and chili cook-offs, and plenty of fried rattlesnake meat to snack on. Animal rights activists and environmentalists from all over the world have protested and criticized this event for many years. However, the event continues and the local rattlesnake population seems to be very little affected by this human tradition.

In the name of entertainment (sometimes thinly disguised as education), circuses, dog races, horse races, and marine parks often use animals. Unfortunately, some of these animals are not well treated. Orcas and dolphins in marine parks live only 25 percent as long as animals in the wild. These animals regularly swim long distances, up to 100 kilometers (62 miles) per day, in the wild. When kept in small pools the animals are not able to swim such long distances, hence, they suffer from stress and increased rates of disease. Circus elephants also experience stress when kept in captivity for entertainment purposes. Since 1990, circus elephants have killed 43 people. Elephants are not normally aggressive animals, but the stress of captivity can cause these highly intelligent animals to go insane.

Animals and World Religions

Religion, whether organized or not, is an intimate part of human culture. All of the world's major religions have explicit or implicit principles concerning the proper character of the human-animal relationship. Most of the world's religions recognize the importance of animals and the animal-human interaction. However, few major religions hold ceremonies to mark the birth or death of animals that are the equivalent of ceremonies marking the birth or death of humans. This seems to indicate that many world religions relegate animal life to a secondary status when compared to human life. Nonetheless, ethics and morality concerning the use of animals is an important issue that most world religions consider to be within their domain. Sometimes, the religion's standpoint on issues relating to animals is clearly stated in holy writings. In other instances, an interpretation of a written passage is made by a person or official body within the religion.

With few exceptions, the general attitude of most of the world's religions toward the relation of humans and animals can be characterized by five general principles. 1) Human life is more valuable than animal life because humans have a "soul" (or something equivalent to a soul). (2) Humans have a God-given authority over other animals. This is usually expressed as "dominion" or "stewardship." (3) The right of humans to consume animals for nutrition and to use the labor of animals is recognized by several, but not all world religions. (4) Cruelty to animals—pointless acts that will cause an animal to experience pain or suffering—is prohibited by most religions because it displays attributes that are undesirable in civilized societies. Even religions that previously or currently practice animal sacrifice often specify that the animal be killed in as painless a manner as possible. (5) Most religions urge kindness toward animals.

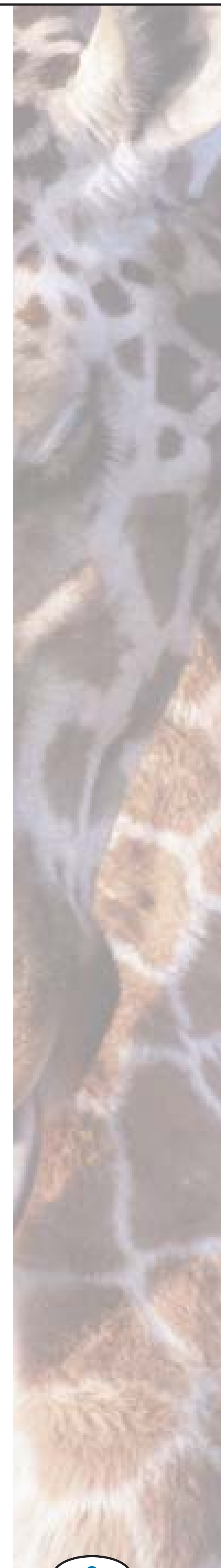
All of the world's major religions have explicit or implicit principles concerning the proper character of human–animal relationships. These Hindu women are petting a sacred cow during a religious festival in Nepal.

Christianity. For many Christians, an indicator of the desired relationship of humans to animals is found in Matthew 10:29–31 in the Christian New Testament. The verses suggest that, although the life of a sparrow is of much less value than a human life, "not a sparrow dies without God taking notice." For Christians, humans may have a soul but God still considers the life of a sparrow important enough to take notice of its passing.

Judaism. The God-given authority of humans over animals is recognized by Judaism, but not without restrictions. The prohibition of cruelty is so strong in Jewish law that the slaughter of animals for human consumption is carefully scrutinized by a specialist in the field. If there is any indication that the animal suffered unnecessarily, it is considered unclean (unfit for human consumption). There are exceptions to this rule for medical research. The Polish rabbi Moses ben Israel Isserles (1525–1572) taught that anything necessary for medical or other useful purposes is excluded from the prohibition of cruelty to animals.

Islam. The right of humans to consume animals for nutrition and to use their labor is recognized by most Muslims. The Qur'an is neutral on the subject of the consumption of meat. However, moderation in all things, including eating, is encouraged (Qur'an 7:31; 5:87). If animals are slaughtered for food, the slaughter must be done in strict accordance with Islamic law and in such a way as to cause as little pain as possible. Most Islamic scholars hold that the Qur'an prohibits animal cruelty, which is defined as causing unavoidable pain and suffering. This last prohibition is generally applied to sport hunting as well.

Hinduism. The Hindu religions also denounce cruelty to animals. The *Bhagavad Gita* (verse 5:18) proclaims that a self-realized soul is able to understand the equality of all beings. To a Hindu, animal souls are the same as human souls, progressing to higher means of conscious expression in each life. Hinduism teaches that every soul takes on a life for a specific purpose and that to kill an animal stops the progression of the soul and may cause



great suffering. For this reason, most devout or orthodox Hindus do not consume meat or use meat products in any form.

Many Westerners have difficulty understanding why a country as poor as India allows cows to wander the streets, break into gardens, and pilfer food from market stalls. To a devout Hindu, the cow is sacred. The *Mahabharata*, an epic poem of ancient India, teaches that spiritual sacrifice must be accompanied by milk curds and ghee (clarified butter). Ghee and the cow that produces ghee becomes the very root of spiritual sacrifice. Hindus hold cows sacred because cows are the symbol of everything that is alive. In the same way that Roman Catholics and many other Christians revere Mary as the Mother of God, Hindus revere the cow as the mother of life. To a Hindu, there is no greater sacrilege than harming a cow. Even the taking of a human life lacks the symbolic defilement attached to cow slaughter.

Buddhism. Like Hinduism, Buddhism also teaches reincarnation, the belief that sentient beings are subject to rebirth as other sentient beings and that consciousness cannot be killed. The interconnectedness of all living organisms is an important precept of the faith. The first of the Five Precepts, the foundation of Buddhist ethical conduct, is not to harm sentient beings.

The relationship between humans and animals is evident in the literature, folklore, and practices of cultures around the world and through the centuries. Yet ambiguity and inconsistency often characterize this relationship. We love our pets and we depend on our domestic animals for food and valuable products, yet we sometimes mistreat our pets and we have almost completely separated ourselves from domestic animals.

Anthrozoology. There is a growing body of literature and an emerging scientific discipline concerning the human-animal relationship, sometimes called *anthrozoology*. The field includes social scientists, psychologists, zoologists, ethologists, historians, philosophers, veterinarians, and physicians. Several groups have been organized to study the human-animal relationship, such as CENSHARE at the University of Minnesota. However, these groups tend to focus on the relationship between humans and their pets. Issues concerning factory farming, vivisection, zoos, and pet-abandonment have generally been addressed by animal rights activists, ethicists and moral philosophers, such as Peter Singer and Thomas Regan. Singer writes about the ethical treatment of animals as a part of human ethics in general.

Humans are dependent on domestic animals for food and companionship. Perhaps the increasing study of human-animal relationships can help us better understand our relationship to the animal species on which we depend and that share our homes and our planet. SEE ALSO Animal Rights; Human–Animal Conflicts; Hunter-Gatherers; Hunting.

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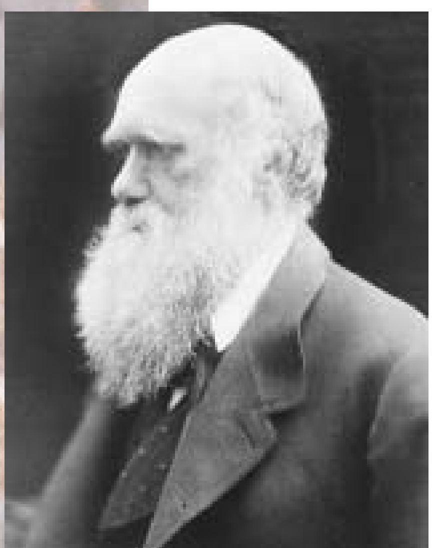

Charles Darwin's theory of evolution, with its emphasis on natural selection, was the first to win wide approval from the scientific community.

Darwin, Charles

Naturalist
1809–1882

Charles Darwin was born on February 12, 1809 in Shrewsbury, England. He died at the age of seventy-three on April 19, 1882. Darwin revolutionized biology with his theory of evolution by **natural selection**. Although others contributed to the theory of evolution, Darwin was the first to win wide approval from the world's experts in biology.

Darwin was the son of a physician and the grandson of the physician and **naturalist** Erasmus Darwin. In the 1790s Erasmus Darwin proposed a theory of evolution. Darwin studied medicine at Edinburgh University and religion at Cambridge University. He received a Bachelor of Arts degree from Cambridge in 1831. There, his interest in biology was encouraged by his friendship with John Stevens Henslow, who studied plants. Henslow recommended Darwin as naturalist for a scientific expedition to South America. In 1831 Darwin began the five-year journey aboard the ship HMS *Beagle*. He gained valuable knowledge about the plants, animals, and natural features of the lands that he visited. In 1839 Darwin married his first cousin, Emma Wedgewood. They had ten children, seven surviving past childhood.

By 1846 Darwin had published several works on his discoveries about coral reefs and volcanic islands. For his writings and other scientific activities, he became greatly respected in the scientific community. Darwin spent years developing his theory on evolution. It is believed that he waited a long time to share it with the world because he feared the religious **controversy** that would result. He finally was moved to go public when he received a paper from Alfred Wallace in 1858. Wallace had the same ideas that Darwin had been pondering for 20 years. Darwin and Wallace presented their theories in a joint paper to the Linnean Society in 1858. In 1859 Darwin published his famous book *On the Origin of Species by Means of Natural Selection* *or The Preservation of Favoured Races in the Struggle for Life*. While the theory was accepted quickly in most scientific circles, religious leaders strongly opposed it. Many religious persons felt that the theory was inconsistent with the biblical book of Genesis. They feared that God had no place in Darwin's world. They claimed that in Darwin's theory, man was descended from apes and not placed in a superior position over other animals.

natural selection a process by which organisms best suited to their environment are most likely to survive and reproduce

naturalist a scientist who studies nature and relationships among organisms

controversy a discussion marked by the expression of opposing views

Darwin expanded his theory in other publications. His theories included the following: (1) most evolutionary changes were very gradual, requiring millions of years; (2) natural selection was the driving force behind evolutionary change; and (3) today's millions of species branched out from a single, original life form.

Darwin's theories spurred further research in biology. Charles Darwin is considered one of the greatest figures in the history of biology. SEE ALSO ADAPTATIONS; BIOLOGICAL EVOLUTION; NATURAL SELECTION.

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DDT

DDT (dichloro-diphenyl-trichloro-ethane) is an insecticide that was first used worldwide in 1946 to increase agricultural production and to reduce disease vectors (carriers). Although formulated in 1874, DDT's insecticidal properties were not discovered until 1936. Paul Muller of Switzerland won the Nobel Prize for that discovery in 1948.

The neurotoxin DDT interferes with the **action potential** along **neurons**. It affects insects and vertebrates by means of this same primary mechanism. It has a greater effect on insects simply because they are smaller and absorb it more readily. At a high enough dosage, DDT can have as detrimental an effect on vertebrates, including humans. Symptoms of DDT toxicity include apprehension, headache, anorexia, nausea, hyper-excitability, muscle fibrillation, respiratory arrest, coma, and death.

action potential a rapid change in the electric charge of the cell membrane

neurons nerve cells

DDT is relatively inert and stable, and is nearly insoluble in water. This combination of attributes allows it to be stored easily in fat. As a result, fatty tissues act as biological magnifiers by slowing the excretion of DDT after it is absorbed. Like other fat-soluble compounds, DDT is transferred up the food chain more efficiently than are water-soluble compounds, thereby achieving higher concentrations among carnivores. Because DDT toxicity is a function of concentration, this **biomagnification** is most likely to cause problems for a predator species, such as eagles, ospreys, and falcons, at the end of a long food chain.

biomagnification increasing levels of toxic chemicals through each trophic level of a food chain

An airplane dusts DDT over sheep in Medford, Oregon, in 1948. First used worldwide as an insecticide in 1946, DDT came under fire in subsequent decades for its detrimental effect on vertebrates.

During the 1950s, United States efforts to control Dutch elm disease consisted primarily of killing its vector, elm bark beetles, with DDT. Soon after, communities in the Midwest and Northeast began to notice an accumulation of dead robins and other birds. Roy Barker discovered that earthworms were consuming DDT sprayed on the elm trees which was seeping into the soil. Robins in turn ate the earthworms, receiving a lethal dose of DDT from as few as eleven worms. Birds that did not die often suffered reduced fertility.

Other predatory bird species also appeared to decline during the 1940s and 1950s. Hawk Mountain, Pennsylvania, is a stopover for many migrating hawks and eagles. From 1935 to 1939, 40 percent of the eagles were yearlings. Between 1955 and 1959, only 20 percent were yearlings. The percentage of juveniles in eagle populations along the Mississippi, Illinois, and Susquehanna Rivers also declined after 1947. In 1950, there were two hundred mating pairs of ospreys at the mouth of the Connecticut River; by 1970 the number had dropped to six. One study suggested that DDT interfered with **calcium** deposition in eggshells, thereby potentially reducing the reproduction rate of susceptible bird species. However, subsequent studies found no correlation between DDT levels and eggshell thickness either in nature or in controlled experiments.

calcium a mineral form of calcium carbonate

DDT may adversely affect whole ecosystems. In the 1950s, the Canadian government instituted a policy of eradicating the spruce budworm. This native insect attacks several species of evergreens. Millions of acres of the Northwest Miramichi watershed were sprayed to save balsams, the pulp industry's most valuable cash crop. Soon trout and salmon began to turn up dead along the streams. Their prey, caddis fly larvae, stonefly nymphs, and blackfly larvae, were being killed along with the spruce budworm. In 1959, the watershed produced less than a third of the smolt (young salmon) it had produced before the most recent spraying.

Rachel Carson's book *Silent Spring*, was released in 1962 and documented the adverse effects of DDT on the environment. Her book catalyzed the modern American environmental movement. Over the years a variety of objections have been made to her characterization of DDT as an absolute detriment to human and ecological health. For example, studies on the role of DDT in breast cancer have yielded ambiguous results. It is also possible that the correlation between DDT use and the decline of fish and bird populations was caused by the simultaneous use of other pollutants such as PCBs.

The Environmental Protection Agency banned DDT in 1971 as a potential human carcinogen. Since then most countries have banned the chemical for agricultural purposes. However, DDT continues to be a cheap and effective way to kill mosquitoes that transmit malaria, requiring lower concentrations than those for agricultural use.

In 2000, more than 100 governmental and nongovernmental agencies gathered to formulate a treaty to completely phase out DDT and eleven other pollutants. The World Health Organization warned that a sudden worldwide ban on DDT could result in an epidemic of malaria in countries that cannot afford other effective insecticides. Until safe, affordable alternatives are developed, DDT will continue to be used in many countries where malaria is endemic, and its residues will be found in soils and human breast milk around the world. SEE ALSO Carson, Rachel; Pesticides; Silent Spring.

Brian R. West

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Defense

Animal defense mechanisms include a stunning array of behaviors and adaptations. Defensive behavior of prey takes four forms: anti-detection, anti-attack, anti-capture, and anti-consumption. Every animal has perfected some form of anti-predator adaptation, whether they attempt to go undetected by camouflaging themselves against their surroundings, or keep themselves from being eaten because they are wildly colored and dangerous-looking.

Camouflage and Mimicry

Cryptic coloration and behavior, also known as camouflage and mimicry, are common methods of anti-detection in insects, birds, fish, amphibians, and mammals. Combining camouflage with hiding behavior is a phenomenon widely used among insects. Cryptic moths and butterflies have wing colors and patterns that mimic the plants found in their environments. The

Porcupines display sets of spiny quills as part of their unique defense system.

Catocala moth has whitish wings with dark linear patterns resembling birch bark so that when it rests upon a birch tree it is barely detectable.

Many animals mimic leaves. Again, most tend to be insects. Probably the most successful of all leaf-mimickers are the leaf insects of the genus *Phyllium*, the so-called walking leaf, from Malaysia and Indonesia. Its detailed body parts perfectly resemble a cluster of green leaves and leaf fragments. The disguise is enhanced by its behavior. By moving very slowly, advancing one leg at a time, it sways slightly like leaves being nudged by a gentle breeze.

Chemical defenses. Even cryptic prey can be detected by keen predators. Some animals have the ability to ward off enemies with noxious tissues, stinging hairs, sticky secretions, painful injections, and foul-smelling excretions. The creatures that rely on chemical defenses also tend to have warning coloration, meaning that their bodies are boldly hued in red, black, orange, or bright yellow. This helps to remind predators of past unpleasant experiences with these species. After having eaten a warning-colored toxic prey, many predators quickly learn to retreat whenever they see the same warning display. Some of the most poisonous species of all are the South American arrow-poison frogs, in the genus *Dendrobates*. These frogs are brilliantly colored with patterns of red, yellow, or white on backgrounds of black or electric blue. Their poisons, which affect the central nervous system, are so deadly that Colombian Indians use it to poison their arrowheads.

Batesian mimicry. Some edible prey have evolved to resemble bad-tasting species in an effort to take advantage of the visual response predators have to particular color patterns. These deceptive species are called Batesian mimics, named for the English **naturalist** Henry Bates, who discovered their ex-

naturalist a scientist who studies nature and relationships among organisms istence in Brazil during the 1800s. One Batesian mimic is the tephritid fly, which possesses a leglike pattern on its wings. It can wave these wings in ways that deceptively imitate the aggressive signals of predatory jumping spiders and ward off any possible fly-eating spiders lurking nearby.

Batesian mimicry can include acoustical, as well as visual, deception. For example, the ground-nesting burrowing owl makes the same sound as a rattlesnake. The owl and the rattlesnake share an underground habitat which makes the deception even more convincing.

Other Anti-Capture Methods

What if cryptic or warning behavior still doesn't keep the predator from closing in on its prey? Some animals use anti-capture methods. By startling the predator momentarily, the animal has a chance to escape. The catocala moth mentioned earlier shows only its white and dark-gray wings while resting. If attacked by a blue jay, the moth can display its hind wings, which are orange, yellow, or red bands on a dark background. The sudden flash of color will surprise the jay, who may inadvertently release the moth.

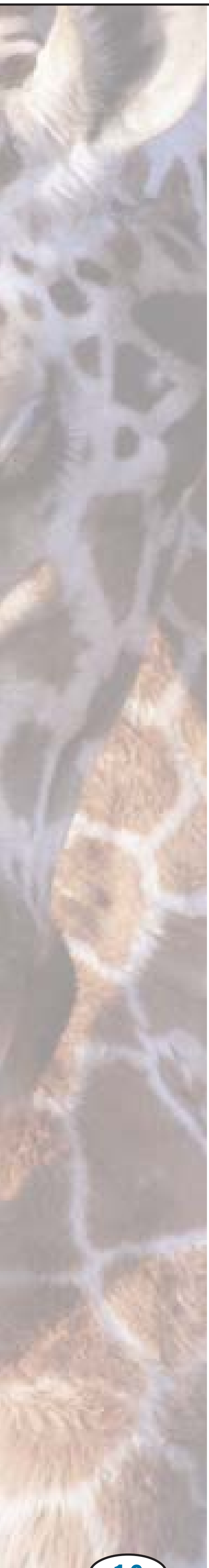
Another anti-capture weapon is sheer vigilance, or remaining alert so as to detect a rapidly approaching enemy in time to take effective action. Vertebrate prey are always scanning, sniffing, or listening for danger. The principle that many eyes, noses, or ears are better than a few could contribute to the tendency of animals to form flocks, herds, and other social groups. It also has been proven that the more animals scanning for danger, the faster the response to that danger.

Alarm calls. Most flock animals rely on alarm signals, or special calls that alert the others in the flock to a possible hazard. The risk of the signal-giver being singled out for predatory attention is lessened because the group flees together, which confuses the predator. In fact, non-calling animals attempting to escape are more than ten times as likely to be killed than alarm-givers. Ground squirrels that live in high densities in mountain meadows give a high-pitched whistle as they dash for cover when a hawk or falcon is spotted. The species has a separate alarm call for terrestrial predators such as coyotes.

Surviving Attack

What happens to the animals that wind up captured? If the prey can somehow convince its captor to let it go, being captured does not mean certain death. Sometimes, chemical deterrents are used to save the life of animal prey. Some salamanders excrete an adhesive that is used to ward off their enemies. If captured by a garter snake, for example, the salamander writhes and thrashes while releasing secretions from the tail and body. The snake can become so coated by the glue that its body becomes stuck to itself and it is rendered completely helpless.

Another way of surviving attack is to induce the predator to strike a body part other than the head. This is critical because brain damage quickly immobilizes prey and removes all chance of survival. This is why animals often hide their heads when under attack. Some animals have evolved false heads on body parts that can be sacrificed without causing death. Hairstreak butterflies have false heads on their hind wings so that when birds attack, the butterfly has a chance to fly away unharmed.



Expendable body parts are another lure used by animal prey. Some lizards, such as the young skins, have brightly colored tails. Skinks twitch their brightly colored tails when threatened to distract the predator's attention from their heads. When a snake attacks the tail, it breaks off and continues to wildly thrash on the ground. Distracted further, the predator generally attempts to subdue and eat the thrashing tail, giving the skink time to escape. SEE ALSO BEHAVIOR; CAMOUFLAGE; MIMICRY.

Ann Guidry

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Desert Adaptations *See Water Economy in Desert Organisms.*

Devonian

The Devonian period, from 437 to 408 million years ago, was named for the English county where it was first identified. It has sometimes been called the Age of Fishes. Spectacular fish fossils abound in the massive Old Red Sandstone sediments that covered a large portion of Laurasia, the supercontinent that would later split apart to form Europe, Greenland, and North America. These fossils indicate that a vast radiation (or divergence) in size and function was taking place among Devonian vertebrates. The jawless Agnathans had multiplied into many groups distributed around the world by the late Silurian (438 mya). Then, in the Devonian, came the fish, which developed jaws and were such successful competitors that the Agnathans were reduced almost to extinction, with only the lampreys and hagfish as their descendants.

Vast schools of eight-to-ten-inch spined fishes, the Acanthodians, swam in the mid-deep waters (beyond the continental shelf). Some were toothless, but many had razor-sharp teeth and devoured huge quantities of the bony fish, which also swam in great numbers in the clear warm seas. The bony fish included the ray fin, the lungfish, and the fleshy, lobe-finned ancestors of amphibians. Enormous placoderms, up to thirty feet in length, dominated the oceans with their armored bodies and tooth-lined, hinged jaws. Early sharks arose, possibly from placoderms, whom they would replace as the

Devonain period and surrounding time periods.

Era	Period	Epoch	Million Years Before Present
Paleozoic	Permian		286
	Pennsylvanian		320
	Missipian		360
	Devonian		408
	Silurian		438
	Ordovician		505
	Cambrian		570

reigning predators of the deep by the end of the Devonian period. And vast coral reefs, some hundreds of miles long, transformed the shallow waters into virtual metropolises swarming with marine life at all levels.

Even more exciting than the proliferation of sea **fauna** was the evolutionary step toward dry land. Fish began exploring up the **brackish estuaries** into freshwater, followed by ravenous six-foot sea scorpions, the fearsome Eurypterids. The lobe-finned fish ventured into shallower and shallower water, eventually developing the rudimentary **lungs** that would allow them to breathe air. Next, their explorations on the muddy shores encouraged innovations in skeletons and fins that allowed them to support their weight in the stronger pull of gravity of the new environment. Gradually, the lower paired fins developed into the four limbs of amphibians. The most complete fossil of an early tetrapod (four-limbed) amphibian comes from the tropical swamps of Devonian Greenland. *Ichthyostega* was a lumbering, forty-inch carnivore, the ancestor of all existing land vertebrates.

fauna animals

brackish a mixture of salt water and fresh water

estuaries areas of brackish water where rivers meet the ocean

lungs sac-like, spongy organs where gas exchange takes place

Yet another major innovation occurred in the Devonian. As the earliest plants and invertebrates made their way onto land, they formed cooperative communities that make possible life as it exists today. Preserved in the Rhynie Cherts of Scotland are perfect slices of pondside life from the period. The minerals (silicon) in the water formed fossil images of the plants. These fossils show the first plants that grew and decomposed to form the first humus-rich soils on the Earth. Living amongst them were the earliest terrestrial **arthropods**: scorpions, mites, and spider-like arachnids. These tiny animals are responsible for breaking down organic material and releasing the nutrients back into the soil. Without this decomposition activity there could be no larger plants and therefore no land animals. This 400-million-year-old partnership between microscopic plants and animals is a fundamental feature of life as we know it. SEE ALSO Geologic Time Scale.

arthropods members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

Nancy Weaver

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1937–

In 1997, Jared Diamond won the Pulitzer Prize for Nonfiction with his book *Guns, Germs and Steel*, an analysis of the geographical and environmental origins of the long-term distribution of wealth and power in different regions of the world. Born in Boston, Massachusetts, on September 7, 1937,

Jared Diamond won a Pulitzer Prize for his analysis of the geographical and environmental origins of the long-term distribution of wealth and power.

Diamond was raised in an intellectually stimulating household by a physician father, interested in the **genetics** of childhood diseases, and a mother who was a linguist and teacher. Diamond became an avid bird watcher at the age of seven. All these influences led in 1958 to a biology degree from Harvard, where he studied biological research, language, history and writing. Diamond earned a Ph.D. in **physiology** from Cambridge, and then a professorship at UCLA in 1968 where he taught molecular physiology, evolutionary biology, and evolutionary **biogeography**.

Through years of fieldwork in South America, southern Africa, Indonesia, Australia, and New Guinea, he wrote more than 200 papers on physiology, **ecology**, and **ornithology**. Diamond also began writing science books for popular audiences. *The Third Chimpanzee: The Evolution and Future of the Human Animal*, 1992, discusses possible theories for the divergence between humans and chimps, who share 98.4 percent of the same genetic material. *Why Is Sex Fun? The Evolution of Human Sexuality*, 1997, examines aspects of human sexuality such as why only humans and pilot whales undergo menopause and why humans, dolphins, and chimpanzees are the only species to have sex for pleasure—that is, when the female is not fertile and there is no possibility of reproduction.

It was in the 1970s, while studying the ecological diversity of bird fauna in New Guinea, that Diamond was asked by his local guide why the white men had all the cargo, or technological goods. Thinking about it, Diamond couldn't come up with an answer. When he pursued the answer back in the United States with other scientists, the answers he received seemed to always come down to: We (being western Europe and the United States) are smarter than they are. Reflecting on his experiences in the jungle, Diamond knew that was untrue. The tribesmen were not only intelligent, but also far more observant and competent in their environment than Diamond thought he would ever be. *Guns, Germs and Steel*, he later said, was written to demolish the intellectual basis for racism. The book proposes that certain geographical regions of the globe lent themselves to the development of agriculture, which in turn encouraged technological growth. Diamond hoped that his work would show that historical studies of human beings can be pursued as scientifically as studies of dinosaurs—and can teach us what shaped the modern world, and what might shape our future.

Nancy Weaver

genetics the branch of biology that studies heredity

physiology the study of the normal function of living things or their parts

biogeography the study of the distribution of animals over an area

ecology the study of how organisms interact with their environment

orinthology the study of birds

Diffusion *See Transport.*

Digestion

Digestion is the process of breaking down food into molecules that cells can absorb. Carbohydrates, proteins, nucleic acids, and fats are broken down into their smallest units (monomers) by digestive enzymes. These hydrolytic enzymes break chemical bonds through a reaction that requires water. Each hydrolytic enzyme is named after the substances it hydrolyzes. For example, carbohydrases break carbohydrates into single sugars (monosaccharides), proteases break proteins into amino acids, nucleases break nucleic acids into nucleotides, and lipases hydrolyze fats to fatty acids.

The Digestive System

The digestive system of humans consists of a one-way digestive tract with several specialized chambers along the way—mouth, stomach, small intestine, and large intestine. Each chamber has a specific function. In the human digestive system, digestion starts in the mouth. There food is physically digested by the action of our jaws and teeth, which break it down into smaller pieces, increasing the surface area for the digestive enzymes to work on. While being chewed, the food is mixed with saliva. Saliva makes the food slippery for swallowing, and also contains the enzyme amylase, a carbohydrase that breaks down starch into smaller polysaccharides. Once food is swallowed it passes along the digestive system through the activity of peristalsis (wavelike smooth muscle contractions). The passage of food from one chamber to the next is regulated by sphincters, or ringlike muscles.

Once the food arrives in the stomach, it is mixed with gastric juice, which contains hydrochloric acid (HCL) and pepsin. HCL kills most swallowed bacteria, and breaks down most food into individual cells, further increasing the surface area for enzyme attack. Pepsin (a protease) begins the hydrolysis of proteins into smaller polypeptides. The main site of human digestion and absorption of nutrients is the small intestine. There accessory glands of the digestive system, such as the pancreas and the liver, secrete their products into the digestive tract. The pancreas secretes bicarbonate ions that neutralize the acid from the stomach, protecting the digestive enzymes of the small intestine. The pancreas also releases a carbohydrase (pancreatic amylase), which continues the carbohydrate digestion started by salivary amylase in the mouth. The resulting disaccharides (e.g., maltose) are further hydrolyzed into monosaccharides (e.g., glucose) by enzymes (e.g., maltase), which are built into the membranes of cells lining the small intestine. This is also where sugar is absorbed from the lumen of the digestive tract into the cells lining the digestive tract.

Other enzymes that are produced and released by the pancreas are proteases (e.g., trypsin), nucleases, and lipases. Proteases attached to the membrane of cells lining the walls of the digestive tract are responsible for hydrolysis of small peptides to amino acids (which are then absorbed), and attached nucleases process nucleotides whose components are also taken up.

For the pancreatic lipases to be efficient, the lipid clumps that form in the watery environment of the digestive tract have to be broken into tiny droplets, which will increase the surface area for the lipases to work on. This is the function of bile salts, which are produced by the liver and stored in the gall bladder before being released into the small intestine. The fatty acids resulting from the action of the lipases are then absorbed.

While digestion and absorption of nutrients are taking place in the small intestine, peristalsis slowly pushes the content of the small intestine into the large intestine, where water and ion absorption are taking place. In the large intestine, populations of bacteria live on material that is not digestible by humans. As a byproduct of their metabolism, they produce gas as well as vitamins such as vitamin K that can be absorbed.

Control and Digestion

How is it possible to digest food molecules and not the cells of the digestive system itself, which is made of the same molecules? Most enzymes are produced in an inactive form called **zymogens**, that do not affect the cells that produce them. These zymogens are then released into the digestive system where they are activated. The cells lining the digestive tract are protected from the active enzymes by a thick layer of mucus. However, the mucus lining is constantly eroded, and if the lining is eroded faster (e.g., by acid-resistant bacteria) than it is regenerated, stomach ulcers may occur.

zymogens inactive building-blocks of an enzyme

To make efficient use of all the nutrients contained in food, control and coordination of the digestion process is crucial. This is accomplished by several negative feedback systems. For example, when we see, smell or taste food, our brain signals the stomach to secrete gastric juice. When food proteins are actually present in the stomach, they trigger the release of the hormone gastrin into the blood stream. This hormone causes the cells in the stomach wall to release even more gastric juice, ensuring that proteins in the stomach are properly predigested. If the stomach becomes too acidic, the release of gastrin—and thus the production of gastric juice—ceases. When the acidic content of the stomach enters the small intestine, another hormone, secretin, is released into the blood stream from the cells lining the small intestine. Secretin causes the pancreas to dump bicarbonate from the pancreas into the small intestine, buffering the acid. When amino acids or fatty acids are detected in the small intestine, another hormone, choleocystokinin (CCK), is released from the intestinal cells into the blood. CCK triggers the gall bladder to release bile and the pancreas to release its digestive enzymes. At the same time, CCK inhibits the peristalsis of the stomach thus slowing down food transport. This allows enough time for the digestion of the food already present in the small intestine before more food from the stomach arrives. SEE ALSO DIGESTIVE SYSTEM; HOMEOSTASIS.

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Digestive System

The digestive systems of animals are quite diverse. Sponges, the simplest animals, do not have specialized digestive systems. Food particles filtered from the water are simply digested within individual cells (intracellular digestion). One of the first steps toward a complex digestive system in animals, and the processing of larger prey, is the evolution of a **gastrovascular cavity**, a digestive sac with a single opening to the external environment. The gastrovascular cavity serves as a protected space for extracellular di-

gastrovascular cavity a single cavity where digestions occurs gestion inside the animal, and at the same time allows distribution of the digested material to most cells of the body. Following extracellular digestion in the gastrovascular cavity, the digestion products from carbohydrates, proteins, and fats are taken up by cells lining the gastrovascular cavity, where digestion is completed intracellularly.

A One-Way Digestive Tract

Cnidarians and flatworms have a gastrovascular cavity. Cnidarians, such as the *hydra*, use their tentacles to move food through their mouth into their gastrovascular cavity. Then the cells lining this cavity excrete digestive **enzymes** that will start extracellular digestion and break the prey into smaller pieces. Any undigested remnants of the prey are expelled through the mouth opening. Like cnidarians, flatworms have a gastrovascular cavity with a single opening, but the cavity itself is highly folded. These folds greatly increase the surface area and extend throughout the body, bringing nutrients within the reach of all cells.

cnidarians aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

enzymes proteins that act as catalysts to start biochemical reactions

The gastrovascular cavity of cnidarians and flatworms allows them to digest larger prey than they could with intracellular digestion. However, the effectiveness of a gastrovascular cavity in supplying the animal with nutrients is limited. Because there is only one opening to the external environment through which prey is taken in and remnants are expelled, the animals have to complete digestion of the first prey and expel its remnants before taking in another prey. With the evolution of a second opening in the digestive system, the digestive system became a digestive tract, or alimentary canal, making it a one-way system between mouth and anus. Food could now be taken in and processed continuously, providing the animal with more nutrients. Most animals—including vertebrates, arthropods, **mollusks**, round worms and earthworms—have this form of digestive tract.

mollusks a large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

A one-way digestive tract is efficient because it allows the food to pass through a series of specialized regions. Such regions may be specialized for protein, fat, or carbohydrate digestion, making each step more efficient. Other regions may be used for food storage or for preparing the food for chemical digestion by physically grinding it into smaller pieces, which exposes more surface area to the action of digestive enzymes. These specialized regions eventually evolved into organs as parts of a complex digestive organ system. However, because nutrient dispersal, by the digestive system itself to all cells of the body, was no longer feasible with such a specialized digestive system (and animals became larger and bulkier) a separate cardiovascular system evolved to serve that function.

Simple animals such as earthworms suck soil into the mouth with the pharynx, pass it through the esophagus into the crop, where it is moistened and stored. From there it is moved into the **gizzard**, which contains small grains of sand that help grind down the food. The actual digestion and **absorption** of nutrients takes place in the intestine, and anything that remains is excreted through the anus. Insects also move food from the mouth through the esophagus into a crop (all parts of the foregut) for food storage and moistening. From there it is moved to a midgut where digestion and nutrient absorption through specialized extensions, or ceca, takes place. The hindgut functions mainly to reclaim water and ions from the gut content that would otherwise be lost in the feces.

gizzard a muscular part of the stomach of some animals where food is ground

absorption the movement of water and nutrients

This young South African spotted hyena licks its mother's mouth to stimulate regurgitation of partially chewed, digested food. The parental act of chewing and digesting food before it is eaten makes consumption easier for many juvenile animals.

Physical Digestion of Vertebrates

During the evolution of vertebrates, two trends can be recognized. First, animals became larger, requiring a more efficient digestive system to meet their nutritional needs. Second, some animals moved from living in water to living on land. This meant they required more energy for locomotion and a more efficient digestive system to provide that energy.

smooth muscle the muscle of internal organs that are not under conscious control

enzyme a protein that acts as a catalyst to start a biochemical reaction

In vertebrates, the physical digestion of food begins in the mouth. Birds crunch seeds with their beaks, and mammals use their powerful jaws and specialized teeth to chew food into smaller pieces, increasing the surface area for digestive enzymes to work on. Salivary glands in the mouth coat the food with saliva to make it slippery for swallowing. After swallowing, the food is moved along the digestive tract with the help of involuntary **smooth muscle** contractions, called peristalsis. Sphincters regulate the passage of food from one chamber of the digestive tract into the next. First the food passes through the esophagus into the stomach. In the stomach, the food is stored and mixed with gastric juice. The gastric juice kills most swallowed bacteria, breaks down most food into individual cells (increasing the surface area for **enzyme** attack), and begins the digestion of proteins. Birds may store food in a crop without digesting it before passing it into the stomach. This allows parent birds to regurgitate food from their crops for their nestlings. Some birds move food from the stomach into a muscular gizzard containing swallowed stones that grind down seeds before digestion continues in the small intestine. The small intestine is the major site of digestion and absorption in vertebrates, and has three distinct regions—the duodenum, the jejunum, and the ileum. Accessory glands such as the pancreas and liver secrete digestive enzymes and other products into the duodenum. The jejunum also releases digestive enzymes. These enzymes digest carbohydrates, proteins, nucleic acids, and fat, and the products of the digestion are absorbed by cells lining the small intestine, especially the ileum. The large intestine is connected to the small intestine. The major function of the large intestine is to reabsorb water that was added to the gut content in the small intestine, and to absorb inorganic ions from the digested food. As a result the feces become more solid. The large intestine also contains many bacteria, which may produce gases as

byproduct of their metabolism, but also vitamins, such as vitamin K, that are absorbed into the blood. Feces are stored in the rectum until they can be eliminated through the anus.

Many grazing animals (e.g., deer, cattle, sheep, giraffes) who swallow grass hastily without chewing while watching out for predators, have a two-part stomach. In the first part of the stomach, the unchewed grass is fermented and predigested by bacteria before it is regurgitated back up into the mouth. There it can be chewed more thoroughly when the animal is in a safe place. After chewing, the food is swallowed again and passes into the second section where digestion takes place. **Herbivores** generally have a longer and more complex intestine than carnivores. This allows them to get as many nutrients as possible out of their more nutrient-poor food. SEE ALSO Digestion.

herbivores animals who eat plants only

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Dinosaurs

The history of the Dinosauria begins with one of the dinosaur's small extinct ancestors called *Petrolacosaurus.* Around 270 million years ago, this animal was a member of the group of early land vertebrates called the diapsids that had skulls with two openings behind the eye socket (other evolutionary groups, like fish and amphibians, had one opening or none at all). The diapsids are believed to be the ancestors of the lepidosaurs (modern lizards and snakes) as well as of the archosaurs, the group that led to the dinosaurs.The lepidosaurs achieved great evolutionary success. The extra openings in their skulls led to the interesting structures found in modern snakes, including a light and flexible skull that allows them to catch and eat prey larger than their mouths.

Ancestry: Euparkeria

The first known archosaurs appeared in the Permian Period (319 to 286 million years ago) and they were well on their way to becoming large-sized animals by the early Triassic (about 245 million years ago). When discussing dinosaur ancestry, paleontologists prefer to examine an interesting little archosaur known as *Euparkeria. Euparkeria* had anatomical characteristics of most archosaurs (and eventually the dinosaurs), including deeply rooted, sharp, serrated teeth; two holes behind the eyes; and a broad space in front of the eye sockets. Their jaws had a distinctive opening that was different in shape and position from other tetrapods, and their spine had small bony plates suggestive of the beginning of armor plating. Perhaps the most important feature of *Euparkeria* is the arrangement of their hipbones.

As the archosaurs evolved, many species developed hipbones that allowed the angle of their hind limbs to change from a sprawling posture, such as a lizard or crocodile has, to an erect one, like a bird. The limbs came under the body instead of being spread out to the side. This leg position provided a firmer basis of support for a larger and heavier body. Dinosaurs became the largest land animals, and part of their ability to become so large was a direct result of this change in posture. When the legs are spread out to the side they can only support so much weight before the joints that attach them to the body give out. With the legs underneath the body, they form a kind of column that can support a great deal more weight. This means a larger animal can move around without being slow and sluggish or breaking its bones. This change in body posture is one of the main reasons dinosaurs were able to become so large.

One important group of archosaurs was the thecodonts, which included *Euparkeria*. During the Triassic period, thecodonts continued to evolve and undergo changes in body shape. By the end of the Triassic 213 million years ago), there were two groups of thecodonts, the saurischians and the ornithischians. The saurischians ate both plants and meat. Their pelvis was distinctive in that the three bones that made up the hip—the ilium, the ischium, and the pubis—were joined so that they angled away from each other in a triangular shape. There were two distinct groups of saurischians, the theropods ("beast feet") and the sauropods.

carnivorous describes animals that eat other animals

The theropods were **carnivorous** dinosaurs that walked upright on two feet. Some of the most famous dinosaurs we know today are theropods, including *Tyrannosaurus rex*, *Velociraptor*, and other swift and dangerous predators. The other group of saurischians, the sauropods, were herbivores and moved about on four legs. Some sauropods, including *Brachiosaurus*, *Camarasaurus*, and *Ultrasaurus*, were the largest animals that ever lived on Earth. The other evolutionary offshoot of the ancestral thecodonts was the ornithischians. The hip structure of the ornithischians differed from that of the saurischians in that their forward-extending pubis bone was turned toward the back. Because this bone structure also occurs in modern birds, the ornithischians are called bird-hipped dinosaurs. (The ornithischians are not ancestors of birds, they just have a similar hip structure.) The legs, feet, and anklebones of ornithischians were similar to those of the saurischians.

A peculiar adaptation of ornithischians was the beaklike covering of the front of the mouth, which is characteristic of the ceratopsians and duck-billed dinosaurs. Ornithischians also had a complex network of bony rods along their spine which supported the spine. All ornithischians were herbivores. The group contains some of the more distinctive-looking dinosaurs, including *Stegosaurus*, which had a series of large, triangular, horn-covered bony plates along its back and tail; the heavily armored *Ankylosaurus;* and the ceratopsians, including *Triceratops*, with its huge bony hood and horns.

The First True Dinosaurs

The first groups of true dinosaurs, the coelurosaurs, appeared about 210 million years ago in the late Triassic period. These dinosaurs were carnivorous theropods. They were agile and lightly built; most species were smaller than an adult human. Some of the best fossil specimens of the coelurosaur known as *Coelophysis* were discovered in the United States in New Mexico.

Other coelurosaurs were the smaller *Ornitholestes*, a heavily jawed predator with nostrils that faced upward on its skull, and *Coelosaurus* perhaps the best-known coelorosaur. All coelorosaur feet had three toes pointing forward and a fourth facing back. The fifth toe was greatly reduced. This pattern persisted throughout the history of all the dinosaurs and is one way to document change within the group.

From the remains of dinosaurs that appear in the fossil record, paleontologists can infer what those animals looked like, how they moved, and what and how they ate. But paleontologists today are also asking: What dinosaur behavior can we infer from fossils? The Maiasaura ("Good Mother" dinosaur) eggs and young found in Montana in 1978 are an excellent example of one way paleontologists can hypothesize dinosaur behavior. In this case, the young dinosaurs at the site were too big to fit in the fossil eggs in nests that were found nearby. Paleontologists think that the parent dinosaurs brought food to the baby dinosaurs and protected them from predators. Also, since many nests were discovered together in a small area, the scientists think that these dinosaurs many have lived together in some sort of herd.

This *Triceratops* skull is on display in the Graves Museum of Archaeology and Natural History in Dania, Florida. The *Triceratops* skull made up nearly one-third the length of its body. The skull featured a large "frill" (bony plate) at the dinosaur's neck, two large horns placed just above its eyes, and a nose that looked like a bird's beak.

The thinking is that if the baby dinosaurs were too big to fit in the eggs, but were still in the nest they probably remained in nest for some time after hatching. They would have to had food brought to them by the parents until they were large enough to forage for food on their own. Many birds care for their young this way by bringing them food until the fledglings are old enough to feed and fly on their own. This is another piece of evidence that links birds and dinosaurs.

At the end of the Cretaceous era (around 64 million years ago), something happened that caused the remaining dinosaurs to die out. No one knows for sure what the event was. Many scientists believe an asteroid hit Earth, causing harsh atmospheric conditions that led to the dinosaurs' extinction. However, very few species of dinosaurs remained by the end of the Cretaceous. Scientists will probably never know what actually happened to the dinosaurs. Most think they are still here as birds. This is not difficult to imagine when you look closely at the characteristics of birds. It is comforting to imagine that these fantastic and lively creatures are still among us, only much smaller.

Recent discoveries of many species of feathered dinosaurs in China have really supported this idea. Most scientists know agree that birds are very closely related to dinosaurs, if not actually dinosaurs themselves. The so-called "missing links" between dinosaurs and birds have been found.

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Diurnal

Diurnal organisms are those that are active mainly during the day. When activity patterns of an organism occur in cycles of about twenty-four hours, the pattern is called a **circadian rhythm**. Diurnal animals, which sleep during the night and are active during the day, or, conversely, **nocturnal** animals, which sleep during the day and are active at night, follow a circadian rhythm. Scientists believe that circadian rhythms are controlled by an internal timing mechanism called a biological clock. The exact nature of this internal timing is not known, but varying levels of hormones are thought to play a role.

circadian rhythm a daily, 24-hour cycle of behavior in response to internal biological cues

nocturnal active at night

Scientists generally concur that the evolution of species on Earth has proceeded in the direction to take full advantage of all possible niches (the specialized role of an animal in its environment). Thus some organisms have evolved to be better suited for nighttime, which is relatively darker, cooler, and more humid. Other creatures have become more specialized for daytime, which is lighter, warmer, and drier. In a sense, then, organisms work in "shifts" so as to use the environment at all times. This allows a greater number of organisms to occupy the same area without excessive competition for space and food at any one time. The day shift includes animals such as humans, dogs, songbirds, elephants, squirrels, gorillas, deer, hawks, lizards, butterflies, honeybees, and chimpanzees. The night shift includes such animals as owls, bats, and mice.

Some animals have both nocturnal and diurnal species. In the tropics, mosquitoes transmit two serious human illnesses, malaria and dengue fever. The *Aedes aegypti* mosquito, which carries dengue fever, is diurnal. The *Anopheles* mosquito, which carries malaria, is nocturnal.

Adaptations of animals to diurnal activities are evidenced by the differing properties of some animals' eyes. For example, nocturnal birds like the owl generally have larger eyes than do diurnal birds like the hawk, for which more light is available. Larger eyeballs assist the nocturnal species in getting as much light as possible to the **retina**. SEE ALSO NOCTURNAL.

retina a layer of rods and cones that line the inner surface of the eye

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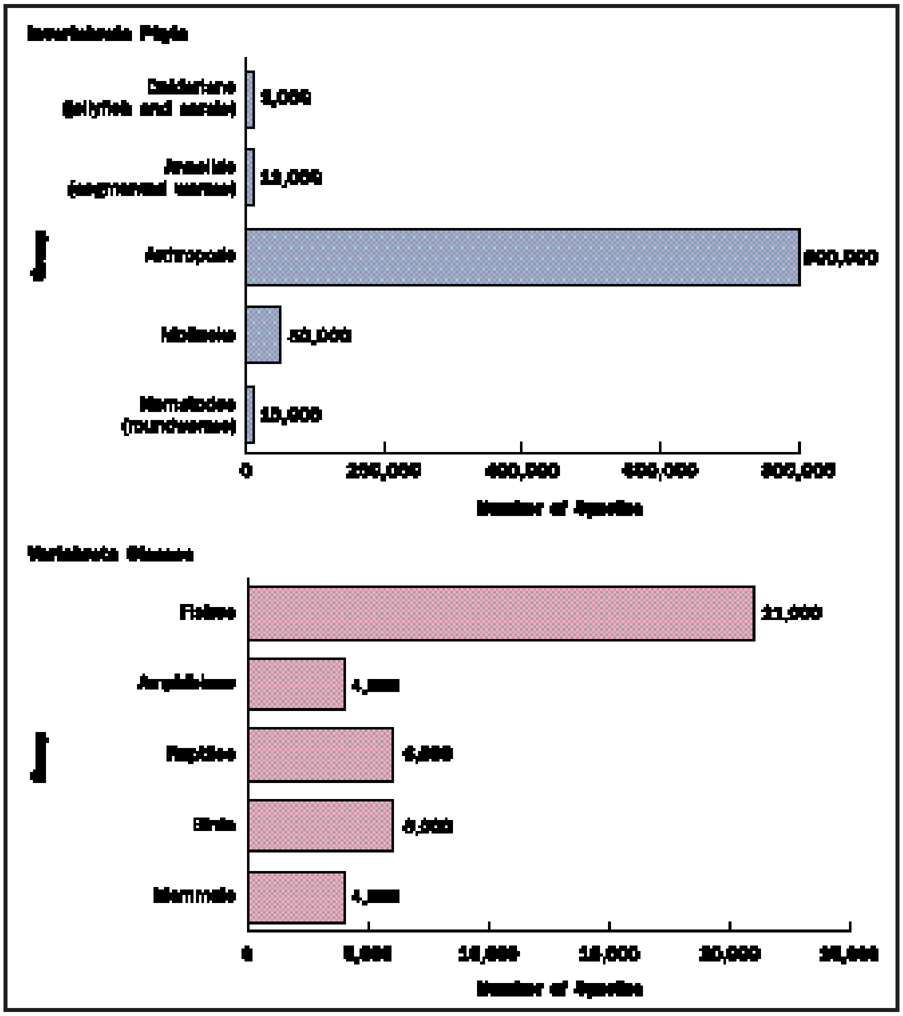
Diversity of Major Groups

archae an ancient lineage of prokaryotes that live in extreme environments

horseshoe crabs "living fossils" in the class of arthropods

crustaceans arthropods with hard shells, jointed bodies, and appendages that mainly live in the water

The diversity, or variety, of animal species in the major groups is staggering. Scientists currently recognize more than one million species of animals, and this number does not include all species of bacteria, **archae**, and protozoa. Invertebrates make up 95 percent of the more than one million known species. Arthropods—spiders, **horseshoe crabs**, **crustaceans**, insects, centipedes, millipedes, and scorpions—are the most successful phylum in the animal kingdom. Arthropods account for 80 percent of all



Graphic representation of the wide diversity of life forms on Earth.

known species of animals. Insects are the most successful arthropods. Scientists estimate that there are one billion insects for each human on Earth! SEE ALSO BIOLOGICAL EVOLUTION; PHYLOGENETIC RELATIONSHIP OF MAJOR GROUPS.

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Domestic Animals

The domestication of animals for agricultural purposes dates back to the beginning of the Neolithic period, 9,000 years ago. Early agriculturalists in the Fertile Crescent of the Near East began breeding goats first, then sheep, pigs, and cattle. The stimulus for this advance was probably **global warming** at the end of the Ice Age, which caused drought in the Near East and

global warming a slow and steady increase in the global temperature forced people to congregate around reliable sources of water. The subsequent increase in **population density** strained the ability of hunting and gathering to meet the demand for food. Herding animals provided a reliable source of protein-rich food during times of scarcity.

population density the number of individuals of one species that live in a given area

A domestic animal is characterized by several attributes. First, it is bred in captivity for economic profit. Second, humans control its breeding, territory organization, and food supply. Animals bred in captivity tend to have different anatomies and behavior from their wild ancestors. Stress and dependence on humans causes hormonal imbalances and disrupts growth in different parts of the organism. Captive breeding exaggerates these effects, leading to the retention of juvenile characteristics, such as submissive behavior, a smaller body, fat deposition under the skin, shortening of the jaws, and smaller teeth and brain. Domestic animals also tend to appear quite different from their wild ancestors, as animal breeders selected them for a variety of idiosyncratic traits in order to identify them easily as property.

Dogs

The first animal species to become domesticated was the dog (*Canis familiarus*), occurring more than 12,000 years ago in west Asia. Modern-day mastiffs and greyhounds have changed little from their ancestors 4,000 years ago in Egypt and Asia. Each of the more than 400 breeds of dog is the same species. Many experts think dogs descended from the wolf (*Canis lupus*). Other researchers suggest that the domestic dog may have descended from a now extinct wild dog. In either case, breeders selected dogs to look different from their ancestors by favoring those with black, white, or spotted coats, long ears, and curled tails. Dogs possess many juvenile characteristics of wolves, including submissive behavior, short jaws, and smaller brains.

Some believe that dogs descended from wolves and that dogs were easily domesticated because of the similarity between wolves' and humans' social behavior. Both species are acutely aware of social hierarchies, making group living more organized and complex than in any other species. When wolves began to scavenge around human settlements, people adopted pups to serve as guards and hunting companions. The human-raised wolves adapted well to human society and likely treated their human companions as if they were a wolf pack. Eventually, humans started to control the breeding of these proto-domestic wolves and the evolution of *Canis familiarus* began.

Livestock

Livestock were the next species to be domesticated. Archaeological evidence of domestic sheep and goats in the Jordan Valley dates back to 7,000 B.C.E. Sheep were domesticated from the Asiatic moufflon (*Ovis orientalis*), a grass grazer found in hills and foothills. Domestic goats were derived from the bezoar goat (*Capra aegagrus*), a hardy browser found in mountainous terrain. Both species were relatively easy to breed in captivity because they were social and adapted to harsh environmental conditions.

Domestic humpless cattle.

Domestic humpless cattle (*Bos taurus*) appear in the archaeological record 6,000 years ago in Egypt and Mesopotamia. Their ancestor was the wild ox (*Bos primigenius*), a browsing and grazing **ruminant** in forests and scrub, now extinct. They provided a multitude of uses,

ruminant a plant-eating animal with a multicompartment stomach such as cows and sheep

Ranchers herding cattle in Utah's Salt Lake Valley. The domestication of animals—including sheep, pigs, goats, and cattle—for agricultural purposes dates back thousands of years.

including labor, milk, meat, bone, and tallow (for burning). Domestic humped cattle (*Bos indicus*) were domesticated independently in Southeast Asia. The domestic yak, water buffalo, and mithan were each domesticated independently from a different bovine species.

Pigs. Pigs were domesticated from the wild boar (*Sus scrofa*) around the same time as cattle. They resemble dogs and humans more than other livestock in several ways. Pigs enjoy body contact with other family members and build nests and beds. They are physically weak at birth, requiring significant parental investment. These similarities may underlie the variation in cultural attitudes toward pigs as agricultural products. Whereas Muslims, Hindus, and some Christians traditionally considered pigs taboo as a source of protein, the Chinese bred both pigs and dogs specifically for their meat.

Horses

Horses were domesticated in the third millennium B.C.E. in Russia and western Asia from the wild horse (*Equus ferus*). In early 2001, scientists from the University of California, Los Angeles, and three Swedish universities published research indicating that the domestic horse was so genetically diverse, it could not have originated at one place. **Mitochondrial DNA**, which is genetically transmitted from mother to children, indicated several different matrilineal (female-based) lines. Based on this finding, the researchers suggested that wild horses were tamed independently in several different parts of the world. The "idea" of domesticating horses may have originated in one place, probably central Asia, but various cultures captured and tamed their own horses.

mitochondrial DNA DNA found within the mitochondria that control protein development in the mitochondria

Horses are grass grazers, making them especially well suited to dry plains. At first they were used for food, then as vehicles for travel. Their ability to carry people had an enormous impact on human economies by speeding travel and transport and was probably a necessary step in the development of civilization.

Cats

Domestic cats are an exception to the rule of domestication. Feral cats (*Felis silvestris*) helped rid rats and mice from stored grains once agriculture became widespread. Because cats are territorial, nocturnal carnivores, controlled breeding was exceptionally difficult. Consequently, there are relatively few cat breeds even after thousands of years of domestication, and those that exist are not much different from their wild ancestor or each other. The weakness of the effects of domestication on cats has made it difficult to determine when or where they were domesticated, but archaeological evidence indicates that ancient Egyptians kept cats as pets by 1000 B.C.E. SEE ALSO ANIMAL RIGHTS; BIOETHICS; FARMING; HUNTER-GATHERERS.

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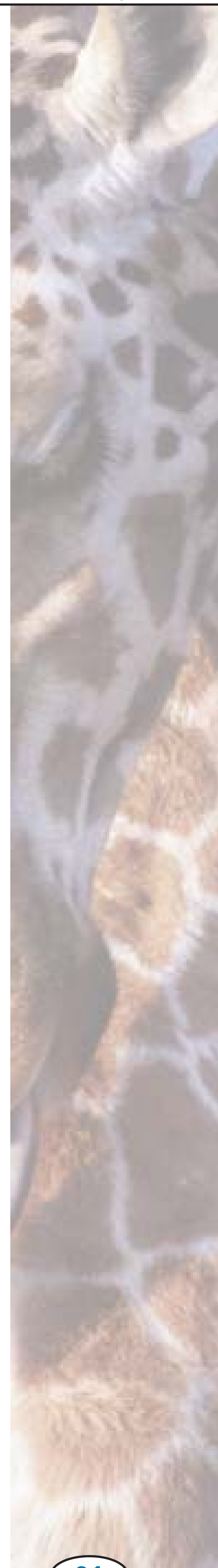
Dominance Hierarchy

Dominance hierarchies characterize many species in which individuals live in close proximity to one another. The dominance hierarchy is a social structure within a group of animals in which certain individuals are dominant over others, and are therefore able to claim access to better resources in the form of food, mates, shelter, and other desirable commodities.

The evolution of dominance hierarchies in a species is indicative that there is competition for resources. Members of a dominance hierarchy are aware of how they are positioned within that hierarchy and they behave appropriately. Of particular importance, the establishment of dominance hierarchies allows for the resolution of conflict between individuals without costly fighting that can result in serious injury or even death. In species where organized group living is essential to survival, it also serves to maintain order among pack members.



Establishment of Dominance Hierarchies

Dominance hierarchies are often established through ritualized displays or mild fighting, rather than all-out battle. The loser in a battle for dominance typically moves away from a choice habitat or a disputed mate. Among primates, dominance conflicts frequently involve no more than the display of enlarged canines, sometimes through yawning. Bears, also, will roar or wave their open mouths at social inferiors. Behaviors like these do not require fighting, but do result in the prominent exhibition of potentially formidable fighting weapons. In other cases, as in elephant seals, there actually can be prolonged, often bloody fighting. However, once the hierarchy is established, subsequent fighting is less frequent. In many cases, there is a strong correlation between dominance and large size.

Dominance hierarchies have to be reestablished when certain individuals feel prepared to move up within the hierarchy, or when new individuals are introduced into an area. During such time a series of challenges may occur. This can be a stressful period for all individuals involved.

Dominance and Mate Competition

Mate competition is extremely common in the animal kingdom, and many dominance hierarchies relate to competition either for mates, or for those resources such as admirable territories that will attract them. In most cases males compete for females, although there are also a few instances of females fighting for males.

There are clearly advantages to dominance. Dominant males have been shown in many species to copulate more frequently or to produce more offspring. In cowbirds, for example, only the dominant male is allowed to sing the songs that are most effective in attracting females. If subordinate males attempt to sing these highly charged songs, they are attacked, often brutally, by more dominant individuals.

Elephant seals are another group in which reproductive success is linked to dominance. Dominance battles in this species involve two males posturing chest to chest and attempting to bite each other, with the loser ultimately retreating. In a few species, such as wolves, the dominant members of a group are the only ones that reproduce.

One tell-tale sign of competition for mates is **sexual size dimorphism**, which describes a situation where one sex of a given species has much greater body size than the other. In the case of mate competition, it is the males that are larger than females. (There are other species where the females are larger, including, the large majority of frogs. However, in these species the large size of females appears to be associated with increased fertility rather than with the establishment of dominance.)

sexual size dimorphism a noticeable difference in size between the sexes

Sexual size dimorphism is often particularly pronounced in species where it is possible for a single male to monopolize many females, as in elephant seals. In fact, a study across various pinniped species (seals, sea lions, etc.) suggests that the degree of sexual size dimorphism is positively correlated with the size of the harem.

The spotted hyena. A particularly interesting example of the dominance hierarchy is that of the spotted hyena. It is the largest species of hyena and has also been called the laughing hyena because of the calls that individuals

Dominance hierarchies are often established through mild fighting. In this case, the dominant grey wolf establishes superiority by nosing a lower-ranking wolf into submission onto the ground.

make when they are in danger. Spotted hyenas live in social groups that vary greatly in size, with the largest having as many as eighty members. Each group defends a territory and hunting occurs in packs.

What is unusual about social organization in this species is that females are dominant within the group and at the same time possess reproductive organs that very much resemble those of males. In fact, female genitalia resemble the scrotum and testes of males so closely that it is almost impossible to determine the sex of individuals in the field.

One early hypothesis to explain this male-mimicking anatomy was that females evolved it in order to participate in the hyena greeting ritual, in which members of the same social group sniff each others' erect penises when they meet again after an absence. Because greeting behavior is important to group solidarity, it was argued that females evolved male-like anatomy so they could participate as well.

However, the greeting ritual theory has since been abandoned in favor of an argument based on fighting for dominance within the hierarchy. There are numerous benefits to being the dominant female within a spotted hyena clan. Females who are high in the hierarchy have priority at kills, and obtain more food than subordinate females or males. Dominant females tend to be the largest hyenas of a pack. They also tend to produce dominant offspring. The production of a dominant male is particularly advantageous because only the dominant male within a pack mates.

Many scientists believe that because aggressive behavior is advantageous in competitions for dominance, female hyenas have evolved high circulating levels of androgens (male sex hormones) such as testosterone, which promote aggression. The curious male-mimicking genitalia are now believed to be a mere side effect of the unusually high testosterone levels. The testosterone circulating in the female's bloodstream while she is pregnant results in the masculinization of the anatomy of both her male and female offspring. It was indeed confirmed that female spotted hyenas do in fact have unusually high testosterone concentrations in their blood. SEE ALSO BEHAVIOR; SOCIAL ANIMALS.

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Drosophila

The common fruit fly *Drosophila melanogaster* is a human **commensal** typically seen hovering around garbage cans or the bananas in kitchen fruit bowls. These small flies have been model organisms for genetic studies since about 1910. The reason these flies have been so useful to biologists is because they are small and thus take up little lab space, they are easily cultured, they have a short generation time, and they are extremely fertile.

commensal a symbiotic relationship wherein one species benefits and the other is neither helped nor harmed

In 1910 Thomas Hunt Morgan of Columbia University in New York City discovered a white-eyed mutant in *Drosophila melanogaster* which differed from the standard red-eyed fruit fly. Mutations such as this allow geneticists to narrow down the chromosomal location of the gene or genes responsible for a particular phenotype, such as eye color. Since then thousands of other mutations in *Drosophila* have been identified and mapped, including mutations that alter behavior and learning. At the genetic level, more is known about *Drosophila* than any other multicellular organism. Furthermore, much of our knowledge of *Drosophila* is relevant to humans. For example, genetic mutations causing tumors in flies have homologues in other animals. With the sequencing of the entire genome of *Drosophila* in 2000, *Drosophila* will continue to be an important tool in understanding how the genotype controls the phenotype of complex organisms.

One aspect of biology in which *Drosophila* proved to be extremely useful was in the study of development. The life cycle of *Drosophila* is made up of four stages: egg, larva, pupa, and adult. Eggs are typically laid in a food source such as a rotting fruit and develop into larvae after about one day.

A fruit fly, also known as *Drosophila melanogaster.* Fruit flies are are a favorite subject of genetic studies, in part due to their compact size and short developmental cycle.

The larvae resemble small segmented worms, and rove about eating the food for several days until they pupate. At pupation the larvae encase themselves and remain stationary for four days as they **metamorphose** into adult flies. As are all arthropods, the adult flies are composed of three main sections—the head, thorax, and abdomen.

metamorphose a drastic change from a larva to an adult

In 1995, three developmental biologists—Americans Edward B. Lewis and Eric F. Wieschaus, and German Christiane Nüsslein-Volhard—won the Nobel Prize for Physiology or Medicine for determining the genes that control the developmental processes in *Drosophila.* They showed that once maternally transcribed genes determine the **anterior/posterior** polarity of the egg, the zygote's own genes control the rest of development. First the zygote's gap genes divide the embryo into broad bands. This activates the pair-rule genes which further divide the embryo into seven bands, each representing two of the larval segments. The pair-rule genes then activate the segment polarity genes, which establish the anterior/posterior polarity of each segment. Finally, the segment polarity genes activate the homeotic selector genes, which establish segment identity in both the larval and adult stages.

anterior referring to the head end of an organism

posterior behind or the back

Interestingly, complexes of the homeotic selector genes are arranged along the chromosome in the same general order that they are expressed along the length of the fly. For example, genes transcribed in the first segments of the fly are located in front of the genes transcribed in the last segments. Also, the first homeotic gene in the complex is active slightly earlier than the second gene and so on. The homeotic selector genes of *Drosophila* were later found to be arranged in the same order as the **homologous** homeotic selector genes in humans and other animals. This implies that the ordering of the homeotic selector gene complex has been conserved since the beginning of animal evolution.

homologous similar but not identical

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Echinodermata

The six thousand species of marine animals in the phylum Echinodermata ("spiny-skinned") are, like **annelids**, arthropods, chordates, and **mollusks**, characterized by a true **coelom**, or body cavity. However, echinoderms differ from all other coelomates (except for chordates) in their embryonic development. Very early in this development, a ball of cells called a blastula develops an infolding called a blastopore, which eventually reaches the other side of the embryo and forms the digestive tract. If the blastopore forms a mouth, the embryo is a called a **protostome**, meaning that the mouth (*stoma*) forms first (*proto*) after the anus. If the blastopore forms an anus, it is called a **deuterostome**, meaning that the mouth (*stoma*) forms second (*deutero*) after the anus. Echinoderm embryos are deuterostomes. This difference in development is so fundamental that protostomes and deuterostomes are thought to have diverged before any other branchings that led to the modern coelomate **phyla**. In other words, echinoderms and chordates are more closely related to each other than to any other organisms.

Although both are deuterostomes, echinoderms and chordates have significant differences. All echinoderms have a **calcium** carbonate skeleton just beneath the skin which typically bears projecting spines, hence the name of the phylum. Like **cnidarians** (jellyfish), echinoderms are **radially symmetrical** as adults, whereas chordates are **bilaterally symmetrical**. However, larval echinoderms are also bilaterally symmetrical. The late development of radial symmetry in echinoderms indicates that it is relatively recently evolved in the taxon. Modern echinoderms probably evolved from a mobile, bilaterally symmetrical ancestor by adding a sessile life stage, which then evolved radial symmetry. Many echinoderm species have since evolved mobility as radially symmetrical adults.

Echinoderms possess a unique water vascular system, which provides structural support for a set of tube feet used for locomotion. This system consists of internal canals lined with protruding tube feet and muscular sacs called ampullae. This system is also connected to the outside of the organism by an opening called a madreporite, through which water goes in and out of the system. When the ampullae contract, water is pushed into the tube feet, making them rigid. Most echinoderms have muscles in the ends of the tube feet that contract to create suction between the foot and a surface upon which locomotion occurs. The tube feet are also used for gas exchange.

annelids segmented worms

mollusks a large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

coelom a body cavity

protostome an animal in which the initial depression that starts during gastrulation becomes the mouth

deuterostome an animal in which the first opening does not form the mouth, but becomes the anus

phyla broad, principal divisions of a kingdom

calcium a soft, silvery white metal with a chemical symbol of Ca

cnidarians aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

radially symmetrical describes an animal that features a wheel-like symmetry in which its body parts radiate out from a central point

bilaterally symmetrical describes an animal that can be separated into two identical mirror image halves

Echinoderms, such as this orange-footed sea cucumber, have a calcium carbonate skeleton just beneath the skin which typically bears projecting spines.

Phylum Echinodermata is made up of five classes: Asteroidea (sea stars), Ophiuroidea (brittle stars), Echinoidea (sea urchins and sand dollars), Crinoidea (sea lilies and feather stars), and Holothuroidea (sea cucumbers). Sea stars have the typical echinoderm **body plan**—a central disk from which five or more arms radiate. They have no head or brain, and their sensory perception consists of eyespots at the end of the arms and neurosensory cells scattered throughout the **epidermis**. A ring of nerves around the mouth connects to nerve cords extending down the arms and coordinates movement. Sea stars feed on **bivalve mollusks** by prying them open with their arms and tube feet, then turning their stomachs inside out into the opening to digest the prey while it is still in its shell.

body plan the overall organization of an animal's body

epidermis the protective portion of the outer portion of the skin found in some animals, it is composed of two layers of cells where the outer layer is continuously shed and replaced by the inner layer

bivalve mollusks mollusks with two shells such as clams

Brittle stars look like sea stars but have thinner arms. Like sea stars, they are mobile, but their tube feet lack suction and are not used for locomotion. Also like sea stars, brittle stars can regenerate limbs that have been lost. Incredibly, a leg can regenerate an entire body. Some species reproduce asexually by dividing and regenerating.

Sea urchins and sand dollars do not have arms, but retain radial symmetry in the rows of tube feet poking out of their hard skeleton. Whereas urchins are spherical, sand dollars are flattened along the axis of radial symmetry. They are armed with movable spines that can be poisonous. Many species have powerful jawlike structures called "Aristotle's lanterns," which they use for grazing on algae and other food attached to a surface, such as rock or coral. As with sea stars and brittle stars, the mouths of urchins and sand dollars are located on the bottom of the body.

Scientists believe that sea lilies and feather stars resemble the first echinoderms because they are sessile and their mouths and arms are oriented upward to gather food from the water. This was probably the intermediate evolutionary step through which the other echinoderms passed on their way to a more mobile adult stage. In fact, 500-million-year-old sea lily fossils are virtually indistinguishable from modern species.

Sea cucumbers are the most recently evolved echinoderms. They have lost most of the skeleton, which remains in the form of small bony particles in the skin. Although they retain five rows of tube feet, they are elongated from head to tail and display partial bilateral symmetry; some tropical species attain lengths of several meters. Sea cucumbers are the most mobile class of echinoderms, eating **plankton** from the water column or digging into the bottom sediments. They also have the ability to regenerate their guts after they expel them in response to predators, presumably as a deterrent.

plankton microscopic organisms that float or swim weakly near the surface of ponds, lakes, and oceans

Echinoderms play important roles in the ecological community of species. Ecologist Robert Payne conducted a famous experiment in Pacific-coast tide pools in which he removed *Pisaster*, a species of sea star. Because sea stars prey on mussels, removing them resulted in an explosion in the mussel population and disrupted the ecological balance of the entire community. Sea stars are so important to tide-pool communities that they are considered a "**keystone species**."

keystone species a species that controls the environment and thereby determines the other species that can survive in its presence

Echinoderms reproduce sexually, with male and female individuals releasing **gametes** into the water. The larvae that result are small and lightweight, like many other floating organisms. They transform into the relatively immobile adult form in order to grow and produce more gametes.

gametes reproductive cells that only have one set of chromosomes

Why did echinoderms evolve such a peculiar adult form of **sexual reproduction**? Why do the larvae not grow bigger and reproduce themselves? Like insects, echinoderms have evolved a strategy of specializing in different activities at different stages in the life cycle. The larval stage specializes in dispersal, which is important for finding new habitats and avoiding competitors. The adult stage specializes in growth and reproduction by moving only enough to capture prey or graze. The ability to **metamorphose** from a dispersal stage to a growth stage allowed echinoderms to perform each function more effectively than their ancestors did. But other primitive deuterostomes failed to evolve this sophisticated adaptation; one of them gave rise to the chordates, and eventually humans. SEE ALSO KEYSTONE SPECIES; PHYLOGENETIC RELATIONSHIPS OF MAJOR GROUPS.

sexual reproduction a reproduction method where two parents give rise to an offspring with a different genetic makeup from either parent

metamorphose changing drastically from a larva to an adult

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Echolocation

Echolocation is the process of using sound waves to locate objects that may be invisible or at a distance. Some bats use sound to locate their insect prey. Bats have vocal chords modified to emit the high-frequency sounds needed for good resolution and specially adapted ears to receive the sound. Animals also use echolocation for orientation, avoiding obstacles, finding food, and for social interactions. The animal produces sounds and listens for the echoes reflected from surfaces and objects in its environment. By analyzing the information contained in these echoes, the animal can perceive the objects.

In all species that use echolocation, the sound pulses are short bursts at relatively high frequencies, ranging from about 1,000 Hz in birds to at least 200,000 Hz in whales. Bats use frequencies from about 30,000 Hz to about 120,000 Hz. The pulses are repeated at varying rates depending on what the animal is doing. A flying bat will emit about one pulse per second. In a hunting bat close to its target, the rate may increase to several hundred pulses per second.

microchiroptera small bats that use echolocation

megachiroptera fruit bats and flying foxes

baleen fringed filter plates that hang from the roof of a whale's mouth

krill an order of crustaceans that serves a food source for many fish, whales, and birds

insectivores animals who eats insects

Most bats, including all small bats (suborder ***Microchiroptera***) and one genus of large bats (***Megachiroptera***) use echolocation. Other animals thought to use echolocation are a few species of shrews and two kinds of birds. Echolocation is also used by most toothed whales and porpoises (*Odontoceti*). **Baleen** whales (those that exist primarily on **krill** and similar organisms) do not use echolocation.

Echolocation in Bats

There are two groups of bats, large bats and small bats. Large bats eat fruit and find their way around using their excellent eyesight. Small bats are mostly **insectivores** that find their flying prey at dusk using echolocation. Bats produce sounds with their larynx, or voice box, which has adapted to produce loud, high-frequency sounds. The quality, frequency, duration, and repetition rate of the sounds produced varies with the species of bat and with the situation. For example, as a bat closes in on its prey, it will repeat the pulses of sound more frequently.

sonar the bouncing of sound off distant objects as a method of navigation or finding food

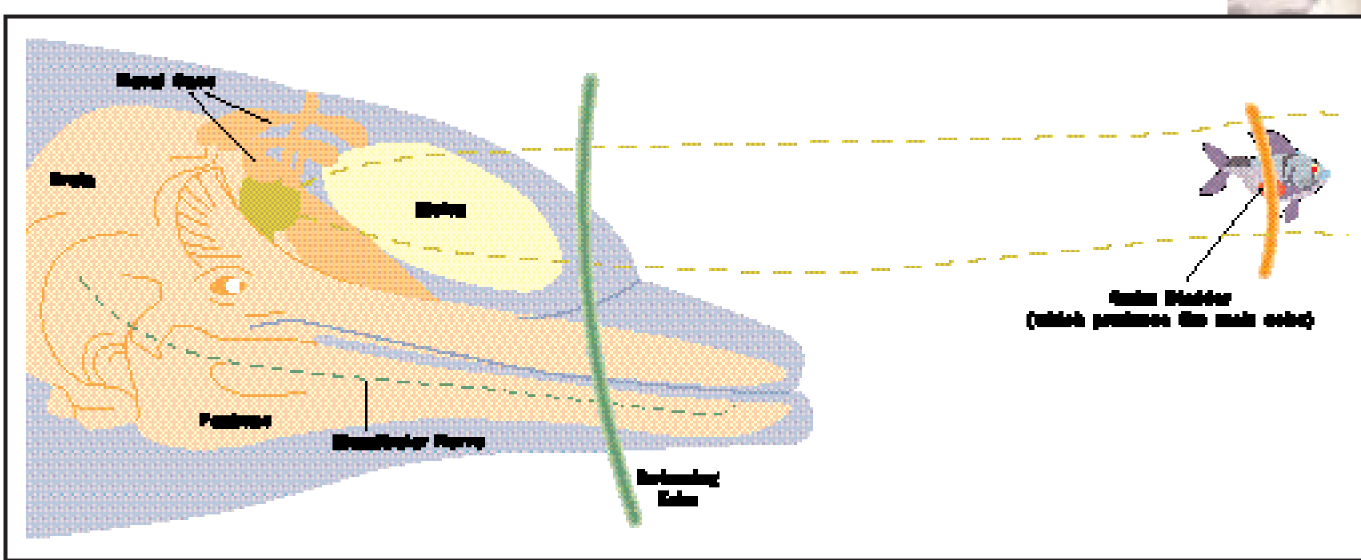
wavelength the distance between the peaks or crests of waves

Although the frequency of bat cries varies among species, the cries usually occur in a range between 30,000 and 80,000 Hz. The use of such high frequencies is an essential feature of the bat's **sonar** system. Because the target object (a moth or other small insect) is so small, a high-frequency, very short-**wavelength** sound must be used. A sound wave with a frequency of 80,000 Hz has a wavelength of around 4 millimeters (1/8 inch), which is suitable for locating a small moth.

Bat ears are well adapted to receive high-frequency sounds. In most bat species, the size of the outer ear is large relative to the size of the head. In some species that use relatively faint sounds, the outer ear is twice the size of the rest of the head. The large surface of the outer ear acts as an efficient collector of sounds. The outer ear is tuned to receive the frequencies emitted by the bat larynx, which helps the bat to hear the sounds it produces and tune out other sounds. The outer ear is also very mobile and can be rotated and tilted in various ways. The bat ear canal also contains a special organ that allows the canal to be closed to reduce the entrance of excessively loud sounds.

behavioral relating to actions or a series of actions as a response to stimuli

Neurophysiological and **behavioral** studies of bat hearing have revealed some curious features. One such feature is that bats do not respond behaviorally to frequencies below 10,000 Hz, although studies demonstrate that



Dolphins use echolocation to orient themselves in their surroundings. Redrawn from the *Greenpeace Book of Dolphins*, 1990.

they can hear these frequencies. This lack of a response is probably due to the bat's dependency on hearing for echolocation. Below 10,000 Hz, the wavelength is too long to be of any use in finding prey. It is also a frequency range where environmental noise is likely to occur, so bats have evolved the ability to selectively ignore sounds that are distracting and are not useful in finding prey. Researchers have also observed that bats are not easily disturbed by extraneous sounds of low frequencies, even very loud sounds. This peculiarity of hearing in bats may account for their resistance to distracting sounds.

Echolocation in Other Mammals

Dolphins and toothed whales use echolocation to orient themselves and locate objects in the water. These animals probably rely on sound production and reception to navigate, communicate, and hunt in dark or murky waters where sight is of little use. They produce sounds with their larynx and a complex system of cavities connected to their blowhole. The sounds used in echolocation are a rapid series of clicks. The clicks contain a wide range of frequencies, but most of the sound energy is in the 50,000 to 200,000 Hz range. These high frequencies are necessary for echolocation in water. Because the speed of sound in water is five times greater than in air, the wavelength of a sound of a given frequency is five times longer in water than in air. To achieve the same resolution, the frequency must be five times higher.

All toothed whales, including dolphins, have a fat-filled organ in the front part of the head called a melon. The melon acts like a lens for sound waves, focusing the sound waves into a narrow beam. Dolphins and other toothed whales generate a wide variety of clicks, whistles, and other noises used in communication and echolocation. The clicks they use for echolocation are of a higher frequency than those used for other forms of communication. This improves resolution and allows smaller prey to be located. The clicks are generated in a series of interconnected passages behind the melon. When the sound strikes an object such as a prey fish, some of the sound is reflected back toward the dolphin. Another fat-filled cavity in the dolphin's lower jaw acts as a receptor for this sound. The sound is carried from the fat-filled cavity to the middle ear and perceived by the animal's brain.

As soon as an echo from one click is received, the dolphin generates another click. The time lapse between click and echo enables the dolphin to determine the distance between it and the object. The difference in sound intensity received by each ear allows the animal to determine the direction. By emitting a series of clicks and listening to the echoes, the dolphin is able to locate and follow its prey. SEE ALSO Acoustic Signals.

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Ecologist

If a butterfly flaps its wings in the Amazon, it causes a typhoon in Asia. This half-joke by ecologists illustrates their belief that all life on Earth is connected in a delicate and barely understood balance. Ecologists study the web of relationships between the plants, animals, microorganisms, climate, and geography of a given habitat.

The term "ecology" was devised by German zoologist Ernst Haeckel in the mid-1800s to mean the study of home. In his time, most scientists studied species in isolation. Haeckel realized the importance of looking at the links between animals and the places in which they live.

Biologist Rachel Carson enlarged on the ecological principle of the interconnectedness of life with her books in the 1950s about the sea. She described how living creatures interact to form communities of mutual dependency and how the vast currents of air and water connect the activities of one habitat with all others on Earth.

Once considered by science to be hostile and competitive with one another, species are now known to cooperate in elaborate ways, suggesting to some ecologists that the entire planet behaves as a single living organism, with the health of any one part mirrored in the whole.

The necessary coursework for a college degree in ecology includes chemistry, calculus, physics, genetics, biostatistics, and geology or biogeography. Ecologists also study neurobiology; cellular, developmental and molecular biology; physiology; and behavior. Their training consists of laboratory work and at least one semester of fieldwork.

Virtually any question concerning how life operates is open to an ecologist. Some of the fascinating puzzles investigated by ecologists include how **pesticides** cause bird species to decline, why pollution from fossil fuels could affect the atmosphere, and even how the flight of a butterfly might cause a typhoon.

pesticides substances that control the spread of harmful or destructive organisms

Nancy Weaver

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Ecology

Ecology is a branch of science that studies the ways in which plants and animals interact with one another and with their surroundings. Ernst Haeckel, a German zoologist, invented the word "ecology" in 1869. It comes from the Greek words *oikos*, which means "household," and *logos*, which means "discourse" or "study." In *The Riddle of the Universe*, Haeckel applied the term *oekologie* to the "relation of the animal both to its organic as well as its inorganic environment."

For many years, ecology was an obscure branch of biology. In the late twentieth century, however, as environmentalism became a popular movement, ecology moved to the forefront of public opinion and also rose to prominence as a discipline. Some of the late twentieth and early twenty-first centuries' thorniest problems—expanding populations, food scarcity, and environmental pollution—were and are essentially problems of ecology.

Ecologists study organisms in various kinds of environments by looking for patterns of interaction. An organism's environment includes both other organisms and physical surroundings. It involves relationships among individuals within a population and among individuals of different populations. These interactions among individuals, among populations, and between organisms and their environment form ecological systems, or **ecosystems**.

ecosystems self-sustaining collections of organisms and their environments

Background

The origins of ecology lie in the natural history studies of the Greeks, particularly the philosopher and scientist Theophrastus (c. 372–d. 287 B.C.E.), a contemporary and friend of the philosopher Aristotle. Theophrastus first described the interrelationships among organisms and between organisms and their nonliving environment.

In the early twentieth century, botanists in Europe and America began to study communities of plants that seemed to depend on each other. The Europeans looked at the composition, structure, and distribution of plant

Some of modern ecology's essential issues, such as environmental pollution and overpopulation, are cause for global concern.

communities. The American botanists studied how plant communities changed over time. Animal ecology developed along separate lines until American zoologists began to study the interrelation of plant and animal communities as a whole.

Around the same time, biologists began to study the interaction of predators and prey, competition among species, and territoriality (especially in nesting birds). Austrian zoologist Konrad Lorenz studied instinctive and **learned behavior** (such as imprinting in birds). In 1920 German biologist August Thienemann proposed the concept of **trophic levels** and energy flow in ecosystems. English biologist Charles Sutherland Elton developed the concept of ecological niches and trophic pyramids. Nutrient cycling was studied in the 1940s and 1950s.

learned behavior behavior that develops in reaction to the environment

trophic levels divisions of species in an ecosystem by their main source of nutrition

Modern ecology is now based on the idea of the ecosystem, a well-defined unit including the organisms and the nonliving environment in an identifiable region. Ecosystems have several structured interrelationships, and they function by maintaining a flow of energy and a cycling of materials through a series of processes such as the food chain. Ecosystems become more complex as they mature. Complex ecosystems are more stable. The organisms in an ecosystem occupy a niche, which includes their feeding and other behaviors as well as their physical position in the ecosystem.

Subdivisions of Ecology

Ecology is a multidisciplinary science. It draws from such disciplines as plant and animal biology, **taxonomy**, physiology, genetics, behavior, meteorology, pedology (the study of soils), geology, sociology, anthropology, physics, chemistry, and mathematics. Plant ecology centers on a descriptive study of

taxonomy the science of classifying living organisms

the relationships of plants to other plants and their environment. Animal ecology studies population dynamics, distribution, behavior, and the interrelationships of animals and their environment. Plant ecology can often focus on just the plants. Because, however, animals depend on plants for food and shelter, animal ecology must include plant ecology. This is particularly true in areas of applied ecology, such as wildlife management.

Even within one of the subdivisions of ecology, ecologists usually concentrate on particular taxonomic groups, so that there are fields of insect ecology or the ecology of large mammals. Other ecologists may study particular ecosystems, such as marine environments or tropical rain forests. In applied ecology, basic ecological principles are applied to the management of plants and animals. Applied ecologists also study the effect of humans on their environment and on the survival of other species. Theoretical ecologists develop mathematical models and computer simulations of particular practical problems.

The study of an individual organism in relation to its environment is known as autecology. The study of groups of organisms in relation to each other and to their environment is called synecology. Autecology is closest to the original concept of ecology. When an individual organism is studied, it is possible to change variables in a controlled way. Thus, autecology is an inductive, empirical science. Synecology is more descriptive and deductive.

There are several other subdivisions of ecology. Ecological geography is the study of the geographic distribution of plants and animals. Population ecology is the study of population growth, mortality, **birthrates**, competition, and predator-prey relationships. Ecological genetics is the study of the genetics and ecology of local races and distinct species. Behavioral ecology is the study of the behavioral responses and social interactions of animals to their environment. Community ecology is the study of groups of organisms in a community. Systems ecology is the analysis and understanding of the structure and function of ecosystems by the use of applied mathematics, mathematical models, and computer programs. Finally, paleoecology is the study of the ecology of fossil organisms.

birthrates ratios of the number of births in an area in a year to the total population of the area

Methods

Ecologists work with living systems possessing numerous variables, so the techniques used by the other sciences are not directly applicable. It is obvious that an individual organism removed from its environment cannot be studied in the laboratory with any hope of **learning** about its relation to its environment. Ecologists must deal with many different variables, only a few of which can be controlled. Some of the variables are probably not known. Consequently, ecological measurements may never be as accurate or precise as measurements made in physics or chemistry.

learning modifications to behavior motivated by experience

In spite of these problems, statistical procedures and computer modeling are providing improved understanding of population interactions and ecosystem function. Computer modeling is becoming increasingly important in applied ecology, especially in the management of natural resources and of agricultural problems that have an ecological basis.

Several different modern techniques have improved the ecologist's ability to study animals in relation to their environment. Various techniques of telemetry can be used. For example, animals can be fitted with a radio transmitter and a global positioning system to provide a constant flow of information including body temperature, respiration, and position. Radioisotopes can be used to track nutrient cycling in an ecosystem. Laboratory microcosms can be constructed using living and nonliving material from natural ecosystems and can be held under conditions similar to those found in the field.

Interdependence in Nature

Ecology emphasizes the interaction between every organism with other organisms and with the natural resources in the environment, such as air, soil, and water. Nineteenth-century British naturalist Charles Darwin emphasized this interdependence in *On the Origin of Species*: "It is interesting to contemplate a tangled bank, clothed with plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp Earth, and to reflect that these elaborately constructed forms, so different from each other, and so dependent upon each other in so complex a manner, have all been produced by laws acting around us."

The well-established principles of ecology make it clear that humans cannot regard themselves as separate from and independent of the natural world. Nature is not just a place a person visits during a drive in the country. Changes made to the environment affect all the organisms in it. When vehicles and factories emit pollutants, plants and animals (including humans) are affected. Water contaminated by waste cannot support a mature, complex, stable ecosystem. Even the vast oceans cannot escape pollution.

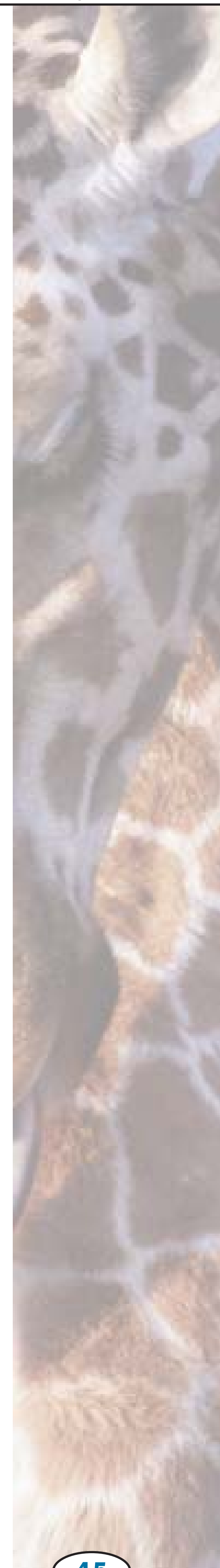
Applications of Ecology

Early in the twentieth century, southern Ohio suffered massive flooding. To prevent a repeat of the disaster, residents in the area constructed large earthen dams across river valleys to contain floodwater. The dam slopes, however, were unstable and washed away easily. Ecologists were called on to devise a system for stabilizing the earthen dams. They recommended planting the fast-growing grasses alfalfa and clover. This was followed by planting bromegrass and Japanese honeysuckle. The combination of plants quickly produced a strong turf that was able to hold the soil and gravel in place.

Migratory waterfowl declined during the early part of the twentieth century. To reverse the trend, ecologists used banding and other techniques to study the migratory patterns and feeding habits. They discovered that springtime hunting was adversely affecting the population, but the major problem was the loss of breeding areas and resting areas. Wetlands were being drained across the northern prairies. Some of these wetlands were not well-suited for crops while others had stored water. Draining had reduced breeding and resting sites and contributed to downstream flooding.

keystone species a species that controls the environment and thereby determines the other species that can survive in its presence

Not all species in an ecosystem are of equal importance. Some, known as **keystone species**, are critical. For example, alligators in the Florida Everglades dig deep holes to collect mud and grass for nests. These holes become permanent ponds that survive periods of drought and provide a reliable source of water for many other species in the ecosystem.



Famous Ecological Mistakes

Well-meaning conservation efforts often turn out to be disasters when ecological relationships are not taken into consideration. To increase the number of deer in Grand Canyon National Park and the Kaibab National Forest, most American mountain lions or cougars (*Puma concolor*) were hunted out in the early part of the twentieth century. With no cougar to keep their numbers in check, the number of deer increased dramatically.

The deer stripped the forest of all undergrowth. They even ate the lower branches from the evergreen trees in the forest as high up as they could reach by standing on their hind legs. This gave the forest an unnatural appearance. With food supplies exhausted, the deer became feeble and many died of starvation. To reverse the damage, deer hunting was allowed and the remaining cougars were protected. The forest and the deer herd slowly recovered.

The Future

All over the world, human activity is dramatically altering natural environments. Natural communities are being replaced with human-made communities. These altered communities, however, still obey the same ecological principles. If these human-made communities are to thrive, people must recognize the ecological principles at work and strive for complex, diverse, and mature ecosystems. People must also recognize the interdependence of humans and the natural world and that human activities can adversely alter the natural balance. SEE ALSO ECOSYSTEM; HABITAT.

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Ecosystem

An ecosystem consists of a biological community and the **abiotic factors** on which it relies. These factors include sunlight, water, elements, and minerals. Energy flows one way through an ecosystem, starting as sunlight absorbed by primary producers, passing through several levels of consumers,

abiotic factors pertaining to nonliving environmental factors such as temperature, water, and nutrients and eventually dissipating as heat. Materials cycle through an ecosystem by alternating between **biotic** and abiotic stages.

biotic pertaining to living organisms in an environment

The sun is the ultimate source of energy for most ecosystems. The distribution of solar energy around the world is dictated by the position of the sun and air and water movement. The variation in solar energy causes variation in temperature and rainfall in time and space, which in turn influences the type of ecosystem found in each place.

trophic levels divisions of species in an ecosystem by their main source of nutrition

Ecosystems contain interconnected food chains known as food webs through which energy flows. Each food chain consists of a sequence of predator-prey relationships at different **trophic levels**. Each predator species can have more than one prey species and vice versa. Primary producers, which provide 99 percent of all organic material, are photosynthetic plants and algae. Primary consumers, or herbivores, eat primary producers; secondary consumers, or carnivores, eat herbivores. Tertiary consumers eat other carnivores. Most ecosystems contain no more than two carnivorous trophic levels, because only about 10 percent of the energy contained in the **biomass** at one level is passed on to the next.

biomass the dry weight of organic matter comprising of organisms in a particular habitat

Detrivores, or decomposers, form yet another trophic level by scavenging or decomposing dead organic material. Decomposers are capable of gaining energy from materials that no other animals can, such as cellulose or nitrogenous waste, and may consume up to 90 percent of primary production (energy produced by plants) in forests.

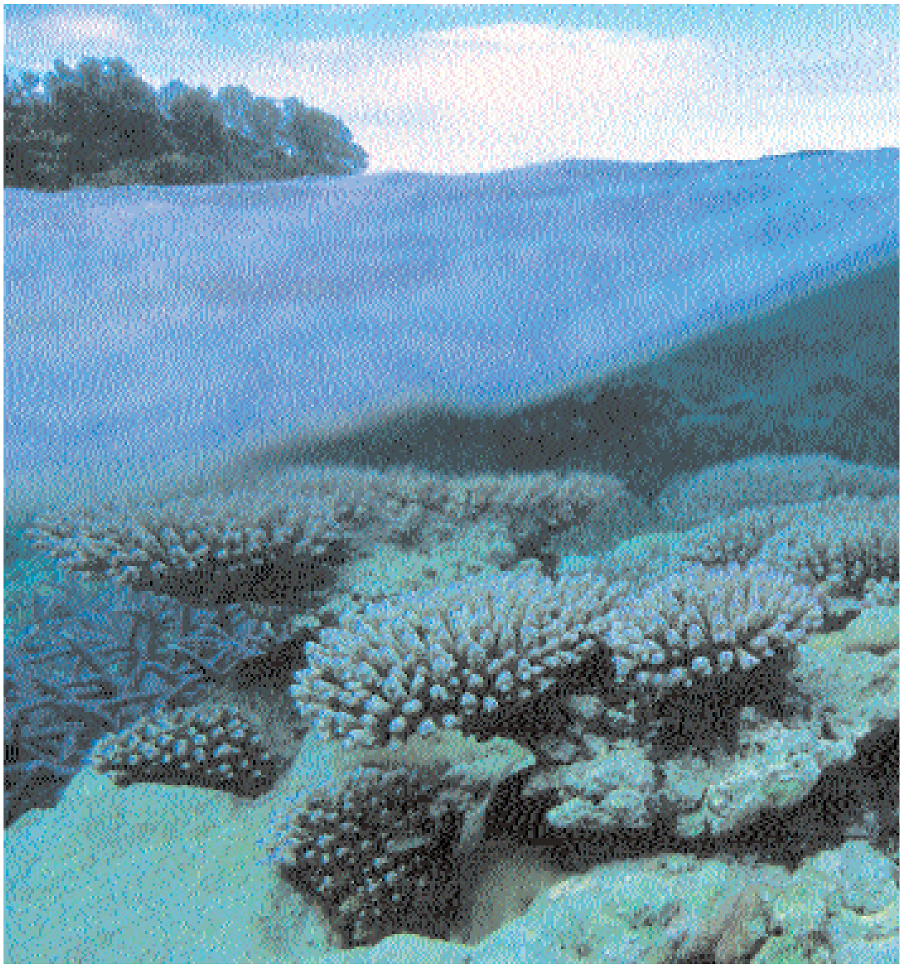
Trophic levels are characterized by their productivity. Gross productivity is the rate at which energy is assimilated by organisms. Gross productivity minus the amount of energy left over after the cost of metabolic activity is net productivity. Net productivity can be measured as accumulated biomass, which is the total dry weight of organic materials, and is the energy that is available to organisms at the next trophic level. The difference between gross and net productivity limits the number of trophic levels in an ecosystem. At some point, there is not enough residual energy to support a healthy population of predators.

The loss of energy at each trophic level would seem to dictate a pyramidal structure in which each trophic level contains less biomass than the one beneath it. However, productivity is a function of both biomass and reproduction rate. For example, a phytoplankton population often reproduces fast enough to support a larger population of **zooplankton**.

zooplankton small animals that float or weakly move through the water

Whole ecosystems can also be measured for their productivity. Algal beds and reefs, due to their rapid reproduction rates, are the most productive ecosystems on Earth. Temperate forests, however, contain the most biomass. Swamps and marshes rank as high as tropical rain forests in productivity, whereas the desert and the open ocean rank the lowest. Cultivated land has only average productivity.

Materials flow through ecosystems in biogeochemical cycles. These cycles include the atmosphere, the lithosphere (Earth's crust), and the hydrosphere (bodies of water). Decomposers play an important role in material cycling by separating inorganic materials, such as nitrogen, from organic compounds. A generalized biogeochemical cycle consists of available and



This coral reef in Palau offers a prime example of an ecosystem in delicate balance.

unavailable organic components and available and unavailable inorganic components.

Inorganic materials become organic through assimilation and **photosynthesis**. Organic materials become inorganic due to respiration, decomposition, and excretion. Sedimentation causes inorganic material to become unavailable, whereas erosion releases it. Fossilization stores organic material as fossil fuel, whereas erosion and combustion release fossil fuels as inorganic material.

photosynthesis the combination of chemical compounds in the presence of sunlight

The water cycle plays a significant role in terrestrial ecosystems because it is the major component, by weight, of all organisms. Water evaporates from oceans, rivers, and lakes and transpires from plants into the atmosphere. Precipitation occurs over land when the atmospheric water condenses, followed by runoff and percolation through the soil into ground water. Eventually, the water returns to the atmosphere by evaporation or transpiration, but in the meantime it can be assimilated by organisms.

Nitrogen also plays a vital role in ecosystems because it is necessary for the synthesis of both amino and nucleic acids, which makeup proteins and DNA. In order for plants to assimilate nitrogen, it must be in the inorganic form of nitrate (NO_3). Bacteria convert ammonia (NH_3) or ammonium (NH_4) into nitrate by nitrification, which requires the addition of oxygen.

A generalized biogeochemical cycle.

	Available	Unavailable
Organic	Organisms Detritus	Coal, petroleum oil, natural gas
Inorganic	Atmosphere Soil Water	Minerals in rocks

Plants convert nitrates into ammonium in order to synthesize organic compounds. Decomposers complete the cycle by ammonification, the separation of inorganic nitrogen from dead organic material. Nitrogen is lost from this cycle by denitrification, in which bacteria break down nitrates into oxygen and nitrogen in poorly aerated soils. Nitrogen is added to the cycle by nitrogen-fixing bacteria, which incorporate atmospheric nitrogen into organic compounds.

The fundamental element in organic molecules is carbon. Plants assimilate carbon from the atmosphere in the form of carbon dioxide, which is broken down during photosynthesis to produce oxygen and carbohydrate. Respiration in plants and animals reverses this process by using carbohydrate to fuel the conversion of oxygen into carbon dioxide. Thus, carbon may be thought of as cycling between gaseous and organic states.

nucleotides the building blocks of a nucleic acid that are composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

Phosphorus is necessary for the synthesis of ATP (adenosine triphosphate) and nitrogen-containing molecules called **nucleotides**. Phosphorus is separated from organic compounds by decomposers or excreted by animals as phosphates. Plants and algae then assimilate phosphates from the soil and water to produce organic compounds.

Humans affect the function of ecosystems in many ways. One effect is the increase in atmospheric carbon dioxide from the burning of fossil fuels, which was negligible until industrialization. Another is the diversion of water from rivers and ground water into reservoirs. Industrial fertilization has increased the level of phosphates in many waterways, causing blooms of phytoplankton that choke the oxygen out of the water. The long-term effects of human influence on ecosystems remain to be determined. SEE ALSO Biomes; Habitat.

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Egg

The egg, or ovum, is the gamete (reproductive sex cell) produced by most female animals. It is fertilized by the sperm, which is the male gamete. The term "egg" is commonly used to include the acellular structures that surround the ovum.

In "higher" animals, including arthropods (such as crabs and insects), most fish, most amphibians, many reptiles (including birds), and some mammals (the echidna and the platypus), the egg is a relatively large structure in which the young matures outside the mother's body. This form of reproduction is called **oviparous**, or egg-laying. In the **viviparous**, or live-bearing, form of reproduction used by some fish, amphibians, and reptiles, as well as most mammals, the developing egg remains within the mother's body.

oviparous having offspring that hatch from eggs external to the body

viviparous having young born alive after being nourished by a placenta between the mother and offspring

The eggs of both amphibians and **amniotes** (reptiles and mammals) generally contain a protective covering and the cells from which the young develop. The protective covering may take on a number of different forms, depending on the animal. In amphibians the coating is gelatinous and clear. In amniotes, it may be leathery like the egg of a reptile, or hard like the egg of a bird. In live-bearing species of lizards and snakes, the shell is a thin membrane through which materials can easily pass.

amniotes vertebrates which have a fluid-filled sac that surrounds the embryo

In most amphibian and amniote eggs of both oviparous or viviparous species, a large yolk mass within the egg nourishes the developing embryo. In some viviparous reptiles and most mammals, nutrition comes directly from the mother through a specialized aggregation of blood vessels. In mammals, this structure is called a **placenta**.

placenta the structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

The structure, size, and number of eggs produced depend on the lifestyle and environment of the animal that makes them, and there is a fair amount of variation. There are two general strategies involving the size and number of eggs: the mother's limited energy resources will either go toward making a smaller number of larger offspring or a larger number of smaller offspring.

Some species produce many offspring to increase the number that survive in a harsh environment. In this strategy, survival is largely dependent on chance, and many of the young die. Species that invest more energy into a smaller group of larger young increase the chance that each individual will survive, based on the assumption that larger young are stronger than smaller young.

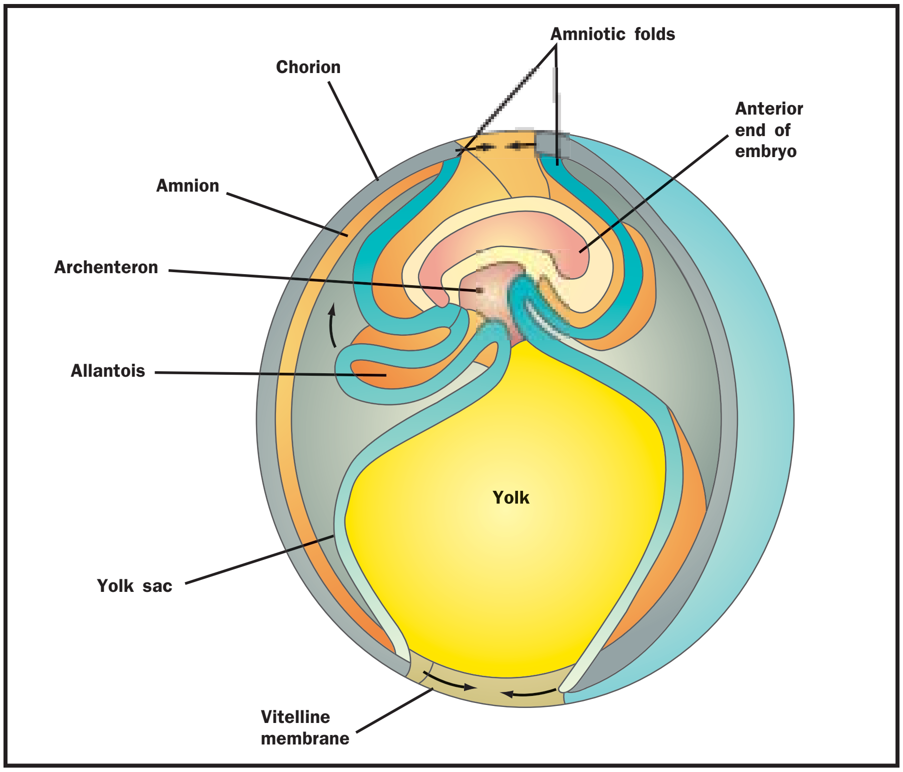
Both oviparous and viviparous strategies are represented among amphibians (frogs, **salamanders**, and the often-hiding, wormlike caecilians). The eggs of oviparous amphibians vary greatly in size. In addition, because the gelatinous membrane that surrounds an amphibian egg is not safe from losing internal fluids, desiccation (drying out) is a serious threat.

salamanders four-legged amphibians with elongated bodies

Most species lay their eggs in or near water, although some salamanders will bury their eggs to keep them moist and cool. Because an amphibian egg is not waterproof, it exchanges fluids and gases easily with the surrounding water. This is critical for supplying the egg with oxygen and for releasing harmful waste products from the confines of the egg.

The eggs of reptiles (including birds) and mammals have features that protect them from the challenges posed by a terrestrial (land) environment. In oviparous amniotes, the eggs are protected by a sturdy shell that safeguards the embryo against desiccation, although some air and moisture can pass through the shell.

The amniote egg has several specialized compartments. The yolk sac holds the yolk that feeds the embryo. The allantois, which is an extension



The development of embryonic membranes in a chicken egg. Redrawn from Campbell, *Biology*, 1993.

of the embryo's gut, stores solid waste products. Both the yolk sac and the allantois are connected to the developing embryo.

Various other egg layers and membranes form around the ovum as it passes from the ovary through a muscular tube called the oviduct to the cloaca. The materials that make up these layers and membranes are secreted by specialized glands that line the oviduct. A clear fluid layer called the albumen—the "egg white" of a chicken egg—supplies the embryo with water and inorganic nutrients and cushions the embryo from impact if the egg is jarred or dropped.

Albumen contains a protein (also called albumen), which binds to water and inorganic nutrients and aids in their transport. These nutrients diffuse through (pass through) the walls of the blood vessels that connect the embryo (through the umbilical cord) to the mother (at the placenta, or aggregation of vessels at the wall of the uterus/oviduct).

The albumen is enveloped within the chorion, a thin membrane which also surrounds the embryo, yolk sac, and allantois. The chorion regulates the passage of gas and moisture into and out of the egg. Finally, a shell surrounds and protects the entire egg. The shell allows moisture and gas to pass through it. The shells of most lizards and snakes have a leathery consistency, whereas birds have hard, **calcified** shells that resist denting. SEE ALSO Embryonic Development.

calcified made hard through the deposition of calcium salts

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Elton, Charles Sutherland

British Biologist
1900–1991

Charles Sutherland Elton was born in Liverpool, England. Elton is considered the father of animal ecology. Ecology is the study of the relations between living creatures and their natural environment.

Elton was educated at Liverpool College and then at New College, Oxford. In 1922 he graduated from Oxford with a degree in zoology. At that time, most scientists studying animals emphasized their physical makeup and performed studies in laboratories. However, Elton was more interested in the scientific study of animals in their habitats. While still in college, Elton began this study, making numerous journeys to the Arctic.

In 1927 Elton published his first book, *Animal Ecology*. It was considered brilliant, and established many of the basic principles of modern animal ecology. He discussed food chains and the food cycle, niches, and the "pyramid of numbers." The pyramid of numbers is an observation about food relationships. A large number of plants feed a smaller number of animals, and these animals in turn provide food for an even smaller number of meat-eating animals. Elton addressed evolution in his 1930 book *Animal Ecology and Evolution*.

Elton concentrated his studies on how the number of animals in a population was affected by a changing environment. In 1932, he established the Bureau of Animal Population at Oxford, which for thirty-five years served as an important center for worldwide studies of ecology. In 1932 Elton became the editor for the newly established *Journal of Animal Ecology*.

In 1936 he was appointed to prestigious positions at Oxford and Corpus Christi College. Elton's research on mice populations enabled him to assist his country during World War II with the control of rodent pests. He published two books on rodents, *Voles, Mice and Lemmings* in 1942 and *The Control of Rats and Mice* in 1954. Other important books were *The Ecology of Invasions of Animals and Plants* (1958) and *The Pattern of Animal Communities* (1966).

In 1953 Elton was elected a member of the Royal Society of London and a foreign member of the American Academy of Arts and Sciences. He was awarded the Gold Medal of the Linnean Society in 1967 and the Royal Society's Darwin Medal in 1970. Elton retired from his studies in 1967.

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Embryology

Embryology is the biological field of study that examines the early development of organisms. In general, a developing organism is considered an embryo until the point at which all the essential tissues and organ systems have developed. In humans, the embryonic stage covers approximately the first two months of pregnancy.

fertilization the fusion of male and female gametes

zygote a fertilized egg

cleavage the process of cytokinesis in animal cells; as cells multiply, the plasma membrane pinches off to make two cells from one

gastrulation the formation of a gastrula from a blastula

mesoderm the middle layer of cells in embryonic cells

Certain key events occur during the embryonic development of all multicellular animals. These include **fertilization**, the union of the sperm and egg to form the fertilized egg, or **zygote**; **cleavage**, when the fertilized egg divides in organized cycles to produce multicellularity; **gastrulation**, in which the three primary germ layers, the ectoderm, **mesoderm**, and endoderm, are differentiated; and finally organogenesis, during which the organs develop.

Two general approaches are often taken in the study of embryology: These are descriptive embryology and experimental embryology. Descriptive embryology dates from antiquity, and attempts to describe the normal sequence of developmental events that occur during embryonic development in a given organism. This information can be used to explain how adult anatomy is achieved. Understanding normal development also allows scientists to understand the origin of common birth defects.

Scientists interested in embryology study images such as this close-up of a 17.5 day old rat embryo without its yolk sac.

Experimental embryology attempts to shed light on the basic processes involved in development, particularly at the cellular level. Experimental embryologists want to discover how development is controlled and how ever more complex structures and organs are produced. They tend to focus on one of a few model organisms about which considerable developmental and genetic information is already known. These model organisms include the mouse, the chicken, the fruit fly *Drosophila melanogaster*, the African clawed frog *Xenopus laevis*, and the nematode *Caenorhabditis elegans*. One particularly effective approach in experimental embryology has been that of developmental genetics, which studies the effect of mutant genes on developmental processes. By comparing the developmental results of mutant versus normal genes, the role of individual genes in development can be assessed. This experimental strategy usually involves screening large numbers of animals for developmental abnormalities. SEE ALSO EMBRYONIC DEVELOPMENT.

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Embryonic Development

All embryonic structures are derived from a single cell formed by the union of two gametes. Every individual organism began as a single cell, which divided and differentiated into various types of cells that make up the diverse tissues and complex structures found in the adult. **Ontogeny**, or the development of an organism from fertilization to adult, begins with the **fusion** of two cells, the sperm and egg. The sperm and egg are **haploid cells** formed through the process of **meiosis**. The haploid cells have no function outside of their involvement in reproduction.

ontogeny the embryonic development of an organism

fusion coming together

haploid cells cells with only one set of chromosomes

meiosis a specialized type of cell division that results in four sex cells or gametes that have half the genetic material of the parent cell

Many invertebrates have isolecithal eggs (yolk is evenly distributed throughout the egg). These eggs have relatively little yolk and various patterns of holoblastic cleavage (the cells divide completely and evenly). The **arthropod** egg has a moderate amount of yolk, concentrated in the egg's center. The eggs of amphibians and **cartilaginous** fishes have a moderate amount of yolk, mostly in the lower half of the egg (the vegetal hemisphere). Birds have extremely telolecithal eggs (yolk is concentrated in the vegetal pole, opposite the nucleus) that have a large amount of yolk.

arthropod a phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

cartilaginous made of cartilage

A shell membrane surrounds the embryo, yolk, and albumin, or egg white. It offers mechanical protection and provides a surface for diffusion of oxygen and other gases. Within the egg the allantois acts as a compartment for the storage of nitrogenous excretory products such as **uric acid**, and may remain after birth or hatching as the urinary bladder. The **amnion** is filled with amniotic fluid to cushion the embryo that it surrounds. The chorion surrounds the amnion and yolk sac. Mammalian eggs contain some yolk but not nearly as much as found in bird eggs. The typical mammalian egg contains little yolk which is evenly distributed throughout the egg (it is microlecithal and isolecithal).

uric acid insoluble form of nitrogenous waste excreted by many different types of animals

amnion the membrane that forms a sac around an embryo

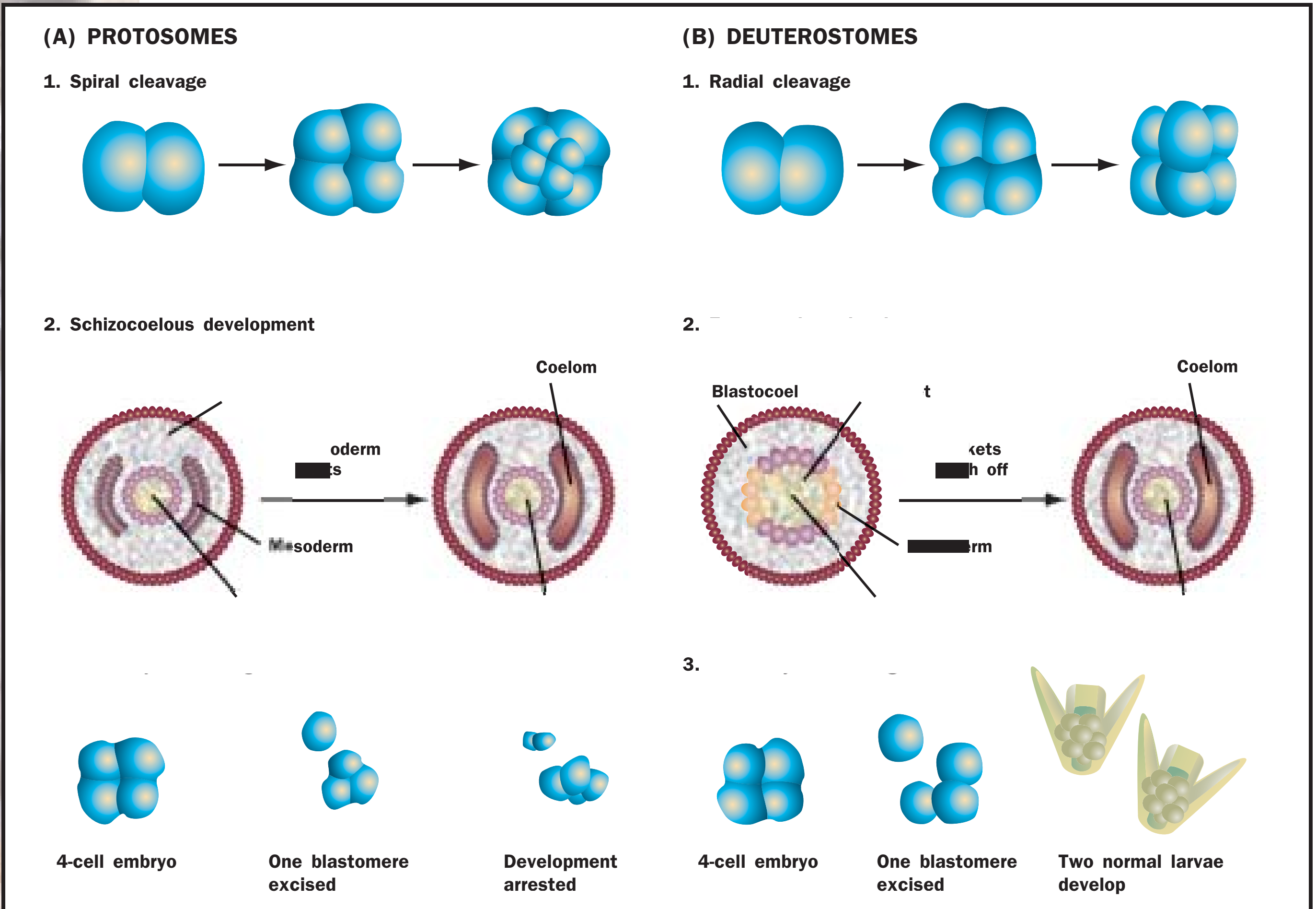
Stages of Development

In **deuterostomes** (one of two major groups of coelomate animals that includes echinoderms and chordates), early cleavage divisions are radial. In contrast, protostomes typically display spiral cleavage. Early cleavage divisions in most embryos are reductive, which means that they divide the original contents of the egg without an increase in the total cellular volume of the embryo. The average diameter of a cell decreases as cleavage continues so that the surface area increases relative to cellular volume.

deuterostomes animals in which the first opening does not form the mouth, but becomes the anus

Gastrulation occurs after several cycles of cleavage events. Several important events occur during gastrulation in multicellular animals:

- The three primary germ layers, ectoderm, mesoderm, and endoderm, are established.
- The basic body plan is established, including the physical construction of the primary body axes.
- Cells are brought into new positions, allowing them to interact with cells that were initially not near them. These cellular interactions alter the fate of individual cells, which begin to look and behave differently. This phenomenon is known as induction (cell–cell interactions which lead to cellular differentiation) and is a critical step in the formation of tissue layers.



A comparison of development cycles in protosomes and deuterostomes. Redrawn from Gilbert, 1994.

During **invagination**, a sheet of **epithelial cells** (cells that are in close contact with each other and adhere to a basement membrane) bends inward to form a "pocket." During ingression, cells leave an epithelial sheet by transforming into freely migrating mesenchyme cells. During involution, a sheet of tissue spreads inward from the lip of the newly formed cavity. As material moves in from the external portion of the sheet, material that was originally at the lip spreads further into the cavity, eventually forming a sheet of tissue that lines the invagination below the exterior tissue layers.

Intercalation is an expansion process during which cells from different layers lose contact with their neighbors and rearrange into a single layer, which increases in surface area and expands laterally. Intercalation is an important morphogenetic movement involved in the construction of the primary body axis in amphibians. A specialized form of intercalation is convergent extension. An epithelial sheet converges toward a central site, followed by its extension along a single axis through intercalation of the cells of the epithelium (picture a pile of poker chips arranging themselves into a stack). This rearrangement of epithelial cells is an important event during both **gastrulation** and subsequent neurulation. Convergent extension of the marginal zone (the region of intermediate pigmentation between the pigmented animal hemisphere and the unpigmented vegetal hemisphere) creates the **anterior-posterior**, or forward-backward axis. During neurulation,

invagination a stage in embryonic development where a cell layer buckles inward

epithelial cells cells that occur in tightly packed sheets that line organs and body cavities

intercalation placing or inserting between

gastrulation the formation of a gastrula from a blastula

anterior referring to the head end of an organism

posterior behind or the back

convergent extension of the central region of the neural plate (the region of embryonic **ectodermal** cells that lie directly above the **notochord**) occurs as the neural axis elongates and the neural tube closes. Also, during intercalation two or more rows of cells move between one another, creating an array of cells that is longer (in one or more dimensions) but thinner than the cell rows from which it formed. The overall change in shape of the tissue results from this cell rearrangement.

ectodermal relating to the outermost of the three germ layers in animal embryos

notochord a rod of cartilage that runs down the back of chordates

Intercalation can be a powerful means of expanding a tissue sheet. During convergent extension, two or more rows of cells intercalate. Cells converge by intercalating perpendicular to the axis of extension, resulting in the overall extension of the tissue in a preferred direction. Primary mesenchyme cells undergo ingression at the onset of gastrulation. During epiboly, a sheet of cells spreads by thinning which is accomplished by changes in the shape or position of cells.

In deuterostomes, the vegetal plate (a thin sheet of epithelial cells) undergoes invagination to produce the archenteron (the cavity formed by the endoderm during gastrulation). The blastopore (the external opening of the archenteron) forms the anus of the larva later in development. Secondary invagination involves the elongation of the archenteron across the blastocoel (the fluid-filled cavity of the blastula, as the embryo is known at this stage), where it attaches to the ectoderm near the animal pole (the pole nearest the nucleus) of the embryo. The onset of secondary invagination correlates with the appearance of long, thin filopodia extended by secondary mesenchyme cells at the tip of the archenteron.

One characteristic found in vertebrates is neural crest cells, derived from ectodermal cells. They develop along the top of the neural tube. As the neural folds close, most neural crest cells change into mesenchyme, an embryonic tissue that consists of star-shaped cells from all three germ layers. Mesechymal derivatives eventually give rise to the visceral skeleton (**gill arches**, some of which will develop into jaws), pigment cells, sensory and postganglionic **neurons** (the dentine-producing cells of teeth), Schwann cells that help protect neurons, and bony scales. **Differentiation** and derivation of tissues and organs during development is called organogenesis. After the production of the neural tube, differentiation of the germ layers occurs rapidly, and organogenesis begins, in which the primary tissues differentiate into specific organs and tissues.

gill arches arches of cartilage that support the gills of fishes and some amphibians

neurons nerve cells

differentiation differences in structure and function of cells in multicellular organisms as the cells become specialized

Neurulation creates three important structures in the embryos of higher vertebrates:

- The neural tube, which gives rise the central nervous system;
- The neural crest, which gives rise to a diverse set of cell types; and
- A true epidermis, which covers over the neural tube.

Examples of Development

Four examples illustrate some aspects of embryonic development. All four are **metazoans**: Platyhelminthes (a nematode), Echinodermata (a sea urchin), and Chordata (represented by a frog, a bird, and a mammal).

metazoans a subphylum of animals that have many cells, some of which are organized into tissues

A worm. *Caenorhabditis elegans* (*C. elegans*) is a free-living nematode with two sexes: a self-fertilizing hermaphrodite and a male. The general body

concentric having the same center

pseudocoelom a body cavity that is not entirely surrounded by mesoderm

gonads the male and female sex organs that produce sex cells

osmoregulatory system a system that regulates the water balance between an organism and its environment

morphogenesis the development of body shape and organization during ontogeny

mitosis a type of cell division that results in two identical daughter cells from a single parent cell

plan of this worm is in the form of two **concentric** tubes separated by a space called the **pseudocoelom**. The intestine forms the inner tube and the outer tube consists of cuticle, hypodermis, musculature, and nerve cells. In the adult, the pseudocoelomic space also contains the tubular **gonad**. The shape of the worm is maintained by internal hydrostatic pressure, controlled by an **osmoregulatory system**.

C. elegans is a primitive organism yet it shares many embryological characteristics with members of higher phyla. The worm is conceived as a single cell that undergoes a complex process of development, starting with embryonic cleavage, proceeding through **morphogenesis** and growth to the adult worm-like animal.

Shortly after fertilization, the maternal pronucleus (the sperm nucleus and egg nucleus within the fertilized egg before their fusion to form the diploid zygote nucleus) migrates from the anterior to the posterior through the pseudocleavage furrow. It meets the paternal pronucleus in the rear, and they migrate forward before fusing and entering **mitosis**. Eggs are laid at about the time of gastrulation and hatch into first-stage juveniles. At hatching there are 558 cells in the hermaphrodite and 560 in the male. The animal matures through four larval stages, punctuated by molts and characterized by additional divisions of a few cells. These result primarily in elaboration of the nervous system and development of the secondary sexual characteristics.

Gonadogenesis, the formation of reproductive organs, begins in the first larval stage and ends in the fourth larval stage.

Sea urchins. Like all echinoderms, the purple sea urchin (*Strongylocentrotus purpuratus*) undergoes radial cleavage, as do typical deuterostomes, such as chordates, ascidians, and other echinoderms. As in embryonic cleavages in other metazoans, sea urchin cleavage divisions are reductive, that is, the cleavages result in more cells but without an increase in the total cellular volume of the embryo. The first two cleavages are meridional, meaning that the cleavage furrow passes through the animal and vegetal poles. The next cleavage is equatorial, that is, it passes through the embryo's midsection. The fourth cleavage is unequal. In deuterostome development, early cleavage divisions are radial. Protostomes typically display spiral cleavage. Early cleavage divisions in most embryos are reductive, dividing the original contents of the egg without increasing the total cellular volume of the embryo. The average diameter of a cell decreases as cleavage continues, and there is an increase in surface area relative to cellular volume. The embryo at this stage (known as the morula) is shaped like a blackberry made up of small, homogeneous cells. During the third cleavage, the surface area roughly doubles. The embryo then enters the blastula stage.

The blastula is a hollow ball of cells organized into an epithelial monolayer. The vegetal pole epithelium thickens to form the vegetal plate, which will give rise to primary mesenchyme cells and the archenteron during gastrulation. The epithelium is lined on its outer, or apical, surface by two extracellular matrice, an inner apical lamina and a hyaline layer outside it. Both are attached to the apices ("tips") of the cells in the wall of the blastula, which extend microvilli into these extracellular **matrix** layers.

matrix the nonliving component of connective tissue

Sea urchin gastrulae (as the embryo is called at this stage) elongate their archenterons via convergent extension during gastrulation. The epithelial cells of the archenteron rearrange as it elongates. Secondary invagination involves autonomous extension of the archenteron in the early phase of elongation, followed by mesenchyme-dependent pulling in the second phase. The sea urchin embryo possesses extracellular matrix layers lining the inside and outside of the embryo. The outer layer is divided into two layers, an apical lamina directly attached to the apical ends of the cells, and a hyaline layer on top of the first layer.

A frog. *Xenopus laevis* is a frog commonly used in embryological studies. The egg of this species is a huge cell, with a volume that is over one million times larger than a normal **somatic** frog cell. During embryonic development, the egg is converted into a tadpole containing millions of cells but with the same volume of material.

somatic having to do with the body

After fertilization, the cortical reaction (a wave of chemicals is released from the egg plasma membrane after fusion of the sperm and egg) results in loss of contact between the surface of the egg and the vitelline envelope (an extracellular membrane that encloses the embryo), permitting the reorientation of the egg via gravity. The varying densities of yolk in the egg result in a consistent orientation. The upper hemisphere of the egg, the animal pole, is dark. The lower hemisphere, the vegetal pole, is light. When it is deposited in the water and ready for fertilization, the haploid egg is at metaphase of meiosis II (the **chromosomes** are aligned at separate poles during second phase of reductive division).

chromosomes structures in the cell that carry genetic information

Entrance of the sperm initiates a sequence of fertilization events. After meiosis II is completed, the **cytoplasm** (the contents of the cell outside the nucleus and within the plasma membrane) of the egg rotates about 30 degrees relative to the poles, which is revealed by the appearance of a light-colored band, the gray crescent. This crescent forms opposite the point where the sperm entered. The crescent establishes the future pattern of the animal: its **dorsal** and **ventral** surfaces; its anterior and posterior; and its left and right sides.

cytoplasm fluid in eukaryotes surrounding the nucleus and organelles

dorsal the back surface of an animal with bilateral symmetry

ventral the belly surface of an animal with bilateral symmetry

The haploid sperm and egg nuclei fuse to form the diploid nucleus of the zygote. The zygote nucleus undergoes several cycles of mitosis (the nuclear division that follows duplication of the chromosomes, resulting in daughter nuclei with the same chromosome content as the parent nucleus). During cytokinesis, a belt of actin filaments forms around the perimeter of the cell, midway between the poles. As the belt tightens, the cell is pinched into two daughter cells. The first cleavage occurs shortly after the zygote nucleus forms and begins with the appearance of a furrow that runs longitudinally through the poles of the egg, passing through the point of sperm entry and bisecting the gray crescent. This divides the egg into two halves, forming the two-cell stage. During the second cleavage, the cleavage furrow again runs through the poles but at right angles to the first furrow, forming the four-cell stage. The third cleavage furrow runs horizontally but in a plane closer to the animal than to the vegetal pole. It produces the eight-cell stage.

The next few cleavages proceed in a similar fashion, producing a sixteen-cell and then a thirty-two-cell embryo. As cleavage continues, the cells in the animal pole begin dividing more rapidly than those in the vegetal pole and thus become smaller and more numerous. Subsequent cleavages produce a hollow ball comprised of thousands of cells called the blastula, which contains a fluid-filled cavity, the blastocoel.

Gastrulation begins with the invagination of cells in the region of the embryo once occupied by the middle of the gray crescent. This produces an opening, the blastopore, that will be the future anus and a cluster of cells that develops into the Spemann organizer (a cluster of cells which act as powerful inducer of surrounding cells). As gastrulation continues, three distinct germ layers are formed: ectoderm, mesoderm, and endoderm.

spinal cord thick, whitish bundle of nerve tissue that extends from the base of the brain to the body

The ectoderm eventually forms the skin, brain, **spinal cord**, and other neurons. The mesoderm forms the notocord, muscles, blood, bone, and sex organs. The endoderm eventually forms the linings of the gut, lungs, and bladder, as well as of the liver and pancreas.

The Spemann organizer, which is mostly mesoderm, develops into the notochord, the precursor of the vertebral column, and induces the ectoderm lying above it to begin to form neural tissue instead of skin. This ectoderm will develop into two longitudinal folds, forming the neural folds stage. Eventually, the lips of the folds fuse to form the neural tube—which later develops into the brain and spinal cord—and the embryo elongates, forming an anterior-posterior, or front-rear, axis.

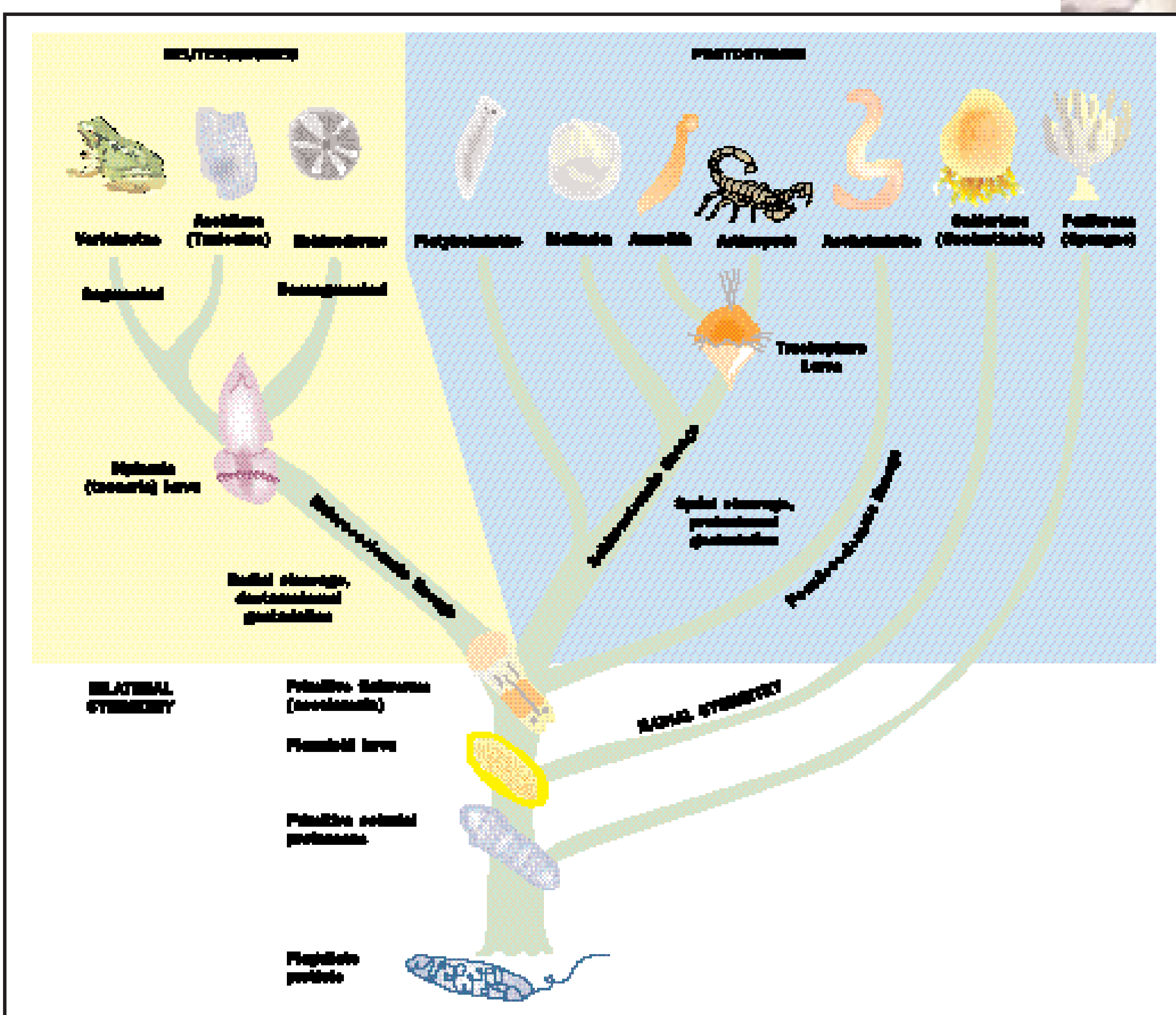
Each of the various layers of cells in the frog gastrula has a definite and different fate. Embryonic cells form many of the specialized structures in the tadpole, including neurons, blood cells, muscle cells, and epithelial cells.

Neurulation in *Xenopus* involves neural fold elevation and invagination of the neural plate to form the neural tube. The neural axis elongates as neurulation proceeds. The induction of convergence and extension behavior in cells of the neural tube is associated with neural induction, also known as primary embryonic induction.

The chicken (*Gallus gallus*). The chicken ovum consists of the yellow yolk and a small yolk-free area called the blastoderm (blastodisc or germinal disc). The nucleus of the ovum is in the blastodisc. The blastodisc appears as a small whitish area on the upper surface of the yolk. Albumin is added to the ovum as it moves down the hen's oviduct. Eventually, two shell membranes and a calcareous shell are added to form the complete egg.

Because of the large amount of yolk present in the chicken egg, cleavage, morphogenesis, and differentiation are confined to the blastoderm. Initially, the blastoderm becomes several cell layers thick and a cavity, called the subgerminal cavity, is formed under these layers. This stage of the embryo is comparable to the sea urchin morula. As cleavage continues and more cells are formed, the blastoderm splits to form two layers, a dorsal epiblast (ectoderm) and ventral hypoblast (endoderm). This embryonic stage corresponds to the sea urchin blastula and the cavity separating these two layers is called the blastocoel. Development to this stage takes place while the egg is still in the oviduct of the hen.

Gastrulation occurs by a process of involution. Involution is the curling inward and in-growth of a group of cells. Cells of the blastoderm surface migrate backward and medially (toward the middle of the embryo) and involute, or turn in, along a line called the primitive streak. These involuted



Comparison of development cycles in protosomes and deuterostomes. Redrawn from Gilbert, 1994.

cells will form the mesoderm germ layer. As gastrulation progresses, the anterior end of the streak moves backward so that the anterior region of the embryo is formed first. The primitive streak is functionally the same as the blastopore of the sea urchin gastrula.

The three germ layers, ectoderm, endoderm, and mesoderm, are created by involution following gastrulation. The coelom results from a separation of the lateral mesoderm. The involuted cells form the notochord anterior to the primitive streak and the lateral mesoderm (**somites**) laterally. After gastrulation, the process of neurulation, or formation of the neural tube and associated structures, takes place.

somites a block of mesoderm along each side of a chordate embryo

Neurulation occurs at or near the end of gastrulation and transforms the gastrula into a neurula by establishing the central nervous system. The ectoderm gives rise to neural folds flanking a neural groove along an axis from the blastopore toward the future head. These folds sink into the dorsum (back) of the embryo and meet mid-dorsally, forming a neural tube of which the anterior part becomes the brain and the rest the spinal cord. A population of mesodermal cells called the chordamesoderm aggregates, or gathers, to form the notochord. The chordamesoderm is required for the formation of the neural tube. During neurulation the portion of chordamesoderm that will form the notochord induces neural plate formation, which is the first stage in the formation of the neural tube. This process is characterized in most vertebrates by three stages. During the neural plate stage, the ectoderm on the dorsal side of the embryo overlying the notochord thickens to form the neural plate. During the neural fold stage, the thickened ectoderm curves inward, leaving an elevated area along the neural groove. The neural fold is wider in the anterior portion of the vertebrate embryo, which is the region where the brain will be formed. During the neural tube stage, the neural folds move closer together and fuse. The neural groove becomes the cavity within the neural tube, which will later contain cerebrospinal fluid that aids in the function of the central nervous system.

The mouse (*Mus musculus*). Embryos of the mouse develop in a very different environment than do those of the chicken. The relatively low yolk content in the typical, small mammalian egg requires that the embryo quickly implant, or adhere to the inner lining of the uterus, in order to obtain nutrients from the mother. Early cleavage in mammalian embryos is followed by the blastocyst stage. There are two groups of cells present at this stage. The outer layer of cells, called the trophoblast, and the inner mass of cells, called the blastocyst, will together go on to form the embryo.

During implantation of the fertilized ovum in the uterus the placenta is formed, which is a structure for physiological exchange between the fetus and the mother. The placenta consists of both a maternal contribution, the endometrium of the uterus, and a fetal contribution, the trophoblast. It is believed that the latter is used as an immunological barrier that prevents rejection of the fetus, and its paternal chromosomes, by the mother. The shape of the placenta varies, depending on the species. The inner cell mass of the blastocyst develops into the blastodisk, similar to that in chickens. Early stages of development of the mammalian embryo, such as the primitive streak stage, neurulation, and germ layer differentiation, are similar to those in birds and reptiles. The primary difference found in mammals is the development of the umbilical cord. The umbilical cord contains the allantois and yolk sac as well as circulatory system structures that connect the embryo to the placenta. SEE ALSO EMBRYOLOGY.

Andrew G. Gluesenkamp

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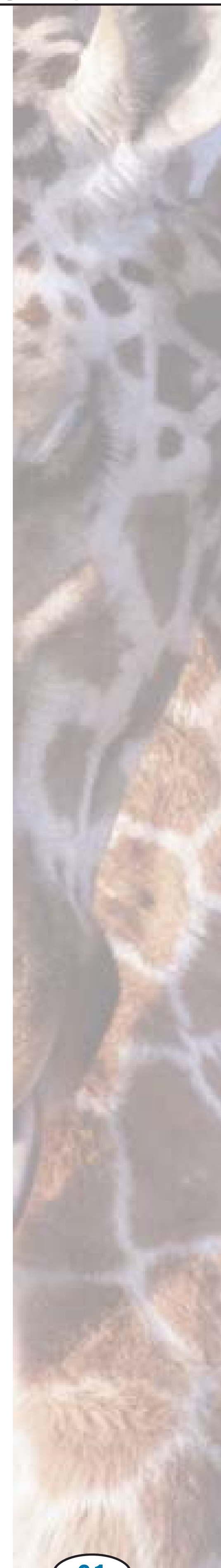

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Endangered Species

An endangered species is one that is likely to become extinct throughout all or part of its geographic range unless steps are taken to prevent its loss. Many of the species currently disappearing are tropical plants and insects that have not even been described by science but whose small ranges are being destroyed by deforestation. These species may contain valuable pharmaceuticals which could lead to cures for diseases, but they are also the irreplaceable products of millions of years of evolution.

The U.S. Endangered Species Act (ESA) protects any endangered species as well as the critical habitat on which it relies. Critical habitat does not necessarily include the entire ecosystem across the species' range. The ESA is the strongest ecological law in the world today because it has the power to restrict or eliminate human impact across an entire species range. Because the economic stakes can be high, officially designating a species as endangered can be a controversial process.

Given the costs of protecting endangered species, it is crucial to be certain that species are in fact endangered. The first step is to document a decline in population number. Doing so requires at least two population samples, using the same sampling methods, at different times. Even if a particular population shows no sign of decline, the species as a whole may decline as a result of range contraction and local population extinction; for example, deforestation eliminates whole populations while others remain intact.

Causes of Decline

Once a decline is established, the cause must be identified. First, natural history must be investigated in order to construct a list of possible agents. These may include prey extinction, pollutants, habitat change, habitat fragmentation, overharvesting, introduced species, disease, or **inbreeding depression**. Diagnosis requires the elimination of alternative hypotheses by observation and experiment.

inbreeding depression loss of fitness due to breeding with close relatives

A classic case of population decline was the decline and extinction of ten species of forest birds in Guam in the late 1960s. **Pesticide** use, hunting, competition from introduced bird species, habitat change, and disease were all measured and found to be uncorrelated with population densities of the forest birds. The only variable that was correlated with the decrease

pesticide any substance that controls the spread of harmful or destructive organisms

The bald eagle, an enduring symbol of the United States, remains an endangered species.

of the birds' range was the range of the brown tree snake, a species that was accidentally introduced to the island via an airplane wheel well in 1967. Subsequent live bait trapping indicated that brown tree snake predation on forest birds was higher where the birds were declining. An associated prediction that the snake would cause small mammal populations to decline was also supported.

Habitat change. Habitat change is any change in the suite of resources and environmental conditions on which a species depends. It is not enough to know that habitat change or loss is causing species decline; the particular factors relevant to the species must be discovered. For example, the northern spotted owl nests in the tops of dead firs. These "snags" are commonly found in old-growth forests. Young forests provide marginal habitat. Nevertheless, understanding the owl's behavior, hunting habits, nesting habits, and other factors may allow some human activity in owl habitat without endangering the owl.

Habitat fragmentation. This is a particularly harmful form of habitat change. Fragmentation is the loss of bits and pieces of habitat because of human activity, resulting in a patchwork habitat. Not only does this reduce the overall species range, it also changes the ratio of edge habitat to central habitat. For example, tropical forest fragmentation favors species that specialize in relatively open, sunny spaces such as treefalls, rather than the cooler, darker forest. This may cause forest specialists to decline as a result of competition as well as habitat loss. Demonstrating an effect of habitat fragmentation on population decline requires documenting fragment sizes and population densities.

Introduced species. Introduced species, such as the brown tree snake, have been responsible for 40 percent of all extinctions. The Nile perch, introduced into Lake Victoria (located in east Africa) in the nineteenth century, caused the extinction of 200 species of cichlid by predation. To detect the impact of an introduced species, the timing of the introduction is compared to that of population decline. If there is a correlation, an experiment must demonstrate that the removal of the introduced species reverses the decline. Removal may involve surrounding the endangered species habitat with fencing or by poisoning the suspected introduced species. Unfortunately, it is difficult to remove a single species from a habitat without changing other variables. And introduced species, once established, are nearly impossible to eradicate.

Chains of extinction can make the diagnosis of species decline more complex. For example, Mauritanian kestrels declined because geckos, their food source, were eliminated by deforestation. Atlantic eelgrass limpets disappeared when a mold killed the eelgrass in which they lived. Black-footed ferrets declined along with their prey, the prairie dog. Saving one species may require saving several others as well.

Environmental contaminants. These may also play a role in species decline. The mechanism by which organochlorides, such as DDT, can cause eggshell thinning in raptors was discovered in the 1960s, and DDT was soon banned in the United States and other countries. Blaming a chemical for the decline of a species, however, can result in banning a harmless substance while ignoring the actual problem. For example, eggshell thinning due to insufficient calcium deposition occurred in the Netherlands in the 1980s, well after DDT had been banned. Further investigation concluded that **acid rain** had leached calcium from the soil, reducing the amount found in the calcium carbonate shells of snails; the birds were unable to obtain sufficient calcium from feeding on snails.

acid rain acidic precipitation in the form of rain

Disease. This factor is thought to have contributed to the decline of many species. Infections can cross from one species to another (called transspecies infections); for example, an introduced species can carry novel **pathogens** with it into a community that has evolved no resistance to it. Often, disease is the result of stress on the species' immune system from another source, such as pollution. Although the disappearance of amphibians around the world remains a mystery, it is likely exacerbated by the effect of acid rain on immune function in aquatic species. Establishing such a connection requires investigating beyond the appearance of disease into underlying causes.

pathogens disease-causing agents such as bacteria, fungi, and viruses

Hunting. Overharvesting occurs when the number of individuals lost to hunting consistently exceeds the number gained from intrinsic population growth in the absence of harvesting. Overharvesting is a particularly difficult factor to measure because both annual harvests and population sizes vary in time and space. Furthermore, hunting yields are often underreported, especially if they are illegal.

Inbreeding depression. This may be a factor in the decline of a population once the number of individuals is small. Inbreeding depression is the result of closely related individuals breeding, causing **recessive** harmful mutations to be passed on by both parents and therefore be expressed in subsequent generations. There is no evidence that inbreeding depression has ever caused extinction in the wild, though it can be a problem for captive-bred populations. It is likely that once a population is small enough for inbreeding depression to become relevant, extinction is inevitable for other reasons.

recessive hidden trait that is masked by a dominant trait

The Northern Spotted Owl

The case of the northern spotted owl in the Pacific Northwest region of the United States illustrates many of the issues surrounding the designation of an endangered species. The species is currently listed as threatened, meaning that it is at risk of becoming endangered in the foreseeable future. Its critical habitat is old-growth and late-successional forest with a dense canopy and open understory, which it requires for successful roosting. Such forests are extremely valuable to the timber industry. Since the spotted owl was listed as threatened in 1990, debate raged in the Pacific Northwest over the relative merits of a protection plan and the logging industry it would impact. At the beginning of the twenty-first century, there was no plan to protect the species, even though it was known that habitat destruction due to logging had caused the species' decline.

The current rate of extinction is greater than at any time in the last 65 million years. There have been only about five such mass extinctions in the history of the Earth, and they all occurred as a result of catastrophic changes in the environment. At no other time has the practices of a single species, humans, caused so many extinctions. SEE ALSO DDT; EXTINCTION; EXOTIC SPECIES; HABITAT LOSS; HABITAT RESTORATION; THREATENED SPECIES.

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exoskeleton hard outer protective covering common in invertebrates such as insects

molting the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

metamorphosis a drastic change from a larva to an adult

Haemolymph is the "blood" of invertebrates. Similar to mammalian blood, it carries nutrients to cells and waste away from cells. Haemolymph does not carry oxygen to cells like mammalian blood.

Hemolymph functions the same way as haemolymph, but works for insects instead of invertebrates.

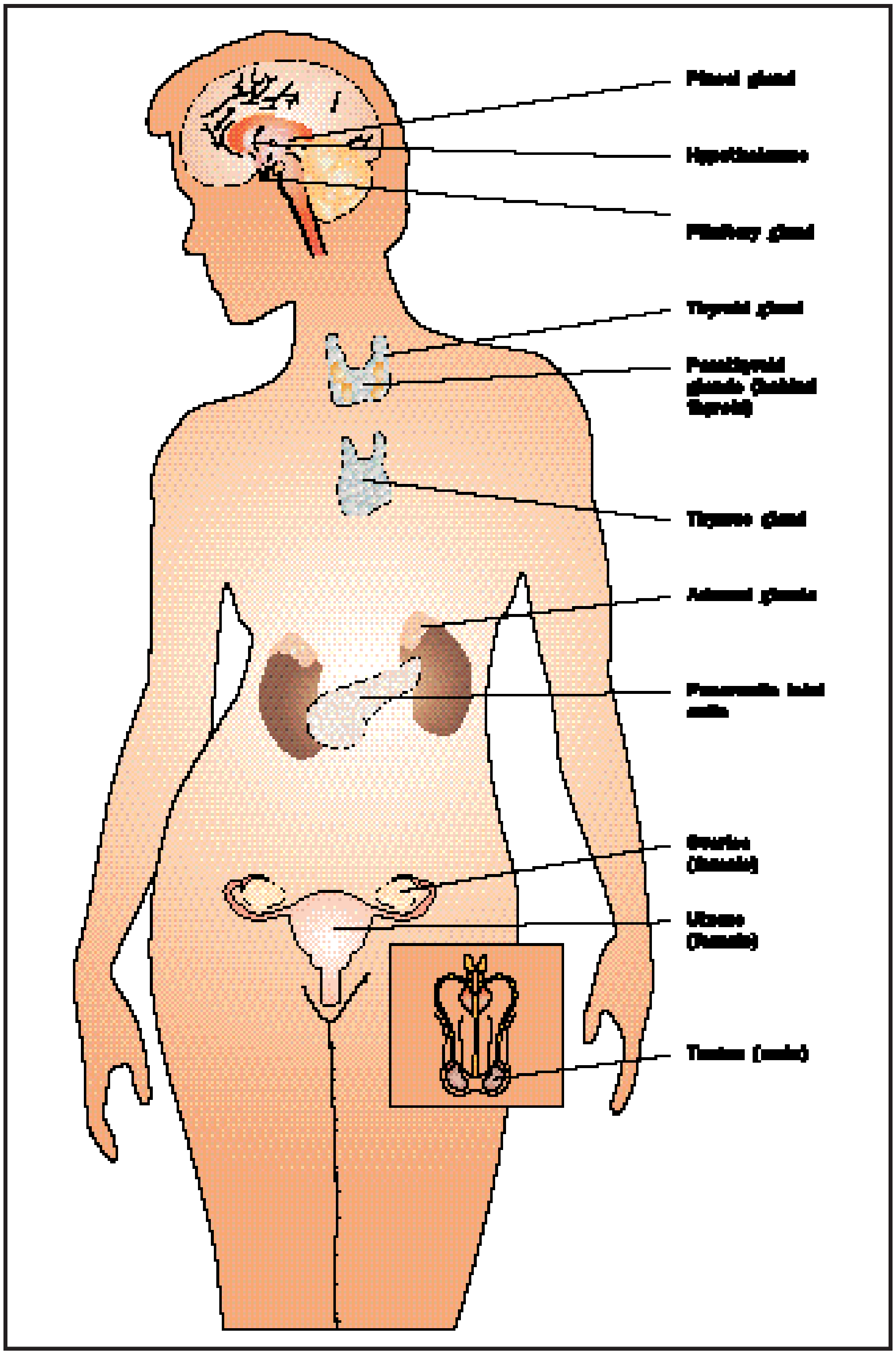
Endocrine System

The endocrine system is part of the regulatory system in animals and helps maintain the internal balance of the body. Both vertebrates and invertebrates have endocrine systems. The endocrine system regulates many functions of the body, including growth and metabolism, water balance, sugar and calcium balance in the bloodstream, and several functions related to sexual maturity and reproduction. Two major functions under endocrine control in invertebrates are the shedding of the **exoskeleton** for growth, called **molting**, and **metamorphosis**, functions that do not occur in vertebrates.

The endocrine system is not as fast to respond to stimuli as is the nervous system (the other major regulatory system in animals), which can respond in less than a second. The endocrine system can respond within minutes, and the effects usually last longer than the effects of the nervous system.

The endocrine system is made up of organs that produce chemical messengers called hormones. Hormones are released directly into the bloodstream in vertebrates and the haemolymph in invertebrates. Hormones circulate with the blood, so they are everywhere in the body.

Only certain cells, however, are capable of responding to these chemical messengers. These are target cells, which have special receptors for different kinds of hormones. Every chemical messenger has a unique shape.



The endocrine organs and their locations in humans. Redrawn from Johnson, 1998.

The target cell has a receptor that corresponds to the shape of the messenger. Most receptors are outside of a cell, embedded in the cell membrane.

When a messenger binds to the target, a different messenger is released inside of the cell. This second signal inside the cell is called a secondary messenger. This secondary messenger then triggers other changes inside the cell, such as the release of a substance. Other target cells have receptors on the inside of the cells. Specifically, some hormones can go inside of the cell and bind to a receptor that turns on and off DNA **transcription** of specific genes.

transcription a process wherein enzymes are used to make an RNA copy of a strand of DNA

Endocrine Organs and Effects

The endocrine system works through the same process in vertebrates and invertebrates, although the organs and chemical messengers involved differ. In invertebrates, the nervous system has modified cells that secrete most types of hormones. The hormones released from within the nervous system regulate the other endocrine organs in invertebrates.

These other organs include the corpora cardiaca, the prothoracic glands, and the corpora allata. The corpora cardiaca are located next to the brain and secrete hormones that control the prothoracic glands. The prothoracic glands are located behind the brain and secrete **ecdysone**, which stimulates and controls molting, as well as other hormones involved in the molting process. The corpora allata is located near the digestive system and secretes juvenile **hormone**. Juvenile hormone is involved in growth, metamorphosis, and reproduction. The **gonads** (ovaries and testes) also secrete hormones in the invertebrates and are involved in reproduction.

ecdysone hormone that triggers molting in arthropods

hormone a chemical signal secreted by glands that travel through the bloodstream to regulate the body's activities

gonads the male and female sex organs that produce sex cells

hypothalamus part of the upper end of the brain stem that regulates activities in the nervous and endrocrine systems

Vertebrates have more endocrine organs than invertebrates. The **hypothalamus**, pituitary gland, and pineal gland are located in the brain. The hypothalamus controls the pituitary gland. The pituitary gland controls water regulation and endocrine production of the gonads, and stimulates growth as well. The pineal gland controls biological rhythms such as sleep by producing melatonin.

All other endocrine organs are located in the body cavity. The pancreas controls blood sugar levels by secreting two hormones that have the opposing functions of raising and lowering blood sugar levels. The thyroid and parathyroid control calcium levels in a manner similar to the pancreas: one hormone raises calcium and another lowers calcium levels. The thyroid also controls metabolism. The adrenal glands are located above the kidney. They are involved in both long-term and short-term stress responses. The thymus is involved in immune responses. The gonads are involved in many functions.

The gonads consist of the ovaries and testes and in vertebrates control development and growth in addition to regulating reproduction. The gonads secrete steroid hormones. Steroids are one of the chemical messengers that have receptors inside of target cells and most cells have steroid receptors, so that steroids affect the entire body.

The gonads produce three classes of steroid hormones: androgens that include testosterone, estrogens, and progestins. Both testes and ovaries produce all three steroid types, but in different proportions. In humans, steroids determine the sex of a fetus during development. If androgens are present at high levels during fetal development, then the fetus develops as a male. If androgens are not present at high levels, then the fetus develops as a female.

Steroids are also responsible for sexual maturation and the development of secondary sex characteristics during puberty in humans. Secondary sex characteristics in males caused by high levels of androgens include changing patterns in hair growth such as baldness and facial hair growth and deepening of the voice. Estrogen in females cause secondary sex characteristics

such as the development of breasts. Progestins in females cause reproductive cycles and menstruation.

Supplemental Hormones for Humans

Humans sometimes take hormones by pills or injections to alter or supplement the body's own production of hormones. The best example of necessary hormone supplements is insulin replacement for diabetes mellitus. The pancreas secretes insulin, which lowers blood sugar levels, and glucagon, which raises blood sugar levels. When someone is diabetic, the body does not produce enough insulin and blood sugar remains at too high a level for normal water and metabolic functions.

Type I diabetes mellitus starts during childhood and is an autoimmune disease. Someone with Type I diabetes mellitus must take injections of insulin to control blood sugar levels. The insulin is either extracted from the organs of other animals or is produced by bioengineering bacteria to produce insulin. Those having Type II diabetes mellitus are often over forty years old and can control blood sugar levels with special diets and exercise.

Another common form of hormones taken by humans is steroids. A practice that is neither legal nor safe is that of individuals, usually males, taking steroids to increase muscle growth. Athletes of all types do this, not just bodybuilders. Androgens facilitate the acquisition of muscle mass, which is why men are more muscular than are women. However, taking supplemental androgens will cause the body to shut down its own production of androgens and interfere with the body's reproductive functions.

Common side effects of taking androgens include shrinking of the testes, impotence, the development of female secondary sex characters such as breasts, and a serious risk of heart attack. Additionally, sources for these androgens are usually other animals such as horses and illegal androgens are often impure, containing antibodies from the source animals. These antibodies can cause severe immune responses in humans and can even be fatal.

Birth control pills are another common form of steroids taken by humans. Birth control pills contain man-made estrogens and progestins. Birth control pills prevent ovulation, the development and release of an egg by the female, by disrupting the normal cycle of hormones that comprise the female menstrual cycle.

Environmental estrogens are chemicals that are thought to function as chemical messengers in animals. Examples of environmental estrogens include plastics and by-products of manufacturing. It is not completely understood at this point whether or not environmental estrogens can affect animals, and if so, to what degree.

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Endosymbiosis

Endosymbiosis is a mutually beneficial relationship between a host organism and an internal associate organism. The term is derived from the prefix "endo," meaning within, and the word symbiosis, which refers to a mutually beneficial relationship between two closely associated organisms. Another term for symbiosis is **mutualism**, which highlights the fact that both organisms are benefiting from the relationship.

mutualism ecological relationship beneficial to all involved organisms

Examples of Endosymbiosis

A well-known example of endosymbiosis is the relationship between a termite and the microorganisms in its gut. The termite consumes wood, but it cannot digest it without the help of protozoans in the termite's gut that break down the cellulose to a form that the termite can metabolize. Thus, the termite supplies food for the protozoan, and the protozoan provides food for the termite. In this example, the protozoan is the endosymbiont, or the internal organism in the endosymbiotic relationship.

There are a variety of levels of dependency between the two associates, including at one extreme an entirely voluntary relationship in which each partner can survive alone, and at the other extreme a situation where both are entirely dependent on the other. Also, the endosymbiont can be at different places within the host organism, from within a body cavity such as the gut to within individual cells. Endosymbiosis also plays a role in evolution, affecting the structure, behavior, and life history of the associated organisms.

Although there are various levels of dependency between the two organisms in an endosymbiotic relationship, it is nearly always advantageous for the two to stay together. An example that demonstrates this is the mutualism between corals and their endosymbiotic algae. The type of algae involved here are called dinoflagellates, and they are specialized to photosynthesize or use organic foods as their energy source. However, certain nutrients are not readily available in the ocean, so it is beneficial for the dinoflagelletes to live within the corals, where the nutrients are available. Similarly, corals can gather some dissolved organic carbon from the water or from prey items, but it is much easier and faster to gather them from the photosynthetic activity of dinoflagellate **endosymbionts**. A side effect of photosynthesis is that calcium carbonate is precipitated from the water that forms the coral structures of coral reefs.

endosymbionts the hypothesis that certain organelles in eukaryotes are prokaryotes that have a symbiotic relationship and live within the eukaryote

Both of these organisms have been cultured independently in the laboratory to show the extent of their interdependence. Under these circumstances, both have significantly reduced growth rates. Sometimes they even stop growing and rely on energy reserves. When they are allowed to circulate in the same water, but not make contact, their growth nearly doubles.

When put into contact, growth is even greater, indicating that actual contact can spur a higher than normal release and uptake of chemicals they exchange. Clearly, then, it is to the advantage of both to remain together.

Some sea anemones with these dinoflagellate endosymbionts have adapted their behavior to the needs of their algae. For example, free-swimming jellyfish will make vertical migrations to layers of water that are rich in ammonium for the dinoflagellates. During the day, **sessile** sea anemones expose those parts of their bodies where the dinoflagellates are located to allow for photosynthesis. At night they retract those parts and expose their stinging tentacles to catch prey in order to sequester food and provide nitrogen to their endosymbionts. These examples of behavior modifications by the host associate organism show how the two organisms have evolved to benefit one another, and, in turn, themselves.

sessile immobile, attached

Locations of Endosymbionts

Endosymbionts can live within their associate organism at a variety of places. They can be within a cavity of the organism, within cavities and within cells, or entirely within cells. Intracellularly, the location can be in cells that have special vacuoles for the isolation of the endosymbiont from the interior of the cell, or in cells that maintain the endosymbiont directly within the cell fluid.

Termites and their protozoan gut inhabitants are one example of the endosymbiont living within a cavity of the associate organism. Another common example is the **fauna** in the stomach of ruminating animals, or animals that regurgitate and rechew food particles, such as deer, cattle, and antelope. Stomachs of **ruminants** have chambers, the first of which is called the rumen and is specially designed to maintain populations of bacteria and protozoa that break down the food of their host using fermentation. The rumen is supplied with food and kept within a certain range of pH by specialized salivary glands. This affords the microbial community with a substrate to feed off of and a favorable environment to do so. There are a diverse number of microorganisms living there, including bacteria that digest cellulose, protozoa that digest cellulose with the help of their own endosymbionts, and others still that are predators on these protozoa. An entire community of different species with different lifestyles lives there.

fauna animals

ruminants plant-eating animals with a multi-compartment stomach such as cows and sheep

A common example of the endosymbiont living within the cells of the host is that of bacteria in the cells of insects. The cells of cockroaches contain bacteria, and cockroaches exhibit slowed development if the bacteria are killed with antibiotics. The growth of the cockroach can be restored, however, with certain additions to its diet that the bacteria presumably were providing.

The transmission of these bacteria from one cockroach to an offspring is hereditary, although not genetically based, because the bacteria invade the cytoplasm of the egg. Then, when the egg is fertilized and develops, it already has the endosymbiont that the mother had.

Another example of maternal transmission can be found in ruminating animals. In these animals, the mother passes the rumen microorganisms to her baby after it is born through her saliva and ruminated food, which contain all the microbial species the baby will need in life. If a baby ruminating animal is not allowed to be in contact with its mother, the baby may never get the microbes necessary for it to be able to digest plant material and will die.

Endosymbiotic Evolution

From behaviors such as the migration of jellyfish to different water layers, and special structures such as the rumen of the stomach, it is clear that endosymbiosis involves complex interactions and that these organisms have evolved together for many generations in order to develop such interactions.

eukaryotic cells cells that contain a membrane-bound nucleus and membrane-bound organelles

prokaryotes single-celled organisms that lack a true cell nucleus

Perhaps the oldest and most widespread example of this endosymbiotic co-evolution is in the origin of **eukaryotic cells**. They evolved from prokaryotic cells, with the primary differences being that eukaryotic cells are larger and more complex, containing a separate nucleus and numerous organelles (such as mitochondria), whereas prokaryotic cells are smaller with a few organelles floating freely in the cellular fluid. Examples of **prokaryotes** are simple unicellular organisms such as bacteria. Most multicellular complex organisms, however, from protozoans to fungus to animals, are eukaryotes.

How did eukaryotic cells arise? Athough there is no direct evidence, the most plausible theory is that an early prokaryotic cell, the ancestor to the mitochondrion, entered another prokaryotic cell, either as a food item or a parasite. Over time, the relationship between the two became endosymbiotic, with the mitochondrion supplying energy to the host associate and the host providing the proper environment and nutrients to the mitochondrion. Thus, a cell with a distinct organelle, or a eukaryotic cell, emerged. This means that every single cell in all prokaryotic organisms has endosymbiotic organelles.

Several characteristics of mitochondria support this widely accepted theory of an endosymbiotic evolution giving rise to eukaryotic cells:

- The mutually beneficial relationship between the cell, which provides nutrients and an environment for the organelle, and the mitochondrion, which provides energy for the cell, is seen in many other endosymbiotic systems, including those mentioned above.
- The modern role of the mitochondrion is to provide energy in a usable form for the cell.
- The mitochondrion has a genome within it that lets it reproduce itself and be largely independent from the cell and the cell's genome, which resides in the nucleus. Finally, the mitochondrion does not divide and reproduce in the same manner as the host cell. In sexually reproducing animals, for example, the mitochondria of the offspring are not a mix of both parents' mitochondria. Instead, they are all inherited from the mother. Thus, the mitochondria do not recombine as does the rest of the cell during sexual reproduction. Rather, they act more as independent organisms, maintaining their identity from host to host. SEE ALSO Interspecies Interactions.

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Entomology

Entomology is the study of insects. It is a major branch of animal zoology. Insects are one of the most successful and diverse groups of living organisms in the world today. Approximately 1.5 million species of insects have been identified by scientists as of the end of the twentieth century. However, it is estimated there may be as many as twice that number on Earth. The number of insect species is greater than the number of all other species of organisms combined. It is estimated that there are about 200 million insects for every living human. Insects are members of the kingdom Animalia, the phylum Arthropoda, and the class Insecta. Insects share the major group Arthropoda with creatures such as crabs, lobsters, shrimp, spiders, scorpions, ticks, mites, centipedes, and millipedes. Common insects include ants, butterflies, bees, cockroaches, beetles, flies, grasshoppers, mosquitoes, dragonflies, moths, wasps, and termites.

Insects have a tough **exoskeleton** (external skeleton) and three pairs of walking legs. The majority of insects have wings, and those with wings have two pairs, except flies, which have only one pair. Their bodies are divided into three regions: the head, thorax, and abdomen. All insects hatch from an egg in a form which is different from that of the adult insect. A well-known example of this is the caterpillar (the larval stage) and butterfly (the adult stage). Insects are characterized by their small sizes and short lifespans.

exoskeleton hard outer protective covering common in invertebrates such as insects

Scientists believe that insects have inhabited Earth for about 380 million years. They occupy nearly every type of environment except for salt water. They are most numerous in tropical climates and on land. Their enormous success is believed to be due to three main factors: their exoskeleton, size, and diet. Their tough exoskeleton protects them against physical damage and water loss. Their small size allows them to occupy many small areas unavailable to larger animals. Small size also allows for a faster reproductive rate. Finally, insects eat almost anything and everything.

Insects play many important roles in nature. Insects such as bees, butterflies, moths, and flies pollinate flowering plants. Many insects aid in the decomposition process and nutrient cycling, or exchange. Insects are important food sources for other animals, such as birds, and also eat other insects, thus keeping insect populations in control.

An entomologist looks through a microscope during a study of grasshoppers. Entomology is the study of insects and the further discovery of new kinds of insects on Earth.

Most entomologists work in the field of economic entomology, which is also called applied entomology. They study the small minority of insects that are harmful to humans. Harmful insects include those that destroy crops and buildings and those that transmit diseases to humans. Insects that feed on plants such as grasshoppers destroy plant crops and timber. Other insects transmit plant diseases. Insects such as termites destroy wood buildings. Bloodsucking insects such as mosquitoes, lice, and fleas transmit some of the most serious infectious diseases in the world. These include malaria, dengue fever, yellow fever, bubonic plague, and typhus.

Scientists attempt to reduce the number of insect pests through a variety of ways. Cultural controls include the draining of swamps where mosquitoes breed. Chemical controls include the use of pesticides and insect repellants. Biological controls include the use of animals that naturally prey on insect pests.

People are also inadvertently decreasing the number of insects by destroying their natural habitats. Destruction of natural areas by human activities is wiping out species of insects that we will never even know existed. What wondrous creatures are we missing?

Denise Prendergast

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Environment

The term "environment" means the surroundings of a living creature. It can also refer to all the factors of the external world that affect biological and social activities. There are abiotic (nonliving) environmental factors such as sunlight, air, and water. There are also biotic (living or recently living) environmental factors such as plants, animal predators, and food. The total environment of an organism is the sum total of the biotic and abiotic environments. The study of the relationships between living creatures and their environments is called **ecology**.

ecology the study of how organisms interact with their environment

A human's abiotic environment includes things such as weather (sunlight, wind, air temperature) and items which give protection from the weather (clothes or houses). Other abiotic factors are the soil and water, and chemicals in the soil and water. A human's biotic environment includes things such as food (plants and animals), other humans, animals, trees, and grasses. The biotic environment also includes how living creatures interact with each other and their abiotic environments. Therefore, a human's biotic environment also consists of social or cultural surroundings. Humans learn from each other how to behave in socially acceptable ways. They also pass along knowledge about language, science, and art.

The major components of Earth's physical environment are the atmosphere, climate and weather, land, and bodies of water such as lakes, rivers, and oceans. The term "environment" is commonly associated with the impact that humans have made on the natural world. Increasing human population and industrial activities have led to problems associated with the pollution of air, water, and soil. Pollution has a negative impact on humans in terms of health and quality of life, as well as on other animals and plants.

Human activities such as the dumping of industrial wastewater and poorly treated sewage water have led to the pollution of fresh and salt water. Groundwater, water beneath the land surface that often serves as drinking water for humans, has also been negatively affected. Accidental oil spills from ships and untreated storm-water runoff from urban and agricultural areas also degrade bodies of water.

Air pollution results from human activities such as burning fossil fuels (oil, coal, and gasoline) to create electricity and power automobiles, and manufacturing industrial products such as chemicals and plastic. Burning fossil fuels releases carbon dioxide into the atmosphere, adding billions of extra tons of carbon to the natural carbon cycle. Deforestation and poor soil management also add carbon. Most scientists believe that the increased

carbon dioxide in the atmosphere contributes to the potentially devastating warming of the global climate, the so-called "greenhouse effect." Another human impact on the atmosphere has been depletion of the ozone layer. The ozone layer helps filter ultraviolet light and protects Earth's surface from harmful doses of radiation. Many scientists believe that chlorofluorocarbons used as coolants in air conditioners and refrigeration units destroy ozone when released into the atmosphere.

Land pollution is caused by poor agricultural practices, mining for coal and minerals, and dumping industrial and urban wastes. The widespread usage of pesticides has led to pollution of both soils and bodies of water.

As more and more environmental problems become evident, humans will have to assess their activities and their impact on the natural world. SEE ALSO BIOME; ECOSYSTEM; HABITAT.

Denise Prendergast

Environmental Degradation

biotic pertaining to living organisms in an environment

abiotic nonliving parts of the environment

Humans, like all organisms on Earth, interact with both the **biotic** (living) and **abiotic** (nonliving) factors in their environment. Environmental degradation occurs when a potentially renewable resource—one of the biotic or abiotic factors humans need and use—such as soil, grassland, forest, or wildlife—is extracted at a rate faster than the resource can be replaced, and thus becomes depleted. If the rate of use of the resource remains high, the resource can become nonrenewable on a human time scale or even become nonexistent.

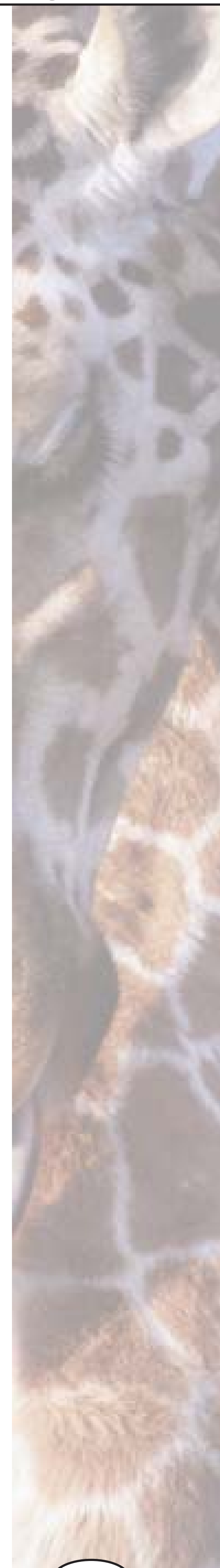
Toxic debris washed ashore at the Padre Island National Seashore in Texas.

For example, topsoil is important to farmers because crops are grown in topsoil. It can take as many as 200 years to form 1 centimeter (0.40 inches) of topsoil through natural processes. Topsoil can also be lost through various causes. One of the main causes of topsoil loss is erosion. Erosion can happen when water washes soil downhill or when wind blows unprotected soil away. Worldwide, topsoil is being lost to erosion much more quickly than it is being replaced.

If topsoil loss is allowed to continue unchecked, the land can be rendered permanently infertile through a process known as desertification. Many areas of the world suffer from desertification. Grasslands do not receive much rain. If the soil cover is removed by overgrazing or by poor farming practices, the topsoil can be rapidly removed by wind erosion. This happened in parts of Texas and Oklahoma during the 1930s, leading to dust-bowl conditions. Although drought contributed to dust-bowl formation, the main cause was overgrazing and poor farming practices.

biodiversity the variety of organisms found in an ecosystem

Loss of **biodiversity** is an important aspect of environmental degradation. Biologists agree that species are becoming extinct at an alarming rate. Biodiversity is also being lost at the ecosystem level due to environmental degradation. Tropical forests are recognized as the most diverse ecosystems on Earth and are experiencing the highest rate of ecosystem loss, but temperate habitats are also suffering degradation. Because the temperate parts of the world were settled first, the loss of biodiversity has been greatest there.



The quantitative loss of ecosystems is easy to measure. When a native prairie is converted to a cornfield or an open field is paved over to make a parking lot, the number of hectares can easily be calculated. Qualitative ecosystem degradation is harder to measure. The structure, function, or composition of an ecosystem can slowly change until the habitat is lost.

The Population Factor

Who is responsible for degrading the environment? We all are. Ordinary human activity from even the most responsible individuals inevitably pollutes and degrades the environment to some extent. We degrade the environment directly when we consume resources (for example, burning wood in a fireplace), and indirectly when we extract resources and transform them into products we need or want.

In 1999, the number of people on Earth exceeded 6 billion. The population of the world increased fourfold in the twentieth century. This rapid increase in population was accompanied by an even more rapid increase in the use of resources to support the growing population and to raise living standards. During the twentieth century, global energy use increased by a factor of 20. Following World War II, the world became even more dependent on extractive industries, such as mining and oil exploration, to supply the various minerals and fossil fuels required to support a higher standard of living. Energy shortages have an even greater impact on developing nations that are heavily dependent on subsidized fuel supplies to maintain food production.

The role of agriculture. During the twentieth century, agriculturally productive land has been extensively modified to make it even more productive. This includes the widespread use during the twentieth century of chemical fertilizers (often produced from oil) pesticides, and extensive irrigation. To supply the needs of extensive irrigation, surface water has been diverted and many wells have been drilled seeking ever more subsurface water. At the same time that industrial agriculture was growing, agriculturally productive land was being lost to urban development and industry. In the twenty first century, competition for remaining land and water resources is expected to continue to increase.

Modern agriculture has been able to produce an enormous amount of food. Intensive agriculture is able to produce more food per hectare, but increases the need for fresh water and chemicals for pesticides and fertilizer. Much of the rise in the food supply since 1950 has been due to greatly expanded irrigation and the use of pesticides and fertilizers. However, reservoirs will eventually silt up and aquifers (subsurface water supplies) will be depleted. Irrigation with surface or subsurface water can also cause salt to accumulate in the soil. As the irrigation water soaks into the soil and evaporates, it leaves the minerals behind. Eventually, these minerals, including sodium chloride and other salts can build up to the point that the soil is rendered unsuitable for growing anything. This has already happened in much of the central valley of California. In addition, the simple ecosystems used by modern industrial agriculture are much less resilient than the complex ecosystems they replace. High-yield crops in **monocultures** are more susceptible to insect infestations and disease than traditionally farmed crops.

monocultures the cultivation of single crops over large areas

High-yield agricultural practices can also lead to soil erosion, and thus a further loss of topsoil.

Forests suffer similar pressures. Trees are harvested for timber and pulp. Land is cleared for agriculture. Mixed, old-growth forests are replaced with trees all of the same species planted at the same time. These forest monocultures suffer many of the same problems as food crop monocultures. They suffer from insect infestations and are much less stable than a diverse ecosystem. Grasslands have also been extensively modified and in many areas suffer desertification. As a consequence, there are significant losses of productivity in agricultural and forest lands from overcultivation, overgrazing, desertification, and deforestation around the world. The human population is expected to continue to grow rapidly during the twenty-first century. As it does, many of the environmental resources on which humans depend are being degraded.

Resource use. According to one simple model developed by G. Tyler Miller in *Living in the Environment*, the total environmental degradation, or total environmental impact, of a population depends on three factors: (1) the number of people, (2) the average number of units (kilograms, liters or pounds, gallons) of resources used by each person, and (3) how each person uses those resources. According to this model, there are different ways overpopulation can cause the environment to become unable to support the rate of resource consumption.

In some regions of the world, people use a relatively small number of units of any given resource, but there are so many people that the resource is still depleted. This is called people overpopulation and it is the principal cause of environmental degradation in the world's poorer developing nations. Because the population is already consuming the minimum amount of resources possible to sustain life, reducing consumption is not possible. In order to prevent or limit resource depletion, some countries have instituted family planning or have strictly limited the number of children allowed in each family.

In other regions there are relatively few people, but each person uses (on the average) so many units of a resource that the resource still becomes depleted. Miller calls this consumption overpopulation. The United States has the highest level of consumption of any nation, although the level of resource consumption in many other nations is rapidly increasing. Reducing resource consumption is certainly possible, but is politically unpopular. Many economists connect the high standard of living in the United States to a high level of resource consumption, and possible reductions in standards of living are never popular.

Population distribution. There are several other factors related to environmental degradation. The first is population distribution. When large numbers of people are concentrated in a small area together with industrial activity, air and water pollution can rise to unacceptable levels. Other factors are wasteful patterns of consumption and overconsumption. When people consume more than they need to maintain a high standard of living or fail to effectively control waste through recycling and conservation, then environmental degradation can occur.

Another factor related to environmental degradation is **carrying capacity**, the maximum population of a given species that an ecosystem can support for an extended period of time. Every habitat, ecosystem, or **biome** has a carrying capacity for the best population level of any particular species. This is the level that maintains ecosystem diversity (including genetic diversity) without depleting ecosystem resources. Humans now inhabit every portion of Earth and occupy a variety of different ecosystems. Discussions of carrying capacity for human population must include the whole Earth as an ecosystem. There is much debate and discussion of Earth's carrying capacity. Many scientists feel that Earth is already overpopulated and that drastic measures must be taken immediately to reduce population and resource consumption. Others feel, just as strongly, that Earth can support far more people than it does now at a high standard of living. New technology, including extractive technologies and genetic engineering of food crops, will continue to increase Earth's carrying capacity.

carrying capacity the maximum population that can be supported by the resources

biome major type of ecological community

global warming a slow and steady increase in the global temperature

A Global Issue

Environmental degradation affects everyone. International environmental concerns frequently focus on large-scale problems such as desertification or **global warming**. However, vulnerable groups, such as impoverished people living in marginal areas, are more concerned with local issues. They may worry about the loss of rangeland, soil erosion, or the need for more intensive farming. These and similar issues affect poor people because they are directly related to the household food supply and food security. Environmental degradation results in decreased production and lowered income. As the land is more intensively farmed, soil fertility decreases and crop yields are reduced. Unfortunately, rural poor people have few choices other than to overusing the limited resources available. The resulting environmental degradation can trigger a downward spiral in which the intensive use of resources results in more environmental degradation, which requires even more intensive use of resources. SEE ALSO Habitat Loss.

Elliot Richmond

Many of the resources to which humans have free access such as clean air, open oceans and the fishes in these oceans, wildlife, migratory birds, atmospheric gases, and stratospheric ozone are held in common. Everyone has the opportunity to use or even abuse these resources. Because it is each individual's self-interest to extract as much of a resource as possible, resources can easily be overharvested or converted to nonrenewable resources. This is often called the "tragedy of the commons," after the practice of grazing sheep or other animals on property held in common by the whole community. When there are relatively few users, the use of resources held in common has little effect. When there are many users, the cumulative effect of many people trying to maximize their use of the same resource can lead to degradation or destruction of the resource. Humans may be able to avoid the tragedy of the commons if they can convert their thinking from a self-centered viewpoint to a broader perspective.

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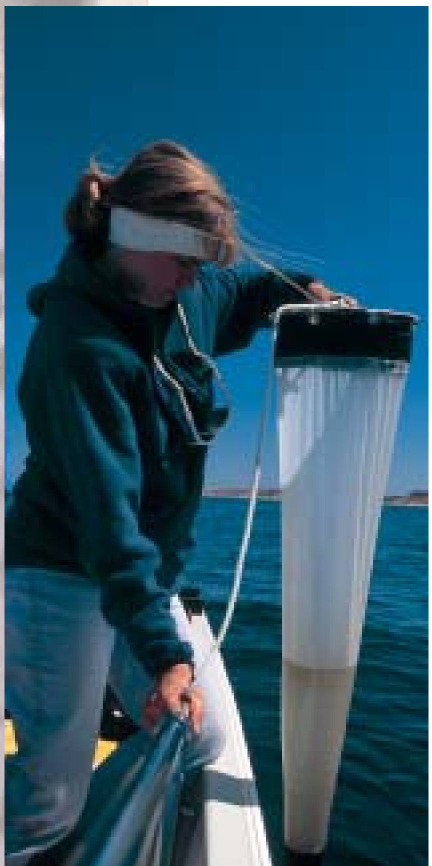
Environmental Impact



A scientist takes a water sample from Monterey Bay in California to determine the environmental impact of pollution in the area's water.

The term environmental impact is a legal term introduced by the National Environmental Policy Act of 1969. This act requires federal agencies to conduct studies to determine the possible consequences for the environment of planned activity. Many states have enacted similar legislation. The results of the study are published as an environmental impact statement. These legal documents are often the basis on which an agency decides whether or not to proceed with a project.

All animals interact with their environment, so all animal activity, including human activity, has some environmental impact. However, human impact on Earth's environment far exceeds that of other species. Humans have altered the environment and landscape on a global scale.

Most species inhabit fairly limited regions within Earth's biosphere, but humans occupy every biome. Humans have the advantage of a high level of technology. Technology has enabled humans to create artificial environments that allow survival even in the harshest environments. Technology allows humans to move food and other materials thousands of kilometers from areas where the resources are plentiful to areas where resources are scarce.

Our ability to live just about anywhere in the world comes at a cost to the environment. Most animals require only a few resources to survive, such as air, food, water, and nesting material. These resources are obtained from a relatively small area. In contrast, humans living in highly industrialized nations rely on thousands of products that come from all parts of the world.

The worldwide extent of human activity, the shift to intensive agriculture, the demand for mineral and other resources, and rising standards of living have all created numerous global environmental problems as well as many regional and local environmental problems. These problems are our environmental impact.

There are several significant environmental issues, including the acquisition and use of natural resources, rapid population growth, soil erosion, desertification, diminishing water supplies, deforestation, loss of biodiversity, global warming, and **acid rain**.

acid rain acidic precipitation in the form of rain

Resource Acquisition

All organisms interact with their environment to acquire and use resources and thus have an impact on their environment. Most of the time, this is a sustainable impact in that resources are replaced at about the same rate as they are removed and waste is produced in amounts that can be easily absorbed by the ecosystem. Consequently, most animals living in a natural environment have no significant long-term environmental impact.

The maximum viable population of a particular species that an environment can support indefinitely is referred to as the carrying capacity. For most organisms, carrying capacity is determined by the ability of an ecosystem to provide resources, such as food, water, and shelter, and its ability to assimilate, dilute, or detoxify wastes.

Early humans interacted with their environment in a sustainable manner, and their environmental impact was localized and short term. How-

ever, the development of intensive agriculture (following the invention of the metal plow) beginning about 5,000 B.C.E. allowed humans to increase the carrying capacity of their environment. During this agricultural revolution, humans came to see the environment as something to be tamed and exploited. Farmers were able to produce a surplus of food that could be traded for other goods and services. This trade led to increased urbanization with the development of trade centers.

During the first half of the nineteenth century, the Industrial Revolution made manufactured goods cheap and readily available to everyone. The mechanization of agriculture allowed an even greater rise in food production and increased urbanization. The Industrial Revolution, therefore, expanded the carrying capacity of the environment even more. As methods of resource acquisition developed, including methods of mining, fishing, farming, and logging, humans have had an increasingly significant, and often harmful, impact on the environment.

Population Growth

Many environmentalists consider population growth to be the principal environmental problem facing the world today. Sometime during 1999, world population exceeded 6 billion. If the current rate of population growth continues, the world's population will exceed 10 billion by 2030, and will continue to double about every twenty-five years. A larger population creates a greater demand on energy and other resources to maintain current living standards.

Desertification

When topsoil is removed, forests are cut down, or grasses are overgrazed, the land can be permanently changed. The process of degrading grassland to infertile conditions is known as desertification. Many grasslands grow in semi-arid regions of the world. These areas average between 25 and 75 centimeters (10 and 30 inches) of precipitation per year. This rain or snow is trapped by a thick layer of humus-rich topsoil. Overgrazing can remove the grass cover, exposing the topsoil to wind and water erosion. Poor farming practices can also expose topsoil. In the 1930s in portions of Texas, Oklahoma, Kansas, and Colorado, overgrazing and poor farming practices combined with extended drought to create dust-bowl conditions. Once the topsoil is lost, it can take hundreds of years to replace.

Diminishing Water Supplies

Water comes from two sources, surface water and ground water. In many parts of the world, there is insufficient surface water to supply the needs of agriculture, so water is pumped from deep wells. Often, the aquifers supplying these wells are recharged only very slowly, if at all. Some of these deep wells pump water that was deposited in the aquifer during the Pleistocene, over 18,000 years ago. Since the climate has now changed, the water cannot be replaced.

Intensive agriculture requires lots of water. Industry, agriculture, and human populations also have a need for abundant supplies of water. Many experts believe the unavailability of sufficient supplies of fresh water will be the most serious long-range problem confronting the United States and many other parts of the world in the years to come.

Deforestation

Deforestation occurs when trees are removed from a forest faster than they can be replaced by natural growth or replanting. Sometimes deforestation is deliberate. When Europeans first arrived, a dense hardwood forest covered much of the eastern United States. Settlers cut down the trees for fuel and building materials and cleared the land for farming.

In tropical regions of the world, the same thing happens today. Trees are removed to open up land for farming. Unfortunately, the soil under tropical forests is poor and lacks essential nutrients due to the heavy rainfall, so the land cannot support agriculture in the long term. After two or three years, the cleared land no longer supports crops and more trees are cut down. Harvesting tropical hardwoods for building materials also contributes to deforestation. The result of clearing land and cutting down hardwoods is an alarming loss of tropical and other forests worldwide.

Biodiversity

Worldwide, species are being lost at a rate equal to or greater than at any other time in the history of life on Earth. Entire ecosystems are lost through environmental degradation. The world's tropical forests contain the greatest variety of organisms on Earth. As these forests are cut down for timber or converted to rangeland, there is a great loss of species and diminished biodiversity. Temperate forests and other temperate habitats are also suffering degradation. While it is easy to measure the number of hectares of forest or grassland converted to cornfields or to parking lots, it is much harder to characterize the slow degradation in an ecosystem's structure, function, or composition.

Global Warming

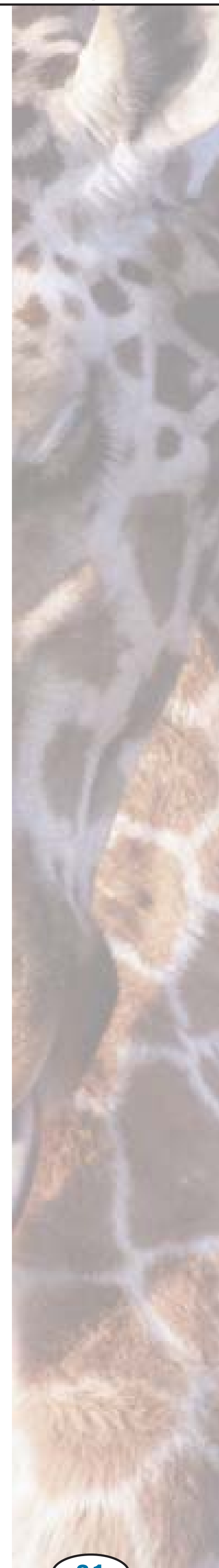
Research strongly indicates that the atmosphere of Earth is gradually warming. The best estimates are that the temperature has increased by 0.5°C (1.0°F) in the last century. This is a small but significant increase. What scientists cannot agree on is what causes global warming. Many researchers are convinced the data show unequivocally that global warming is directly related to the increase in greenhouse gases, such as carbon dioxide. Others feel it may simply be a short-term climactic phenomenon.

Acid Rain

acidic having the properties of an acid

Because acid "rain" may come in the form of rain, snow, fog, or dew, the best term is acid deposition. All rain is slightly **acidic**. As water falls through the atmosphere, it absorbs carbon dioxide. The carbon dioxide reacts with the water to form carbonic acid. This is normal and healthy. Plants and animals easily tolerate this natural acid rain.

The problem arises when other compounds dissolve in rainwater and make the rain even more acidic. Sulfur dioxide is emitted from power plants that burn high-sulfur coal, and from other sources that burn fuel with a high sulfur content. Sulfur dioxide particles can be carried over long distances by



winds and fall to the ground far from where they originated. If the sulfur dioxide dissolves in water in clouds, it forms sulfuric acid. Power plants and automobiles also emit oxides of nitrogen, which can dissolve in water to form nitric and other acids.

Natural precipitation has a pH of about 5.6. The pH of pure water is 7.0. A pH of 5.5 will reduce the ability of trout and salmon to reproduce. If the pH falls below 5.1, several serious effects can occur. Acid rain with a pH below 5.1 can damage buildings and statues, kill fish and aquatic plants, weaken trees, disrupt the nitrogen cycle, and stunt the growth of crops.

There is no escaping the conclusion that human activity has dramatically changed our planet, mostly for the worse. Many of these changes, such as open pit copper mines, are simply unsightly. Other changes, such as air and water pollution, have great potential to do harm to humans and other life. As we struggle with raising the standard of living of people all over the world, it is important to look for techniques of resource extraction and utilization that can minimize the adverse impact human activity has on the environment. All human and animal activity affects the environment in some way, but human activity need not harm our environment. SEE ALSO Global Warming.

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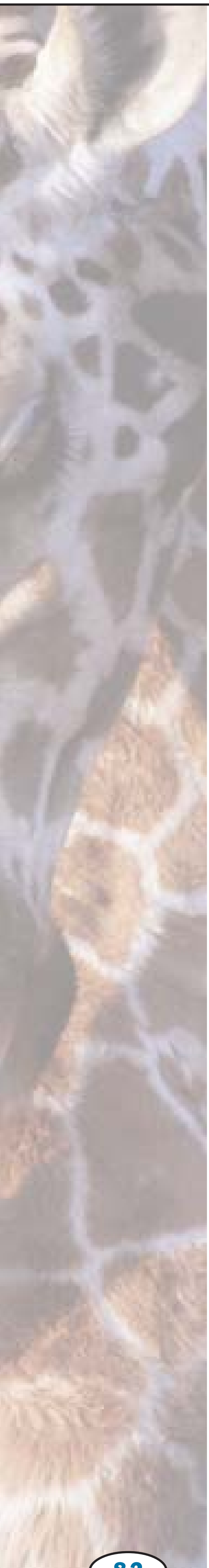

Environmental Lawyer

pesticide any substance that controls the spread of harmful or destructive organisms

The field of environmental law began after World War II (1939–1945) as a response to growing public concern about the impact of the massive amounts of toxic chemicals used in the fields of agriculture and public health. American biologist Rachel Carson's 1962 book *Silent Spring*, which served as both a warning about the dangers of unregulated **pesticide** use and a reminder that human health is inextricably linked to the health of the planet, mobilized people around the world. The first lawyers to work with this growing "environmental" movement helped grassroots organizations investigate chemical claims and lobby for laws to regulate the proliferation of poisons flushed into the water and air and dumped by the planeload over farmland. Thanks to public pressure, the U.S. government in 1970 created the Environmental Protection Agency, charging it with enforcing environmental protection of land, air, water, and other species.

Environmental lawyers choose from three broad areas in which to work. Many enter government agencies, writing laws and enforcing them, investigating violations, and prosecuting the violators. Many other lawyers choose to work for industry helping companies to understand and comply with the changing laws, permits, and regulations. These lawyers also defend their clients in violation lawsuits and help them to lobby for decreased regulations. The smallest group of environmental lawyers is composed of those who work as public advocates for citizen's groups, from the local to the international level. These lawyers describe their work as the least well paid yet the most rewarding in allowing them to use their career to pursue their ideals, whether they are protecting neighborhoods, clean air and water, wilderness, or other species.

The requirements for becoming an environmental lawyer are the same as for any law degree. A candidate with a bachelor's or master's degree applies to a three-year law program with a set curriculum. Elective courses could include studying the Clean Air Act, Superfund cleanup laws, or the laws governing mineral resources. Although not a requirement, a background in ecology, biology, chemistry, or engineering helps lawyers understand complicated pollution questions. The most important quality to bring to environmental law is a reverence for life and an understanding of the interconnectedness of all beings.

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Ethology

innate behavior behavior that develops without influence from the environment

The study of behavior is divided into two sub-categories: learned behavior and **innate behavior**. Ethology is the study of innate, or instinctive, behavior. Scientists in this field study the mechanisms underlying specific behavior, as well as their evolution. Ethologists were the first to systematically and scientifically measure the natural activities of animals.

Ethology had its origins in a middle ground between the behaviorists, who believed that all behavior must be learned, and the classicists, who held that all behavior was inborn. According to ethologists, animals are genetically predisposed to learn behaviors that benefit their species, but this natural behavior can be modified, within limits.

The field of ethology was pioneered by three prominent European scientists during the first half of the twentieth century: Konrad Lorenz, Nikolaas Tinbergen, and Karl von Frisch. Lorenz, an Austrian scientist and physician, is referred to as the founder of modern ethology. He discovered the process of imprinting, by which newly hatched ducklings and goslings follow the first animal they see and hear as if it was their mother. Lorenz also conceived of the **fight or flight response**, a theory that attributes an animal's reaction to conflict as a compromise between two inner drives: to attack or to flee. Nikolaas Tinbergen began by studying the homing behavior of wasps and later worked with Lorenz. Tinbergen applied ethological concepts to anthropology, the study of human interactions, by linking human instinct to rituals. Karl von Frisch studied the sensory systems of fish, discovering that fish are able to see many colors and have relatively sensitive hearing. Von Frisch also demonstrated that honeybees have a sophisticated ability to use the sun's position for orientation and to utilize different dances to indicate a target's direction and distance from the honeycomb. These three researchers won the Nobel Prize in Physiology or Medicine in 1973 for their combined contributions to the field of ethology.

fight or flight response an automatic, chemically controlled response to a stimulus that causes increased heart and breathing rates for increased activity

Neuroethology, a discipline that originated in the 1960s, combines ethology with neurobiology. It draws connections between outwardly observable, innate behaviors and the activity of particular regions of the brain.

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Eukaryota

The Eukaryota are one of the two major groups of biological organisms. The other is the **Prokaryota**, which contains the eubacteria and archaebacteria.

prokaryota a group of organisms that lack a membrane-bound nucleus and membrane-bound organelles

Differences Between Eukaryotic and Prokaryotic Cells

The key feature of all eukaryotes is that they possess eukaryotic cells. These differ from prokaryotic cells in several important respects. Eukaryotic cells are more complex and highly organized than prokaryotic cells. They are also, on average, ten times larger. Only eukaryotic cells have membrane-bound **organelles**. The organelles are separated from the cytoplasm by plasma membranes.

organelles membrane-bound structures found within a cell

In eukaryotic cells, the DNA is contained within a nucleus, an organelle bound by a double membrane. Eukaryotic DNA is linear, with a beginning and an end, and is divided into a number of separate chromosomes. Prokaryotic cells, on the other hand, have only a single circular-shaped chromosome of DNA that is not contained in a nucleus. One consequence of this difference is that eukaryotes can have much larger amounts of DNA than prokaryotes, which is necessary for the evolution of complex organisms.

ATP

ATP, or adenosine-triphosphate, is the organic molecule that forms the basis of energy in all living organisms. ATP is used in all cellular processes that require energy.

Other important eukaryotic organelles include the mitochondria, which are responsible for the cell's metabolism (the conversion of food into usable energy resources in the form of ATP), and the chloroplasts, which allow those species engaging in photosynthesis to use light energy to fix carbon, that is, to take in atmospheric carbon in the form of carbon dioxide and incorporate it into organic molecules for use by the organism. While both of these functions are also performed by prokaryotes, the machinery for these processes is not organized into organelles.

Eukaryotic cells also have an extensive system of internal membranes, including the endoplasmic reticulum (responsible for the synthesis of proteins) and the Golgi apparatus (responsible for processing and packaging proteins from the endoplasmic reticulum), which are not found in prokaryotic cells. Finally, unlike prokaryotes, not all eukaryotes have cell walls, and the cell walls of eukaryote species are composed of different materials from prokaryotic cell walls.

The Endosymbiotic Theory of the Origin of Eukaryotic Cells

Because of the relative simplicity of prokaryotic cells, it has long been supposed that they preceded eukaryotic cells in time. The endosymbiotic hypothesis for the origin of eukaryotic cells was first proposed by Lynn Margulis in her 1981 book, *Symbiosis in Cell Evolution.* The endosymbiotic hypothesis ("endo" means "within," "symbiosis" is a situation in which organisms live together in close association) suggests that eukaryotic cells arose when certain prokaryotic cells acquired **endosymbionts**, in this case other prokaryotic cells that lived within them. It is believed that the endosymbionts derived benefits from the host such as protection and organic nutrients, while the host obtained ATP (from the prokaryotes which evolved into mitochondria) or access to the products of photosynthesis (from the prokaryotes which evolved into chloroplasts).

endosymbionts the hypothesis that certain organelles in eukaryotes are prokaryotes that have a symbiotic relationship and live within the eukaryote

What were these prokaryotic symbionts? Likely candidates have been identified: mitochondria may have originated from endosymbiotic aerobic bacteria, while chloroplasts probably arose from endosymbiotic cyanobacteria, a prokaryotic group that had already evolved photosynthesis. There is considerable evidence supporting this hypothesis. Within eukaryotic cells, mitochondria and chloroplasts both have their own genetic material, separate from that of the nuclear DNA. It is in the form of a single circular chromosome, much like that seen in prokaryotes. Also, mitochondria and chloroplasts possess their own protein-synthesizing machinery, which again resembles that found in prokaryotes.

The evolution of the eukaryotic cell represented an advance in the degree of complexity present in cells. It allowed for the evolution of further

complexity of organization, including multicellular organisms. SEE ALSO Prokaryota.

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Evolution *See Biological Evolution.*

Evolutionary Stable Strategy

An evolutionary stable strategy describes tactics employed by individual organisms when competing with one another for a given resource. These tactics can be behavioral or structural, and the organism does not consciously choose them, but adopts them as a natural consequence of evolution. Both structures and behaviors are heritable (capable of being inherited), and as some are successful and some fail, only the better ones are passed on. It is important to differentiate between a strategy employed by an individual, such as displaying brighter-colored feathers, and a strategic decision an individual might consciously make, such as going to medical school, because only heritable strategies get passed on to offspring. Decisions such as going to medical school, however strong in a family, are not heritable.

The idea of evolutionary stable strategy (ESS) was first conceived by the British biologist John Maynard Smith in 1974. The idea is that one strategy in a given contest, on average, will win over any other strategy. The strategy should also have the benefit of doing well when pitted against opponents employing the same strategy. This is important, because a successful strategy is likely to be common and an organism will probably have to compete with others who are employing it. There does not necessarily have to be a single evolutionary strategy. It can be a combination of strategies, or a combination of individuals who each employ only one strategy.

The workings of an evolutionary stable strategy can be illustrated by looking at a simple system of two strategies. Suppose a given population of organisms has to compete for food. In this particular population, there only two possible strategies. Individuals can act like "hawks," which will fight over a piece of food viciously and retreat only when seriously injured, or they can act like "doves," which will try to puff their chests out and pretend to be tough, but run away at the threat of any serious challenge. Hawks will always beat doves. When hawks fight hawks, there will be a winner and a loser, but the loser will be seriously injured. Doves fighting doves will display at one another for a period of time before giving up. Neither will be injured, but they will have wasted some of the time they could have spent looking for food.

Illustration of the Dawkins system.

		Opponent	
		Hawk	Dove
Player	Hawk	50 or –100, average –25	Always 50
	Dove	Always 0	40 or –10, average 15

Which is the better strategy? That is, is it better to be a hawk and win against all doves, but at the risk of serious injury, or is it better to be a dove and risk being trounced by hawks? To answer this question, the British evolutionary biologist Richard Dawkins assigned arbitrary scores to wins and losses. He awarded 50 points for a win, zero points for losing, minus 100 points for serious injury, and minus 10 points for wasting time with excessive displays. Under Dawkins's system, assuming a record of equal wins and losses for evenly matched competitors, a bird population consisting exclusively of doves would reward individuals with an average of 15 points per contest. If a dove wins a contest against a dove, he gets 50 points less 10 points for wasting time, for a total of 40 points. The loser gets minus 10. If an individual wins half his contests, his score averages to 15 points (40 points minus 10 points divided by 2).

However, we cannot assume that a population of only doves would be evolutionarily stable. Although such a population seems beneficial for all the individuals involved, what happens if a mutation takes place, or a sudden immagrant flies in, and a hawk appears in the population? The hawk will win all his contests, and reproduce quickly and often. Before long, the successful hawks could possibly drive the doves into extinction. However, at a price of minus 100 points per loss, a hawk surrounded exclusively by hawks will average minus 25 points, whereas a dove surrounded by hawks will score zero. So in a population of only hawks, doves will tend to do better. A population of only hawks would not be evolutionarily stable, either. Over time, a single strategy cannot sustain itself.

So what strategy is evolutionarily stable? In this particular population, the stable strategy is a mixture of doves and hawks. This could mean that individuals never change their strategies and that a combination of both strategies is stable, or that individuals may employ either strategy and switch strategies as often as they please. In this case, the average individual will employ the most advantageous proportions of either strategy. In a system with 12 individuals—5 doves and 7 hawks—the average payoff for any individual is 6.25. Thus, we could have 5 individuals that were always doves and 7 that were always hawks, or 12 individuals that were doves 5/12 of the time and hawks the rest.

Of course, this is a very simple system. If individuals switch strategies, it is assumed that the organism's opponents are unable to guess its intentions. If the organism could not disguise its intentions, enemies could quickly learn to detect outward signs of strategy choice and adjust their tactics accordingly. For example, if an individual scratched at the sand every time before deciding to be a dove, its opponents could learn to be a hawk every time sand was scratched, and they would always win.

In nature, of course, different strategies are tried all the time. Instead of just two, there is a nearly infinite number of potential tactics, and it is reasonable to imagine that mutations are happening at a constant rate that introduces new tactics, or reintroduces old ones, into the system. These new strategies may topple the old ESS, or they may not. A preexisting ESS has probably been challenged by any number of alternate strategies and has survived, but it might be expected that only a completely new and innovative strategy would have a fighting chance at defeating it.

In 1980, the American political scientist Robert Axelrod created a contest related to the hawks-vs.-doves scenario, but allowed fifteen different strategies to compete in a computer simulation. After hundreds of rounds, a consistent winner cropped up, which may be safely called the evolutionary stable strategy. Fifteen opponents with a variety of tactics could not defeat it. Axelrod held another contest, this one with sixty-three entrants, and came up with the same winning strategy.

Such contests happen constantly in nature. New strategies evolve and pit themselves against the present evolutionary stable strategy. Given the diversity of the opponents that show up, the strategy is tested in a variety of directions. A true ESS will be unshakeable regardless of the opponents. Of course, in nature, changes in an organism's physical environment or species invasion can change all the rules of the game, and strategies may topple and be replaced by others better suited to the new environment.

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Excretory and Reproductive Systems

Excretory and reproductive systems each have important but different functions in animals. The excretory system maintains water, ion, and nitrogen balance within the body and eliminates wastes. The reproductive system creates new individuals of a species. Both the excretory and reproductive systems are under endocrine control but are also influenced by the external environment.

The Reproductive System

The reproductive system functions to produce more individuals of a species. The reproductive system is regulated by the endocrine system and is affected by environmental conditions outside of the animal and internal conditions inside the animal. Reproductive cycles are influenced by the time of year, amount of daylight and rainfall, and temperature, in addition to nutrition and general health of the animal.

The main organs in the reproductive system are the **gonads**, which include the ovary and testis. The ovaries produce eggs and the testes produce sperm. The egg and the sperm are **gametes** that combine to form a **zygote** in a process called fertilization. The zygote will grow and develop into a new individual of the species.

gonads the male and female sex organs that produce sex cells

gametes reproductive cells that only have one set of chromosomes

zygote a fertilized egg

Timber rattlesnakes during mating.

The egg and sperm both carry DNA, the material that contains the genetic instructions for the growth and development of a new individual. Gametes are produced through **meiosis** and contain only one-half of the genetic information of the parent. When the gametes come together and form a zygote, the zygote will have half of its genetic information from the egg and half from the sperm.

meiosis a specialized type of cell division that results in four sex cells or gametes that have half the genetic material of the parent cell

In vertebrates such as humans, egg and sperm come separately from different individuals. Humans and most other animals (both vertebrates and invertebrates) have different sexes commonly called males and females. In the case of animals without separate sexes, one individual produces both eggs and sperm and is called a **hermaphrodite**. Most hermaphrodites, including many **annelids**, pair with another individual and exchange eggs and sperm rather than fertilizing themselves. Some platyhelminthes self fertilize. Other animals switch between being male and female, a condition called sequential hermaphroditism.

hermaphrodite an animal with both male and female sex organs

annelids segmented worms

In addition to sexual reproduction, the fusion of the egg and sperm, some animals can reproduce asexually. In asexual reproduction, genetic material is not combined. Therefore, it produces an offspring that is genetically identical to the parent. Types of asexual reproduction include budding, fission, and parthenogenesis. Parthenogenesis occurs in rotifers, some bees, wasps, ants, and several species of fish, lizards, and amphibians. Some animals switch between sexual and asexual reproduction, and some reproduce only asexually.

Fertilization can happen internally or externally. External fertilization occurs in most sea-living creatures as well as freshwater fish and amphibians. In external fertilization both eggs and sperm are shed into water and fertilization, development, and growth of the zygote all take place outside the body. Internal fertilization occurs when egg and sperm are joined inside of the body. The zygote can develop inside of the reproductive tract, as in mammals. Birds and reptiles have internal fertilization but lay eggs. The zygote develops inside the egg but outside of the body. Invertebrates that have internal fertilization also lay eggs.

The Excretory System

Vertebrates have a closed circulatory system, which means that they have arteries and veins that transport blood. Cellular metabolism produces waste and uses nutrients and water. The circulatory system carries water and nutrients to cells and carries waste products away from cells. Water and nutrients come from ingestion and digestion. Waste removal is critical to maintaining internal **homeostasis**.

Nitrogen is the most toxic byproduct of cellular metabolism. The body must excrete nitrogen. Nitrogen is commonly produced as ammonia from cells. Many animals will convert ammonia, which is extremely toxic, into a less toxic form of nitrogenous waste. These include **urea** and **uric acid**.

The habitat of an animal determines which kind of nitrogenous waste it produces. Most aquatic animals, both invertebrates and freshwater fish, excrete ammonia. Ammonia dissolves in water and is easy to transport outside of the body by **diffusion** when an animal is surrounded by water. This happens primarily through the skin in invertebrates and through the **gills** of fishes. Ammonia must be diluted by a great deal of water to be nontoxic. There is not enough water in land animals to dilute ammonia enough, so ammonia is turned into either urea or uric acid.

homeostasis a state of equilibrium in an animal's internal environment that maintains optimum conditions for life

urea a soluble form of nitrogenous waste excreted by many different types of animals

uric acid an insoluble form of nitrogenous waste excreted by many different types of animals

diffusion the movement of molecules from a region of higher concentration to a region of lower concentrations

gills the site of gas exchange between the blood of aquatic animals such as fish and the surrounding water

Which of these an animal produces is linked to where the offspring develop. Animals characterized by internal development of offspring such as mammals make urea. So do animals that have eggs which develop in water, such as amphibians, sharks, and some fish that live in saltwater.

Urea is not very toxic and can be concentrated by the kidney to conserve water. Urea is dissolved in water, so transport of waste out of a developing egg that is sitting in freshwater is done by diffusion. Uric acid is not water soluble and is excreted in a paste. Birds, reptiles, and insects all produce uric acid. These animals develop in an egg on land, and waste must accumulate in the egg as the individual grows and develops. Because uric acid is not water soluble, it can sit in the egg and not be reabsorbed by the developing zygote.

Water balance in the body is maintained through a process called osmoregulation. The vertebrate kidney is a specialized organ that both concentrates urea or uric acid and maintains water balance, mostly by filtering the blood. When blood passes through the kidney, water is reabsorbed and reused by the body. Additionally, almost all sugar, salts, and other nutrients are reabsorbed by the body from the kidney. Waste products are taken out and eliminated, the main waste product being nitrogenous waste. The kidney contains about 20 percent of the blood volume at any one time.

In invertebrates, a variety of specialized structures exist for waste removal. Flame bulb protonephridia in planaria are the most primitive specialized osmoregulation structure in invertebrates. Annelids have an excretory system called the metanephridium, and it functions for both osmoregulation and nitrogenous waste removal. Insects use Malpighian tubules for both osmoregulation and filtering the hemolymph. SEE ALSO Catadromous—Diadromous and Anadromous Fishes; Fertilization; Ontogeny.

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Exotic Species

Exotic species, which are also known as alien species, invasive species, nonindigenous species, and bioinvaders, are species of plants or animals that are growing in a nonnative environment. Alien species have been moved by humans to areas outside of their native ranges. Once transported, they become removed from the predators, parasites, and diseases that kept them in balance in their native environments. As a result of the loss of these controls, they often become pests in the areas into which they are introduced.

Many plants and animals can disperse naturally into new habitats. The colonization of North America by cattle egrets from Africa, and the slow spread of the nine-banded armadillo into Texas and Louisiana occurred without human intervention. But the most destructive invasions are invariably those caused by human activity, whether deliberate or inadvertent.

The introduction of exotic species into the United States probably began with the first colonists that came ashore. When the Pilgrims landed at Plymouth in 1620, various non-native rodents, such as *Rattus*, and the house mouse, *Mus musculus*, almost certainly disembarked right along with them. The problem of exotic species became even more acute in the eighteenth and nineteenth centuries, as the United States entered world trade.

Environmental Impact

Nonnative species are not always harmful. Ninety-eight percent of the food grown in the United States come from nonnative species of wheat, barley, rice, cattle, and poultry. The nonnative honeybee is essential in growing plant crops, as well as generally benefiting flower pollination. Non-native species add $500 billion a year to the United States economy.

However, many nonnative species do enormous environmental damage. Research has shown that more than 40 percent of species on the U.S. Department of the Interior's lists of endangered or threatened species are at risk primarily because of nonindigenous species.

The economic damage caused by rats is huge. Rats alone do more than $19 billion of damage per year. Damage caused by alien insects cost $20 billion. Altogether, the more than 30,000 nonnative species in the United States cost the country $123 billion a year in economic losses, according to a June 12, 1999 report by Cornell University ecologists. In that report, David Pimentel of Cornell said that the United States has become the land of a billion rats.

Constant motion allows these fire ants to breathe in the water.

Invading species can cause complex changes within the structure and function of their new ecosystem. Their presence can lead to the restructuring of established food webs, the importation of new diseases to the new surroundings, and competition with indigenous organisms for space and food. Other ecological changes may occur when the invading organisms reproduce with native species, possibly altering the gene pool. This may lead to hybridization and homogeneity, which reduces biodiversity, the primary element associated with an ecosystem's ability to adapt to natural or human-induced changes.

How Do They Get Here?

Introductions of nonnative species can be planned, incidental, accidental, or unintentional. They can also be caused by a natural disaster. Scientists have made several attempts to identify the possible pathways of introduction, with varied success.

The most common method of introduction into marine environments is through the ballast water of shipping vessels. A cargo ship floats high in the water and is very unstable when it is empty. To stabilize the ship, the crew fills the ballast tanks with water. When the tanks are filled, marine organisms are pumped in along with the water. Then, when the ballast water is discharged at the next port of call, exotic species can be introduced. Scientists estimate that as many as 3,000 alien species per day are transported around the world in the ballast water of ships.

Aquaculture, the cultivation of natural products of water such as fish, also introduces invading organisms. Although nonnative species can provide inexpensive food and sources of recreation for human communities, these same species can cause environmental damage if they are released or escape.

Extent of the Problem

Every state in the United States and nearly all communities have been affected by bioinvaders. However, two states have been especially hard hit—Hawaii and Florida—and for similar reasons. Both states are geographically isolated and both have a semitropical-to-tropical climate.

Hawaii. Hawaii has been geographically isolated from the rest of the world for millions of years. Because of this isolation, Hawaii originally had thousands of species that existed nowhere else on Earth. But it has suffered the highest rate of extinctions of any area of the United States and one of the highest rates anywhere in the world, with hundreds and possibly thousands of unique species already extinct. The tropical climate of Hawaii allows invasive plants and animals to thrive. Nonnative plants and animals frequently displace native species. Predation by nonnative rats, feral cats, dogs, and mongooses has led to the extinction of many species of birds. Habitat destruction by feral pigs has altered landscapes. To compound the problem, nonnative species are usually more aggressive at colonizing disturbed ground left behind by the feral pigs.

Florida. Like Hawaii, Florida has a subtropical-to-tropical climate that allows many plants and animals to thrive. The state is protected by ocean on three sides. On the fourth side, it is geographically isolated from the states further north by differences in climate. Because of this isolation, Florida is considered to have been somewhat species-poor, with many niches available for invasive species to colonize.

Florida now lays claim to 63 percent of the nonindigenous bird species, 25 percent of nonindigenous plants, 25 percent of land mammal species, and the largest number of established nonindigenous amphibian and reptilian species in the United States. Overall, approximately 42 percent of Florida's reptiles, 23 percent of its mammals, 22 percent of its amphibians, 16 percent of its fishes, 15 percent of its **flora**, and 5 percent of its birds are naturalized nonindigenous species.

flora plants

Florida's nonindigenous species cause severe problems for the state's ecology, economy, and resource management. This is largely because of their impact on fishing and water sports, the degradation of wildlife habitat, the reduction of biological diversity, and the alteration of natural ecosystems.

Well Known Invaders

Thousands of invasive species worldwide are notorious for their distinctive habits, destructive potential, or ecological damage. Other invaders seem to be having little environmental impact. A few of the more well-known exotic species in the United States are discussed here.

African Clawed Frog. The African Clawed frog, *Xenopus laevis*, was widely used in human pregnancy testing in the 1940s and 1950s, and as a result was shipped all over the world. The frog is native to southern Africa, but is now found around the world in suitable habitats, probably due to accidental or deliberate releases. It is voracious and prolific, preying on insect larvae, small fish, and tadpoles. It is a completely aquatic frog. The state of Washington prohibits importation of *Xenopus*, and other states require a permit for possessing it. *Xenopus* remains a popular laboratory animal and is still available as a pet in some areas. The environmental damage caused by *Xenopus* is due to its voracious appetite and fecundity. The frog competes with native species for small fish, insect larvae, amphibians, and other prey. However, researchers disagree as to the extent of environmental damage it causes.

Mediterranean Gecko. This small gecko (*Hemidactylus turcicus*) is a native of the Mediterranean, and apparently first arrived in the United States on cargo ships unloading in New Orleans. Some areas may also have been colonized by escaped pets. The lizard is primarily nocturnal, preferring rocky walls near bright lights. It is found all along the Gulf Coast of the United States and as far west as Arizona. Because there are no other nocturnal, insectivorous lizards in areas the gecko have colonized, it does not appear to be causing any environmental damage.

Zebra Mussel. Zebra Mussels (*Dreissena polymorpha*) originated in the Balkans, Poland, and areas within the former Soviet Union. The species was introduced into the Great Lakes in the ballast water of ships in 1988. It has been spread by barge traffic into all the major East Coast rivers of the United States that are connected through canals to the Great Lakes. At first, the zebra mussel was believed to be intolerant of the warm water in the southern parts of the United States, but it is now established in the lower Mississippi River. Many of the small lakes near the Great Lakes are not connected to the Great Lakes by waterways, but they still have zebra mussels. In these cases, the mussels were probably transported on boats moved from lake to lake on trailers. They would not necessarily have to be moved from lake to lake on the same day, because in cool, humid conditions, zebra mussels can stay alive out of water for several days.

The economic impact of zebra mussels is due to their habit of colonizing the pipes that supply water to electric power plants and public water supplies. The colonies can become so dense that flow through the pipes is restricted. At one power plant in Michigan, zebra mussel densities were as high as 700,000 individuals per square meter (80,000 per square foot), and the diameters of pipes had been reduced by two-thirds at some Michigan water-treatment facilities.

Imported Fire Ants. There are two species of imported fire ants, *Solenopsis invicta*, the red fire ant, and *Solenopsis richteri*, the black fire ant. *S richteri* was introduced first, but the much more aggressive red fire ant has displaced it and the native fire ant species across most of the south. Currently, *S richteri* is found only in a few areas of northeast Mississippi, northwest Alabama and southern Tennessee. The attempts to control these invaders have been controversial. Early efforts to eradicate the ants with the widespread application of pesticides severely damaged the environment and may have contributed to the spread of the insect. Recently, a small parasitic fly (*Psuedacteon*) which offers promise as a fire ant control has been successfully bred, and test releases are underway. Techniques are now being developed to breed large numbers of the tiny flies for more widespread release.

The red fire ant is well established from North Carolina to eastern Texas, although the further extension of its range may be limited by geographical factors such as dry summers or cold winters. The two fire ant

species inhabit approximately 93,120,000 hectares (23,010,4531 acres) in nine southern states, making them a familiar feature of life in these areas. There are probably about 10 billion colonies. The ants are feared because, when a nest is disturbed, the ants swarm over any nearby object, delivering multiple, painful stings to the intruder. However, the greatest economic impact of the imported fire ant comes from their attraction to electrical equipment. Short circuits, fires, and other damage can occur after ants colonize the equipment.

Reptiles and amphibians. The native range of the giant toad (*Bufo marinus*) extends from southern Texas, through Mexico and Central America, to Brazil in South America. This marine toad is widespread, occurring outside its natural range in places such as Australia, Fiji, Guam, Hawaii, Japan, New Guinea, the Philippines, the Solomon Islands, Tonga, several islands in the West Indies, and southern Florida. In 1955 an accidental release of 100 frogs led to an established population around Miami International Airport. This population has now spread throughout southern Florida and into the fringes of Everglades National Park through an extensive system of canals and drainage ditches.

Giant toads have replaced the native toad *Bufo terrestris* in much of its range. Marine toads have voracious appetites and eat small, moving or nonmoving objects such as other toads, insects, snails, snakes, garbage, and dog food. If bitten by a pet, the toads release a milky bufotoxin from their parotid glands. Bufotoxin causes profuse salvation, twitching; vomiting; shallow breathing and collapse of the hind limbs. The toxin has been known to cause death in small mammals. The long-term environmental impact of this animal is unknown.

Birds. The parakeet or budgerigar (*Melopsittacus undulatus*), commonly known as the budgie, is indigenous to interior Australia. Budgerigars are popular as caged birds throughout the world, but escaped or released birds have become established as wildlife in Florida. Another small parrot, the Monk parakeet (*Myopsitta monachus*), is native to South America. It has established colonies in several cities around the United States, including one in Austin, Texas. This parrot is considered a pest in its native territory, causing substantial damage to grains and fruit crops. It is also a very aggressive bird, competing with other species for food sources. There are several reports of Monk parakeets attacking and killing other birds. The overall environmental impact of these birds is unknown at this time.

In the 1850s and 1860s, the weaver finch, *Passer domesticus* (also called the house sparrow) was deliberately introduced into North America at several different times and places. In 1853, a group of 100 birds from England were released in Brooklyn, New York, in a misguided attempt to control canker worms. Since its introduction, it has rapidly and aggressively colonized almost all of North America, displacing native birds by competing for nest sites and food. It is also hardy and fecund.

Where do we go from here? Many scientists think that the spread of exotic species is one of the most serious, yet largely unrecognized, threats to our environment. Nonnative animal species cause enormous economic each year to crops, waterways, and natural environments in the United States. Safeguarding our natural heritage from alien and exotic species involves

stopping additional introductions, the early detection and quick eradication of pests, integrated systems for the control and management of existing pests, and the restoration of native species and ecosystems.

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Expenditure Per Progeny

The goal of each living thing is to pass on its own genetic information. The limited resources of the world have created a complex, biological community under intense selective pressure. In order to ensure survival of oneself and one's genes, an individual must utilize a competitive reproduction strategy. Genetic adaptations occur over time to make organisms run faster, grow more efficiently, or better detect their food. These evolutionary "decisions" are fairly easy to make: the tradeoff of spending energy on stronger muscles is easily worth it if stronger muscles keep their owner alive.

Numerous reproduction strategies and compromises are evident in nature, and certain constraints favor one or another. If you were given power to design a completely new organism, you would be forced to make a number of decisions regarding its production. Eggs or live young? How many eggs? How much time invested in raising them? Do the males care for the young? The females? Both? Neither? Organisms evolve to take the best strategy under the given circumstances, and one “choice” they have to make is how to allocate energy towards reproduction.

One variable is how many offspring to have. For example, long-term studies of the great tit, a bird in Britain, show that the optimal number of eggs for a great tit is about eight. If a pair of birds raises a larger brood, chicks in that brood get fed less often. They eat fewer caterpillars and weigh less when leaving the nest. However, heavier chicks tend to live longer and healthier lives.

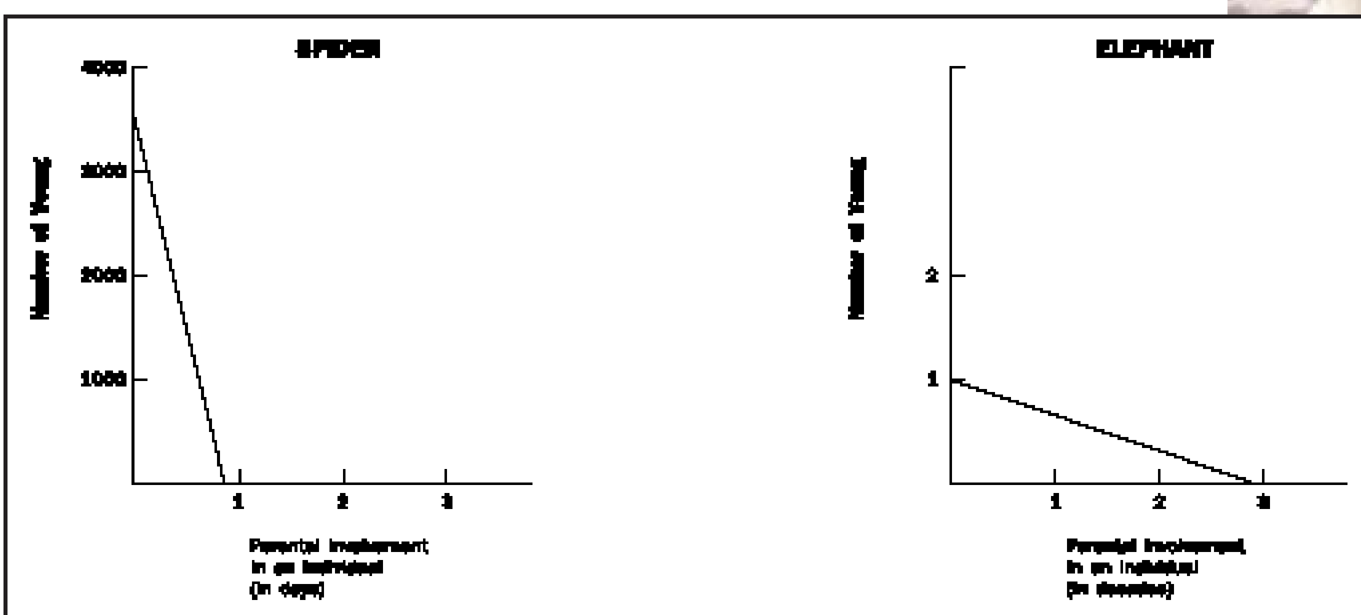
So if a parent wants to maximize the number of healthy young it can have, and maximize the chance that all of those young will live to be old enough to reproduce and generate healthy offspring of their own, it cannot raise too many. If it raises fewer than the optimal number, its chicks might well turn out healthy, but there will be less of them to pass on the family genes.

Christopher M. Perrins showed in 1979 that if the size of broods are artificially manipulated by sneaking into nests and adding or removing eggs, the optimum number is between eight and twelve eggs. We know this because Perrins tried to recapture chicks from the nests later on; he had the best luck recapturing chicks from the nests with eight to twelve eggs. More eggs meant the chicks were less healthy overall; fewer eggs simply meant there were fewer chicks to start with.

This assumes that parents will expend about the same amount of energy on a brood of chicks regardless of brood size. Raising chicks is an enormously expensive endeavor: parents must expend energy in making the eggs, making the nest, sitting on the nest and protecting it, and getting food for the brood once it hatches. Great tits bring back an item of food every thirty seconds as long as there is daylight. Plus there is the matter of multiple breeding seasons. Is it better to work like a horse for one season on one brood and be tired and inefficient for subsequent seasons, or more slowly expend oneself? In the end, each chick receives a certain amount of energy in metabolic production, feeding, and raising. This amount is known as the expenditure per progeny.

Predictably, differing species exhibit a wide range of “decisions” regarding expenditure per progeny. An organism as physiologically and socially complex as a human being requires a lot of energy to develop inside and outside of the womb, so any one individual offspring represents an enormous investment. The evolutionary “hope” is that an incredibly complex, adaptable individual will be able to reproduce, and thus only a few are made. This is a good thing, because human beings are so energetically expensive!

Contrast this reproductive strategy with that of a spider. Spiders have no social development and require little to no care after birth. They are also small and comparatively easy to make. Thus, a reproducing spider will invest all of her energy into making thousands and thousands of eggs. While



A comparison of the energy expended per progeny between a spider and an elephant.

baby spiders possess negligible learning capacity and are not as equipped as human beings to deal with complex, new situations, it is reasonable to assume that if a parent generates thousands of them, at least a few of them will make it to reproductive age.

Making energetic decisions like these, or tradeoffs, is part of the process of evolutionary development. As changing environmental circumstances dictate what might be the most effective reproductive strategy, parents must allocate their energies accordingly. SEE ALSO Reproduction, Asexual and Sexual.

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Extinction

Extinction is the irreversible disappearance of all signs of life pertaining to a particular group of organisms. This group can be any of the accepted categories of taxonomic nomenclature, including kingdom, phylum, class, order, family, genus, species, and even subspecies. Most often, extinction is used in reference to the species level organism. The organism may have gone extinct at any time within the past 600 million years of the **fossil record** or may be in the process of going extinct today. Furthermore, this phenomenon does not pertain only to animals but is also applicable to plants, fungi, protists, bacteria, and archaebacteria.

fossil record a collection of all known fossils

Many situations can theoretically lead to the extinction of an organism. Determining the cause of extinction is very difficult, especially when information from the fossil record must be used to reconstruct a sequence of events. In many cases, a direct explanation is not forthcoming, and many hypotheses must be examined. Unfortunately, present-day cases of extinction are becoming increasingly common, leading to the need to predict and counteract the disappearance of currently living organisms. Extinction is a natural occurrence well documented in prehuman fossil deposits, and there is evidence that it may allow opportunistic evolution of species that had previously been overshadowed. Human domination of the biosphere, however, is accelerating the extinction rate. For many reasons, human lives are negatively affected by mass extinctions, and humans are struggling to oppose further loss.

Causes of Extinction

Many mechanisms account for extinction. Although organisms depend on other species in their ecosystem for food and population control, this delicate balance may be upset through the pressure of interspecies interactions. If an organism serves as the food source for another, it may be overpredated or overharvested, leading to the death of all members of the taxonomic group. This can occur if the predator/herbivore evolves keener sensory or cognitive capabilities, making it a more efficient consumer. It can also be the result of a food web disruption, such as when an environmental change suddenly favors the propagation of the predator/herbivore without offering such a benefit to the prey. Similarly, when two species occupy the same environmental **niche**, meaning that they prefer similar habitats and food types, they can be in direct competition for limited resources. If the competing species is better able to inhabit that niche, by gaining more territory and consuming more food, it can drive its competitors to extinction. Humans sometimes hunt animals for sport. This is not exactly predation or competition, but it can also result in the death of an entire species, for example, the dodo bird.

niche how an organism uses the biotic and abiotic resources of its environment

Environmental alteration can also lead to extinction. This may be part of a global climate change, one of Earth's natural climate fluctuations. In this case, one might expect to find a high number of global extinctions, especially among animals in regions greatly affected by the temperature and weather pattern differences. The microenvironment also undergoes change over time. For example, a new mountain range may form along a plain, an island may sink into the ocean, and a river may divert its course. Each of these examples would strongly affect the organisms that depend on those particular microenvironments for sustenance. In some cases, this local regional change can be called **habitat loss**. This term describes the destruction of a particular type of habitat, such as decline of biodiversity in the North American natural plains, beginning in the nineteenth century.

habitat loss the destruction of habitats through natural or artificial means

Evolution can also be considered a direct mode of extinction. Taxonomic boundaries are sometimes very arbitrary, meaning that the distinction between groups is unclear. The lines between groups are drawn using evidence about the organism's habitat, body shape (or morphology), and living habits; most often, however, only the morphology can be relied upon. Some species in the fossil record show gradual change in morphology over evolutionary time. Paleontologists, scientists who research extinct organisms, must sometimes examine a progression from one body type to another

Event	Species Involved in Great Extinction	Probable Cause of Great Extinction
Cambrian mass extinction	Trilobites; brachiopods; conodonts	
Ordovician mass extinction	Trilobites; archaeocyathids	
Devonian mass extinction	Stromatoporoids; corals; brachiopods; trilobites; conodonts; acritarchs; all jawless fishes; placoderms	Global Cooling Events
Permian mass extinction	Trilobites; corals; blastoids; acanthodians; placoderms; pelycosaurs	
End-Cretaceous mass extinction	Pterosaurs; belemnoids; many plant species; marine reptiles; mollusks; echinoids; fishes	Volcanic Activity or Meteorite Impacts

Five great extinction events.

and determine at what point the original species can be called a new species. Nonetheless, the original species can no longer exist when the new species begins, and this in itself is a kind of extinction.

Factors that Can Contribute to Extinction

Several factors influence the likelihood that an organism will go extinct. Some species have a very small range, so that they are very susceptible to small-scale changes in the environment. This is an extremely common explanation for the extinction of subspecies. Subspecies sometimes evolve when isolated populations of a species living at the boundaries of its natural range develop distinct behaviors and appearances that distinguish them from the parent species. Given a long enough period of separation from the parent species, these subspecies would develop into an entirely novel organism. Despite this, they often are subject to extinction because their small population size and range cause them to either die out or to be reassimilated into the parent species.

A particular type of feeding pattern is another extinction factor. Whereas generalist feeders, which rely on many sources of nutrition, can switch to a different diet if their food source were to disappear, specialist feeders, which consume only one particular food source, cannot and are therefore highly susceptible to extinction.

Some organisms can be said to have a very delicate niche dynamic for a combination of the above reasons. For example, olive ridley sea turtles return to the same beach year after year to lay eggs. The eggs are highly predated by local animals, and the beaches are often brightly lit and filled with human tourists, factors that decrease the fitness of the mothers and the young. The turtles, however, seem physiologically incapable of choosing other sites for nesting because of their dependence on a particular sort of fine-grained sand and on particular temperature patterns at the chosen beaches.

Once species numbers decline to a small amount of individuals, extinction speed is increased by a factor known as **inbreeding depression**.

inbreeding depression loss of fitness due to breeding with close relatives

In 2000, the population of California condors had climbed to eighty-seven, from a low of thirty in 1967. But of that number only 3 lived in the wild.

This occurs when so few individuals remain in a species that they are forced to mate with members of their own families out of necessity. The smaller gene pool causes increased incidence of genetic disorders, general poor health, and increased susceptibility to disease, all of which increase the species' decline.

Difficulties Determining When an Extinction Has Occurred

Extinctions are not always easy to pinpoint or determine. When a fossil organism stops appearing in the fossil record, this may be explained by a variety of reasons. It may be that environmental conditions during the following period did not favor fossil formation, so that the species survived but was no longer fossilized. Another possibility is that only a small population of a widely dispersed species may live in the region that allows fossilization; if this local population goes extinct, the entire species will disappear from the fossil record, but that does not necessarily mean that the entire species has also gone extinct. Another explanation is that the species may have merely migrated from a fossil-friendly environment to a fossil-unfriendly habitat, or perhaps to a region for which the fossil bed has not yet been found. A confounding factor in determining extinction can be as simple as researcher bias. Organisms seem to go extinct at the boundaries between geological periods of Earth's history, but this may be due to a quirk of the field of paleontology: Paleontologists often study only one period in the rock strata. They categorize all organisms that appear at the beginning of their period, and may not realize that the scientists researching an earlier period have already named the same species. Thus although it appears that an organism has become extinct, in reality it has just been mistakenly renamed.

Paleontologists try to account for all of these sources of error through thorough study and the use of probability equations, but the fossil record is irregular and difficult to interpret. For example, in the mid-twentieth century, the coelacanth, a species of bony fish that scientists had falsely declared extinct, was rediscovered as a living species. Coelacanths were thought to have gone extinct 70 million years ago because they disappeared from the fossil record. This mistake was remedied in 1938 when a fisherman caught a living coelacanth off the coast of southeastern Africa.

Reasons for Preventing Extinctions

Although extinction is a natural occurrence, there are many reasons to actively protect existing species from extinction. More and more, ecosystems are viewed as integrated modules, so that the extinction of one species in the ecosystem can disrupt all of the other species' population dynamics. If humans ignore the extinction of a seemingly uninteresting species, this could cause widespread extinctions in many other organisms. In general, biodiversity (the presence of a high number of species in an environment) is equated with a healthy ecosystem, and high extinction rates decrease biodiversity. Often, an environment of low biodiversity reveals what humans consider to be pests. These are merely organisms that are able to survive in an ecosystem reduced and dominated by humans. People naturally prefer a healthier ecosystem, with clean breathing air, green surroundings, and a wide variety of species. There is a value to the beauty of the environment, which is damaged by high extinctions. Furthermore, humans directly depend on some species for medical benefits, such as medicine, tissue and organ donations, and animal models of human disease. Organisms that go extinct can no longer be researched as possible cures for human ailments or be studied by engineers as models for building computers, machinery, and vehicles.

Preventing extinction is a political as well as a biological priority. The needs of humans often overshadow the decline of endangered species. For example, the economy of many Third World countries depends on agriculture. If natural ecosystems such as rain forests must be destroyed to support the agricultural needs of these nations, many species are put at risk and forced into extinction. Without that source of income, however, the peoples of these countries could languish and starve. A balance between preserving the rain forest habitat and ensuring the well-being of the humans must be sought.

CALIFORNIA CONDOR

California condors are the largest birds in North America, weighing up to 11.5 kilograms (25 pounds), with a wingspan of more than 2.7 meters (9 feet). In 1967 condors had declined to approximately thirty individuals. In 2000, eighty-seven condors were living, but only three were in the wild. While captive breeding programs have improved the outlook for condors, their future now depends entirely on human intervention.

Methods of Preventing Extinction

There are several contemporary means of preserving a particular species. Active breeding programs at nature reserves and at zoos attempt to maintain a sizable population of individuals to avoid inbreeding depression. When animals such as cheetahs are the victims of inbreeding depression, specialized veterinarians and behaviorists monitor their health and attempt to circumvent the danger of disease. Hunting and fishing regulations attempt to predict population flux and disallow overharvesting of game animals. Specialized herbariums and eco-landscaping firms are working to restore lost habitats within depleted landscapes.

Despite these endeavors, there is still an acute danger that many of the world's habitats will be thrown into disarray by human intervention. The shrinkage and parceling of natural habitats is especially damaging to animals with large ranges, such as Siberian tigers, bald eagles, and buffalo. Nature preserves are under constant study to improve the efficiency of the surroundings in order to prevent extinction. see also Feeding Strategies; Fossil Record; Habitat Loss; Habitat Restoration; Hunting; Paleontology; Zoological Parks.

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Extremophile

Most animals live in conditions where the temperature is between 4°C and 40°C (39°F–104°F), the pH (which measures acidity and alkalinity) is between 5 and 9, and oxygen is abundant. Some animals, called extremophiles, live in conditions that are outside these ranges. The term "extremophile" is given to micro-organisms that live in extreme environments. These environments range from hot springs to sea ice to brine lakes to deep-ocean hydrothermal (hot water) vents. Each of these environments has conditions that are considered punishing or even unbearable for most animals. However, extremophiles thrive under these conditions. Extremophiles may also provide a glimpse of what the earliest forms of life looked like.

Archae an ancient linage of prokaryotes that live in extreme environments

Extremophiles are part of a new kingdom of animals called **Archae**. The members of this kingdom look like bacteria and were considered a phylum in the Kingdom Monera. In the late-twentieth century, however, scientists separated the Archae from other bacteria based on their genetic and biochemical makeup.

Extremophiles are loosely grouped into categories on the basis of where they live. Thermophiles are found living in temperature extremes. Some thermophiles are found in hot springs with water temperatures that approach boiling. The hydrothermal vents along the **midoceanic ridges** support extremophiles that not only tolerate high temperatures and **acidic** conditions but also metabolize, or process, hydrogen sulfide, which is poisonous to most animals. At the other extreme, some extremophiles thrive in very cold conditions. These are found in sea ice and on glaciers.

These iceworms in a snowfield pollen feeder are examples of extremophiles, or the ability of animals to live in extraordinary climates.

midoceanic ridges long chains of mountains found on the ocean floor where tectonic plates are pulling apart

acidic having the properties of an acid

alkaline having the properties of a base

Other examples of extreme environments include natural salt lakes such as the Dead Sea and Great Salt Lake. The extremophiles living there are called halophiles. Still other extremophiles live in highly acidic or highly **alkaline** environments. Acidophiles thrive in environments with a pH less than 5 while alkaliphiles live in environments with a pH greater than 9. Acidophiles are found in places such as hydrothermal vents while alkaliphiles are found in soda lakes such as are found in Egypt and the western United States. A final major group of extremophiles are the methanogens. They are found living in places with little oxygen, such as swamps and the intestinal tracts of animals. Methanogens do not use oxygen to metabolize their food and they produce methane gas as a waste product.

Scientists have known about extremophiles for more than forty years. Most scientists considered them curiosities in the animal kingdom. Scientists became interested in extremophiles because of their enzymes. Because extremophiles live in extreme conditions, their enzymes must also work under these conditions. Enzymes extracted from extremophiles have grown into a multibillion dollar industry. The enzymes are used in industrial and medical applications that range from making stone-washed jeans to creating artificial sweeteners to conducting genetic tests.

The enzyme-based process known as PCR is used to amplify DNA for genetic identification or genetic testing for disease and conditions. The enzyme reactions used in the procedure occur slowly at room temperatures. By using enzymes from a thermophile, the reactions are performed at a much higher temperature and so at a faster rate.

In recent years, scientists have began searching extreme environments on earth in hope of discovering clues for finding extraterrestrial life. As scientists searched extreme environments, they found more and more kinds of extremophiles. Many environments that scientists had in the past considered sterile were discovered to be the home of many different organisms. Some scientists came to believe that the total mass of all extremophiles on Earth exceeded the mass of all humans on Earth. SEE ALSO ADAPTATIONS, BIOLOGICAL EVOLUTION, KINGDOMS OF LIFE.

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Farmer

Farmers make a living by managing or operating farms, places where plants (crops) or animals (livestock) are raised to be sold to others. Crops include grains such as wheat, vegetables, fruits; fibers such as cotton; nuts; flowers; and landscaping plants. The type of crop grown on a particular farm depends on the climate, soil, and layout of the land, whether it is low-lying or mountainous, for example. There are livestock, dairy, and poultry farmers, as well as farmers that raise bees and fish.

Farming is financially a risky business, with success depending on weather conditions, plant and animal diseases, insect problems, prices of fuel and other expenses, and market demand. Farmers may work on large commercial farms or on smaller farms which may be family owned. The work is very demanding physically and takes place mostly outdoors. During the growing season, farmers may work almost constantly, seven days a week. Animals must be cared for every day. Farmers must have both labor and management skills. They decide which crops to plant and which fertilizers to use. They need to know how to care for their livestock and keep the barns, pens, and other farm buildings in good condition. Farmers work with tools and machinery and maintain equipment and facilities. They must have good financial skills, including keeping records of expenses, taxes, and loans. Also, farmers must understand the various laws that apply to their business. Computers have become increasingly more important in farming to keep track of finances, manage inventory data, and track schedules for applying pesticides or breeding livestock.

Becoming a farmer does not generally require formal training or education. The enormous knowledge that is necessary for this profession is often acquired by a person raised on a farm. In grade and high school, it is good training to participate in agricultural programs run by organizations such as 4-H. However, even a person raised on a farm can benefit from getting an education at a university. A bachelor's degree in agricultural sciences, which include courses in farming, producing crops, and raising livestock, can be helpful, along with courses in crop, dairy, and animal sciences. Business courses such as economics, accounting, and marketing are also useful. SEE ALSO Apiculture; Aquaculture; Farming.

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Farming

Farming, or agriculture, is the science or art of cultivating the soil, growing and harvesting crops, and the raising of animals. Beginning some 10,000 years ago, people in various places around the world began to grow plants

This farmer in Sri Lanka uses two oxen to plow through a muddy rice paddy. Many farmers around the world still utilize ancient farming and cultivation methods.

and domesticate animals. Slowly and over time, farming made living in one place possible, encouraged innovations in tools, and allowed a dramatic increase in population. All civilizations, from the earliest we know about down to our own, have evolved from this ability intentionally to grow plants and raise animals for larger groups of people.

Ancient stories and the oldest oral traditions speak of the origins of plants and animals. In the classic mythologies of all world cultures, agriculture came as a divine gift. In most stories a god or goddess came to instruct the people in the arts of growing plants and raising animals. In the Mediterranean region instruction came from a goddess, Isis in Egypt, Demeter in Greece, Ceres in Rome. From cuneiform tablets we learn that the source for agriculture for the Babylonians, and Chaldeans was a god named Oannes, who appeared to these people of the Persian Gulf coast and taught them to grow crops and raise animals. In Chinese mythology P'a Ku separated the heavens and Earth, created the sun, moon, and stars, and produced plants and animals. The Aztec and Mayan people thought that corn was on Earth before humans. In all of the myths and stories about the origin of agriculture, knowledge is gratefully received as a blessing from the gods or goddesses.

From Hunting and Gathering to Farming

Our modern scientific stories suggest that, for several million years or more, our human ancestors survived by hunting wild animals and gathering wild plants. Then, from about 10,000 and to about 4,500 years ago, hunter-gatherer societies in at least seven regions of the world independently domesticated selected species of plants and animals. This time period is often referred to as the Neolithic Revolution. This development toward farming and the domestication of animals in the Middle East, southeast Asia, northern China, Africa, southern Mexico, Guatemala, and Peru profoundly altered the direction of humankind.

As these new agricultural systems emerged, they allowed human populations to increase, as well as setting the stage for the creation of complex human societies far beyond what had developed in hunting and gathering times. Large farming villages appeared as people gathered and settled in permanent villages. Villages turned into towns and cities, and eventually into city-states that dictated the production of food. These changes eventually led to the industrial and technological world that we live in today.

The question of why and how agriculture or farming became important in human societies continues to be investigated. One notable theory suggests that farming of some kind was practiced by hunters and gathering peoples all along. This "proto" farming encouraged certain plants and animals and resulted in increasing available foods. Other theories speculate that farming was less costly and safer than hunting and gathering or that climatic changes reduced the number of big game animals and made farming necessary to support a larger number of people. Farming may have allowed people to live in less hospitable environments such as semideserts and mountainous regions. Still other theories propose that changing climatic conditions eventually encouraged people to move into fertile riverine environments or people living in more marginal habitats encouraged the growth of certain plants that led to the deliberate planting of seeds and the cultivation of certain plants.

The Domestication of Plants and Animals

As people made the shift to farming they experimented with domesticating useful and familiar plants and animals. Perhaps this process started with a wild plant that people liked and used as an important food crop. Observation and experimentation resulted in plants that could be cultivated and relied upon. The big seeded grasses of the Middle East, rice in Asia, and the *zea* grasses that became corn in the Americas fulfilled this role. South Americans cultivated the potato, chocolate, and tomatoes.

Many early farmers domesticated animals as well as plants. People observed animals in the wild that were not solitary and not too large, fierce, or migratory. Many mammals can be tamed easily by capturing young animals and raising them in captivity. The domestication process requires rearing many animals over many generations and eventually altering the gene structure.

For example, in the Middle East we find species of goats and sheep that were domesticated from wild animals. In the wild they are relatively slow and docile, and both species lived in social groups ruled by a strong leader. Over time, these once-wild sheep and goats have undergone a reduction in size, a complete loss of horns in the female sheep, and **mutations** for wool. In goats, twisted horns and long hair called mohair appeared. Breeds of cattle appeared with long horns, short horns, crumpled horns, or humps. The earliest South American farmers found and domesticated llamas and alpacas. Other animals that lived on the outskirts of human settlements, such as dogs and pigs, developed relationships with humans before people settled as farmers. Small animals such as rabbits, turkeys, and guinea pigs were probably caught and enclosed.

mutations abrupt changes in the genes of an organism

Humans rely on other animal and plant species to produce food. Farming eventually succeeded because people figured out ways to coax more food from the environment than would otherwise be possible. The adoption of farming enabled human population to rise from an estimated 8 million present 10,000 years ago, to between 100 million and 300 million at the time of Christ, to 6 billion in the year 2000.

Biodiversity

Biodiversity is the vast and varied combination of habitats and the many species of plants and animals that thrive in combination with each other. One of the serious environmental problems humankind faces today is the loss of that biodiversity. Scientists feel that this is the direct result of the transformation of natural landscapes by people for farming and grazing uses. These lands include breaking up and clearing large tracts of wild lands and wetlands. The logging and clearing of tropical and temperate forests have contributed to the loss and decline of many species of plants and animals along with their genetic and ecological complexity. This biodiversity is lost when tens, hundreds, and thousands of farmers clear land to increase yield, when loggers clear forests to provide lumber for houses and furniture, and when city dwellers need more land for homes, schools, and factories. Cutting old-growth forests to make room for cultivated fields has encouraged erosion on slopes and mountains. Swamps have been drained and rivers damned and diverted to provide water for irrigation. Overgrazing of grasslands and the use of toxic fertilizers and pesticides have polluted lakes, rivers, and streams.

The accumulated actions of all of these people over time have led to a massive extinction of species of plants and animals. Although this process has been going on since humans began to farm, the pace of change has accelerated since the seventeenth and eighteenth centuries because of the industrial and agricultural revolutions. Innovations in machinery and genetics allowed for more crops to be grown with less labor and allowed people to do different kinds of work and move into cities. In the twenty-first century, increasing population, the global economy, and modern farming practices have created additional stresses on the environment.

Twenty-first century farming practices encourage cultivation of large-scale monoculture crops and single breeds of animals. Approximately eighty plant crops provide about 90 percent of the world's food sources. A little over fifty animal species account for most of the domestic animal production used for food and fiber. Many scientists believe that this overdependence on a small number of genetically similar plants and animals could have devastating consequences if weather or pests take a toll on large monocrops. Thousands of other plants could be cultivated to prevent such a scenario. In addition, tens of thousands of plants are known to have edible parts that could be used.

Hundreds of thousands of animal species, many of them insects, are needed for pollination and protection of crops. Tens of thousands of microbial species, most of them living in soil or on plants, provide nutrients, act as agents of decomposition, and contribute to the success of living communities of plants and animals. Without this biodiversity many of the fundamental ecological processes that are necessary for all living things to thrive will have a devastating effect on humankind's ability to feed, house, and sustain itself.

The Future

In spite of all the changes in land use and agricultural practices, farming on the modern scale is productive and holds the promise of solving many of the world's food problems. However, its impact must now be considered alongside maintaining or increasing the natural biodiversity necessary for the maintenance of natural systems that sustain all life on Earth.

Scientists and commercial farmers are realizing that greater diversity leads to greater productivity. Research and experimentation is being conducted in areas such as rotations of grasslands for dairy and beef cattle production, precise matching of soil conditions with specific plant species, and the maintenance of seed banks to help protect genetic diversity and increase the number of plants that can be used.

Genetic diversity has also been lost in animals used for food and fiber. The number of breeds used by humankind has declined by nearly thirty since the mid-twentieth century. Scientists and breeders are working together to protect the genetic diversity of rare endangered breeds along with their wild relatives in hopes of maintaining diversity in the available supply of milk, meat, and fibers that people throughout the world depend on.

In addition, scientists are acknowledging that a significant portion of the world's biodiversity is in the hands of small indigenous farmers throughout the world who practice age-old farming and ecological practices. This body of specialized knowledge is invaluable and in danger of being lost unless these individuals can pass their knowledge on to people who can make use of it.

Along with preserving local knowledge, some scientists believe that rural and agricultural landscapes, if properly designed and managed, can help preserve a significant number of plant and animal species. The conservation of local biodiversity depends on how agricultural lands are used and also on the protection of wild lands. Farmers around the world can help maintain the biodiversity needed to maintain all kinds of life on Earth as well as taking care of our expanding human needs. SEE ALSO Apiculture; Aquaculture; Farmer; Hunter-Gatherers.

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1944–

Dr. Anne Fausto-Sterling is a Professor of Biology and Women's Studies at Brown University in Providence, Rhode Island. She teaches in the Department of Molecular and Cell Biology and Biochemistry. Her scholarly interests include developmental genetics, intersexuality (the study of people born with atypical sexual anatomy), and the interplay between science and gender. Her laboratory at Brown researches the evolution of sexual reproduction and **regeneration** in flatworms of the genus *Planaria.*

regeneration regrowing body parts that are lost due to injury

Fausto-Sterling is best known for her work on race, gender roles, and human sexuality. In addition to her teaching and research at Brown University, she has given lectures and held workshops on many campuses across the United States. The message she conveys to her audience is that gender plays an important role in how science is carried out and reported, and that science influences the perception of gender differences. Fausto-Sterling urges students of feminist scholarship to seek a broad understanding of scientific practices and knowledge.

Fausto-Sterling has been a faculty member at Brown for more than twenty-five years and has written a number of influential books on gender, development, and biology. These controversial but popular works (controversial because she criticizes the research practices of her colleagues) examine how race and gender have structured scientific practices and knowledge. In *Myths of Gender: Biological Theories About Men and Women*, Fausto-Sterling evaluates the scientific merit of studies on the biological basis of behavioral differences between men and women. She cautions the public to accept the results of these studies with skepticism, arguing that many theories set forth by this line of research are poorly supported by scientific evidence. In *Sexing the Body: Gender Politics and the Construction of Sexuality*, Fausto-Sterling discusses how human society influences the formation and dissemination of biological knowledge about animal and human sexuality.

Fausto-Sterling has received numerous honors and awards and has been elected to the membership of several prestigious scientific societies. Her honors come from the fields of science and the humanities. She received an honorable mention in *The Best American Essays of 1994* for a piece on

intersexuality entitled "The Five Sexes." In 1995 she received a Women of Distinction Award from the City University of New York. Her biography was also profiled in *No Universal Constants: Journeys of Women in Science and Engineering*. Fausto-Sterling is a Fellow of the American Council of Learned Societies and the Dibner Institute for the History of Science and Technology at the Massachusetts Institute of Technology.

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Feeding

autotrophs organisms that make their own food

heterotrophs organisms that do not make their own food

photosynthesis the combination of chemical compounds in the presence of sunlight

chemosynthesis obtaining energy and making food from inorganic molecules

frugivores fruit-eating animals

Organisms that live on Earth are either **autotrophs** or **heterotrophs**. Autotrophs obtain energy directly from their physical environment through **photosynthesis** or **chemosynthesis**. Heterotrophs must obtain their energy by eating autotrophs or by eating other heterotrophs. Plants are autotrophs, but all animals are heterotrophs. Animals that feed on living organisms or parts of living organisms can be classified into three general groups based on feeding behavior: herbivores, carnivores, and omnivores.

A herbivore is an animal that eats the tissues of green plants and only plants. Herbivores consume many different parts of plants. This group of animals can be further subdivided into such categories as folivores (eaters of leaves), **frugivores** (eaters of fruit), and granivores (seed eaters). Herbivores have special adaptations that allow them to extract sufficient energy and nutrients from plants. For example, herbivores have large stomachs, allowing them to eat a large amount of material. Some herbivores have two stomachs. Food stored in the first stomach is partially broken down by bacteria through a process similar to fermentation. Then the material is regurgitated, chewed some more, swallowed again, and passed to the second stomach. Herbivores have also evolved special teeth adapted for cutting and grinding plant tissue. Herbivores include such animals as grasshoppers, caterpillars, cattle, and antelope.

Carnivores eat other animals. The animals eaten by carnivores may be herbivores, omnivores, or other carnivores. Since animal tissue is more densely packed with nutrients than plant tissue, carnivores have relatively shorter digestive tracts. They have also evolved special teeth suitable for tearing flesh. Some members of order Carnivora, such as cats, have all fanglike teeth ideally suited for cutting or tearing through animal tissue.

Carnivores are all predators. They are generally larger than their prey (but not always; for example, wolves prey on moose and caribou). Predators pursue and capture their prey, so they require a large amount of calories.

Cattle graze at the Simplon Pass in the Switzerland Alps. Cattle are herbivorous, eating only plants and the tissues of green plants.

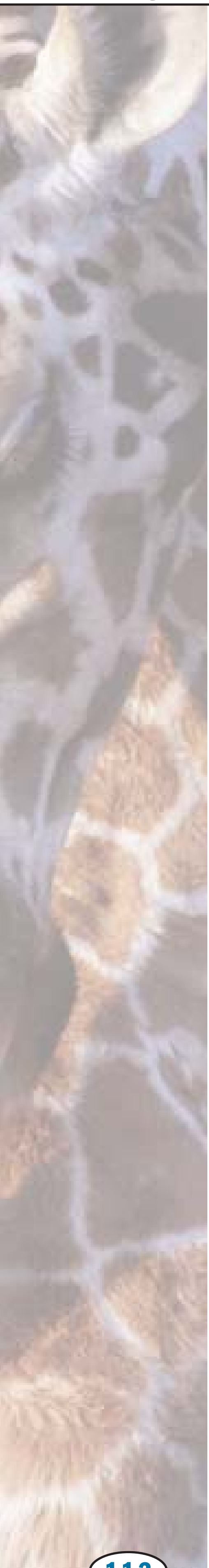
They therefore must catch and eat many individual prey items during their lives.

Carnivores are generally very important to the ecosystems they inhabit. Since carnivores eat other animals and must eat a large number of prey individuals, they almost always act as a check on populations of herbivores. Carnivores include animals such as cats, wolves, shrews, and polar bears. Wolves are classified as carnivores but most of the Canids (which also include foxes, coyotes, and domestic dogs) will eat fruit and berries or other plant tissue when they are hungry and the fruit is available.

Omnivores obtain energy by eating both plant and animal tissue. Some omnivores hunt, pursue, and catch other animals, just as predators do. Most omnivores will readily eat the eggs of other animals. Many omnivores are also **scavengers**. Omnivores eat plants, but not all plants and not all parts of the plants they do eat. Omnivores can eat fruits and tubers. Some grains can be eaten by omnivores.

scavengers animals that feed on the remains of animals that they did not kill

Humans are omnivores who have expanded their food choices by discovering fire and inventing cooking. Cooking animal or plant tissue tends



to break down complex molecules, making more nutrients and calories available. Since omnivores eat both plant and animal tissue, they have evolved several different kinds of teeth, including incisors for shearing plant and animal tissue, canines and bicuspids for tearing and crushing meat, and molars for grinding seeds and other plant tissues. Omnivores include black bears, humans, many apes, cockroaches, chickens, and raccoons.

detritus dead organic matter

Detrivores are a group of organisms that get energy from dead or decaying plant and animal matter. Detrivores can be classified as **detritus** feeders or decomposers. There are no animals that act as decomposers, so animal detrivores are all detritus feeders. Animal detrivores can be considered omnivores that eat the dead remains of other organisms. Earthworms are typical detrivores.

The sun is the source of all energy for life on Earth. Plants harvest sunlight and store the energy in the chemical bonds of carbohydrates, fats, and proteins. Animals obtain their energy from plants. Herbivores obtain solar energy directly by eating plants. Carnivores obtain solar energy indirectly by eating other animals. All animals have evolved feeding behaviors that allow them to obtain sufficient energy and essential nutrients to live, grow, and reproduce. Some animals (herbivores) eat vast quantities of food with low nutritional value. Other animals (carnivores) consume smaller amounts of food with higher nutritional content, but they have to work harder to get it. Still other animals (omnivores) eat a variety of foods allowing them to use whatever food sources are available at any given time.

producers organisms which make up the level of an ecosystem that all other organisms ultimately depend on; usually these are plants

consumers animals that do not make their own food but instead eat other organisms

A trophic level is a group of organisms that all consume the same general types of food in a food web or a food chain. In a typical food web, all **producers** (autotrophs) belong to the first trophic level and all herbivores (primary **consumers**) belong to the second trophic level.

The second trophic level in a grassland ecosystem would be all of the herbivores that eat the grass. This group can include a wide variety of organisms. For example, in the original grasslands of the central United States, the second trophic level included grasshoppers, rabbits, voles and other small rodents, prairie dogs, and American bison (*Bison bison*). Since all of these creatures eat the same grass, they are all at the same trophic level, despite their differences in size, reproductive habits, or any other factors.

The third trophic level includes primary carnivores, such as wolves and warblers. Primary carnivores prey on herbivores. Secondary carnivores, such as falcons and killer whales, prey on primary carnivores as well as herbivores. Omnivores, such as humans, are able to feed at several different trophic levels. SEE ALSO Feeding Strategies; Foraging Strategies.

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Feeding Strategies

All animals must eat to live. Animals obtain energy and essential nutrients from the things that they eat. Since animals cannot harvest energy directly from the sun, they obtain energy to grow, move, and reproduce by consuming other organisms. Herbivores obtain solar energy by eating plants. Carnivores prey on other animals. Omnivores, such as humans, obtain energy by eating both plants and other animals.

Some animals consume enormous quantities of food with little nutritional value. Grazers, for example, eat large quantities of grass and other plants that have a low energy content and nutritional value. These animals have evolved special adaptations, such as two stomachs, that allow them to obtain sufficient energy from grass.

Some predators have developed special adaptations that allow them to consume large quantities of food at one time. Large snakes may catch and consume prey only three or four times a year. Lions and other large cats have adaptations that allow them to gorge on large amounts of meat at one time, then go without eating for several days or weeks.

Other predators take a different approach. The blue whale (*Balaenoptera musculus*), the largest animal that has ever lived, primarily feeds on small, shrimp-like crustaceans called **krill**. Vast quantities of krill must be consumed for the whale to obtain sufficient energy and nutrients. A blue whale may consume four tons of krill per day. The whale shark (*Rhincodon typus*), the largest living fish, feeds mainly on tiny plankton, anchovies, and sardines that it filters from the water.

krill an order of crustaceans that serves as a food source for many fish, whales, and birds

Foraging

Feeding and searching for food take up most of an animal's time. Foraging behavior requires some sort of system for distinguishing food from nonfood and for recognizing desirable food. Omnivores that consume a variety of different foods must learn which foods are good to eat. Sampling is risky, because many possible food items can be poisonous.

Rats need to consume forty different kinds of material including water, amino acids, fatty acids, vitamins, and minerals. The food available at any given time may lack some essential part, requiring the rat to spend extra time searching for foods that contain the missing element. In one study, rats were provided with a variety of foods, including yeast, a source of B-complex vitamins. When the yeast was removed from their diets, they immediately began to consume feces, another good source of B-vitamins. When yeast was reintroduced, they stopped consuming feces.

Humans are the ultimate foragers, regularly consuming an amazing variety of different foods. Yet people are generally cautious about trying new foods. Human cultures are easily identified by the food they eat. Food choices embody the accumulated wisdom of a culture about what is good to eat. However, humans do not seem to make food choices based on the need for essential vitamins and minerals. For example, a craving for fresh fruit does not appear to develop in people suffering from vitamin C deficiency. British sailors had to be required to eat limes in order to counteract scurvy

African wild dogs surround their prey, a wildebeest, on the Serengetti Plains of Tanzania.

caused by vitamin C deficiency. Humans also crave and eat far more fat and salt than is necessary for good health.

Foraging behaviors are learned and are adapted to an animal's lifestyle. Nervous systems are organized to enable animals to make associations between toxic effects and foods ingested hours earlier. Most people have experienced a strong aversion to the kind of food consumed right before an illness that caused nausea and vomiting, even when the food had nothing to do with the illness.

Grazers and Herbivores

frugivores fruit-eating animals

Herbivores consume many different parts of plants. This group of animals can be subdivided into folivores (eaters of leaves), **frugivores** (eaters of fruit), and granivores (seed eaters).

Caterpillars are probably the most familiar example of folivores. Caterpillars must eat large quantities of leaves in order to store enough fat and protein to undergo metamorphosis. However, some plants have developed a defense against caterpillars. In Finland, caterpillars of the moth *Oporinia autumnata* eat leaves of the birch tree. Caterpillars that feed on leaves from trees that were heavily damaged the previous year grow more slowly than caterpillars that feed on lightly damaged trees. Apparently the birch tree has developed chemicals that make the damaged leaves hard to digest.

Species of milkweed have evolved a highly toxic sap that prevents most caterpillars from consuming their leaves. However, the caterpillar of the monarch butterfly has evolved a tolerance for the toxin in milkweed sap and readily consumes it. Toxins from the sap are incorporated into the tissue of the caterpillars, making the caterpillars unpalatable to most predators. However, certain species of orioles have evolved a tolerance for this toxin and readily consume the insect.

Mammalian grazers generally consume a variety of different plants during a day. Only a few, such as the koala of Australia, eat only one type. Large species of grazers tend to be less selective than smaller species. In East Africa, communities of grazing animals have developed a commensal relationship. Elephants and buffalo first eat the tall, coarse grasses and then move on. They are able to consume large quantities of this low-nutrition food source. Zebras follow along behind the elephants, reducing the plant biomass even more. The zebras are followed by still smaller wildebeest, who select among the lower-growing plants that remain after the zebras have fed. Finally the smallest grazers such as Thompson's gazelles are able to reach the young, protein-rich sprouts of grass missed by the wildebeest.

Filter Feeders

Filter feeders are found in many different animal phyla, including **brachiopods**, mollusks, various worms, and chordates. They are indiscriminate eaters. They feed on prey much smaller than themselves that are suspended in water or air. Each filter feeder has some sort of apparatus with which it filters prey from the medium of air or water. The structure of this apparatus determines the size of prey. Filter feeders also have an apparatus for moving the air or water relative to the filter. This can be done by moving the filter. Barnacles wave feather-like fronds through the water, periodically drawing in whatever happens to have been caught. Other animals, such as oysters, pump water through a filter, thus moving the medium. Sometimes the filter feeder is passive and depends on wave action to move the medium. More often the filter feeder expends energy to move the medium through the filter. For example, the blue whale and the whale shark swim through the ocean with gaping mouths. The blue whale is able to gulp an enormous quantity of water because its throat has special pleated folds that allow it to expand to several times its original volume. Then the whale closes its mouth, forcing the water back through a specialized structure known as **baleen**. The whale shark has special structures in its gills that filter small organisms and other debris from the water passing through the gills. Sponges have specialized cells with flagella that keep a constant flow of water through the sponge. Once the energy has been expended to capture the prey, the filter feeder rarely rejects it, thus being indiscriminate eaters.

brachiopods a phylum of marine bivalve mollusks

baleen fringed filter plates that hang from the roof of a whale's mouth

Carnivores

Carnivores are animals that eat other animals. Carnivores can be found in most of the animal phyla. Some mollusks prey on other mollusks; praying mantids eat other insects and anything else they can catch; hawks and eagles eat small mammals, large insects, fish, and other birds. Roadrunners catch and eat large insects, lizards, and small snakes. Many species of fish prey on other fish. Some species of fish that live in the deep ocean, where other animal life is scarce, have jaws so huge they can swallow another fish substantially larger than themselves. All of these animals obtain energy and essential nutrients by eating other animals.

Mammals in the order Carnivora are highly specialized to prey on other animals. They have specialized digestive systems that are inefficient at digesting plants. This order includes dogs, cats, bears, weasels, and seals. Within this group, the cats, family *Felidae*, have evolved to prey almost exclusively on other mammals. Lions have evolved specialized behaviors, teeth, and digestive systems that allow them to pursue and kill much larger mammalian herbivores. They are able to consume huge amounts of meat by gorging on the kill, which they slowly digest. This specialized behavior is necessary because lions may go several days or longer between kills. Cheetahs are even more specialized. They have evolved speed at the expense of strength and are now so specialized that their diet consists almost exclusively of the small gazelles that graze the African plains. Grazers and filter feeders eat vast quantities of food with low nutritional value. Carnivores consume smaller amounts of food with higher nutritional content, but they have to work harder to get it. SEE ALSO Foraging Strategies.

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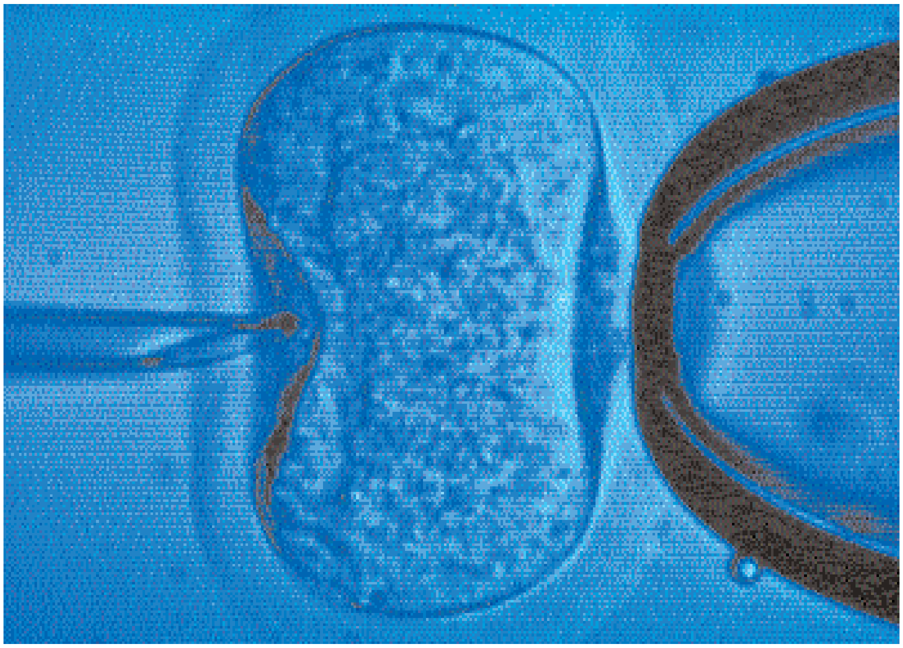
Fertilization

Life can persist in one of two ways. First, living things can spurn death in the hope of living forever. This is usually not possible, because death by predation or other unintentional causes is virtually inevitable. Second, living things can make copies of themselves, or reproduce, as a means of "hedging their bets" against death. Then, all that is required for life to persist is for at least one of the copies, or offspring, to remain alive at any one time. Thus, all living things reproduce.

How does reproduction occur? Some organisms reproduce asexually. The single-celled prokaryotes undergo binary fission, meaning literally "to split in half." Binary fission occurs after the cell has doubled the amount of its cellular constituents. The single circular chromosome is replicated from a single initiation point, the replication fork moving bidirectionally around the chromosome. Finally, inward growth of the plasma membrane separates the large cell into two equal halves. Some multicellular organisms reproduce asexually through budding. For example, in hydra, a relative of the jellyfish, a mass of mitotically dividing cells grows on the parent's side and eventually detaches as a small copy of the parent. However, most multicellular organisms reproduce sexually. Sexual reproduction takes place after the production of special reproductive cells termed **gametes**. Gametes are typically labeled as being of one sex or the other, male or female, with the female gamete being the larger of the two types. Fertilization is the union of a male and a female gamete to form a **zygote**, the developing offspring. There are many ways in which fertilization can occur in nature.

gametes reproductive cells that only have one set of chromosomes

zygote a fertilized egg



This microscopic image demonstrates in vitro fertilization. The needle (at right) injects sperm cells into a human egg (center).

The sexual organs of animals are called gonads. Gametes are made in the gonads—the female gonads produce eggs, the male gonads produce sperm. Human males produce millions of sperm every day. Females produce one mature egg in each menstrual cycle. When a sperm and an egg fuse during fertilization, a diploid zygote is formed. This zygote divides mitotically until it is an adult organism. Animals are unique in that they have a special type of cells called **germ cells**, in the gonads. The sole function of these cells is to undergo meiosis to form the **precursors** of eggs and sperm, oocytes and spermatocytes, which differentiate into the mature gametes necessary for reproduction. One can think of animal bodies, which are made of **somatic** cells derived from the original germ cells, as the machines that germ cells use to ensure their successful passage to the next generation.

germ cells egg or sperm cells, gametes

precursors a substance that give rise to a useful substance

somatic having to do with the body

Animals may release gametes into the external environment to be fertilized, or the male may deposit gametes into the female, allowing fertilization to take place inside the female reproductive tract. External fertilization occurs only in aquatic or moist habitats where gametes will not dry out. **Sessile** animals such as corals often release millions of gametes into the water at one time ensuring that at least some will be fertilized. In such cases, fertilization does not require that members of the opposite sex be near each other, although it is necessary that both males and females release their mature gametes at the same times. They do this by responding to species-specific environmental cues such as light cycles or temperature.

sessile immobile, attached

Some animals, including fish and amphibians, use external fertilization but do so only with a particular mate. When a female is receptive to a particular male, she will lay her clutch of eggs in the water and the male will distribute his sperm over them. In this form of external fertilization, unlike internal fertilization in which the female can store and use sperm from many males, the male is assured of paternity and is therefore much more likely to take care of the offspring.

Internal fertilization requires that the male introduce his sperm directly into the female, so there is a much greater probability that any particular gamete will be fertilized. Furthermore, animals are no longer dependent on water for fertilization and may become completely terrestrial. Animals with internal fertilization, especially females who incur most of the cost of reproduction, are selected to be extremely choosy with whom they mate. If they do not pick healthy mates they may spend precious energy and time raising an offspring that cannot compete with the offspring of choosier parents. There are usually species-specific behaviors, courtship displays, and other physical cues that allow females to pick healthy mates of their own species, a phenomenon known as sexual selection.

At the cellular level, a mammalian sperm must undergo several steps before it can fertilize the egg. The first step is termed the acrosomal reaction, in which enzymes from the sperm cap, or acrosome, are released. These enzymes serve to break down the barrier of follicle cells that surround the egg, as well as the zona pellucida, a **glycoprotein** envelope that encases the egg. The sperm can tunnel through the zona pellucida only if the acrosomal enzymes recognize species-specific molecules of the female's egg. Eventually the sperm gains access to the egg itself, and the sperm and egg plasma membranes fuse. At this stage the egg becomes activated and initiates a rapid sequence of events.

glycoprotein an organic molecule that contains a carbohydrate and a protein

First, the activated egg blocks entry to other sperm, as polyspermy (the fertilization of an egg by more than one sperm) is generally lethal to the developing embryo. When the first sperm fuses with the egg plasma membrane, the egg begins to increase its concentration of positively charged sodium ions from the surrounding environment of the female oviduct. The change in the electric potential across the plasma membrane (the excess positive charge inside the egg) prevents further sperm/egg fusions. Next, development processes begin; the egg increases oxygen consumption and begins protein synthesis. Eventually the nuclei of the sperm and egg fuse to form the diploid nucleus of the new zygote. SEE ALSO Reproduction, Asexual and Sexual.

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Fitness

Fitness is a central concept of evolutionary biology. We will consider individual fitness, followed by fitness as applied to alleles or genotypes.

direct fitness fitness gained through personal reproduction

The **direct fitness** of an individual is related to the number of offspring that that individual produces. Specifically, it is one-half of the number of

offspring produced, because in sexual species, only half of an offspring's genes come from either parent. That proportion, one-half, represents the **degree of relatedness**, or proportion of genes shared, between parent and offspring.

degree of relatedness how closely related members of a population are

Indirect fitness derives from shared genes with kin other than the direct offspring of an individual. This might include cousins, nieces, nephews, siblings, and so on. The indirect fitness of an individual is calculated by adding the relations of that individual multiplied by the degree of relatedness. Inclusive fitness represents the sum of direct and indirect fitness.

indirect fitness fitness gained through aiding the survival of non-descendant kin

The concept of indirect fitness was developed by the evolutionary biologist W. D. Hamilton. The idea originated with attempts to explain **altruistic behavior** in animals. Altruistic behavior is defined as behavior that harms the actor yet benefits the recipient, and includes such actions as alarm calling, which may draw the attention of the predator to the caller.

altruistic behavior the aiding of another individual at one's own risk or expense

According to natural selection theory, altruistic behavior should be eliminated from populations because it hampers individual survival and reproduction. However, Hamilton noted that if altruistic behavior benefits the kin of the actor, that behavior can nonetheless be selected for. This is because kin share genes with the actor. **Hamilton's Rule** dictates when altruistic behavior is beneficial: Altruism is selected for if the cost of a behavior to the actor is less than the benefit to the recipient, multiplied by the recipient's degree of relatedness to the actor. Thus, altruistic acts are more likely if they benefit close kin rather than distant kin, or unrelated individuals.

Hamilton's Rule individuals show less aggression to closely related kin than to more distantly related kin

Kin selection explains a wide variety of altruistic behavior. It also explains the evolution of social systems in which some individuals forego reproduction in order to help parents raise siblings. This is the situation in many pack species, such as wolves. In wolves, packs are often made up of two parents and their offspring from several mating seasons. Only the parents, which are the dominant individuals in the pack, reproduce.

Kin selection also explains more extreme examples of social behavior, such as that found in **eusocial** insects (species in which there are non-reproductive individuals. The primary groups of eusocial insects are the Hymenoptera (ants and bees) and the termites. Both groups have evolved special genetic systems in order to make kin selection more powerful. The Hymenoptera are characterized by **haplodiploidy**, a genetic system in which the males are haploid and females are diploid.

eusocial animals that show a true social organization

haplodiploidy sharing of half the chromosomes between a parent and an offspring

One consequence of haplodiploidy is that females (who are the crucial players in the colony) share a greater proportion of genes with their sisters than they would with their own offspring. It therefore benefits females to care for sisters in the colony rather than try to reproduce on their own. Termites are not haplodiploid, but they do go through repeated cycles of inbreeding, which also results in individuals sharing an unusually large proportion of their genes.

Kin selection is more complicated in the real world than Hamilton's Rule suggests because the expected reproductive success of individuals must also be factored in. For example, even though an offspring only shares half its genes with a parent, the parent may protect an offspring more vigorously than expected because reproductive success of the younger offspring may be greater than that of the more aged parent.

So far, this discussion has focused on individual fitness. Fitness can also be defined for alleles or for genotypes rather than for individuals. Allelic or genotypic fitness describes the relative contribution of one allele or genotype to the next generation as compared to that of possible alternate alleles or genotypes. These forms of fitness are central to population genetics.

polymorphisms having two or more distinct forms in the same population

Genotypes and alleles with higher fitness are selected for in the next generation, and make up a greater proportion of the total gene pool than other genotypes and alleles. All else being equal, alleles with greater fitness will eliminate and replace alleles of lower fitness. However, the fitness of particular alleles or genotypes may depend on numerous external factors, and changes in the relative fitnesses of alternate alleles/genotypes may help maintain **polymorphisms** in populations, situations in which a population has multiple alleles for a given locus.

anemia a condition that results from a decreased number of red blood cells

One external factor determining the fitness of alleles and genotypes is the specific environment in which they are found. One well-studied example is that of the sickle-cell **anemia** allele. This allele is normally disadvantageous because individuals who are homozygous for the allele (that is, carrying two copies of it) have sickle-cell anemia. However, in malaria-prone areas, it has been shown that individuals who are heterozygous (carrying one sickle-cell allele and one normal allele) are more resistant than individuals who have two normal alleles. So, in areas where malaria occurs, the fitness of the sickle-cell allele is higher than in malaria-free areas.

epistasis a phenomenon in which one gene alters the expression of another gene that is independently inherited

Another external factor determining the fitness of a particular allele or genotype is the alleles an individual possesses for other genes. This is called **epistasis**.

frequency-dependent selection a decline in the reproductive success of a particular body type due to that body type becoming common in the population

Yet an additional external factor that may determine the fitness of an allele or genotype is its frequency in the population. This is known as **frequency-dependent selection**. Frequency-dependent selection is known to operate in mimicry systems, in which there are poisonous individuals as well as non-poisonous individuals of the same species that mimic the appearance of poisonous individuals. The fitness of either type depends on the relative frequencies of poisonous and nonpoisonous individuals in the population.

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Fishes *See Osteicthyes.*

Flight

Three different groups of animals—insects, birds, and mammals—include species that have evolved the ability to fly. This ability developed independently in each group through separate evolutionary processes. Recent research has shown that a fourth group of animals, the now-extinct winged reptiles known as Pterosaurs, were probably capable of true flight as well. Whereas the aerodynamics of flight apply equally to all types of flying animals, the mechanical details of flight vary significantly among the groups.

All insects, birds, and mammals that fly move themselves forward by flapping their wings. They do not depend exclusively on gliding and soaring to remain aloft. However, many species of birds combine extensive gliding and soaring with episodes of true flight to conserve energy.

Forward flight is produced in all true flying animals in a similar way. Each animal moves its wings up and down in a circle or figure-eight pattern. The wings are moved downward and backward, producing forward thrust and lift. Then the wings are rotated and moved back to the original position to start a new stroke.

Insects

Insects have two pairs of wings, but one pair may be small and degenerate or modified into wing covers. So insects may use either one or two pairs of wings in flight. In insects with one pair of wings, such as flies, mosquitoes, wasps, and bees, the tip of the wing moves in an oval path. On the down stroke, the wing is held parallel to the body and is moved forward and down. On the upstroke, the wing is turned perpendicular to the body plane.

Wing movement in insects with two pairs of wings, such as dragon flies, is similar, but the front and rear wings move alternately, one wing moving down while the other moves up. Because of the **exoskeleton** anatomical structure of insects, muscles are not attached directly to the wings. Instead, the wings are attached to the thorax (chest area). Four sets of muscles inside the thorax cause it to flex and twist, thus moving the wings.

exoskeleton hard outer protective covering common in invertebrates such as insects

Bats and Birds

Some people think that bats are birds because both fly. Bats and birds do have some common features, such as very lightweight skeletons, but bats are mammals, not birds. The bones of a bat's wing are quite distinct from a bird's. The long bones of a bat's wings are actually finger bones with a thin, leathery membrane stretched between. Only the thumbs of the bat remain as useful digits. The thumbs have strong claws that the bat can use for climbing.

In birds and bats, the muscles that control wing movement are attached directly to the wing bones. Birds have large chest muscles that are attached to a deep, keel-like sternum (breastbone). The depth of the sternum gives the wing muscles additional leverage, allowing for strong flapping motion. Smaller muscles return the wing to the upper position. Pterosaurs also had deep, keel-like sternums.

Birds also have specially designed wing feathers to aid flight. These feathers flatten out, overlap, and lock together on the down stroke to produce lift. As the wing is drawn back up, the individual feathers separate and rotate. This allows air to flow between the feathers, reducing drag. The downward movement of the wing propels the bird forward and provides lift. In forward flight, the body does not remain stationary in the air, so the wing

Because of their very small wings, hummingbirds are barely able to glide at all. Some hummingbirds flap their wings over 100 times per second to manuever.

always moves forward relative to the air. From the viewpoint of the bird, the tip of the wing moves in an oval or figure-eight path, with the wing tip moving forward and downward on the "power" stroke then upward and backward on the return stroke.

Most birds and all bats spend their time in the air in forward flight. Birds fly by flapping or gliding. Bats do not glide efficiently, so they flap continuously. Flapping consumes large amounts of energy. To conserve energy while staying aloft, many birds alternate flapping and gliding. Birds such as woodpeckers and many sparrows flap furiously, then fold their wings and glide through the air like little guided missiles. This produces an undulating motion to their flight path: they move up and forward while flapping, then move down and forward while gliding.

The long wings of many larger birds allow for extended periods of soaring and gliding. In contrast, the short, tiny wings of a hummingbird must be flapped constantly to keep the bird hovering in the air. Not surprisingly, hummingbirds must consume an enormous number of calories each day to provide the energy for their constant flapping.

Hovering is a specialized form of flight that is characteristic of, but not unique to, hummingbirds. Kestrels and kingfishers often hover when hunting. Other birds hover occasionally as well. However, hovering requires large energy expenditures, so it is common only among hummingbirds, whose body mass is very small.

In flight, hummingbirds can move forward, backward, up, or down. Hovering allows hummingbirds to hang motionless while drawing calorie-rich nectar from the blooms of plants. This allows hummingbirds to obtain nectar that would otherwise be out of reach. Hummingbirds have specialized shoulder joints that allow the wing to be rotated completely around to an upside-down position. By rotating the wing this way, the hummingbird is able to gain lift from both the forward and backward strokes of its wing. The wing tip follows a figure-eight pattern as in other birds, but the specialized shoulder joint allows the figure eight to be turned sideways. While performing these adjustments, it is not unusual for hummingbirds to reach a flapping frequency of up to 100 times per second.

Energy Requirements of Birds

The expression "eats like a bird" is often used to describe someone who eats a very small amount of food, but this is not an accurate description. Relative to their body weight, birds eat an enormous amount of food. An active hummingbird may eat three or four times its own body weight in food every day. This would be like an 80 kilogram (180 pound) person eating 240 kilograms (530 pounds) of food each day. Hummingbirds (and other birds) eat so much food because sustained flight requires that their large muscles work constantly, and this expenditure of energy must be replenished continually.

The metabolic rate is the rate at which a bird, or any animal, converts food calories into available energy. Flight takes a large amount of energy, so a high metabolic rate is necessary. To maintain the high metabolic rate necessary to provide energy for flight, birds must consume foods with the greatest possible energy content.

Carbohydrates, fats, and proteins all provide energy. Birds can use as much as 90 percent of the energy found in these foods. The diet of birds varies according to species, but common sources of carbohydrates include seeds, fruit, and flower nectar. Protein comes from such sources as insects, worms, fish, and small mammals, depending on the species, size, and habitat of a bird.

Seeds are rich in carbohydrates and fats, both of which are good sources of calories. Most fruit contains sugar, but fruit is not very high in calories compared to seeds and nuts. That is why fruit-eating birds need to spend long periods of their day feeding to get enough food. Flower nectar, which provides a rapidly metabolized, high-energy source, is mostly sugar dissolved in water. Twenty percent of all bird species utilize this energy source at least part of the time. Although nectar is good for quick energy, it contains little protein or fat. So birds supplement their nectar diet with other sources.

Insects are an excellent food source for birds. Insects are high in protein and fats and therefore contain a lot of energy-producing calories. Most people are surprised to learn that insects provide as much as 50 percent of the calories in a hummingbird's diet! Unfortunately for birds, insects are not always available. Although they are common in spring and summer, they die off during the colder months. Insect-eaters must switch to other foods or move to warmer areas where insects are more common. Birds of prey, including owls and hawks, rely on small mammals and fish as sources of protein.

How Birds Conserve Energy

Because flight requires so much energy, bird species have evolved various energy-saving techniques. Geese, cranes, pelicans, and other large birds often fly in formation. This is an energy saving technique. Each bird's downward wing stroke creates an updraft. By flying in formation, each bird is able to use the updrafts produced by the bird just in front of it. This provides extra lift and saves energy over long distances. The lead bird does not get any benefit, so birds take turns leading the formation. Energy saving formations include the familiar "V" of geese and swans and the ragged diagonal line in which brown pelicans often fly.

Gliding and soaring are two other energy saving techniques. Gliding is "coasting" on the wind in a straight line or gentle curve while gradually losing altitude. Soaring is using air currents to gain altitude.

The long, slender wings of albatrosses and shearwaters are ideal for gliding. Using a combination of gliding and soaring, an albatross can fly over hundreds of kilometers of ocean surface in search of food without flapping. The glide path starts high above the ocean waves with the bird headed downwind and slowly losing altitude in a long, straight glide. Close to the ocean surface, the wind speed is less because of friction between the air and ocean surface. As it gets close to the water surface, the albatross turns into the slower wind and, using its momentum, soars back up to the original altitude, never flapping its wings unless absolutely necessary. It then turns back downwind and repeats the process.

Gulls, hawks, and many other birds soar to take advantage of updrafts created when wind encounters an obstacle such as a cliff or mountain. Birds can soar on these updrafts for long periods of time with little effort.

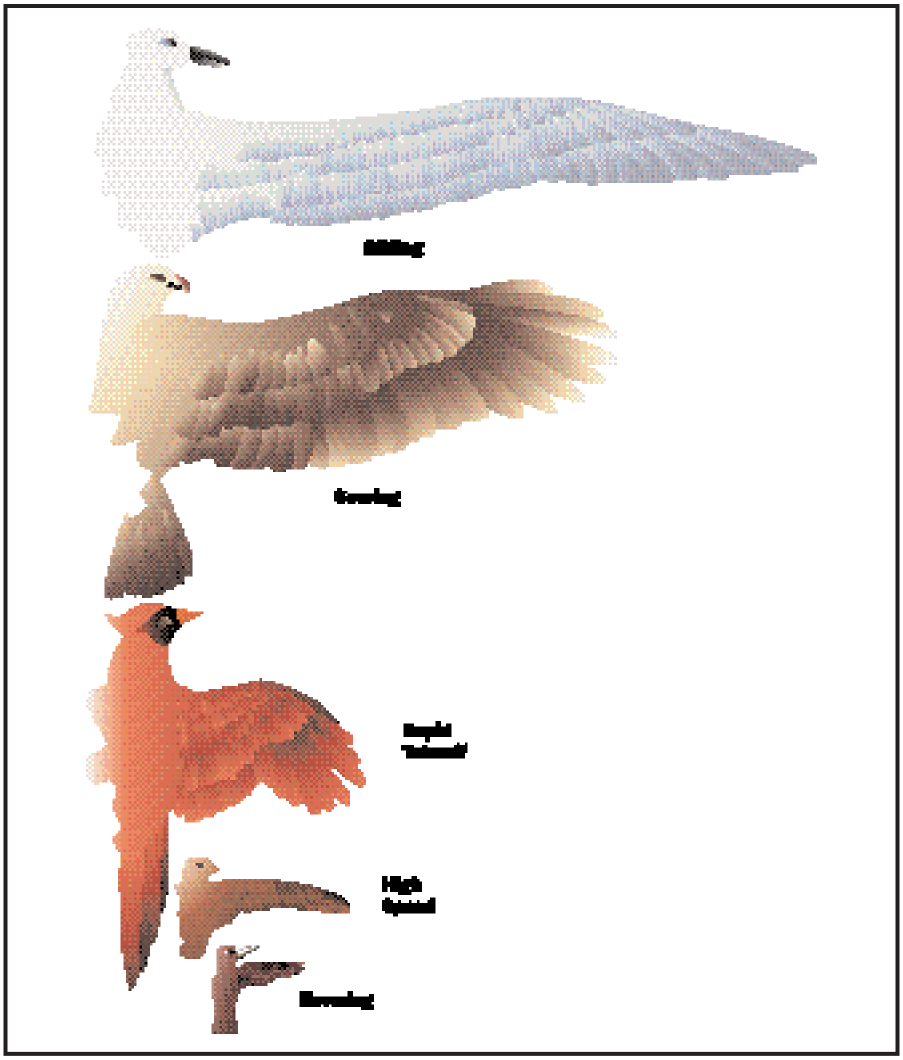
Other species, such as eagles and vultures, take advantage of rising columns of heated air called *thermals* to soar with little effort to great altitudes, from which they glide downward to the next thermal. Their long, broad wing shape allows them to take advantage of these upward air currents. Thermals occur because warm air is less dense than cold air. Denser cold air forces the less dense warm air to move upward as the cold air flows in to replace the warm air. Thermals are often found over plowed fields and darkly colored parking lots. Most birds whose flight patterns rely on thermals are searching for prey or carrion. Some birds, including storks, use thermals to migrate, climbing within one thermal, then gliding downward to the next.

Wing Shape and Flight Behavior

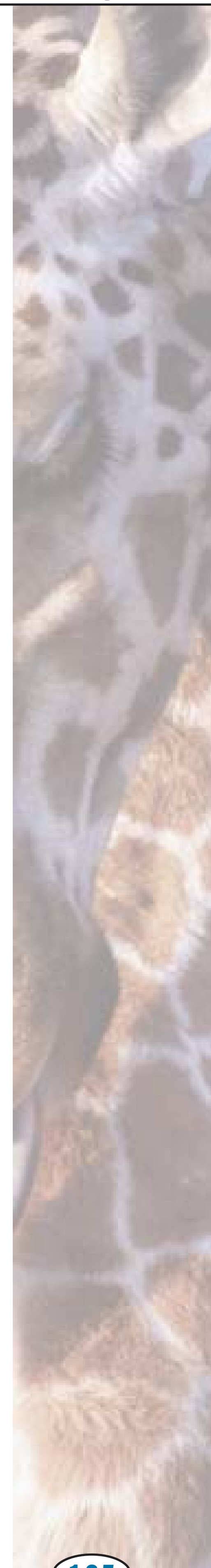
Each different kind of bird has a unique wing shape specially adapted to that bird's flight behavior and habitat. Birds that skim the surface of large bodies of water have glider-like wings that are long but slender and tapered to take advantage of the aerodynamic conditions of their environment. The narrow wings of birds of this type, such as the albatross, minimize drag, whereas the spectacular length of their wings (over 3.3 meters in the Wandering Albatross) provides sufficient lift.

Eagles, vultures, and hawks have wings that are both long and wide. This combination of length and width produces a large wing surface area that is ideal for soaring. These birds also have other specialized adaptations for soaring. For example, at the tips of their wings, each flight feather operates separately and independently of the others. This reduces drag due to turbulence, helps prevent air from spilling over to the top of the wing (which would reduce lift), and increases the bird's ability to make the small flight adjustments necessary for optimal soaring.

Just as the flight patterns of ground-dwelling birds differ from those of sea birds, such as the albatross, or high-altitude birds, such as hawks and eagles, so do their wing shapes. Ground-dwelling birds, including pheasants and turkeys, need to be able to fly rapidly for short distances. Their typical behavior is to remain motionless for as long as possible until a preda-



Wing shapes at various points of flight. Redrawn from *The Bird Site*, 2001.



tor approaches too closely, then explode into flight with much noise, thus distracting and confusing the predator. This kind of flight requires a short, broad wing attached to powerful chest muscles. This wing design also allows the bird to change direction rapidly. However, such a short, rounded wing is not suitable for extended flight. Although they are not ground-dwelling birds, parrots and other tree-dwelling birds also exhibit this type of wing. Because they do not need to fly great distances, their rounded wings enable them to maneuver quickly through the many trees of their forest homes.

High-speed birds, including falcons and swallows, have slender, tapered wings that can be flapped rapidly and efficiently to produce high-speed flight. All birds capable of high-speed flight exhibit this wing shape that produces little drag. Peregrine falcons are widely reported to have the fastest flight of all birds. One falcon overtook an airplane flying at 175 mph. However, this was in a dive. The highest speed ever reported for a bird in level flight was 218 mph for a spine tailed swift, *Hirandapus caudacutus*, in the Cachar Hills of India. This speed was recorded by timing the flight of the bird between two known points using a stopwatch.

It would seem that flight gives enormous evolutionary advantages. The Pterosaurs inhabited a wide variety of different habitats and survived for 140 million years. Bats occur in every part of the world except the Arctic and Antarctic. Worldwide, there are thousands of different species of birds, with 1,700 different species found in North America alone, inhabiting a wide variety of ecological niches. However, the insects are the real success story of flight. Nearly one million insects have been identified, and many entomologists estimate there at least that many more. Insects were the first to evolve the ability to fly, and they have made the most of it! SEE ALSO Gliding and Parachuting; Locomotion.

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Flatworms *See Platyhelmithes.*

Food Web

All organisms, dead or alive, are potential food sources for other organisms. A caterpillar eats a leaf, a robin eats the caterpillar, a hawk eats the robin. Eventually, the tree and the hawk also die and are consumed by decomposers.

Organisms in an ecological community are related to each other through their dependence on other organisms for food. In a food chain a producer is eaten by a herbivore that is in turn eaten by a carnivore. Eventually, the carnivore dies and is eaten by a decomposer. For example, in a lake, phytoplankton are eaten by zooplankton and zooplankton are eaten by small fish. The small fish are eaten by large fish. The large fish eventually die and decompose. Nothing goes to waste. Food chains are channels for the one-way flow of solar energy captured by photosynthesis through the living components of ecosystems. Food chains are also pathways for the recycling of nutrients from producers, through herbivores, carnivores, omnivores, and decomposers, finally returning to the producers.

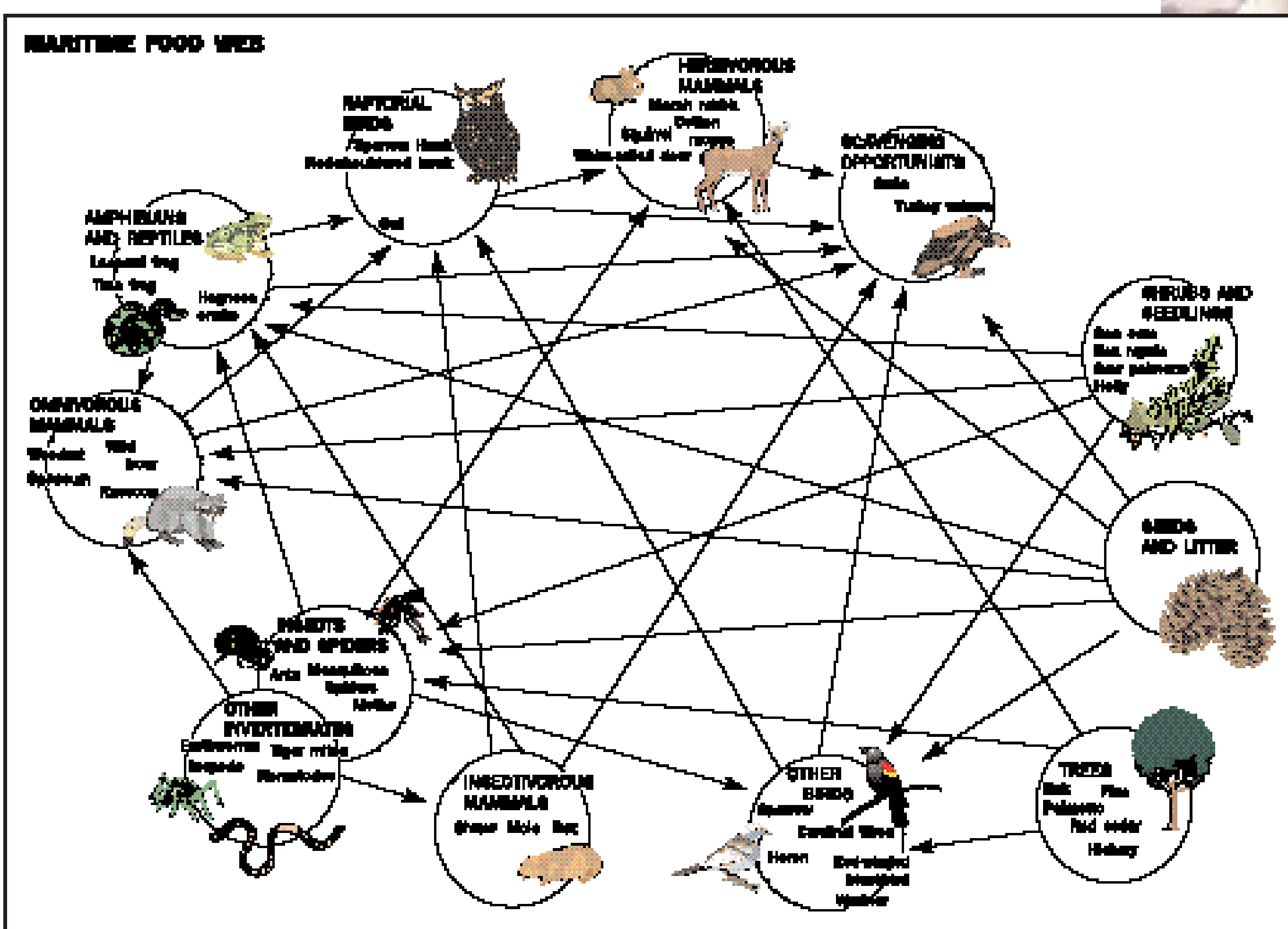
trophic level division of species in an ecosystem by their main source of nutrition

autotrophs organisms that make their own food

photosynthesizing autotrophs animals that produce their own food by using sunlight to convert other substances to food

The perfectly linear relations represented by food chains are almost never found in natural ecosystems. Although all organisms have somewhat specialized diets, most can eat a variety of different foods. Thus, each **trophic level** appears as part of several different interconnected food chains. These food chains combine into highly complex food webs.

As with food chains, a food web’s source of energy is the sun. The solar energy is harvested by producers such as green plants or algae. These producers are known as **autotrophs** or **photosynthesizing autotrophs**. Al-



This maritime food web demonstrates how the different elements of an ecosystem depend upon one another.

most all other organisms obtain their energy, directly or indirectly, from the sun. The exceptions are the communities found around deep ocean thermal vents, which are supported by various bacteria that convert heat energy into stored chemical energy. These bacteria are known as **chemotrophs** or **chemosynthetic autotrophs**.

Autotrophs are always found at the first trophic level. In an ecosystem this trophic level may include monerans, protists, and several different phyla of plants. They can all be placed at the first trophic level because they all have the same source of energy, and the entire food web depends on the energy harvested by them. For example, in a grazing food web, a herbivore eats living plant tissue and is eaten in turn by an array of carnivores and omnivores. Herbivores and the carnivores that prey on them are known as **heterotrophs**. In contrast, a detrivore (also a heterotroph) harvests energy from dead organic material and provides energy for a separate food chain.

Each step in a food web or food chain involves a transfer of matter and energy (in the form of chemical bonds stored in food) from organism to organism. Thus food webs are energy webs because the relationships represented by connections in the web represent the flow of energy from a group of organisms at one trophic level to another group of organisms at a different level. Because energy is lost (as waste heat) at each step, food chains rarely involve more than four or five steps or trophic levels.

chemotrophs animals that make energy and produce food by breaking down inorganic molecules

chemosynthetic autotrophs an organism that uses carbon dioxide as a carbon source but obtains energy by oxidizing inorganic substances

heterotrophs organisms that do not make their own food

At each level the organisms waste much energy in the form of heat generated by normal activity. Only a fraction is stored as food or used for growth. Only about 10 percent of the food entering a link is available for the next organism in the chain. After about five links, there is insufficient energy to support a population of organisms (other than decomposers). For example, in the food chain starting with diatoms and ending with killer whales, only about 0.01 percent of the initial energy stored by the diatoms is delivered to the killer whales.

Energy flow through a food web depends greatly on the nature of the producers at the first trophic level. These are usually photosynthetic plants, phytoplankton, or algae. In forest ecosystems, trees are the largest and most abundant organism. They determine the physical structure of the ecosystem, and they can be eaten directly by small or even very large animals. However, much of the matter and energy harvested by the trees goes to build a supporting structure. These supporting structures are composed of cellulose and other wood fibers that are poor sources of energy (although they may be good sources of valuable minerals and other nutrients).

In contrast, grasses do not invest much energy in supporting structures, so more energy is available per kilogram of plant material present to the grazers that obtain energy from plants. Consequently, all of the above-ground parts of the grass plants are eaten by herbivores.

detritus dead organic matter

Energy spreads out through the food web, from the lowest trophic level to the highest. At the "top of the food chain," large carnivores harvest the remaining energy. However, all things eventually die, no matter where they are in the food web, and the dead organic matter accumulates in the soil, lake bottom, or forest floor. This **detritus** becomes the basis for a completely different ecosystem, the detritus food web.

Detritus feeders and decomposers harvest solar energy from the detritus by breaking down the organic material into simpler organic compounds and inorganic compounds. By this process, the matter is recycled and made available for reuse by plants. The detritus food web is vitally important to all ecosystems on Earth. Without it, dead organic matter would accumulate and bury everything.

Humans are omnivores. They can operate on several trophic levels, eating plants, insects, mammals, birds, fish, mollusks, and many other organisms. Humans can also shorten the food chain when resources are scarce. In areas of the world where the population may be straining resources, people commonly increase the total food supply by eliminating one or more steps in the food chain. For example, to obtain more energy humans can switch from eating herbivores that obtain their energy from cereal grains to eating the cereal grains themselves.

keystone species a species that controls the environment and thereby determines the other species that can survive in its presence

The food web does not tell us everything there is to know about the complex biological communities called ecosystems. Not all relationships are equally important in these dynamic, evolving communities. Food webs contain both strong and weak links. Weak links can often be broken with little impact on the community. On the other hand, some species have a disproportionately large effect on the community in which they occur. Called **keystone species**, they help to maintain diversity by controlling populations of species that would otherwise come to dominate the community. Or they may provide critical resources for a wide range of species.

For example, in the intertidal communities of the Northwest Pacific coast of North America, the starfish *Pisaster ochraceus* feeds on the small mussel *Mytilus californius.* Experiments have shown that when the starfish is artificially removed, the population of mussels explodes, soon covering all available space. Other species are crowded out. The interaction between *Pisaster* and *Mytilus* helps to maintain the species diversity of these intertidal communities.

Research has shown that ecological communities with complex feeding relationships have greater long-term stability and are less affected by external stresses. This suggests an evolutionary basis for the diverse and complex ecological relationships found in many communities of organisms. However, humans often violate this sound ecological principle in order to increase agricultural productivity by creating artificial ecosystems that contain only one plant, such as corn. These systems are called **monocultures**. While greater agricultural productivity is possible with monoculture crops, they are very unstable ecosystems. Disease, drought, or a new insect pest can easily destroy an entire year's harvest. SEE ALSO BIOMASS; FEEDING; FEEDING STRATEGIES; TROPHIC LEVEL.

monocultures cultivation of single crops over large areas

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Foraging Strategies

The term "forage" means to wander in search of food. Every animal has a particular method of locating food, whether they smell it, find it by sight, or detect it by chemical means. Animals seek out food both individually and in groups.

Collecting food as efficiently as possible allows a species to propagate its genes more effectively. The optimal foraging theory, developed by Robert H. MacArthur and E. R. Pianka, states that food gatherers that do a better job of increasing the benefits and of decreasing the costs of foraging should procreate more effectively than those whose feeding activities yield lower net benefits. Foraging decisions are, in effect, cost-benefit problems that animals have to solve.

Food, whether animal or vegetable, provides stimuli that predators can detect. Waste products of animals give off olfactory signals that help predators locate their next meal. For example, when dung-eating beetles smell far-off feces, they quickly take to the air and forge their way along the odor trail leading straight to their primary food source. A more highly specialized adaptation involves the urine and dung of the vole, a small rodent, which does more than release olfactory signals. The waste products of the vole reflect a certain amount of ultraviolet radiation that is invisible to the

This garden dormouse forages for a pear. Animals have a wide variety of foraging methods that are dictated by sight, sense, and smell.

human eye but is clearly evident to the kestrel, a small hawk. From the air the kestrel can detect the ultraviolet markings left by the vole, which increases the kestrel's hunting success.

Foragers do not always work alone. Sometimes their companions inform them of food locations. Social insects such as bees, wasps, ants, and termites have evolved incredible techniques for transferring this kind of information. Probably the most fascinating is the complex dance of the honeybee. It is performed when a forager has found pollen or nectar and has returned to the hive. Depending on the distance and direction of the food source in relation to the sun, the honeybee will perform either a waggle dance or a round dance. The round dance informs other worker bees that a food site is located within fifty meters of the hive. The waggle dance, depending on the number of abdomen waggles and direction faced when waggling, illustrates both the distance and the direction of a food source in relation to the hive. Karl von Frisch spent twenty years experimenting with bees that he had trained to visit particular feeding stations. By studying their dances he determined that their behavior changed significantly depending on the distance and direction of a food source's location.

What about solitary animals who go unaided in the search for prey? Some rely on deceitful measures to catch their dinner. One ingenious method is used by the bolas spider (*Mastophora dizzydeani*), which releases a scent identical to the sex pheromone of certain female moths. When the male moth of the species goes in search of a mate, he may encounter instead a bolas spider armed with a sticky globule attached to a long, silken thread. The spider throws the blob, hits the moth, and then feasts on the captured prey. By employing the deceptive scent, the bolas spider lures insects within attack range. This maximizes the spider's success rate while reducing its energy output.

Because of potentially toxic foods, predators must pay attention to warning coloration and behavior of **fauna** prey and carefully avoid more difficult-to-detect toxins in flora. Herbivores must be able to determine whether the

fauna animals

plant they have selected to eat has low concentrations of toxic terpenoids—poisons that many plants incorporate into their tissues to repel consumers.

A study of the **herbivorous** Costa Rican howler monkeys illustrates how some animals deal with this problem. Foraging very carefully, these monkeys avoid toxic leaves and those low in nutritional value. Although the choices they make in selecting particular leaves may raise the costs of foraging, they ingest fewer poisons and more usable proteins. For example, howlers tend to avoid foraging in common tree species, opting instead to eat the leaves from scarcer species. These preferred tree species, it turns out, have lower levels of alkaloids and tannins. Alkaloids are poisonous to howlers, and tannins make leaves harder to digest. Also, the monkeys tend to feed on only the petiole—the leaf part lowest in toxins—while discarding the more toxic leaf blade.

herbivorous describes animals who eat plants

The optimality theory does not always work in a clear-cut fashion. Some animals must balance the cost of consuming more food per unit of foraging time against the risk of becoming food themselves. For instance, the hoary marmot, a relative of the groundhog, stays close to its burrow on rocky slopes and feeds primarily on the heavily grazed margin of meadow located nearby rather than venturing further into greener pastures. This reduces its risk of becoming prey for an eagle or coyote. Thus, it spends more time looking out for food than for danger. Although this may compromise foraging efficiency in caloric or nutritional terms, it keeps them alive. Whirligig beetles behave in much the same way, restricting their movements to the dense cluster of beetles that form on the water's surface. In this way, they steer clear of being eaten yet sacrifice foraging opportunities that exist beyond the safety of numbers. SEE ALSO Feeding; Feeding Strategies.

Ann Guidry

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Fossey, Dian

American Primatologist
1932–1985

Dian Fossey, born in 1932, was a celebrated mountain gorilla researcher. Fossey initially dreamed of becoming a veterinarian, but her science grades prevented her from pursuing that goal. A fairly antisocial person, she got along well with children and animals as an occupational therapy intern before making her way to Africa at the age of thirty-one. There she was immediately captivated, and she became acquainted with renowned anthropologist Louis Leakey, who was engaged in research. Impressed with her attitude, Leakey sent her to eastern Congo in 1966, and Africa became the setting of her life's work.

Scientist Dian Fossey was well-known for her pioneering work with gorillas.

Fossey enjoyed working in Africa despite horrifying conditions. Shortly after her arrival in the Republic of Congo (later Zaire), the country became embroiled in civil war, and she later escaped to Rwanda. Despite the tense political situation and other extreme difficulties (poachers, disease, lack of funding, and so on), Fossey vigorously protected her subjects of choice, mountain gorillas. She quickly got closer to them than other researchers and managed to become accepted among them. Although some critics argued that her methodology was unscientific, saying it was unquantifiable, Fossey logged thousands of contact hours and observations, frequently finding new groups of animals to work with.

> Louis Leakey believed women were better suited than men to observe and note animal behavior because he thought women were more patient.

Fossey also worked to keep the gorillas' habitat intact. Frequent invasions by poachers and cattle herdsmen destroyed what little mountain gorilla habitat remained. Fiercely independent, she was unwilling to compromise her activities or research methods despite the conflicting opinions of others.

In 1973, Fossey left Africa to begin her graduate studies at Cambridge. After earning her Ph.D in 1976, she was a visiting professor at Cornell University from 1980 to 1982. She also took this time to write *Gorillas in the Mist*, a firsthand account of her experiences. It became an enormously popular book although it was less well received by other primatologists. She returned to Africa in 1983, convinced that her methods of **poaching** prevention would best serve the gorilla population.

poaching hunting outside of hunting season or by using illegal means

In 1985, Fossey was murdered, most likely by poachers. Since her death, there have been few poaching incidents and the mountain gorilla population has been growing. Fossey brought the plight of the mountain gorilla to public consciousness and left behind the Dian Fossey Gorilla Fund for their protection. SEE ALSO Primates.

Ian Quigley

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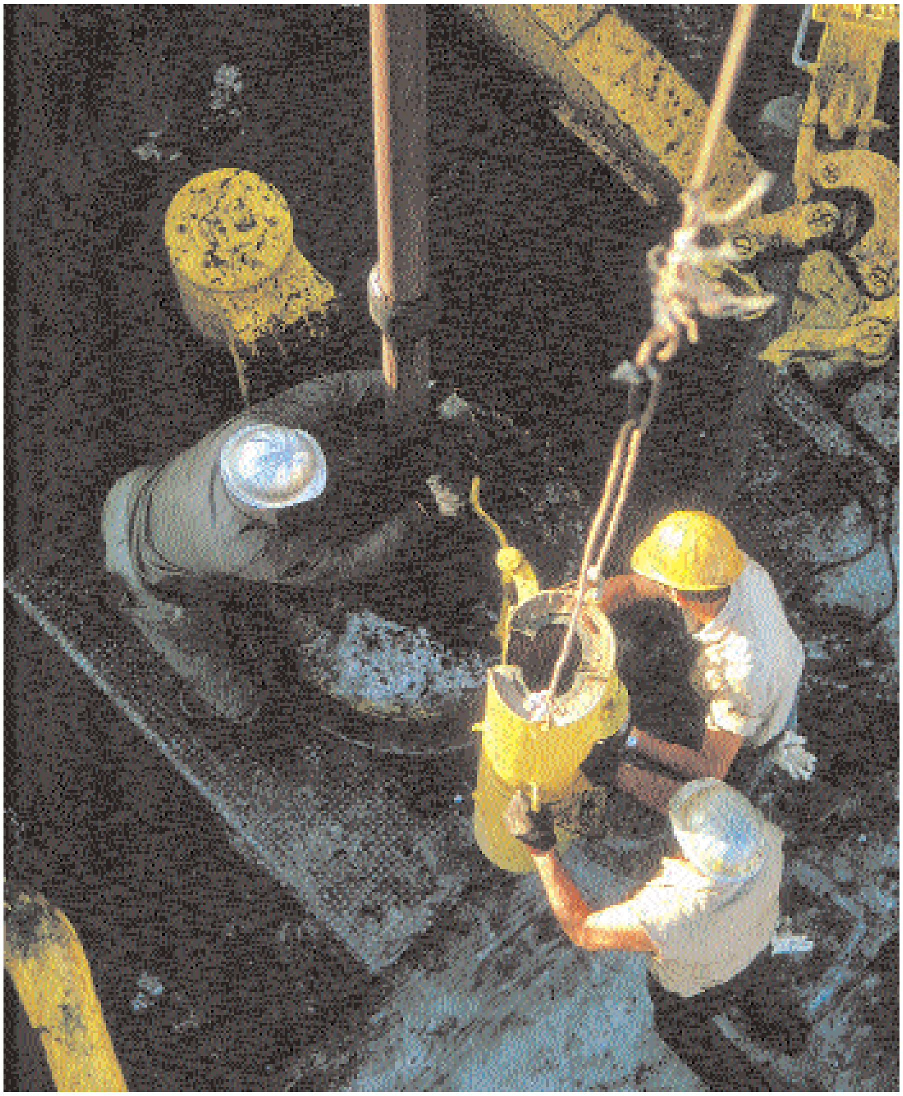
Fossil Fuels

Fossil fuels are buried deposits of plants and animals that have been converted to coal, petroleum, natural gas, or tar by exposure to heat and pressure in the Earth's crust over hundreds of millions of years. The energy in fossil fuels comes from sunlight, either directly or indirectly.

Coal comes primarily from the remains of plants that were buried in anaerobic conditions (without oxygen). Coal ranges from 55 percent to 90 percent carbon mixed with water and other substances including compounds of nitrogen and oxygen. Coal is graded according to hardness and carbon content. The lowest grade, lignite, is soft and brown in color. The hardest, anthracite, is nearly pure carbon. It is so hard it can be polished like a gemstone.



Workers drilling for gas. Natural gas is usually found in varying amounts, along with crude oil and with coal.

Petroleum (crude oil) is a liquid containing primarily hydrocarbon compounds along with small amounts of compounds containing oxygen, sulfur, and nitrogen. Crude oil originates with the buried remains of various types of plankton, primarily diatoms. It varies in consistency from a thin liquid the color of port wine to a thick, black, tarlike substance that must be heated before it will flow. Crude oil is the source of gasoline, jet fuel, diesel, heating oil, bunker oil, plastics, and other compounds.

Natural gas is usually found in varying amounts along with crude oil and with coal. It is also found by itself. Natural gas consists of a mixture of methane (CH_4) and other hydrocarbons such as ethane (C_2H_6), propane (C_3H_8), and butane (C_4H_{10}). Methane is a natural byproduct of the anaerobic decomposition of organic remains.

Oil and Natural Gas

Petroleum ranges in quality from a relatively thin, free-flowing liquid called light or sweet crude to a thick, gooey black liquid with high sulfur content called heavy or sour crude. Because sweet crude is cleaner to burn and easier to transport, it is more valuable. Some oil flows naturally to the surface but most must be pumped. After primary recovery, hot water, steam, or high-pressure carbon dioxide can be injected into adjacent wells to force out some additional wells. Only about one-third of the oil can be extracted in primary and secondary recovery.

Oil, a useful fuel that can power automobiles, trucks, and airplanes, is a relatively inexpensive energy source. It has a high energy content and is easily transported. However, most experts expect little of the world's original oil reserves to remain by the middle of the twenty-first century. If world oil consumption increases at a rate of 2 percent per year, 80 percent of the world's supply will be used up by 2037.

When natural gas deposits are tapped, the gas is pressurized, which causes the propane and heavier hydrocarbons to liquefy. This liquefied petroleum gas (LPG) is stored in pressurized tanks and used in rural areas where natural gas supplies are not available. The remaining gas, mostly methane, is dried, cleaned of hydrogen sulfide, and distributed through pressurized pipelines.

Natural gas is a very clean-burning substance. If the gas is properly treated to remove sulfur and other contaminants, combustion products consist of water and carbon dioxide. Natural gas burns hotter and produces less pollution than any other fossil fuel.

The U.S. Department of Energy has estimated that all known and unknown reserves of natural gas will last until 2045 at present levels of consumption. If consumption rises by 2 percent per year, natural gas reserves will be depleted by 2022.

Coal

Coal is the world's most abundant fossil fuel. The United States, China, and Russia contain about two-thirds of known and estimated undiscovered coal reserves. Much of that coal contains large amounts of sulfur. When coal containing sulfur is burned, sulfur dioxide is created. Sulfur dioxide is one of the primary components of acid rain, so it is a pollutant. It is very difficult to remove the sulfur before the coal is burned, so the sulfur must be removed from the stack gases. Removing the sulfur is costly, although part of the cost can be recovered by selling the byproduct, sulfuric acid. World reserves of coal will last 220 years at current consumption rates and 65 years if consumption rates increase by 2 percent per year. Identified coal reserves in the United States will last about 300 years at current consumption rates.

Coal must be extracted by mining, the most environmentally destructive and expensive form of extraction. The least expensive form of mining is strip mining. The layer of rock and soil over the coal is removed by heavy machines, the coal is extracted by other heavy machines, and the rock and soil are replaced. Existing laws require that strip-mined land be returned to its original contour and replanted in suitable ground cover. When properly done, this restoration leaves the land in good condition.

Unfortunately, much of the land that was strip-mined before the laws were passed has not been restored. This results in erosion and pollution. Much of the coal that can be strip-mined in the United States is in the arid west, where restoration is more difficult and expensive. These requirements have made coal more expensive. Since natural gas is cheaper and burns cleaner, most new electric power plants being built are gas-fired.

Carbon Dioxide

All fossil fuels represent millions of years of stored solar energy. Plants remove carbon dioxide from the air and use the energy of sunlight to separate the carbon from the oxygen. The oxygen is released and the carbon is used to build carbohydrates, fats, and proteins. The carbon stored in fossil fuels is the result of this process. When fossil fuels are burned, this process is reversed. Oxygen from the air combines with carbon in the fossil fuels to form carbon dioxide, which is released into the atmosphere. Carbon dioxide levels in the atmosphere have been increasing steadily since the beginning of the industrial revolution. Most scientists now think that these increasing levels of carbon dioxide in the atmosphere are contributing to **global warming** through a process known as the **greenhouse effect**. SEE ALSO Global Warming.

global warming a slow and steady increase in the global temperature

greenhouse effect a natural phenomenon where atmospheric gases such as carbon dioxide prevent heat from escaping through the atmosphere

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Fossil Record

Geologists and other scientists use fossils to correlate the ages of different rock strata (thin layers or beds of rock that differ in some way from adjacent layers) in different places on Earth. If two different rock strata contain the same set of fossil species, then the two different rock strata were probably deposited about the same time. Fossils also can give clues about the environment of Earth in the past. For example, certain fossils are only found in the ocean. When these fossils are found in a rock strata, it is a sure sign that the rock strata was deposited in an ocean even if it is now on top of a high mountain.

Fossils can also help to establish the relative ages of rocks (which rocks are older and which are younger). If a fossil species can be assigned an absolute date by radioactive dating, then that same fossil species can be used to help determine the absolute dates of other rocks that contain it. The fossil record also gives clues as to how life has evolved.

A fossil is any preserved remains of ancient life. There are several different categories of fossils. Trace fossils include such things as tracks, burrows, and coprolites (fossilized excrement). Body parts or whole bodies of organisms can be preserved by a process known as mineralization, in which minerals gradually replace the organic remains and the fossil is turned to stone.

Molds, casts, and imprints make up another category of fossils. They are formed when the sediment has solidified about an organic object and the object is subsequently dissolved, leaving a hole in the rock—a mold. Deposition of mineral matter from underground solutions may fill the hole, producing a cast. Molds of thin objects (such as leaves of ferns often found in coal) are called imprints.

Organisms with hard tissues are more likely to be preserved. Organisms that are more abundant are more likely to be preserved. Organisms that live in swamps or near water are less likely to decay when they die and are more likely to be preserved. All these factors make the fossil record somewhat incomplete. Nevertheless, the fossil record extends back at least 3.5 billion years. During this immense span of time, tens of millions of different species have lived on Earth.

superposition the order in which sedimentary layers are found with the youngest being on top

sedimentary rock rock that forms when sediments are compacted and cemented together

The fossil record can also be used to determine the ages of rocks. The geological principle of **superposition** states that if rock layers are undisturbed, older rock layers are found below younger layers. If the rock layers contain fossils, then the relative ages of those fossils can be determined from the relative ages of the rock in which they were found. Then those same fossils can be used to help determine the relative ages of rocks found elsewhere. A bed of **sedimentary rock** can be identified by its fossils.

Using these ideas, geologists working in the first part of the nineteenth century at many different places gradually developed a theory of the history of life on Earth. This life history is now known as the geological time scale. Although the early researchers dramatically underestimated the age of Earth, they did establish the principle of determining the age of rocks by looking at the fossils found in those rocks.

Even a superficial examination of the fossil record shows that many species existed in the distant past that no longer exist today. Likewise, even an incomplete fossil record reveals that species living today did not exist in the distant past. Thus the fossil record and the geological time scale provided the background for Charles Darwin and other scientists to develop their theories of evolution. SEE ALSO Biological Evolution; Geological Time Scale; Morphological Evolution in Whales; Tetrapods—From Water to Land.

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Fruit Fly *See Drosophila.*

Functional Morphologist

Functional morphology is a relatively new field in biology. Morphology is the study of the size, shape, and structure of animals, plants, and microorganisms, and the relationships of their internal parts. Unlike anatomy, morphology is not just simple description. It also involves the principles according to which form are related. The organizing principles used by morphology include evolutionary relations, function, and development.

The functional morphologist studies how the shape, or morphology, of an organism or some part of an organism relates to its function. For example, there is a relationship between the shape of a tree and how it is affected by wind. Tall trees grow in protected valleys and can shelter each other. Bristlecone pines, which tend to be small and sturdy, grow where the soil is thin and the wind blows constantly. The form of a bird's wing is related to the speed and manner of its flight. Swifts and falcons are unrelated birds, but both have narrow, sharply pointed wings, ideally suited for rapid flight.

Peregrine falcons have long, slender and pointy wings. Functional morphologists have deduced that the shape of their wings evolved to their present shape to allow the birds to fly quickly.

Functional morphologists study motion, support structures, energetics of motion, neural control of locomotion, and motion occurring at the cellular and molecular levels. Fluid flow in cardiovascular systems, fluid flow in respiration, and feeding strategies are all part of functional morphology. Research in functional morphology is multidisciplinary and has applications in ecology, evolution, and medicine.

A functional morphologist will usually have studied biology with a heavy emphasis in anatomy courses as an undergraduate student. Some physics or even engineering courses are also useful. At the graduate level, courses in biomechanics, comparative vertebrate anatomy, comparative physiology, mathematical and computer modeling, and advanced mechanics are necessary preparation for functional morphology, and the student will also specialize in an area, such as fish feeding behaviors or the mechanics of shark movement.

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Functional Morphology

Functional morphology involves the study of relationships between the structure of an organism and the function of the various parts of an organism. The old adage "form follows function" is a guiding principle of functional morphology. The function of an organ, appendage, tissue, or other body part dictates its form. Furthermore, the function can often be deduced from the form. The idea of relating form and function originated with the French naturalist Georges Cuvier (1769–1832).

The primary task of functional morphology is observing living organisms to see how they live and function. From observations of living organisms, scientists also attempt to discern principles that will allow them to determine function from the forms of fossils, such as bones, shells, or whatever happens to be preserved from organisms that no longer exist.

Theoretical morphology tries to determine the limits of form; not every conceivable form could actually exist in nature.

Functional morphology studies the ways in which structures such as muscles, tendons, and bones can be used to produce a wide variety of different behaviors, including moving, feeding, fighting, and reproducing. Functional morphology integrates concepts from physiology, evolution, development, anatomy, and the physical sciences, and synthesizes the diverse ways that biological and physical factors interact in the lives of organisms. Functional morphology and biomechanics allow scientists to observe and quantify not only how animal skeletons and joints move and how muscles work but also how these things relate to the diversity of animal behaviors.

Functional morphology helps to understand the form of modern animals. For example, even casual observation reveals that elephants have very thick legs relative to their body size when compared with smaller animals such as antelope or horses. This is not just a fluke of nature's design; elephants need thick legs to hold up their body mass. But why are the legs of an elephant proportionately thicker than the legs of smaller animals?

The mass of an object is related to its volume. Imagine an animal, an elk for example, scaled up to be twice as tall (about the height of an elephant) while keeping all proportions the same. An animal twice as tall as another animal of a similar shape will have much more than twice the volume. Because it is also twice as long and twice as wide, the scaled-up elk will have eight times as much volume as the normal-sized elk. Assuming bone and muscle density remain about the same, the scaled-up elk will also have eight times as much mass. However, the legs of the larger elk will only have four times the area of the legs of the normal-sized elk.

According to the principles of engineering, the strength of a column of bone and muscle is proportional to its cross-sectional area. Legs with only four times the cross-sectional area will not be strong enough to hold up eight times the weight. To hold up the scaled-up elk, its legs must be proportionately thicker than the legs of the normal-sized elk. Consequently, in order to attain the great size they have, elephants had to evolve legs proportionately much thicker than those of smaller animals.

Elephants also have large ears. Functional morphology helps to understand this feature as well. As elephants evolved to larger body size, the area of their skin did not increase as rapidly as their volume. Thus, the elephant's skin could not dissipate enough heat to keep the elephant cool. The elephant's relatively large ears, however, significantly increase its ability to give off heat. Forest elephants live in somewhat cooler environments, so their ears are not as large as elephants that spend more time in the sun.

Functional morphology also helps to understand the limits on the size of cells. If a spherical bacterial cell grows to twice its original size, it has eight times the volume but only four times the surface area. Because the cell absorbs nourishment through its surface, it must sustain eight times as much mass with only four times as much nourishment. At some point, a cell will become so large that it cannot absorb enough materials to sustain its mass, and it will then divide. SEE ALSO Allometry.

Elliot Richmond

FUNCTIONAL MORPHOLOGY

A couple walk hand in hand along the beach. Suddenly an ant appears at the top of a sand dune, scaring the wits out of the couple. This is no ordinary ant, this is a *giant* ant the size of an elephant! Since ants are extremely strong for such small animals, this gigantic ant must be unbelievably strong, able to throw automobiles around like toys, right? Actually, no. As an object increases in size, its weight grows much faster than its strength. When an object doubles in size, it becomes four times as strong, but eight times as heavy. The thin legs of the ant are strong enough to support several times its own weight. However, if the ant were scaled up to be as tall as an elephant, its legs would be too flimsy to hold up its own weight.

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Genes

A common feature of organisms is that offspring tend to look like their parents. For example, tall, brown-eyed parents tend to have tall, brown-eyed children. The mechanism by which parents pass on particular traits to their offspring is termed **heredity**. The focus of the following entry will be to explore the role of genes in heredity.

heredity the passing on of characteristics from parents to offspring

What Is a Gene?

Originally, most biologists believed in "blending inheritance," where the joining of a sperm from the father and an egg from the mother yields offspring which have characteristics that are a blend of the characteristics of the two parents. However, Austrian botanist Gregor Mendel's (1822–1884) pioneering work with inheritance in pea plants largely disproved this theory. Mendel showed that for many traits, when a pea plant with one trait (e.g., green pods) is bred to a pea plant with another trait (e.g., yellow pods), the offspring always look like one of the parental types, never a mixing of both (e.g., yellow-green pods are never seen). Mendel proposed that traits are inherited in a "particulate" manner. Parents transmit individual hereditary units to their offspring, and the particular combination of these units in an offspring controls how that offspring will look. These hereditary units are now known as genes. Thus the science of heredity is termed **genetics** and the overall genetic makeup of an organism is termed its **genotype**. The genotype determines the types of traits an organism will have, otherwise known as the organism's **phenotype**.

genetics the branch of biology that studies heredity

genotype the genetic makeup of an organism

phenotype the physical and physiological traits of an animal

Most organisms are diploid, that is, they have two copies of every gene. Different forms of a particular gene are known as **alleles**. In the example above, the gene for pod color had two alleles, green and yellow. Diploid parents make **haploid** eggs and sperm, meaning those gametes have only one copy of each gene. Thus when the egg and sperm fuse, the resulting offspring is a diploid, having one copy of each gene from both parents. An offspring with two copies of the same allele for a particular gene is called a **homozygote**, while an offspring with two different alleles for a particular gene is called a **heterozygote**.

alleles two or more alternate forms of a gene

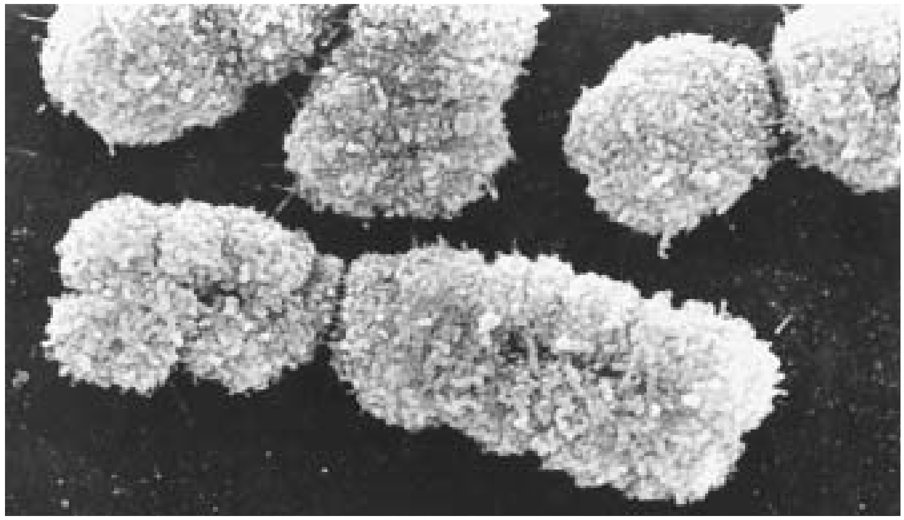
haploid cells with only one set of chromosomes

homozygote an animal with two identical alleles for one trait

heterozygote an organism whose chromosomes contain both genes of a contrasting pair

When an offspring receives different alleles of a particular gene from its parents (e.g., a yellow pod allele from its mother and a green pod allele from its father), one allele is typically **dominant** over the other. In our

dominant an allele that is always an expressed trait



Genes are passed through human reproductive chromosomes, such as these X-chromosomes.

example, green pod is dominant over yellow pod so that an individual with both color alleles will always have green pods. The nondominant allele is known as the **recessive** allele.

recessive a hidden trait that is masked by a dominant trait

Although uncommon, some pairs of alleles do not behave in a completely dominant or recessive manner. For example, the flowers of snapdragons typically come in two colors, red and white. Mating a red-flowered plant with a white-flowered plant yields pink-flowered offspring, which would be expected under the blending inheritance theory. To show that Mendel's laws still hold, a cross may be made between a pink-flowered plant and a white-flowered plant. A proponent of the blending inheritance theory would predict that all offspring from this cross would have light pink flowers, whereas in fact half the offspring have white flowers and the other half have the original pink. When the phenotype of the heterozygote is a combination of the phenotypes of homozygotes for those two alleles, the alleles are said to show **incomplete dominance**.

incomplete dominance a type of inheritance where the offspring have an intermediate appearance of a trait from the parents

Codominance occurs when a heterozygote expresses both of the homozygote phenotypes. Take for example the A and B blood groups of humans, which determine the type of **antigen** a blood cell will produce. If a homozygote for A (written AA) mates with a homozygote for B (BB), the offspring will be heterozygous (genotype AB), and will produce both A antigens and B antigens, not a blending between the two.

codominance an equal expression of two alleles in an heterozygous organism

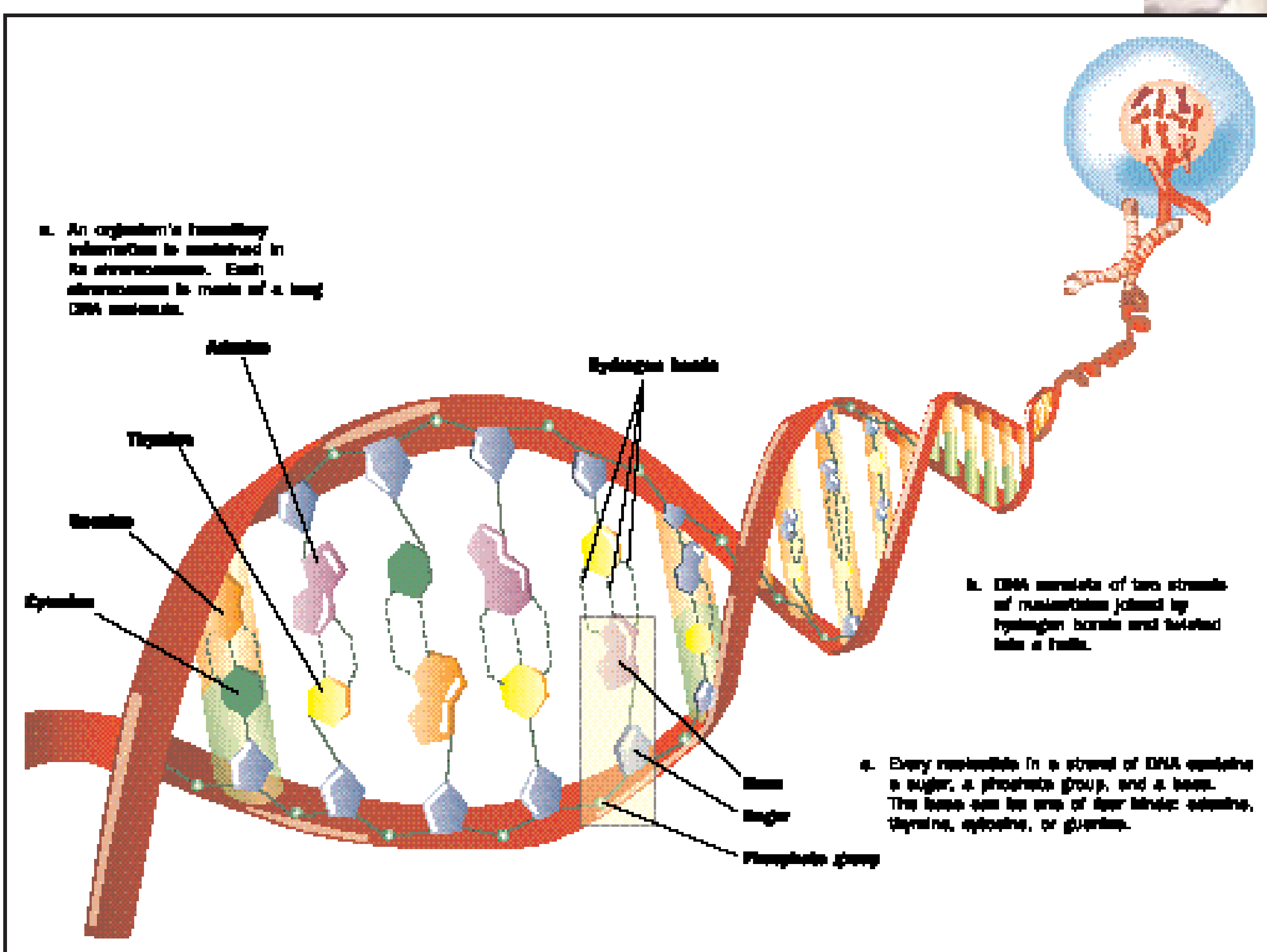
antigen foreign substances that stimulate the production of antibodies in the blood

Other factors may affect whether a normally dominant allele expresses its phenotype. Siamese cats have a dominant black fur allele, but that allele only expresses its phenotype at colder temperatures. These cats tend to have dark ears, paws, and a dark tail but are light-colored in areas of the body closer to the body's warm core. Furthermore, other genes in the **genome**, such as genes that code for modifiers and suppressors, can affect how an allele at one particular gene is expressed.

genome an organism's genetic material

DNA as the Genetic Material

Because genes control the structural and functional properties of organisms, it became increasingly important to biologists in the early twentieth century that they determine what type of molecules genes actually are. It was



Structure of DNA. Redrawn from Johnson, 1998.

tempting to believe that genes were proteins, as it had been established that proteins are an extremely diverse group of molecules that perform a wide variety of specific functions within cells. However, several lines of study eventually led to the conclusion that genes are made of deoxyribonucleic acid, or DNA.

When a diploid organism makes new cells, the new cells are also diploid and are exact copies of the old cells. The mechanism by which cells replicate is termed **mitosis**. However, when adult organisms mate, they make haploid gametes (eggs and sperm) through a process known as **meiosis**. Scientists worked out the steps by which **diploid cells** make diploid copies (mitosis) and haploid copies (meiosis) in the late 1800s. The difference between mitosis and meiosis lies largely in the sorting in the cell nucleus of chromosomes, condensed strands of DNA packaged with various proteins. Interestingly enough, chromosomes seem to move from one generation to the next in a way that mirrors the movement of genes across generations. In adult cells there are two copies of every chromosome, as there are two copies of every gene. Meiosis yields gametes with one copy of each chromosome, and fertilization of the egg by a sperm restores the chromosome number to its original state, paralleling the fact that one copy of each gene from both

mitosis a type of cell division that results in two identical daughter cells from a single parent cell

meiosis a specialized type of cell division that results in four sex cells or gametes that have half the genetic material of the parent cell

diploid cells cells with two sets of chromosomes parents are fused into their diploid offspring. Thus genes appeared to be associated with chromosomes. Furthermore, later studies showed that particular genes could be mapped to precise locations within chromosomes.

bacterium a member of a large group of single-celled prokaryotes

In the 1920s, a British physician named Frederick Griffiths performed a number of experiments with the **bacterium** that causes pneumonia in humans, *Streptococcus pneumoniae*. Griffiths worked with two strains of the bacteria, one that was virulent and caused disease, and another that was avirulent (not virulent). Griffiths found that the avirulent bacteria, in the presence of extract from the virulent strain, could be transformed into a virulent form. This "transforming agent" was studied intensively by the American bacteriologist Oswald Avery and his colleagues over several years. They were able to destroy various chemicals found in the virulent strain extract so as to be able to test the significance each chemical had on virulence individually. In 1944 they concluded that DNA from the virulent strain extract was the transforming agent.

Further proof that DNA is the molecule of inheritance came in 1952 with the publication of a paper by Alfred Hershey and Martha Chase of the Carnegie Laboratory of Genetics. They studied the bacteriophage T2, a virus that infects bacteria such as *Escherichia coli (E. coli)*. It was known that viruses were made almost entirely of protein and DNA, and that some viral component moved into the bacterial cells and caused the bacteria to use its cellular apparatus to make new viruses. Hershey and Chase were able to label the protein component of the virus and the DNA component of the virus in different ways so as to track which component was responsible for controlling the host cell. Their results confirmed that the viral DNA, not protein, was responsible for manipulating the bacterial host cells. It was finally apparent that the genetic material is made of DNA.

How Does the Genotype Determine the Phenotype?

enzymes proteins that act as catalysts to start biochemical reactions

George Beadle and Edward L. Tatum's work on the bread mold *Neurospora crassa* in the 1940s at the California Institute of Technology provided some of the first convincing evidence that the function of genes is to control the production of proteins. *Neurospora* can be grown in the lab on a medium made of a few simple nutrients. However, *Neurospora* mutants that required certain supplements in the medium to be able to grow were known to exist. In these mutants, **enzymes** (proteins that catalyze molecular reactions) that are necessary to the functioning of particular metabolic pathways do not perform properly. Beadle and Tatum irradiated *Neurospora* cells with x-rays to induce a wide variety of mutations that made the *Neurospora* unable to live on the minimal medium. Some of these mutations blocked different steps within the same metabolic pathway. Because the genes controlling different enzymatic steps from the same pathway were mapped to different chromosomal locations, it became clear that particular enzymes correspond to particular genes. In other words, each gene, which is made of DNA, is responsible for the production of one enzyme. It was later shown that genes can "code" for any kind of protein, including enzymes.

nucleotides the building block of a nucleic acid that is composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

Biologists quickly focused on determining the structure of DNA to try to gain insight into the actual mechanism whereby genes control the production of proteins. DNA was found to be a double helix made primarily of the four **nucleotides**: adenine (A), cytosine (C), guanine (G), and thymine

(T). The structural makeup of DNA is shared among all living things, suggesting that the different forms of life have a single common ancestor. The process by which DNA specifies the type of protein to be made was labeled the "central dogma of molecular biology." Genes are first copied from DNA to RNA (ribonucleic acid) in a process termed **transcription**. This RNA, which is referred to as **messenger RNA** or mRNA, then specifies the formation of proteins in a process termed **translation**. Translation involves the breaking up of the DNA into **codons**, combinations of three nucleotides in a row. Each combination of three bases (e.g., ATG, TCA, …) encodes a particular amino acid, the building blocks of proteins. So, despite the small number of nucleotide types that make up DNA, sequences of these nucleotides code for the wide variety of proteins found in organisms.

transcription a process where enzymes are used to make an RNA copy of a strand of DNA

messenger RNA a type of RNA that carries protein synthesis information from the DNA in to the nucleus to the ribosomes

translation a process where the order of bases in messenger RNA codes for the order of amino acids in a protein

codons the genetic code for an amino acid that is represented by three nitrogen bases

organelles membrane-bound structures found within a cell

exons the coding region in a eukaryotic gene that is expressed

introns a non-coding sequence of base pairs in a chromosome

homologous similar but not identical

polymerase an enzyme that links together nucleotides to form nucleic acid

The Structure of Genes

In eukaryotes (organisms that possess membrane-bound **organelles** such as a nucleus), genes are typically made up of **exons** and **introns**. Exons are regions of the gene that code for protein (the codons), while introns are regions of the gene that are transcribed into mRNA but are spliced out before the translation stage. Introns are thought to have evolved to allow exon shuffling, the process whereby an exon from one allele of a gene in a heterozygote may "switch places" with the same exon from the second allele. This mixing and matching of exons in the two copies of a gene allows for rapid evolution of proteins. The exons are switched through a process known as recombination, the physical breaking and piecing together of **homologous** chromosomes. Having introns increases the probability that the locatio of the chromosomal breakpoints during recombination are not in coding DNA and so will not cause deleterious mutations.

There are several other types of noncoding regions within genes. For example, promoters are specific DNA sequences in front of the coding region which allow the RNA **polymerase** enzyme to bind and to start transcription of the gene. Other DNA sequences near the coding region of the gene allow for regulatory enzymes to bind and cause up-regulation (more or faster transcription) or down-regulation (less or slower transcription) of that gene. For example, if a host cell is being attached by a bacteria, enzymes in the host cell bind to and cause the up-regulation of genes coding for proteins that destroy bacterial cells.

Gene Evolution

Genes control the phenotype, the structural and functional properties of an organism. Since it is clear that phenotypes have evolved and diversified over the history of life, it stands to reason that genes controlling the phenotype have evolved as well. How do genes evolve?

The ultimate cause of evolution is the accumulation of mutations in the DNA of an organism. Mutations can be caused by a number of factors, including errors made by DNA polymerase during replication of the genome, by reactive molecules in the cell, and by external factors such as x-rays. Eukaryotes utilize many mechanisms, including repair enzymes, to fix mutations when they occur, but inevitably some mutations are not corrected and are then passed on to future generations. The overwhelming majority of mutations are harmful or neutral with respect to the fitness of the organism

possessing them. However, when advantageous mutations occur, natural selection tends to increase their frequency in a population.

Point mutations. The most common types of mutations are point mutations, mutations that occur within a single gene. Point mutations can be broken up into a number of classes. Because the genetic code is "degenerate," that is, different codons may code for the same amino acid, some mutations are silent. Often a change in the third base of a **codon** (e.g., ACA to ACG) does not change the amino acid that is coded for. Silent mutations have virtually no effect on the fitness of an organism. Missense mutations are mutations that change a codon and change the amino acid that is coded for. A protein with one altered amino acid may be nonfunctional but will more likely just be less efficient in its job than the original. Nonsense mutations are mutations that change a regular codon into a stop codon, prematurely terminating translation of the mRNA. These mutations generally have severe effects on the ability of the protein to perform its required function. Frameshift mutations do not cause base substitutions but instead delete or add nucleotides into a sequence. Imagine a frameshift mutation that adds one nucleotide into a coding sequence. Because the mRNA message is read three nucleotides (one codon) at a time, the one base insertion will cause all the downstream codons to be one base off and to be read wrong. These mutations are extremely disruptive to the genes they occur in.

codon the genetic code for an amino acid that is represented by three nitrogen bases

Gene duplication. Other than point mutation, another way in which a gene might gain a new function is through gene duplication. Occasionally, parts of chromosomes or even whole chromosomes are duplicated. If a gene is duplicated, then one of the duplicates is free to evolve in any direction since the other will continue to fulfill its duties. Gene duplication allows genes to acquire novel functions and to create novel phenotypes. Gene duplication may be extremely important in an evolutionary sense; for example, it appears that the great diversification of vertebrates was accompanied by several genome duplication events.

Although most new point mutations have harmful effects on fitness, the majority of mutations which become "fixed," that is, which reach 100 percent frequency in a population, are neutral or advantageous. This is because natural selection tends to weed out harmful mutations or keep them at extremely low frequencies. Thus when comparing the gene sequences from two closely related species, any differences in the DNA sequences can be attributed to the fixation of neutral or advantageous mutations that have arisen since the time when those species evolved away from their most recent common ancestor. There has been great debate in the scientific literature regarding what proportion of fixed differences between species were actually favored by natural selection. The Japanese geneticist Motoo Kimura, in his controversial 1983 book *The Neutral Theory of Molecular Evolution*, provided compelling evidence to suggest that much of the evolution that genes undergo over time is neutral, and that very few genetic differences between species were favored by selection. SEE ALSO BIOLOGICAL EVOLUTION; GENETICIST; MENDEL, GREGOR; MORPHOLOGY.

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Genetic Engineering

Genetic engineering is the altering of an organism's deoxyribonucleic acid (DNA) to create a desired effect. Genetic engineers follow a set of techniques that allows them to remove genetic material from two or more species, recombine the genetic material (to create **recombinant DNA**), and integrate it into a host's genome, or genetic material. Genetic engineering is used for a variety of scientific, agricultural, and medical purposes.

recombinant DNA DNA that is formed when a fragment of DNA is incorporated into the DNA of a plasmid or virus

Restriction Enzymes

All recombinant DNA technology requires the use of **restriction enzymes**. These enzymes are naturally occurring in bacteria that fight phage, or virus, DNA, but geneticists can use restriction enzymes as tools to cut DNA into manageable fragments.

restriction enzymes bacterial proteins that cut DNA at specific points in the nucleotide sequence

Restriction enzymes recognize specific sequences along the DNA where it can be cut. These sequences contain four or more bases and occur randomly, and each enzyme cuts at a different sequence. Most restriction enzymes cut double-stranded DNA in a staggered fashion, so that a single strand extends from each end. These complementary "sticky" ends tend to bond to each other in solution.

Geneticists often need to isolate specific DNA molecules from a mixture. Restriction enzymes cut DNA into many small fragments. These fragments can be run through an electrophoretic gel, which distributes them according to size. In a technique known as Southern blotting, an absorbent membrane is then placed on the gel, transferring the ordered DNA fragments. Finally, a radioactive DNA probe is applied to the membrane, binding to any complementary DNA sequences and thereby labeling them.

Restriction enzymes can also be used to map genes. Restriction sites often vary by one or more nucleotides within a species. Genetic variation at a restriction site can produce a change in the length of a DNA sequence, also known as restriction fragment length polymorphism (RFLP). RFLP can then be measured, what is often called "DNA fingerprinting." Any genetic variation that is correlated with the RFLP is likely to be in the same part

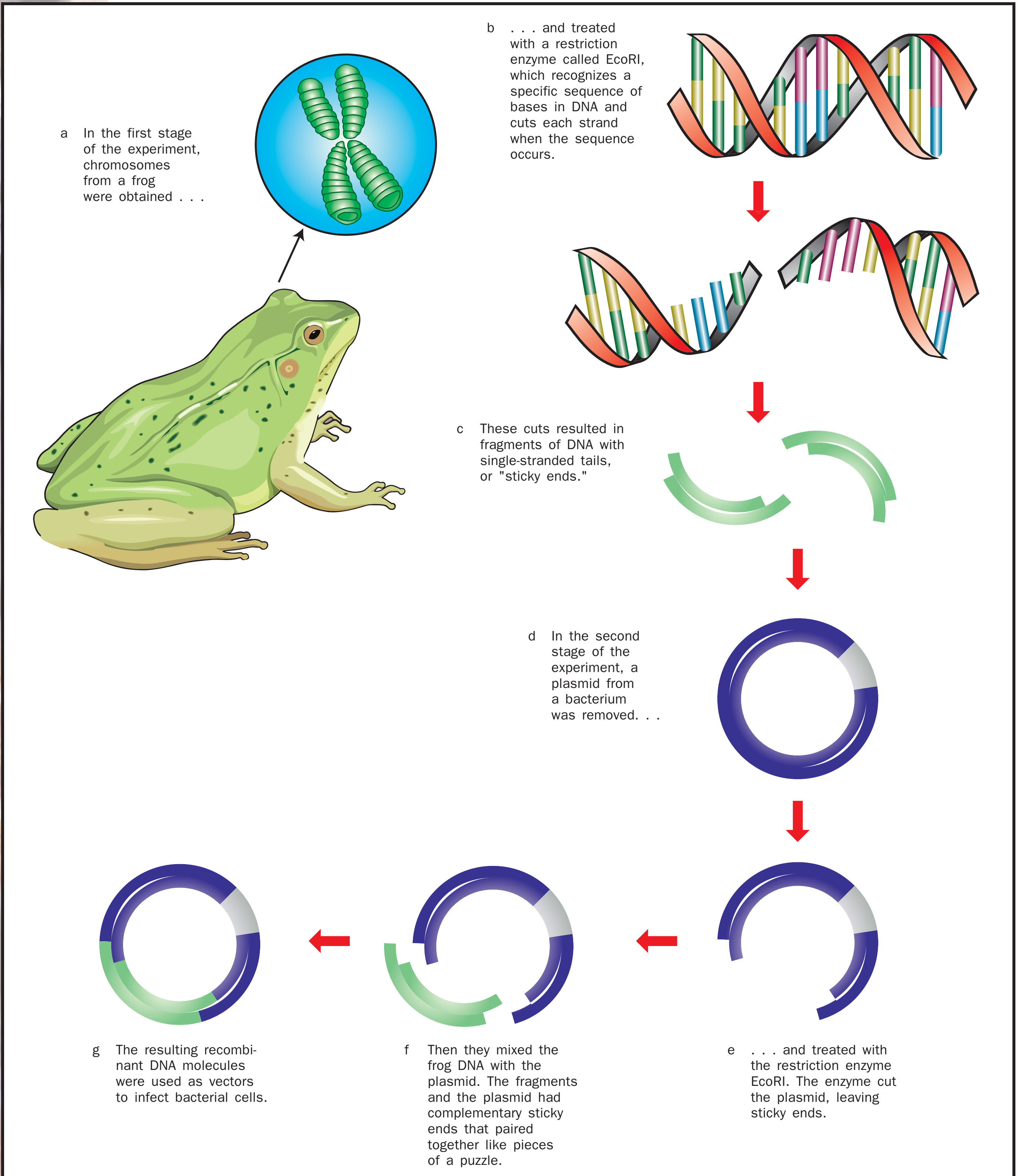


Illustration of plasmids being inserted into a vector. Redrawn from Johnson, 1998.

of the genetic material because correlations between distant genetic locations (loci) tend to break down over time as a result of recombination between chromosomes.

Recombinant DNA

Making recombinant DNA requires isolating the DNA that will be cut, donor DNA, and the DNA into which the donor DNA will be inserted, vector DNA. The combination of donor DNA and vector DNA is recombinant DNA.

A vector is a small piece of DNA that carries the donor DNA into host cells. A common vector is a plasmid, a small ring of bacterial DNA that replicates independently of the main chromosome. Plasmids are useful vectors because they easily enter bacterial cells. A plasmid vector must first be removed from the rest of the bacterial genome. The DNA is removed and centrifuged so that the smaller plasmids sink farther than the larger chromosomes. Alternatively, an alkaline pH degrades genomic DNA but not plasmids, and the genomic DNA can be precipitated out of the solution.

Donor DNA and vector DNA must be digested with a restriction enzyme so that they can be spliced together. Some sticky ends will anneal (bind) vector DNA to donor DNA. Although their initial bonding is temporary, adding DNA ligase creates stronger bonds between the joined ends to make a continuous molecule.

To improve the efficiency of this procedure, annealing between two vector molecules or two donor molecules can be prevented by adding complementary nucleotides to one strand of each molecule, for example, As to the donor molecules and Ts to the vector molecules. Furthermore, two different restriction enzymes may be used for donors and vectors, allowing greater flexibility in choosing splice sites.

Cloning

Plasmid vectors are introduced into bacteria by transformation. The plasmid replicates within each **bacterium**, and the bacteria divide many times. Consequently, a single DNA donor molecule can be amplified into billions of copies. This set of copies is referred to as a clone.

bacterium a member of a large group of single-celled prokaryotes

Most plasmids used to make recombinant DNA carry genes for drug resistance. This feature allows geneticists to apply an antibiotic to select bacteria that have been transformed by the recombinant plasmid. The antibiotics destroy bacteria that do not carry the plasmid. Plasmids also have particular restriction target sites that tailor them to the use of certain restriction enzymes. Vectors can have two different drug resistance genes, one of which contains the restriction site. If an insertion of donor DNA occurs, drug resistance is lost, and application of the drug will destroy all bacteria carrying the insert. In this way bacterial colonies carrying the desired gene can be identified and allowed to grow.

Lambda phage, a bacterial virus, can also be used as a cloning vector. Phage heads selectively package chromosomes about fifty kilobases in length. If a piece of phage DNA is removed and replaced by a donor DNA fragment of approximately the same size, the recombinant DNA can still be packaged. However, if the insertion is not successful, the phage head will not form and the DNA cannot be injected into bacteria. Successful transfection of donor DNA into a bacterial colony can be detected as a plaque indicative of infection.

There are several other types of vectors. Cosmids are hybrids of lambda phages and plasmids. Because they are larger than either phages or plasmids, they are capable of inserting larger DNA fragments. Expression vectors allow foreign genes produce proteins in a bacterium. Yeast artificial chromosomes (YAC) can carry very large inserts into yeast cells for replication. Bacterial artificial chromosomes (BAC) are capable of carrying large inserts into bacteria.

DNA Libraries

One goal of cloning genetic material is to develop a DNA library. A library is a collection of clones covering part or all of the genome of interest. It may consist of phage, bacteria, or yeast, depending on the vector used. A library may be genomic or cDNA. A cDNA library contains only coding DNA because it is synthesized from messenger RNA, which is the template from which proteins are made. A cDNA library is useful to researchers interested in genes that are expressed in particular tissues, from which they can obtain mRNA. Because the donor cDNA encodes protein, what is known as a cDNA expression library can also transcribe and translate genes into proteins.

Once a library is created, it can be screened with a probe to find a gene of interest. A probe is a piece of single-stranded DNA or an antibody that is radioactively labeled. A DNA probe will bind to a complementary strand of DNA in the library, whereas an antibody probe will bind to a protein. cDNA probes can be synthesized as an oligonucleotide, a short piece of synthetic DNA, from the amino acid sequence of the protein of interest. Because of the redundancy of the genetic code, many different cDNA's can code for the same protein. Therefore, a cocktail is often made of many different cDNA oligonucleotides.

Positional cloning is a process of using information about the location of a gene so as to clone it more efficiently. Clones can be ordered by their positions along a chromosome by doing a chromosome walk. A chromosome walk uses the ends of each clone to probe the rest of the library for overlapping clones. If another gene is closely linked to the gene of interest and its position is known, only the clones near the first gene need be probed to find the gene of interest.

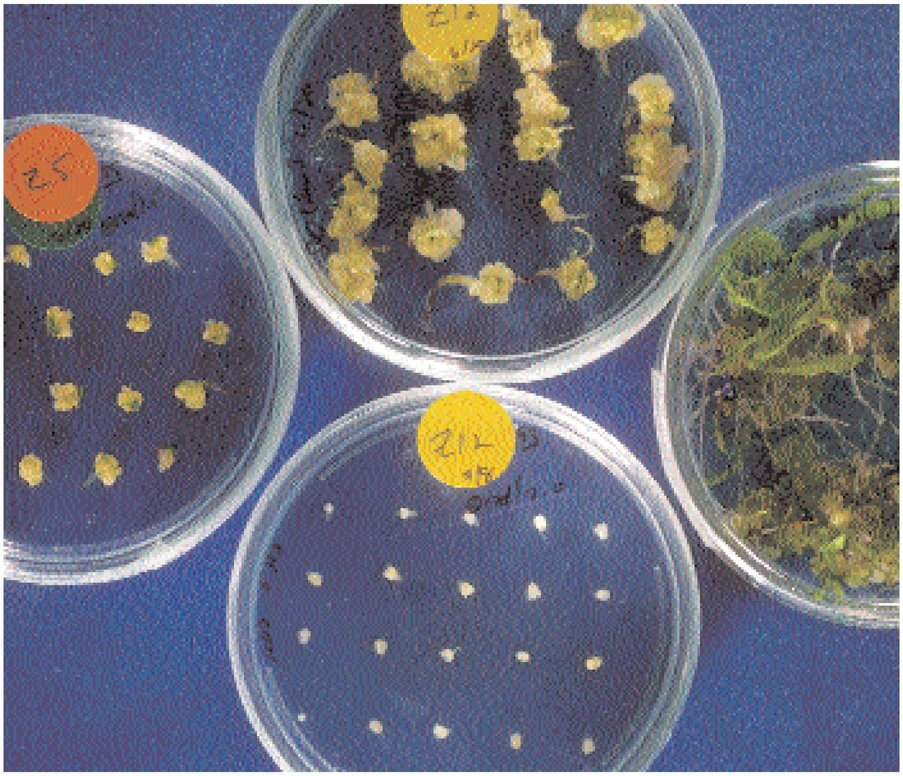
Tagging is a process in which a known DNA sequence (tag) is allowed to insert at random places in a genome. If by chance an insertion occurs in the gene of interest, it will likely cause a mutation that limits the functioning of the gene's product. Mutant lines are selected and used to construct a genomic library, which is then tested with the tag as a probe to identify the gene of interest.

DNA Sequencing

polymerase an enzyme that links together nucleotides to form nucleic acid

primer short preexisting polynucleotide chain to which new deoxyribonucleotides can be added by DNA polymerase

Once a gene is cloned, its DNA sequence can be determined. First, the gene of interest is copied with a **polymerase** enzyme, a **primer** to direct the polymerase to the gene, and nucleotides. The nucleotides are not all the same, however. Some are missing an oxygen atom, which prevents them from adding another nucleotide to the end. Thus, the sequencing reaction results in an array of partial copies of the gene. If the reaction is performed with some deoxygenated thymine, then all of the copies will end in thymine. A



Corn tissues are used by geneticists in an attempt to produce desired traits.

different sequencing reaction can be performed for each deoxygenated base to generate four different sets of partial copies. The next step is to separate the partial copies according to size. Larger fragments travel more slowly through a gel, and mobility through an acrylamide gel is extremely sensitive to size. If one were to run two sets of fragments differing by just one base in size, the difference would be evident as two distinct bands on an acrylamide gel. Thus the products of a sequencing reaction will show up as an array of bands on an acrylamide gel, with each band representing the position of the deoxygenated nucleotide used in the sequencing reaction. Alternatively, just one sequencing reaction may be done with some of each nucleotide deoxygenated if each is labeled with a unique fluorescent dye, resulting in color-coded bands.

If the precise location of a gene is not known, sequencing can reveal its location. A functional gene usually appears as an open reading frame (ORF), which is a sequence of DNA uninterrupted by a stop signal. A sequence can be analyzed by a computer program, which examines all three possible reading frames on each strand. Unusually long ORFs indicate the presence of a gene, because otherwise stop codons are expected to appear at random.

If a gene has been cloned and sequenced, it can be copied from any individual in a population by polymerase chain reaction (PCR). Primers, short oligonucleotides that attach to complementary DNA and act as targets for the polymerase enzyme, are designed from the gene sequence. The strands of DNA are separated at a high temperature. The temperature is lowered again, one primer attaches to each strand of DNA, and the polymerase extends each one in opposite directions. This process is repeated many times by a machine, providing billions of copies of the gene in a few hours. PCR is useful for quickly amplifying DNA from many individuals in a population.

Gene Alteration and Expression

All of the above recombinant techniques allow geneticists to identify and describe genes. Once a gene has been sufficiently characterized, it can be manipulated to produce a desired outcome. In vitro mutagenesis can change a single target nucleotide to another nucleotide. First the gene is cloned into a single-stranded phage vector. An oligonucleotide primer is constructed from the gene's DNA sequence. The primer is complementary to the gene with the exception of the target site, which is changed to the desired nucleotide. (Although not completely complementary to the template DNA, hybridization occurs under certain conditions.) The phage is allowed to replicate so that its copy incorporates the new nucleotide. Continued copying will produce mostly mutant genes, which can be identified with the mutant primer as a probe under conditions that prevent hybridization with nonmutants.

Synthetic oligonucleotides can also be used to construct entire genes up to sixty bases in length. The automated reaction adds bases one at a time to the growing oligonucleotide, which is embedded in a resin. Overlapping oligonucleotides can be pieced together to synthesize longer sequences. Herbert Boyer's lab synthesized the gene for somatostatin, a human growth hormone, in this manner. The scientists added a restriction site to each end of the gene and a methionine codon to one end. Restriction enzymes were used to insert the gene into a bacterial plasmid that carried the same restriction sites. The insertion occurred in the middle of a bacterial beta-galactosidase gene, which the bacteria transcribed and translated. The resulting protein was a chimera (of genetically diverse tissue) of somatostatin and beta-galactosidase, separated by a methionine residue. Cyanogen bromide was used to cleave the protein at the methionine residue and recover the somatostatin.

There are other ways to produce eukaryotic (non-bacterial) gene products in bacteria. For example, phage T7 contains promoters that generate a large amount of protein during a late stage of infection. First, a gene is inserted next to a T7 promoter. The promoter interacts with T7 RNA polymerase, which is synthesized in the presence of lactose. Therefore, the addition of lactose to bacteria carrying the recombinant T7 will produce large quantities of the gene product. Insulin, somatostatin, and many pharmaceutical drugs are now produced with engineered bacteria and fungi.

transgenic an organism that contains genes from another species

Genetic engineering is not restricted to placing eukaryotic genes in bacteria. Eukaryotic cells can be altered by inserting foreign DNA into their genomes. An organism derived from such a cell is referred to as **transgenic**. There are several ways to produce transgenic organisms. For example, the gene of interest (the transgene) can be paired with a eukaryotic promoter in a vector and injected into the nucleus of the organism's gamete. The promoter will cause the gene to be expressed whenever the promoter's natural gene is expressed. This may be useful in determining the expression pattern of the natural gene if the product is not as easily detectable as that of the transgene. Or, the transgene's product alone may be valuable. For example, crops can be endowed with genes for pesticides or metabolizing nitrogen.

Unfortunately, the ecological consequences of introducing transgenic organisms into nature are unknown.

Gene Therapy and Screening

Gene therapy is the insertion of a normal gene into a chromosome carrying a defective copy of the gene. The first case of gene therapy in a mammal was the cure of a growth hormone deficiency in mice. A gene was inserted into the ova of mice carrying two defective promoters for the gene. The gene was paired with a promoter-regulator for the metallothionein gene, which activates in the presence of heavy metals. Offspring carrying the transgene showed higher growth rates in the presence of heavy metals than did those without the transgene, indicating that a functional metallothionein promoter had taken control of the growth hormone gene.

gene therapy a process where normal genes are inserted into DNA to correct a genetic disorder

Human gene therapy can be either germinal or somatic. Germinal gene therapy introduces transgenes into both somatic cells and germ line cells of the early embryo. This therapy has been performed on mice but not humans. Somatic gene therapy inserts transgenes only into affected tissues using a viral vector. This form of therapy has proven successful in treating severe combined immunodeficiency disease and atherosclerosis. Because most transgene vectors insert randomly throughout the genome, one potential side effect of gene therapy is a mutation caused by insertion into a healthy gene.

Although gene therapy for humans remains highly experimental, genetic screening for diseases is already being applied. Embryonic cells are collected from the amniotic fluid or the **placenta**. Some genetic abnormalities can be detected by their effects on restriction sites. A probe constructed from the cDNA of the gene of interest is used to identify fragments of DNA carrying the gene. These fragments are digested by a restriction enzyme whose target site contains the deleterious mutation. Mutant genes will not be cleaved by the restriction enzyme, whereas normal genes will. This can be detected as two different banding patterns on an electrophoretic gel. A related technique takes advantage of the often tight linkage between mutant genes and restriction fragment length polymorphisms (RFLP), which can serve as indicators for the presence of mutant genes.

placenta the structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

PCR can also be used to amplify DNA for sequencing or another form of testing. SEE ALSO Genes; Genetically Engineered Foods; Genetics.

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Genetic Variation in a Population

Genetic variation in a population describes the existence in that population of different alleles, or alternative forms, for a given gene. The presence of genetic variation implies that individuals of the population vary in the alleles

polymorphic referring to a population with two or more distinct forms present

phenotypic variation the differences in physical and physiological traits within a population

they possess, meaning that individuals differ in genotype. Genetic loci for which there are multiple alleles are described as **polymorphic**. Humans, for example, are polymorphic for traits such as eye color and blood type.

Genetic variation is one facet of the more general concept of **phenotypic variation**. Phenotypic variation describes differences in the characteristics of individuals of a population. Phenotypic variation is of interest to biologists because it is what natural selection acts upon: different phenotypes may have different fitnesses, and selection results in fitter phenotypes leaving more descendants.

heritability the ability to pass characteristics from a parent to the offspring

Phenotypic variation arises from either of two sources: genetic variation and environmental variation. However, only differences that arise from genetic variation can be passed on to future generations. Furthermore, only a fraction of the genetic component of variation, the additive genetic variation, is actually heritable. The additive genetic variation divided by the total phenotypic variation yields the **heritability**, which describes how much offspring resemble their parents.

The Amount of Genetic Variation

In the 1960s there was considerable debate regarding how much genetic variation actually exists in populations. The common view was that polymorphic loci are fairly rare. Then, the development of the technique of gel electrophoresis allowed biologists to examine patterns of protein variation across populations and to quantify genetic variation.

Biologists detected surprisingly large amounts of genetic variation. In most vertebrate species, for example, approximately 30 percent of genes were found to be polymorphic. Studies in the 1970s in humans showed that genetic variation occurs at approximately the same levels as in other animal species. The studies in humans also revealed, famously, that so-called human races are not real biological groupings. It was found that there is considerably more genetic variation within races than between them.

Since then it has been the absence of genetic variation that is considered anomalous. Absence of genetic variation in populations generally suggests that there was a population bottleneck in the recent history of the group, a time when the population size became very small. The result of a population bottleneck is that all members of the current population are descended from a small number of individuals, and therefore have only limited genetic variation. Genetic variation is expected to build up over time in these populations as new mutations appear.

How Genetic Variation Is Maintained

The discovery of large amounts of genetic variation in nearly all populations led to the formulation of a different question: How is genetic variation maintained? In many cases, after all, natural selection removes genetic variation by eliminating genotypes that are less fit.

mutation an abrupt change in the genes of an organism

Many factors act to increase or maintain the amount of genetic variation in a population. One of these is **mutation**, which is in fact the ultimate source of all variation. However, mutations do not occur very frequently, only at a rate of approximately one mutation per 100,000 to 1,000,000 genetic loci per generation. This rate is too slow to account for most of the

A group of stallions, mares, and foals graze in the Black Hills of South Dakota. The population's genetic variations resulted in the different hair color evident between the horses.

polymorphisms seen in natural populations. However, mutation probably does explain some of the very rare phenotypes seen occasionally, such as albinism in humans and other mammals.

A second factor contributing to genetic variation in natural populations is selective neutrality. Selective neutrality describes situations in which alternate alleles for a gene differ little in fitness. Because small fitness differences result in only weak natural selection, selection may be overpowered by the random force of genetic drift. Alleles whose frequencies are governed by genetic drift rather than by natural selection are said to be selectively neutral. Under neutrality, allele frequencies vary over time, increasing or decreasing randomly. Over long periods of time, random fluctuations in the relative frequencies of different alleles may result in some being eliminated from the population. However, genetic polymorphisms are long-lived, and novel neutral alleles may arise continually through mutation.

polymorphisms having two or more distinct forms in the same population

Finally, several forms of natural selection act to maintain genetic variation rather than to eliminate it. These include balancing selection, frequency-dependent selection, and changing patterns of natural selection over time and space.

Balancing selection occurs when there is **heterozygote advantage** at a locus, a situation in which the heterozygous genotype (one including two different alleles) has greater fitness than either of the two homozygous genotypes (one including two of the same allele). Under heterozygote advantage, both alleles involved will be maintained in a population.

heterozygote advantage a condition where a heterozygous individual has a reproductive advantage over a homozygous individual

A classic example of heterozygote advantage concerns the allele for sickle-cell **anemia**. Individuals who are homozygous for the sickle-cell allele have sickle-cell anemia, which causes the red blood cells to become

anemia a condition that results from a decreased number of red blood cells sickle-shaped when they release oxygen. These sickle-shaped cells become caught in narrow blood vessels, blocking blood flow. Prior to the development of modern treatments, the disease was associated with very low fitness, since individuals usually died before reproductive age.

Heterozygotes, however, have normal, donut-shaped blood cells and do not suffer from sickle-cell anemia. In addition, they enjoy a benefit of the sickle-cell allele, which offers protection from malaria. Consequently, heterozygous individuals have greater fitness than individuals who have two copies of the normal allele. Heterozygote advantage in this system is believed to have played a critical role in allowing a disease as harmful as sickle-cell anemia to persist in human populations. Evidence for this comes from an examination of the distribution of the sickle-cell allele, which is only found in places where malaria is a danger.

Another form of natural selection that maintains genetic variation in populations is frequency-dependent selection. Under frequency-dependent selection, the fitness of a genotype depends on its relative frequency within the population, with less-common genotypes being more fit than genotypes that occur at high frequency.

Frequency-dependent selection is believed to be fairly common in natural populations. For example, in situations where there is competition for resources, individuals with rare preferences may enjoy greater fitness than those who have more common preferences. Frequency-dependent selection may also play a role in predation: if predators form a search image for more common prey types, focusing on capturing those, less common phenotypes may enjoy better survival.

Finally, changing patterns of selection over time or space can help to maintain genetic variation in a population. If selection patterns fluctuate over time, different alleles or genotypes may enjoy greater fitness at different times. The overall effect may be that both alleles persist in a population. Changing selection pressures over time are encountered by a species of grasshopper characterized by two color morphs, a brown morph and a green morph. Earlier in the year, when the habitat is more brown, the better-camouflaged brown grasshoppers enjoy greater protection from predators. Later in the season, however, the environment is greener and the green grasshoppers have higher fitness.

Another possibility is that selection patterns vary from one place to another as a result of differences in habitat and environment. The prevalence of different genotypes in different habitats, combined with gene flow between habitats, can result in the maintenance of multiple alleles in a population.

One example comes from the allele for resistance to copper toxicity in species of grass. Copper-tolerant alleles are common in areas adjacent to copper mines, where the soil is contaminated. They are not expected in uncontaminated areas, however, where they are less fit than normal alleles. However, because grass species are wind pollinated, gametes can travel considerable distances, and copper-tolerant alleles are often found in areas where they are at a selective disadvantage. SEE ALSO GENES; GENETICS; PEPPERED MOTH; SELECTIVE BREEDING.

Jennifer Yeh

One well-studied example of genetic variation in populations is that of *Biston betularia,* the peppered moth.

There are three color morphs in the peppered moth: a light morph, a dark or melanistic morph, and an intermediate morph. Before the Industrial Revolution, the light morph was the most common form, although melanistic moths were also seen occasionally. However, by the end of the nineteenth century, the melanistic morph had become much more common, and had practically replaced the light morph in certain areas.

Biologists traced this shift to industrial pollution in urban areas. Without camouflaged resting places, the light moths became easy targets for bird predators. This explained both the prevalence of melanistic moths in polluted urban environments, and of light moths in comparatively pristine country habitats.

The puzzling aspect of the peppered moth story is that genetic variation was not entirely eliminated in populations. In urban areas, for example, melanistic moths make up only from 90 to 100 percent of the total population, despite very strong selection. Apparently there are forces other than predation pressure at work. It was hypothesized briefly that heterozygote advantage might be the explanation, but that theory was ultimately rejected. It is now believed that gene flow between country and urban areas, and frequency-dependent selection are viable alternatives. However, much work remains to be done on this historic system.

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Genetically Engineered Foods

Through genetic engineering, scientists are able to alter, add, or remove specific genes from animals. Scientists are even able to add genes from a plant or animal to another plant or animal. The new genetic material in the plant or animal creates what is called a **transgenic** organism. A transgenic organism is one that contains genetic material from two different organisms.

transgenic an organism that contains genes from another species

Genetic engineering is attractive to agriculture because transgenic organisms can be designed with specific characteristics. Transgenic animals may grow faster, produce different proteins, resist disease, eat different foods, or gain weight faster. Transgenic plants may resist freezing, tolerate droughts or excess water, grow in poor soil conditions, resist pests, and resist pesticides. Transgenic plants or animals hold the promise of increasing production with less work and expense. While transgenic organisms may be the key to feeding the rapidly expanding human population, there are potential risks. Eating foods from transgenic organisms may cause allergic reactions or other interactions. Genes from transgenic organisms may find their way into "wild" populations of plants or animals, thereby affecting the genes of that population.

The first genetically engineered food introduced to the market was the Flavr Savr tomato in 1994. The Flavr Savr tomato was not a transgenic organism because new genetic material was not added. Instead, one of the genes in the tomato was altered to slow down the ripening process. The Flavr Savr tomato was engineered to ripen after being picked green and to slow down the chemical reactions that cause spoiling. The result was a tomato that can be picked green, ripen on the shelf on the way to the grocery store, and then remain fresh on the shelf. This type of genetically engineered food is probably safe because no new genetic material was inserted into the tomato plant.

Foods based on transgenic organisms have a higher risk for problems. In 1996 scientists created a transgenic soybean plant which had been altered to include a gene from the Brazil nut to increase its nutritional content. However, it was found that the soybeans from this transgenic plant produced some of the same proteins as Brazil nuts. One of these proteins was one to which some people are allergic. As a result, someone with allergies to Brazil nuts would also have an allergic reaction to the soybeans.

Not all transgenic organisms cause trouble. One of the first food uses for transgenic organisms was in the production of cheese. Cheese is made from milk. One of the first steps in making cheese is to separate the milk into curds (solids) and whey (liquid). This is done with an enzyme called **rennin**. Rennin has traditionally been extracted from the stomachs of slaughtered cows.

rennin an enzyme used in coagulating cheese, is obtained from milk-fed calves

A lab technician picks away corn embryos that will be grown in controlled conditions for a specific result.

In 1990, scientists used genetic engineering to splice the gene from cows that stimulated the production of rennin into yeast cells. The result was yeast cells that produce rennin. The rennin produced by the yeast cells is identical to the rennin produced by cows. The only difference is that the rennin from the yeast cells does not need to be extracted. This has lowered the price and increased the amount of rennin available. As a result, cheese is easier and cheaper to make. Transgenic rennin was approved for use in 1990; there have been no reports of problems and its use continues in about 65 percent of cheese production.

When genetically engineered organisms are used for food, it is easy to see where problems may develop. However, genetically engineered organisms could also pose problems with the environment. Crop pests such as insects damage a large percentage of crops each year. To combat pests, farmers use chemical pesticides. Sometimes these pesticides can cause problems with people who eat the crop or to animals living near the fields. Scientists have started using genetic engineering to make plants that resist crop pests. One way of making corn pest resistant is by inserting a gene from a bacterium, *Bacillus thuringiensis*. The resulting transgenic plant then produces a toxin originally produced by the bacteria. This toxin, *Bt* toxin, is poisonous to the corn borer, a common pest insect. Now, the corn plant itself produces its own pesticide. This means that farmers do not need to use pesticides on their fields, resulting in higher yields and fewer pesticides in the environment. At first glance, this seems like an excellent solution for increasing profits.

Unfortunately, corn borers, like other insects, reproduce quickly. Some of the corn borers were actually resistant to the *Bt* toxin. The corn borers that survived because of their resistance were able to pass the resistance on to their offspring. Now, just like with so many other pesticides, the pests were developing resistance. Scientists believed that this would be a minimal problem, and with limited use of other pesticides, these insects could be controlled. However, when farmers started growing transgenic corn that produced *Bt* toxin, they found an unexpected result.

Corn reproduces by pollen being carried from one plant to another. Unlike many plants, corn pollen is carried by the wind. Cornfields produce incredible amounts of pollen and the pollen often coats everything surrounding the fields. Scientists soon discovered that caterpillars of Monarch butterflies were being killed. The caterpillars eat a plant called milkweed, not corn plants. However, the transgenic corn pollen was deposited on the milkweed and the caterpillars were eating it along with the milkweed. The *Bt* toxin in the pollen was enough to kill the caterpillars.

Because of the benefits that genetically modified organisms provide, their use will probably continue to grow. No one knows how widespread the use of genetically modified organisms is in the United States. In 2000, the amount of transgenic crops was 52 percent of soybeans, 19 percent of corn, and 48 percent of cotton. The U.S. Food and Drug Administration has been working with scientists to devise ways of testing and even labeling foods that are transgenic or are derived from transgenic materials. The debate over genetically engineered foods and products will no doubt continue.
SEE ALSO Bioethics; Farming; Genes; Genetic Engineering; Genetics.

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Geneticist

Geneticists, or genetic scientists, study heredity. Heredity is the process by which certain characteristics of an organism are handed down from parent to offspring. Geneticists study plants and animals, including humans. Geneticists work in three broad fields: biology, medicine, and agriculture. They attempt to increase knowledge about biology in order to understand and cure genetic diseases. Also, they counsel families at risk for genetic diseases or disorders. Geneticists breed new crop plants and livestock that are disease resistant or have other desirable properties. The rapidly growing biotechnology field uses genetics to produce everything from medicines to microchips. Sensitive genetic tests are being increasingly used in criminal cases to identify persons. At the turn of the twenty-first century, geneticists are involved in very important work known as the **Human Genome Project**. This international research program aims to construct detailed maps of the human genome, determine the complete sequence of the 3 billion bits of genetic information, and find the location of the approximately 30,000 human genes. Its results will have major impacts on biology and medicine, especially in relation to the approximately three thousand to four thousand hereditary diseases of humans.

There are four main types of geneticists: those performing basic research; those working in specialized laboratories; genetic counselors; and clinical geneticists. Geneticists in basic research must generally have a doctoral or Ph.D. degree and from two to four years of postdoctoral training. They might hold a faculty position at a university or work at a private research institute or biotechnology firm. Laboratory geneticists apply genetics to agriculture,

Human Genome Project a study by U.S. Department of Energy and the National Institutes of Health to map the entire human genome by 2003 legal or police work, drug development, and clinical medicine. Depending on the position held at the laboratory, this type of geneticist is required to have a bachelor's, master's, doctoral, or medical (M.D.) degree. Genetic counselors have specialized graduate degrees in medical genetics and counseling. They assist families at risk for genetic diseases. Their work can include speaking with the family, interpreting information about genetic conditions, and conducting research. Clinical geneticists must usually have a medical degree. Many work at university medical centers or large hospitals. They work to identify genetic disorders and birth defects and arrange for proper treatment of the patient. Also, they help the patient and family cope with the disorder.

At the high school level, persons interested in becoming a geneticist should study math, chemistry, physics, biology, English, writing, and computer studies. In college, persons wishing to conduct basic research generally major in biology or genetics. Also, they take math, chemistry, and physics courses. A doctoral degree in genetics is generally required to conduct basic research. Clinical geneticists must obtain medical degrees. Genetic counselors usually obtain specialized graduate degrees. Their curriculum consists of two years of master's-level programs with courses and field training in medical genetics and counseling. SEE ALSO Biological Evolution; Genes; Genetics; Mendel, Gregor.

Denise Prendergast

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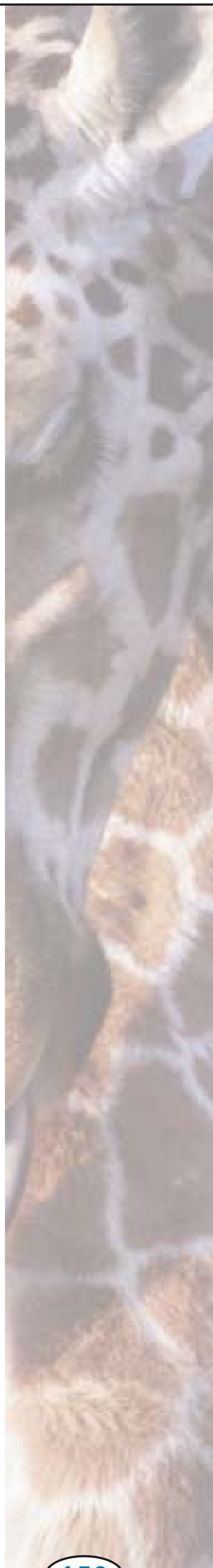
Genetics

heredity the passing on of characteristics from parents to offspring

Genetics is the study of the mode and mechanism of the transmission of heritable information. **Heredity** is the passing of a trait from one generation to the next. The heritable information of an organism is contained in its DNA, and the DNA an organism has is called its genome. DNA passes from cell to cell by cell division and from parent to offspring by reproduction.

genotype the genetic makeup of an organism

The actual unit of inheritance is the gene, a region of DNA that codes for one trait. The sequence of DNA makes up the **genotype** of an individual. A genotype can be for one single gene, for the entire genome of an individual, or anywhere in between. The physical location of a gene on a chromosome is called a locus. The particular copy of a gene at each locus is called an allele. For example, the gene for eye color occurs at one locus and has different alleles that code for blue or brown or green, etc. Diploid eukaryotes have pairs of chromosomes. Therefore, individuals have two copies of each gene, one copy on each chromosome in the pair. The genotype of a diploid organism for one single gene is the pair of alleles for that locus. So the genotype for eye color is composed of two alleles, one on each chromosome in the same location. Alleles interact with each other when they



are expressed. This interaction is referred to as dominance. Sometimes one allele hides the other allele. Other times the alleles are both expressed equally. There can also be complicated interactions between alleles and the environment in expressing a trait.

How a gene is actually manifested into a physical structure is the **phenotype** of an individual. The phenotype is the outward appearance of an organism, the reactivity of a digestive enzyme, or even the presence or absence of a disease. The phenotype of an individual is important because it is what natural selection works on. The genotype determines the phenotype of a trait. Since there are two alleles for each locus and alleles can interact, different combinations of alleles produce different traits, in other words, different genotypes produce different phenotypes. The genotype is the underlying genetic basis of a phenotype.

phenotype physical and physiological traits of an animal

Inheritance Through Reproduction Produces Genetic Variation

The difference among genotypes is referred to as genetic variation. There is genetic variation at one gene when different individuals have different combinations of alleles. Genetic variation also refers to the combination of alleles at different genes. Different phenotypes reflect underlying genetic variation. People with blonde hair and blue eyes have a different genotype and phenotype than people with brown hair and brown eyes. This difference is genetic variation.

In **asexual reproduction**, the parent and offspring have identical DNA. Mitosis is one form of cell division that produces daughter cells that are identical to the mother cell. Asexual reproduction results in clones, organisms that are identical to each other genetically.

asexual reproduction a reproduction method with only one parent, resulting in offspring that are genetically identical to the parent

Sexual reproduction produces offspring that are the combination of the genetic makeup of two individuals. In humans, a baby gets half of its genetic material from its mother and half from its father. Gametes, the sperm and egg, contain only half the genome of an individual; only one of the pair of chromosomes are in each gamete. Reducing the genetic material by half is accomplished through meiosis, cell division that produces gametes. Since gametes have only one copy of all chromosomes when they join to form a zygote, the zygote has two copies of each chromosome like its parents.

sexual reproduction reproduction method where two parents give rise to an offspring with a different genetic makeup from either parent

Organisms that are clones inherit the genotype of their parent since they are genetically identical. In sexually reproducing organisms, the identical genotype of an individual cannot be inherited since each offspring's DNA is made up from one half of the mother's DNA and one half of the father's. In the same way, a phenotype cannot be inherited because it is derived from the genotype. Only genes are inherited. When sexual reproduction occurs, genotypes are split up and new genotypes are formed, making sexual reproduction an important source of genetic variation for evolution.

In his pea experiments, Gregor Mendel observed that each gamete an individual makes is unique. The two processes that make gametes unique are the law of segregation and the independent assortment of homologous chromosomes. In normal meiosis, each gamete ends up with one copy of each chromosome. The law of segregation describes the process of the separation of the two alleles at the same locus on a pair of chromosomes into separate gametes. Independent assortment is when the two chromosomes in

These two calves in Japan were cloned from cells contained in a cow's milk called colostrum, produced in the first week after a cow has delivered.

a pair are randomly distributed during meiosis into the four gametes. Each time four haploid gametes are produced from one parent cell, each gamete has a different combination of one set of chromosomes. Independent assortment is another important source of genetic variation.

Recombination redistributes combinations of alleles of different genes. During meiosis, crossing over happens among the tetrad of chromatids during prophase I. Bits and pieces of homologous chromatids are swapped among chromatids at the chiasmata during crossing over. This means that different alleles for the same gene are being swapped. The result is that for different genes, different alleles are now being combined. For example, suppose the gene for pea-coat texture is on the same chromosome as the gene for pea-coat color. On one chromosome, the allele for round peas is present with the allele for yellow peas. On the homologous chromosome, the combination is the allele for wrinkled peas and for green peas. Recombination through crossing-over events can produce a gamete that has one chromosome with the allele for round peas with the allele for green peas. It could also produce a gamete that has a chromosome with an allele for wrinkled peas with an allele for yellow peas. Of course it is possible to get the parental combinations in gametes as well. Recombination is another very important source of genetic variation.

Genetic mutation is the ultimate source of genetic variation. When DNA is replicated during cell division, mistakes are made at very low levels in copying and dividing chromosomes. These mistakes can lead to changes in the DNA called genetic mutations. Mutations can be in the sequence of the DNA during replication. They can also occur when pieces of different chromosomes get mixed up during cell division, or when whole chromosomes are not divided equally among daughter cells during cell division. Mutations often have negative effects. A mutation in the DNA can produce a phenotype that is not normal. When natural selection acts against these abnormalities, the mutations are called deleterious mutations. Only very rarely does mutation produce a variant of a phenotype that is better than normal. If natural selection favors this phenotype, the mutation is a beneficial mutation and the trait that results from natural selection is an adaptation. Adaptations can spread throughout a population over a few generations.

Genetic Variation and Biological Evolution

Genes are the raw material for biological evolution. Genes are the only things that are inherited in sexually reproducing organisms. Combinations of different alleles for the same gene and different combinations of alleles at different genes make up genetic variation. Genetic variation comes from genetic mutation and from processes related to sexual reproduction, including recombination and independent assortment. Without genetic variation, biological evolution can not take place.

Evolution is a change in the frequency of a gene in a population over time. Natural selection, the most important of the five forces that cause biological evolution, selects on phenotypes of individuals. However the genes, not the genotype or the phenotype, are passed on to the next generation. The other forces that cause evolution do effect the genes. Nonrandom mating pairs up different combinations of genes in new individuals, or keeps existing combinations of genes together. Gene flow from other populations can introduce new genetic variation into a population. Mutation can change the genes directly during cell division and create new genes, both deleterious and beneficial, during reproduction. Random genetic drift can also change the gene frequency in a population. Random genetic drift is a subsampling of a population, for example, if there is a big die off from disease. When only a few individuals are left, only a few alleles are present for each gene, and the combinations that exist are just a few of the possible combinations. Random genetic drift can dramatically change the genetic variation and the gene frequencies of a population, causing much evolution.

Genetics and biological evolution are typically even more complicated. Most traits, such as how tall humans are, do not have categorical differences but vary continuously. For example, humans are not 1.5 to 1.8 meters (5–6 feet) tall, but instead are 5 feet 1 inch or 5 feet 2 inches, and height can be measured in even smaller increments. Quantitative traits such as height typically result from many genes; they are polygenic traits. Alleles at several **loci** interact to produce the overall height of an individual. The environment can interact with the genotype and affect the phenotype of an indi-

loci sites or location

vidual. For example, if a child does not have the proper nutrition growing up, he or she will be shorter as an adult than if well nourished.

Molecular genetics has changed how genetics is performed and what we can understand about the origin and diversity of animals. In April, 2000, Celera Genomics announced it had sequenced the entire genome of one human being. Being able to know the entire genetic sequence of not only one organism, but of several different organisms, will revolutionize genetics. Being able to compare whole genomic sequences of different organisms will provide a new understanding of how evolution created and maintains the diversity of organisms on Earth. SEE ALSO Biological Evolution; Genes; Geneticist; Mendel, Gregor; Morphology.

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Geological Time Scale

Geologic Time Scale

Era	Period	Epoch	Significant Events	Million Years Before Present
Cenozoic	Quartenary	Holocene	recorded human history, rise and fall of civilizations, global warming, habitat destruction, pollution mass extinction	0.01
		Pleistocene	*Homo sapiens*, ice ages	1.6
	Tertiary	Pliocene	global cooling, savannahs, grazing mammals	5.3
		Miocene	global warming, grasslands, *Chalicotherium*	24
		Oligocene		37
		Eocene	modern mammals flourish, ungulates	58
		Paleocene		66
Mesozoic	Cretaceous		last of age of dinosaurs, modern mammals appear, flowering plants, insects	144
	Jurassic		huge plant-eating dinosaurs, carnivorous dinosaurs, first birds, breakup of Pangea	208
	Triassic		lycophytes, glossopterids, and dicynodonts, and the dinosaurs	245
Paleozoic	Permian		Permian ends with largest mass extinction in history of Earth, most marine inverterbrates extinct	286
	Pennsylvanian		vast coal swamps, evolution of amniote egg allowing exploitation of land	320
	Missipian		shallow seas cover most of Earth	360
	Devonian		vascular plants, the first tetrapods, wingless insects, arachnids, brachiopods, corals, and ammonite were also common, many new kinds of fish appeared	408
	Silurian		Coral reefs, rapid spread of jawless fish, first freshwater fish, first fish with jaws, first good evidence of life on land, including relatives of spiders and centipedes	438
	Ordovician		most dry land collected into Gondwana, many marine invertebrates, including graptolites, trilobites, brachiopods, and the conodonts (early vertebrates), red and green algae, primitive fish, cephalopods, corals, crinoids, and gastropods, possibly first land plants	505
	Cambrian		most major groups of animals first appear, Cambrian explosion	570
Proterozoic			stable continents first appear, first abundant fossils of living organisms, mostly bacteria and archeobacteria, first eukaryotes, first evidence of oxygen build-up	2500
Archean			atmosphere of methane, ammonia, rocks and continental plates began to form, oldest fossils consist of bacteria microfossils stromatolites, colonies of photosynthetic bacteria	3800
Hadean			pre-geologic time, Earth in formation	4500

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Gills

Gills and lungs are the two structures commonly used by animals for respiration. Both are characterized by large amounts of surface area that function in gas exchange. The difference between them is that gills involve external extensions from the body surface, whereas lungs possess internal foldings. Gills have evolved independently several times in a variety of animal groups.

Among the **annelids**, certain species of terrestrial worms have long slender, branching gills which extend from the body. **Horseshoe crabs** possess structures known as book gills, which are actually modified appendages that function in gas exchange. **Crustaceans** also have gills that have been modified from **thoracic** or abdominal appendages.

annelids segmented worms

horseshoe crabs a "living fossil" in the class of arthropods

crustaceans arthropods with hard shells and jointed bodies and appendages that mainly live in the water

thoracic the chest area

Gill structures are highly diverse among crustaceans. Generally, the more aquatic crustaceans have more elaborate gills, while the more terrestrial species are characterized by simplified gills. That is a consequence of the greater availability of oxygen on land, from the air, than in water.

In **echinoderms**, the group that includes starfish, the large surface area provided by the many appendages and by the tube feet are used in gas exchange. However, some species supplement these with gills around the oral cavity. **Mollusks** possess gills within their **mantles**. These are oriented to face the water current. Vertebrates such as **salamanders** are also characterized by external gills, which in their case are filamentous structures that extend from the head region. In some species, only the aquatic larvae have gills. However, in many species that remain aquatic their entire lives, the gills may be retained into adulthood.

echinoderms sea animals with radial symmetry such as starfish, sea urchins, and sea cucumbers

mollusks large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

mantles tissues in mollusks that drape over the internal organs and may secrete the shell

salamanders a four-legged amphibian with an elongated body

Fish also use gills in gas exchange. The gills of fish are supported by a series of bony **gill arches**. The gill arches lie between the gill clefts, through which oxygenated water flows. The gill arches support tissue that includes the tiny blood vessels which carry in deoxygenated blood and carry away oxygenated blood, as well as the **gill filaments**, where gas exchange actually occurs. The gill filaments each have numerous secondary gill lamellae that further increase the surface area available for gas exchange.

Fish that have high energy demands, such as those which swim quickly, have more surface area associated with their gills. The **operculum** of bony fishes is a covering that protects the entire gill area. It also covers the operculum chamber, which is essential to the process of pumping water over the gills.

gill arches arches of cartilage that support the gills of fishes and some amphibians

gill filaments the site of gas exchange in aquatic animals such as fish and some amphibians

operculum a flap covering an opening

Gills are used by fish for respiration. Over time, gill structure has evolved independently in several different animal groups to form other skeletal elements.

Gas exchange across the gills occurs in what is described as a counter current fashion. This is a very efficient mode of gas exchange because water flows in one direction and blood flows in the other. The consequence of countercurrent flow is that well-oxygenated blood encounters well-oxygenated water, and is able to pull more oxygen from the water, while less-oxygenated blood encounters less-oxygenated water. Oxygenation thus occurs along the entire pathway where the water and blood are juxtaposed.

Fish push oxygen-rich water across their gills by one of two methods. In ram ventilation, fast-swimming species such as sharks swim with their mouths open. Water is forced into the mouth and out over the gills.

buccal mouth

Most bony fish species, however, employ a second method, **buccal** and opercular pumping. In this method, serial expansions and contractions of the mouth cavity and the opercular cavity occur, resulting in the continuous flow of water over the gills. First, the mouth, or buccal, cavity expands, drawing water in. Then, the mouth closes and the buccal cavity contracts. This forces water to flow over the gills into the opercular cavity. At the same time, the opercular cavity expands, which draws more water in from the buccal cavity. Water exits through the operculum.

Some fish will use buccal and opercular pumping while swimming slowly and ram ventilation when swimming faster. Ram ventilation is essential in some species, which suffocate if they are not able to swim fast enough.

The gill arches have played a crucial role in vertebrate evolution. Over evolutionary time, they have been modified to form other essential skeletal structures. The vertebrate jaw, which characterizes all vertebrates aside from lamprey and hagfish, was modified from a single pair of gill arches.

incus one of three small bones in the inner ear

In mammals there has been a further modification of this pair of gill arches. Mammals have evolved a "new jaw," and the original bones of the jaw joint now function as middle-ear bones in mammals. The **incus** and

malleus are both homologous to the jaw bones in other vertebrates, which are homologous to gill arches in primitive fish groups. The middle-ear bones are involved in conducting sound between the eardrum and the inner ear, where neural processing occurs. The third mammalian middle-ear bone, the **stapes**, occurs in all terrestrial vertebrates, and is also derived from the gill arches. SEE ALSO Blood; Respiratory System.

Jennifer Yeh

malleus outermost of the three inner ear bones

stapes innermost of the three bones found in the inner ear

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Gliding and Parachuting

Many vertebrates have independently evolved the ability to glide. In spite of their name, "flying" squirrels (*Glaucomys volans* and *Glaucomys sabrinus*) glide, not fly, from tree to tree. The little marsupial known as a sugar glider (*Petaurus breviceps*) can also glide from tree to tree. Many other animals practice parachuting. The difference between parachuting and gliding is control. Parachuting is simply slowing the rate of descent with little or no attempt to control direction. Flying squirrels carefully steer themselves as they glide from the crown of one tree to the trunk of another.

Cynocephalus is a group of medium-sized gliding mammals closely related to bats. These mammals hang upside down in trees, leaping into the air to glide in search of fruit to eat. The group *Exocoetus* contains the "flying" fishes. Although a true glider, *Exocoetus* can extend the range of its glide by flapping its **pectoral** fins. Flying fishes glide when startled, as by a predator. They swim rapidly underwater, then launch themselves into the air, where they can glide over long distances. *Rhacophorus* is a tree-dwelling frog with expanded toe membranes that help it fall more slowly after it leaps off a tree. The frog is a true glider, as it can turn and maneuver while airborne.

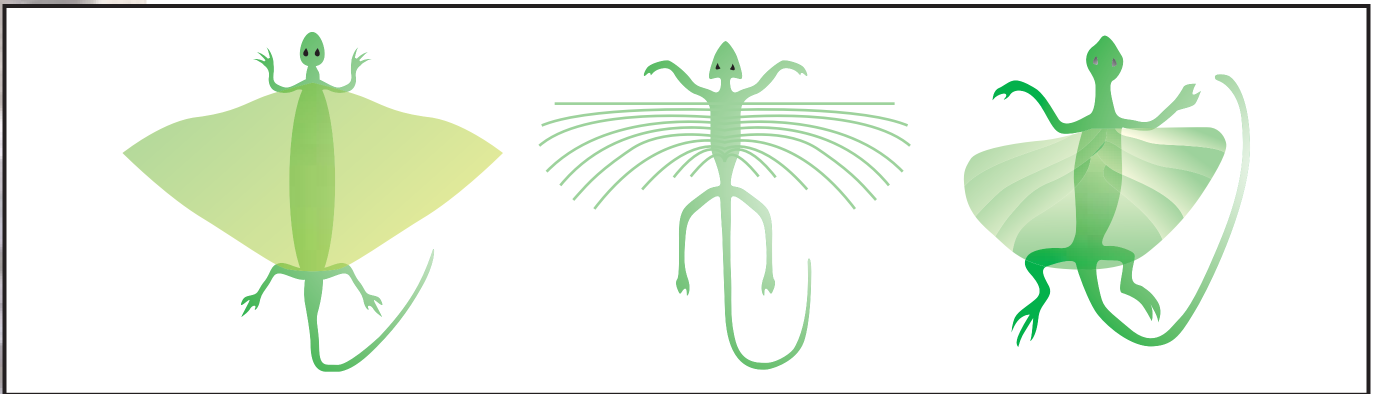
pectoral of, in, or on the chest

All gliders and parachuters can increase the relative width of their bodies, thus increasing the surface area exposed to wind resistance. A few gliding frogs flatten their bodies and spread their limbs outward. Gliding snakes not only flatten their bodies, but also draw in the scales on the lower side of the body to form a kind of trough. Some flying lizards, such as *Draco volans*, have evolved the ability to glide using specialized ribs that spread out like a fan.

Gliding mammals, such as flying squirrels, have a fold of skin on each side of their bodies that extend from the front leg or front wrist back along the side of the body to the hind leg or the ankle. To glide, the squirrel climbs to near the top of a tree and launches itself toward another tree, spreading the fold of skin by holding out its front and rear legs. The glide angle is quite steep, but accurate enough that the squirrel securely lands well

INDEPENDENT EVOLUTION

Many completely unrelated organisms seemed to have evolved similar structures at different times. For example, mollusks, arthropods, and vertebrates all evolved eyes. However they didn't "borrow" the idea from each other. Each class of animal evolved the structure separately from the others. Grasping appendages, eyes, wings, powerful legs for jumping, and many other features of our animal world are simply good ideas that have been discovered many times through the processes of evolution.



The flying lizards (from left to right) *Weigeltosaurus, Icarosaurus,* and *Draco* possess different structural features that allow them to glide.

up on the trunk of the target tree and can climb back to a safe height above ground.

Parachuting lacks the implied directional control of gliding. To parachute, the animal launches itself into the air and controls its fall by spreading toes, limbs, and membranes. Parachuters usually fall to the ground or to a lower branch of a tree. Most gliding and parachuting animals are fairly small. Their surface area is large relative to their weight, so air resistance effectively slows them down. If an animal is small enough, it needs no special adaptation for parachuting. For example, an insect can fall from the top of a tall tree all the way down to the ground without harm. The insect is its own parachute.

Gliding and parachuting are not generally evolutionary steps toward flying. They are independent adaptations acquired by animals that live primarily in forests. However, birds may have evolved the ability to fly as an extension of running along the ground with short, gliding hops that became longer and longer over time, evolving eventually into true flight. Roadrunners (*Geocòccyx californiànus*) regularly display this behavior. Although capable of flight over short distances, they prefer to run and occasionally glide. SEE ALSO Flight.

Elliot Richmond

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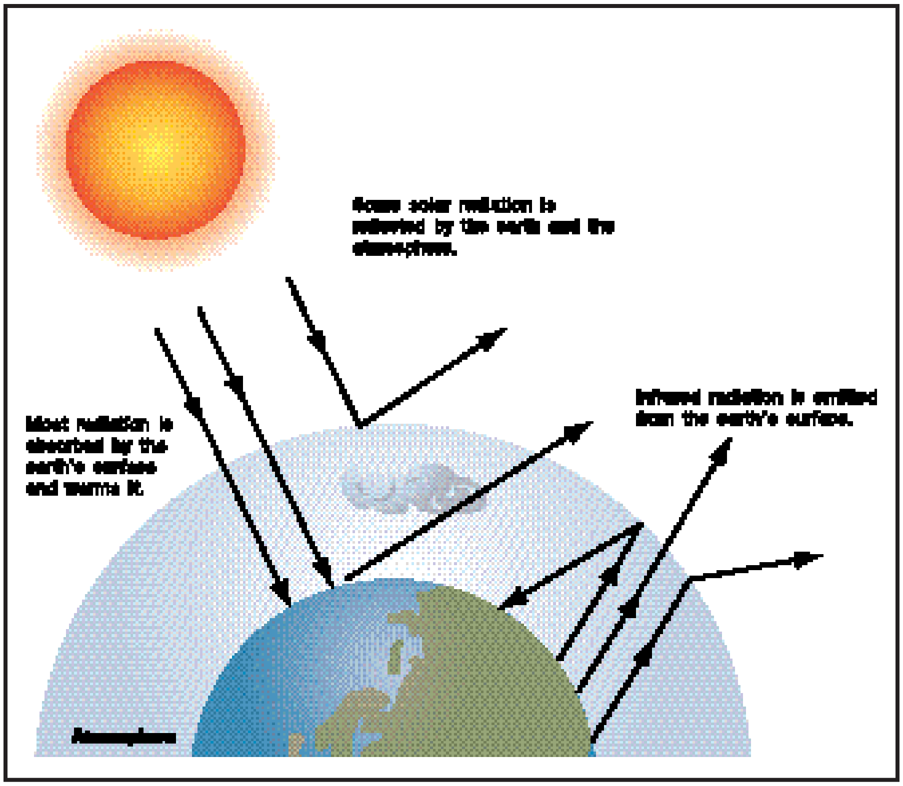
Global Warming

Global warming is an example of global climatic change. To understand the concept of global warming and make decisions about how to respond to the seemingly contradictory information received from various sources, it is important to distinguish between climate and weather. Weather applies to short-term changes in properties of the lower atmosphere such as temperature, relative humidity, precipitation, cloud cover, barometric pressure, and wind speed. Climate is the general pattern of weather conditions, seasonal



The "Greenhouse Effect" involves the effects of both solar and infrared radiation on Earth. Redrawn from Barnes-Svarney, 1995.

variation, and weather extremes over a long time—at least thirty years. A summer with record high temperatures is not a signal that global warming is occurring. A winter with record cold is not proof that global warming is not occurring. Climate change, especially global climate change, must be determined from global averages of weather conditions collected, averaged, and compared over decades.

Climate Change

Earth's climate has changed dramatically many times in the past and will almost certainly change many times in the future. Twenty thousand years ago, the places where Minneapolis, Milwaukee, Chicago, and Detroit now stand were covered with ice. Scientists do not know what caused the ice to spread or what caused it to retreat. Once the ice began to retreat, it did so very rapidly, completely disappearing in a few thousand years. Only a few remnants, such as the Greenland ice sheet, still exist. If the Greenland ice sheet were to melt, global sea levels would rise by 8 to 10 meters (26 to 33 feet), and many major seaports and coastlines would be flooded. If the Antarctic ice sheet melted, Earth's oceans would rise by 100 meters (330 feet).

Humans would survive climate changes of this magnitude, but social and political organizations probably would not. Scientists know this because past civilizations have not survived similar climate changes. Around 1000 C.E., a well-established Norse colony thrived in what is now southern Greenland. The colony had been established during a relatively warm period when the temperatures in the area were 2 to 4°C (4 to 7°F) above average. It vanished almost without trace as the climate returned to normal, an ice sheet moved

Meltwater filling deep crevasses in the surface of the Columbia Glacier in Alaska.

back over pastures, and the advancing sea ice cut off communications. That small temperature change made the difference between a thriving colony and disaster.

Earth's climate is still changing. Research strongly indicates that Earth is gradually warming up. According to the United States Environmental Protection Agency, the best estimates are that Earth's temperature has increased by 0.5°C (1.0°F) in the last century, precipitation has increased by 1 percent, and sea level has risen by 2 to 5 centimeters (1.0 to 2.0 inches). This is strong evidence for a small but significant increase in global average temperature. Almost all scientists agree with these facts. However, scientists cannot agree on what causes global warming. Many researchers are convinced the data show unequivocally that global warming is directly related to the increase in greenhouse gases such as carbon dioxide. Others feel the data simply indicate a short-term climatic phenomenon.

The "greenhouse" effect is somewhat misnamed. A greenhouse gets warm on a sunny winter day because the sunlight passes through the glass, warming the plants and other surfaces in the greenhouse. The plants warm the air, but the warm air cannot escape, so the temperature in the greenhouse rises. The planetary **greenhouse effect** operates a little differently. **Infrared** radiation from the sun passes through the atmosphere and warms the surface of Earth. As the surface warms, it also radiates infrared. However, since the temperature of Earth is much lower than the temperature of the surface of the sun, the infrared radiation emitted by the ground, building, rocks, and plants has a much longer wavelength. Radiation of this longer wavelength cannot pass through the atmosphere, and is absorbed by the air or reflected back to the ground.

greenhouse effect a natural phenomenon where atmospheric gases such as carbon dioxide prevent heat from escaping through the atmosphere

infrared invisible part of the electromagnetic spectrum where the wavelengths are shorter than red, heat is carried on infrared waves

A little greenhouse effect is a good thing. If it were not for the greenhouse effect, Earth's average surface temperature would be well below the freezing point of water and life could not exist. The question is, can we have too much of a good thing? Is it possible that rising temperatures on Earth are due to increased levels of greenhouse gases in the atmosphere?

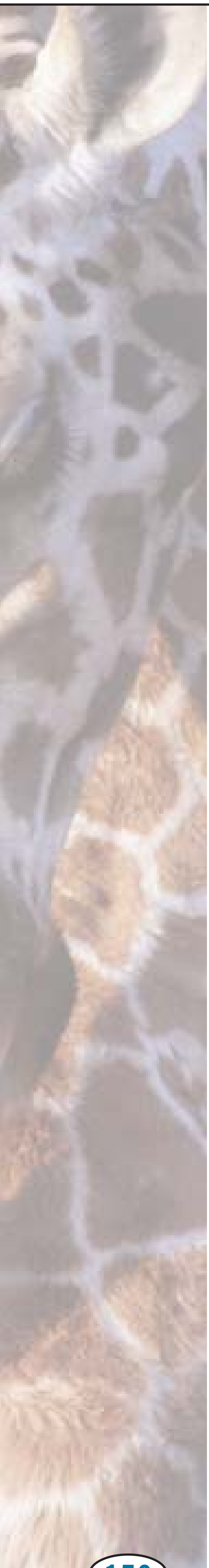
Greenhouse Gases

There are several greenhouse gases. Naturally occurring greenhouse gases include water vapor, carbon dioxide, methane (from plant decay and other sources), nitrous oxide (from volcanoes), and ozone. All these gases can also result from human activity. Carbon dioxide is released when fossil fuels are burned. Methane is emitted from livestock operations and the decomposition of organic waste. Nitrous oxide is emitted by internal combustion engines and by the burning of solid waste. Several synthetic materials are powerful greenhouse gases, including hydrofluorocarbons, perfluorocarbons, and sulfur hexafluoride.

Of all the greenhouse gases, carbon dioxide causes the most concern and is therefore closely monitored. Scientists know that carbon dioxide levels in the atmosphere have increased steadily since the beginning of the Industrial Revolution. Most scientists also agree that the average surface temperature of Earth has increased by about 0.5°C (1°F) over the last 100 years. In addition, most scientists now think there is a direct correlation between the increase of carbon dioxide in the atmosphere and the increase in the global average temperature. What remains uncertain is what will happen in the future and what should be done about it. Although the consensus among scientists is that Earth's temperature will continue to increase over the next 100 years, there is no consensus on the size of the increase. Estimates range from 1°C (2°F) to over 5°C (9°F). A 10°C rise will have little effect and is no cause for alarm. However, a 5°C rise could have disastrous consequences. Sea level could rise by 100 meters (330 feet), deserts could expand dramatically, and precipitation patterns would change in unpredictable ways.

Controversy Over Global Warming

Discussions about global warming have become intensely political, with "conservatives" and "liberals" taking contradictory positions. Two questions related to global warming should be discussed and debated. The first question is whether global warming is occurring and whether humans are causing it. The second question is this—if global warming is occurring and humans are causing it, what should be done about it? This second question is clearly a matter of public policy and political process. Public media,



Congress, and other public forums are the appropriate arenas for the debate about this question.

Many national governments and international organizations continue to raise concerns about global warming and the possible link to carbon dioxide emissions. Most countries are firmly committed to strengthening international response to risks of adverse climate change. Since gases emitted into the atmosphere do not recognize political boundaries, this is a legitimate question of international concern. The United Nations Framework Convention on Climate Change currently provides a vehicle for discussion and continuing scientific research into this difficult problem. SEE ALSO Fossil Fuels.

Elliot Richmond

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Goodall, Jane

British Zoologist
1934–

Jane Goodall, the world's leading expert on chimpanzees, was born in London, England. Almost nothing was known about chimpanzees until Goodall conducted her field studies in East Africa. Her study of these animals in the wild has revealed that chimpanzees have many striking similarities to humans. They are our closest relatives in the animal world, having 98 percent of the same genes.

Goodall grew up on the southern coast of England. From earliest childhood, she was obsessed with animals, her favorite reading being Dr. Doolittle and Tarzan books. Goodall's unusual dream of going to Africa to live with animals was encouraged by her mother. Goodall attended secretarial school, and then got a job. When a friend invited her on a trip to Kenya, she raised money by working as a waitress. At the age of twenty-three, Goodall began her adventure, traveling to Kenya by boat. There she sought out Dr. Louis Leakey, a famous scientist who studied paleontology (the study of ancient life) and anthropology (the study of humans). She became Leakey's assistant, and he soon decided Goodall was the person he had been looking for to lead a study of wild chimpanzees in East Africa. Because the British authorities thought it unsafe for a young woman to live alone among wild animals in Africa, Goodall's mother Vanne agreed to accompany her for the first three months. In 1960, Goodall arrived at Gombe National Park in Tanganyika (now Tanzania).

In the beginning, the chimpanzees were afraid of the young woman who silently and patiently watched them. It took nearly six months for the chim-

Jane Goodall's study of chimpanzees in the wild has made her the world's leading expert on human's closest relatives.

panzees to accept her presence, allowing Goodall to follow them on their daily travels through the forest. She named the chimpanzees and grew to love them. She made one important discovery after another. It was Goodall who first learned that chimpanzees make and use tools to obtain food and defend themselves. Previously, it was believed that only humans made tools. Goodall learned that chimpanzees hunt and are occasional meat eaters. She was also first to document their complex family relationships and emotional attachments.

Goodall left Africa to study **ethology** (the scientific study of animal behavior) at the University of Cambridge. When she received her Ph.D in 1965, she was one of very few candidates to receive a Ph.D. without first having an A.B. degree. She promptly returned to Tanzania to continue her field studies and establish the Gombe Stream Research Centre. Research at this facility is still being conducted to this day, mostly by Tanzanians.

ethology animal behavior

Despite her intense studies, Goodall found the time to marry twice and raise a son, Hugo. She wrote many famous books including *In the Shadow of Man* (1971) and *The Chimpanzees of Gombe: Patterns of Behavior* (1986). Goodall has received numerous awards, including the J. Paul Getty Wildlife Conservation Prize in 1984. In 1977, Goodall established the Jane Goodall Institute, located in Washington D.C., to educate people about chimpanzees and their preservation.

Denise Prendergast

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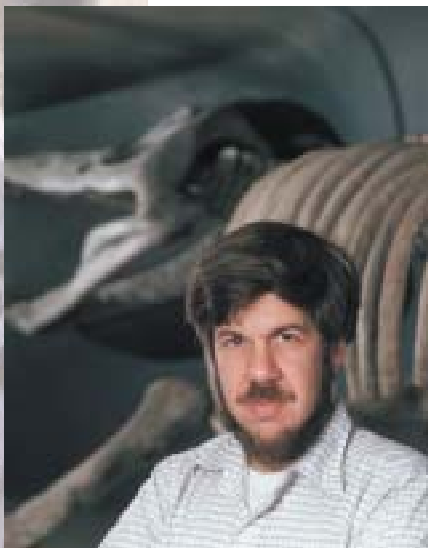

Steven Jay Gould has straddled the scientific and literary communities as a successful author and researcher.

Gould, Stephen Jay

Evolutionary biologist, paleontologist, and science writer
1941–

Stephen Jay Gould (1941–) is an American evolutionary biologist, paleontologist, and science writer. Gould teaches at Harvard University and is known in the lay community for his essays in the *Natural History* journal. In the scientific community he is known for his ideas on evolutionary theory. He has been awarded many literary and academic honors, including the National Book Award and a MacArthur Prize.

Born on September 10, 1941, in New York City, Gould grew up in Queens, New York. His father was a court stenographer and an accomplished amateur naturalist. At five years of age, while taking a trip with his father to the American Museum of Natural History, Gould saw a reconstruction of the dinosaur *Tyrannosaurus rex*. From then on, he was intrigued by science.

During his high school years, Gould was disappointed in the way evolution was depicted in biology textbooks. As a consequence, he began to read the original works of Charles Darwin. Gould received a B.A. from Antioch College in 1963. He was awarded a Ph.D. in paleontology from Columbia University in 1967.

Gould then became assistant professor of geology at Harvard University. In addition, he was appointed curator of invertebrate paleontology at Harvard's Museum of Comparative Zoology. At around this time he expanded his study of land snails to the West Indies and other parts of the world.

In the early 1970s Gould introduced his most noted contribution to evolutionary theory, the concept of punctuated equilibrium. Along with Niles Eldridge, he proposed that new species are created by evolutionary changes that occur in rapid bursts over periods as short as a few thousand years, separated by periods of stability in which there is little further change. This contrasts with Darwin's classical theory in which species develop slowly over millions of years at fairly constant rates.

In 1981 Gould served as expert witness in a lawsuit in Little Rock, Arkansas, that challenged a state requirement that so-called creation science be taught. He challenged the literal interpretation of the Bible, stating that Noah's flood could not account for fossil remains around the world. Partly as a result of Gould's testimony, the State of Arkansas legally acknowledged that creationism was a religion and not a science and therefore could not take the place of a scientific curriculm taught in Arkansas public schools.

Gould is widely known for his many books on natural history, paleontology, and biological evolution, including *The Mismeasure of Man* (1981), *Hen's Teeth and Horse's Toes* (1983), *The Flamingo's Smile* (1985), *Wonderful Life* (1989), and *Eight Little Piggies* (1993).

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Growth and Differentiation of the Nervous System

The nervous system is formed of specialized cells called neurons that use electrical and chemical signals to carry information to and away from the brain. Neurons contact each other, and other tissues, at a specialized region of the cell called a **synapse**. There, chemicals called **neurotransmitters** are released by one **neuron** and received by the other. Long, thin regions of the neuron that carry information from a distant location to the neuronal cell body are called **axons** and **dendrites**. Neurons connect to, or **innervate**, every type of tissue in the body, including bones, skin, organs, and muscles. The information they carry allows organisms to sense the world, think, react, and maintain body function. Normal growth and development of the nervous system is necessary for forming a normal organism.

Genetic Basis of Development

Many of the accepted underlying mechanisms for nervous system development were discovered through research on organisms such as the frog, the fruit fly, and the nematode worm. The results of this research are valid even for human development because of a type of gene called the **Hox genes**. These genes are remarkably similar in nearly all animals, as well as plants and yeast. This is because they are so important for development in all forms of life that they have not changed very much throughout the course of evolution. Hox genes encode proteins that are expressed in different combinations and locations of the embryo. The balance of Hox gene products is so fundamental for development that, by manipulating the amount and location of the Hox proteins, developmental biologists were able to observe improper development of body parts, and misplaced, multiple, or backward limbs in animals such as frogs, chickens, and fruit flies.

Hox genes are responsible for organizing development of the portion of neural tube located within the trunk and limbs of the embryo. Segmentation of internal tissues is an evolutionary remnant from distant ancestors that had clear segmentation, such as earthworms. Thus, in the human embryo, motor and sensory neurons, as well as muscle and bone, are organized into discrete sections called embryological **somites**. The size and location of somites are defined by the extent and location of Hox gene transcription. Somites become functional units in the adult, such that each region contains neurons from the same part of the spinal cord.

Differentiation of the Nervous System

The vertebrate nervous system arises from **ectodermal** tissue of the embryo, which also gives rise to the skin. All ectoderm cells have the ability to develop into neural tissue and skin, but only those cells that are adjacent to the **notochord** do so. The notochord is an elongated, tubelike structure that runs down the midline of the embryo, underneath what will become the **spinal cord**. At the stage when the embryo is still only a sack of cells (gastrula stage), the notochord forms and releases chemicals onto the overlying ectoderm, causing those cells to differentiate into neurons. **Differentiation** is the process by which an embryonic precursor cell develops into a specialized mature cell. The first step in the differentiation of the nervous system is the formation of

synapse the space between nerve cells across which impulses are chemically transmitted

neurotransmitters chemical messengers that are released from one nerve cell that cross the synapse and stimulate the next nerve cell

neuron a nerve cell

axons cytoplasmic extension of a neuron that transmits impulses away from the cell body

dendrites branched extensions of a nerve cell that transmits impulses to the cell body

innervate supplied with nerves

Hox genes also known as selector genes because their expression leads embryonic cell through specific morphologic development

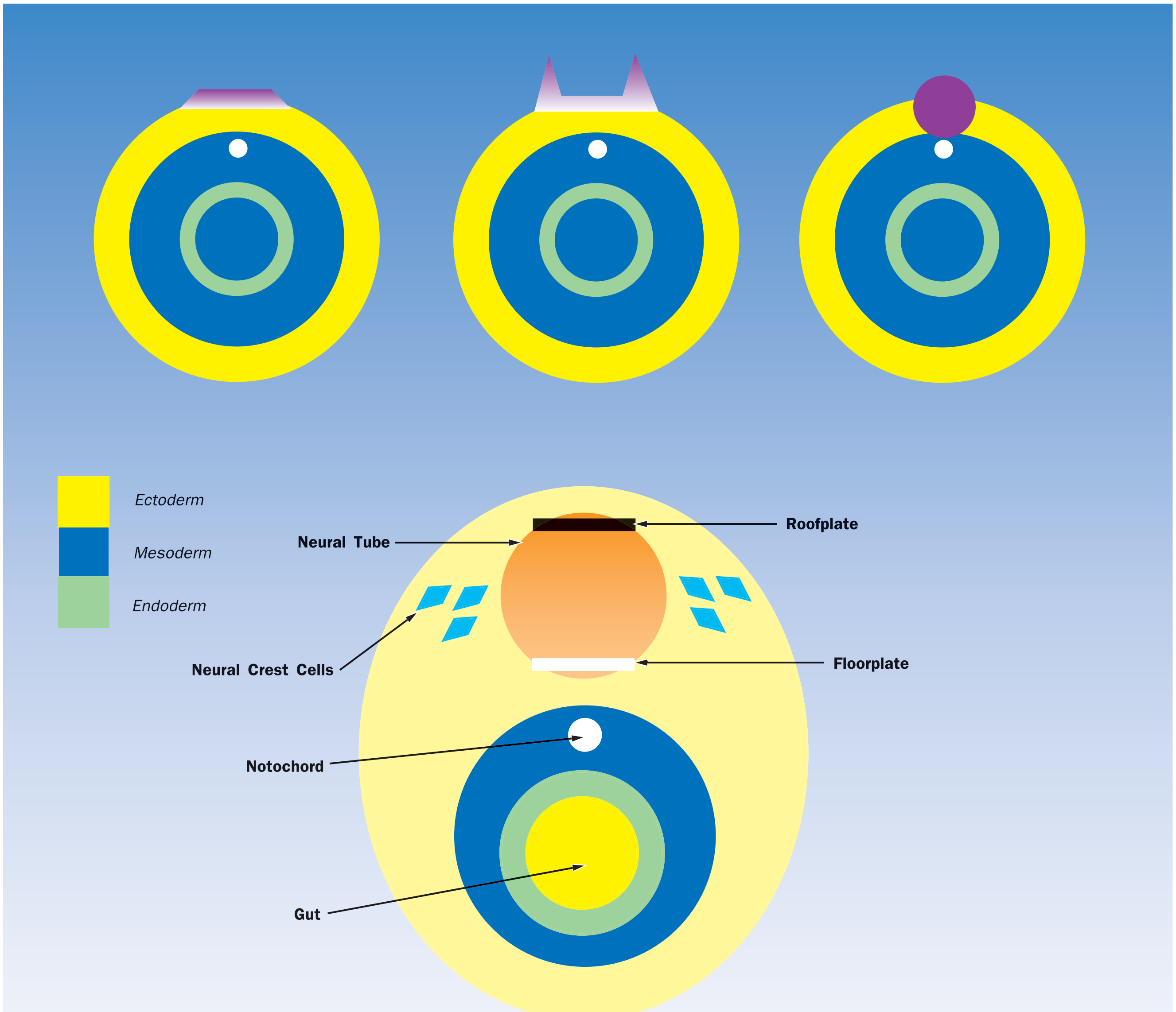
somites a block of mesoderm along each side of a chordate embryo

ectodermal relating to the outermost of the three germ layers in animal embryos

notochord a rod of cartilage that runs down the back of Chordates

spinal cord a thick, whitish bundle of nerve tissue that extends from the base of the brain to the body

differentiation the differences in structure and function of cells in multicellular organisms as the cells become specialized



The neurula is the embryonic stage at which the neural tube forms and begins to differentiate. The neural plate is shown in the upper left figure, forming from the ectoderm. In the middle figure, the neural plate folds upwards, and in the right figure, it seals into the neural tube. In the bottom figure, ectoderm has grown over the neural tube. The floorplate has formed and begins releasing sonic hedgehog (white). The roofplate releases another differentiation factor (black). Neural crest cells (blue diamonds) migrate out of the neural tube to other regions of the body.

Cross section of the neurula.

notochord a rod of cartilage that runs down the back of chordates

a flat strip of cells called the neural plate. This structure is formed from rapidly dividing ectoderm cells. In the second step, the continued propagation of these cells forces the sides of the plate to curve upward into a neural fold, and then in the third step, the ends fuse into a neural tube. The neural tube lies above the **notochord**, and it will eventually give rise to all the nervous tissue in the body, including sensory neurons in toes and fingers, the spinal cord, optic neurons from the eye, and the brain. In the fourth step, ectodermal cells on either side of the neural tube grow over and shield the neural tube from the external environment, eventually becoming the skin that will

overlie the spinal cord. In a rare congenital disease called spina bifida, this skin fails to fuse, and the baby will be born with its spinal cord exposed. When the neural tube is covered, also in the fourth step, a group of cells called neural crest cells migrates out of the neural tube and travels to different parts of the developing embryo. These cells will develop into facial bones, dentine-producing cells (for teeth), the tissue covering the brain, and glial cells, neuronal support cells, in the **peripheral nervous system**.

peripheral nervous system the sensory and motor nerves that connect to the central nervous system

The differentiation of the neural tube is most clearly illustrated by one of the best-known differentiation-inducing chemicals from the notochord, named sonic hedgehog after a Nintendo video game character. Sonic hedgehog is released from the dorsal (toward the back) notochord, and induces a specialized region of the neural tube called the floorplate. The roofplate then develops across from the floorplate at the ventral (toward the front) region, and begins to produce a different differentiating chemical called bone morphogenic protein (BMP). BMP is a completely different molecule than sonic hedgehog and it causes cells to differentiate into a different type of neuron. Large amounts of sonic hedgehog in the local environment of a cell cause it to develop into a motor (muscle-related) neuron, whereas a relatively high concentration of BMP causes differentiation into sensory (touch, temperature, and pain) neurons. This organization persists into adulthood, so that the ventral half of the spinal cord always contains sensory neurons and the dorsal half always contains motor neurons.

The portion of the neural tube located in the embryo's head uses some of the same chemical signals as the spinal cord, but differentiation occurs in a much different manner. Here, the neural tube will form into the brain. First, the tube forms into three distinct regions: the hindbrain, midbrain, and forebrain. Later, these regions specialize into the unique divisions of the mature brain. The hindbrain is very important in development because its sides swell into structures called rhombomeres, which exist only in the embryo. Rhombomeres are fundamental organizing centers because they release many chemicals that tell other parts of the neural tube how to differentiate. In the midbrain, specialized cells called isthmus cells release chemicals that establish an anterior-posterior axis. These chemicals tell cells that are located more anterior (nearer to the top of the head) to develop in a different way from those that are located more posterior (nearer to the spinal cord).

Development of the forebrain is very complex, but it is also mediated by the production of certain inducing chemical factors. Furthermore, development is shaped by the speed of cell division, meaning that regions that grow cells more quickly will be larger in the adult organism. Another means of controlling brain development is through cell migration. Many undifferentiated pre-neuronal cells are "born" near the ventricles, fluid-filled spaces located in the center of the brain, and then migrate to another region. The order of cell generations (i.e., born first, second, third, etc.) will determine what kind of neuron it will differentiate into and where it will eventually settle.

Growth of the Nervous System

As neurons mature, they grow dendrites and axons toward other cells. When dendrites and axons encounter the appropriate target cell, they will form synapses that may last for the life of the organism. Neuronal migration and growth are partly dependent on chemical guidance cues from the tissues through which they grow, and partly on specialized support cells that provide a framework along which migrating neurons can travel. One example of this migration is a sensory neuron in a seven-foot-tall person: the sensory neuron has its cell body in the spinal cord but must extend an axon to the big toe nearly three-and-a-half feet away. Chemicals in the back, thigh, leg, and foot tell the neuron in which direction to grow. Once a synapse is formed between two neurons, or between a motor neuron and a muscle fiber, the target cell releases a chemical trophic factor that sustains the synapse and the survival of the presynaptic neuron. Trophic factors keep the synapse alive and functional, but if the target cell stopped producing them the synapse would disintegrate.

Animals such as humans that are born helpless and underdeveloped do not achieve fully mature nervous systems until sexual maturity. During their first few years of life, human babies have very poor coordination, strength, perception, and cognitive abilities because their nervous system is still forming interconnections. Babies are therefore physically incapable of seeing, feeling, and understanding the world in the same manner as adults. This is one explanation for why memories from early childhood are cloudy and incomplete.

Brain growth after birth occurs by a great increase in the number of neurons and the number of synapses. However, many of these cells and many synapses die off before maturity. This is because the vertebrate method of development uses excess neurons for the embryo to accommodate environmental differences and the possibility of an accident. If the excess neurons are needed, they become active, and if active they will survive. If the neurons remain inactive, they will die. This process is inherent in the development of many organisms, even the human. Thus, if a baby is exposed to many bright colors, variable sounds, and interesting sensations, neurons in its brain will be very active and will survive. If the same baby is hidden from bright colors, hears few sounds, and is given no **tactile** stimulation, many of these neurons will die because they are not being used at an early age. Later in life, the baby in the first situation will be better able to interpret and understand the world than the baby in the second situation.

tactile related to the sense of touch

This example of neuron cell death illustrates critical periods in development. A critical period is a specific length of time in an organism's youth in which it is possible to save neurons from cell death. If the correct stimuli are not presented before the end of the critical period, that individual will never acquire normal abilities. The correct stimulus for a sensory neuron, for example, is touch, and the correct stimulus for a visual neuron is vision. One demonstration of this effect is manipulation of the visual system of the cat. If a kitten's eyes are covered between ten and twenty days after birth, the kitten will be blind for the rest of its life, even after the patches are removed. Human language, vision, hearing, and learning ability all have critical periods. These have been revealed through rare circumstances of neglect in which children are denied exposure to language and/or visual stimuli and tactile stimulation. Psychologists who studied these examples found that, after a certain age, children who have not had access to language or culture are not able to learn how to speak or interact with other humans in a normal manner. SEE ALSO Nervous System.

Rebecca M. Steinberg

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Habitat

A habitat is the environment in which an organism, species, or community lives. Habitats can be classified in a number of ways in order to compare them at different times, across different geographic areas, and in terms of different life history strategies.

Within nearly every type of habitat there exists a species that has adapted to that habitat, from the deep ocean floor to the polar ice caps. These specializations mean that the organism can survive in one type of habitat but not necessarily in another, a concept termed **habitat requirement**. Organisms that are free to move about can choose which habitat they will live in, and these choices are made based on the costs and benefits of each place.

habitat requirement the necessary conditions or resources needed by an organism in its habitat

In order to make comparisons between the many that exist, habitats need to be classified in some manner. First, it is important to understand that what is a good environment to one organism, such as the middle of the ocean for a shark, may not be good for another, such as a desert-dwelling lizard. Thus, classification of habitat types is usually done in reference to a certain species or group of species.

One method of classifying habitats is temporally. Over time a habitat may be constant, with little change from the viewpoint of a particular organism, or it may be seasonal, where there is a predictable pattern of favorable and unfavorable periods for that organism. An example of a constant environment is a cave. A cave's temperature stays at a constant temperature, within a few degrees of the mean annual temperature of the area; therefore, a bat can find refuge from the extreme high and low daily temperatures. The cave is also a consistent shelter for the bat because there is no rain in a cave.

Habitats can also be unpredictable, alternating between favorable and unfavorable periods for variable amounts of time, or ephemeral, meaning there are periods that are predictably short followed by unfavorable periods of variable, frequently extensive duration. To a water-loving amphibian, ephemeral habitats are intermittent streams that only run after heavy rainfalls and dry up to an uninhabitable state between rains.

If classifying habitats spatially, they can either be constant, with a fairly uniform distribution of resources like food and refuge, or they can be patchy, with resources occurring in small, dense locations that are scattered around an area that is otherwise without any resources. It is easy to see how these different habitats could select for different behaviors, including types of locomotion, searching, and communication among individuals to relay locations of food patches or defend territories.

Many species, such as the Canadian polar bear, have adapted to a variety of habitat changes.

Habitats can also be classified by their effects on the growth and life history of the species in question. On the one hand, in size-beneficial habitats large individuals have a greater chance to successfully compete and reproduce within their own species. For example, a large male deer that successfully defends a harem of females is more likely to mate. Also, the risk of predation may be greater for smaller adult deer, which are subject to attacks by wolves.

On the other hand, certain habitats are size-neutral or size-detrimental. In these habitats mortality may occur equally to all individuals, such as when a seasonal spring dries up. Or in such a habitat larger individuals may have a disadvantage; for example, an aerial predator may find it easier to see larger individuals or find it more worthwhile to chase them because of the greater food reward. Additionally, in a resource-rich environment there may be no within-species competition that would favor larger individuals.

The type of growth that is preferred in a given habitat will often correlate to the reproductive strategy of a species. In a size-beneficial habitat it is advantageous to reproduce less frequently and have fewer, larger offspring. This is also called a ***k*-selecting habitat**. A reproductive adult may have to delay reproduction for a long time in order to store the energy necessary to produce a large offspring. That offspring will then have a much better chance at survival. In a size-neutral or detrimental habitat, producing smaller, greater numbers of offspring is often a good strategy. This is also known as an ***r*-selecting habitat**.

***k*-selecting habitat** habitat where there is a high cost of reproduction and is sensitive to the size of the offspring

***r*-selecting habitat** the concept where a high reproductive rate is the chief determinant of life history

Habitats are as varied as the animals that live in them and each could be infinitely described, but another general way to think of them is according to their measurable characteristics, or parameters. Examples of habitat parameters, or characteristics, include temperature, moisture, substrate type, nutrient availability, altitude (or depth in water), and amount of light and wind (or current in water). Each of these parameters shapes the organisms that live there or imposes certain habitat requirements that limit the types of organisms that can move in.

Consider the cave example again. This habitat has a constant temperature, high moisture, low nutrient availability, and no light. Because of these characteristics, organisms that evolved to live in caves lose the ability to withstand temperature extremes and low moisture but in exchange gain the ability to withstand long periods with little food, partially by lowering their metabolism relative to their surface-dwelling relatives.

Other lost features of cave-dwelling organisms are sight, which takes considerable energy, and pigment, two things totally unnecessary in a habitat with constant darkness. These habitat parameters also restrict the kinds of animals that can successfully move into the cave environment. Raccoons, even though they are not cave adapted, can use the cave because they are nocturnal and accustomed to using their keen sense of smell to find their way through the dark and hunt for food.

These examples make it easier to understand the complexity of habitats and their specialized requirements. Because most organisms have adapted to their habitats and may not necessarily survive in another, it is extremely important to maintain habitats in their natural state in order to ensure the survival of the species that live there. SEE ALSO Biomes; Ecosystems; Environment; Habitat Loss; Habitat Restoration.

Jean K. Krejca

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Habitat Loss

Many biologists consider habitat loss, habitat degradation, and habitat fragmentation the primary threats to species survival. Habitat is the place or kind of place where an organism or a community of organisms lives and

This waste wood came from the mining of a tropical rain forest in Borneo.

thrives. Habitat loss occurs when habitat is converted to other uses, such as when a wetland is filled or a prairie is covered by housing developments. Habitat degradation occurs when the habitat is so diminished in quality that species are no longer able to survive. Urban development can degrade a habitat because plants and soil are replaced with asphalt and concrete. Water runs off instead of soaking in. Average temperature goes up because the asphalt and concrete absorbs more solar energy. Fragmentation occurs when terrestrial habitats are separated into small, isolated fragments. Even when the total acreage of habitat appears to be sufficient, the fragmentation prevents species from surviving.

Some species have a very limited habitat. For example, as its name implies, the habitat of the creosote bush grasshopper, *Bootettix argentatus*, is the creosote bush, *Larrea tridentata*. It is found nowhere else. Most animals avoid the creosote bush and find the leaves distasteful or even toxic, whereas this small grasshopper thrives on the leaves. If the creosote bush were to become extinct, so would the little grasshopper.

Fortunately for *Bootettix argentatus*, there are plenty of creosote bushes and neither the plant nor the grasshopper is in danger. This is not true for many other animals. The Texas horned lizard, *Phrynosoma cornatum*, has become so rare in much of its original range that it has been listed as a threatened species. Many people who grew up in Texas and Oklahoma in the 1940s and 1950s remember playing with this docile and easily caught lizard commonly called "horny toad" or "horned frog." The lizard's habitat is open dry country with loose soil (for burrows), supporting grass, mesquite, cactus, and plenty of the large ants they prefer to eat.

Several factors have caused the decline in population of Texas horned lizards (and the other horned lizard species as well). Many are taken for the pet trade. This is unfortunate, as they do not make good pets and most starve to death within a few months. Another factor contributing to the decline is the displacement of native ants by imported fire ants, *Solenopsis invicta*. Texas horned lizards feed almost exclusively on a few species of large red ants, such as harvester ants. Imported fire ants drive harvester ants and other ants out of their range, thus depriving the horned lizards of their primary food supply.

Many biologists believe that the major cause of the decline of the Texas horned lizard is the loss of habitat. The open areas with prickly pear, sparse grass, and mesquite are being converted into farmland and housing subdivisions. Of course, the first thing many homeowners do when moving into a new subdivision is to start eradicating the ants. People do require living space, clean water, food, and a safe environment, but there are many things that humans can do to reduce or prevent loss of habitat.

Causes

Many human activities can cause habitat loss, degradation, or fragmentation. In addition to urbanization, industrial agriculture, improper forest management, overgrazing, poorly managed mining, water development projects, pollution, the introduction of non-native species, and fire suppression all degrade habitat.

Urbanization. Industrial agriculture is the main cause of habitat loss while urbanization is the major hindrance to species recovery. Urbanization is a complex process that involves a progressive increase of the percentage of a population that lives in an urban area and a corresponding decrease in the percentage of people living in rural areas. Urbanization is often accompanied by urban sprawl as the city expands to accommodate an ever-increasing population. Managing urban sprawl is an enormously difficult and political process.

Many urban and suburban developments try to preserve "green belts" for aesthetic and other reasons, but habitat fragmentation still occurs. For example, by the early 1990s urban sprawl in California had reduced the indigenous coastal sage scrub ecosystem by more than 90 percent. Coastal sage is the habitat of the threatened California gnatcatcher. The remaining 10 percent of sage scrub is broken up into small fragments. Instead of four or five large patches containing thousands of hectares, there are now hundreds of widely separated tiny patches of a few hectares each. These patches are too small to support healthy populations of California gnatcatchers.

Industrial agriculture. Nearly half of the land area in the United States is devoted to agriculture. There are 472 million acres in cropland and 587 million acres in range or pasture. According to ecologist Curtis Flather and others, massive single crop industrial agriculture is the leading cause of habitat destruction in the United States, substantially affecting our forests, rangelands, and wetlands. Nearly 90 percent of recent wetland losses are due to agricultural practices.

Deforestation. In many parts of the world, logging, grazing, and mining are the major threats to endangered ecosystems and species. Deforestation occurs when trees are removed at a rate faster than they can be replanted. Habitat degradation occurs when the largest and oldest trees are removed, leaving behind scrubby stands of small and immature trees. Worldwide, deforestation is decimating tropical rain forests with enormous habitat loss.

RATES OF DESTRUCTION OF BRAZIL'S TROPICAL RAIN FORESTS

Brazil, a country that is 8,511,960 square kilometers (3,286,969 square miles), originally was home to 2,860,000 square kilometers of rainforest. In 2001, the coverage had been reduced to 1,800,000 square kilometers. The annual rate of deforestation, then, works out to be 2.3%, or 50,000 square kilometers. This is the equivalent of 1000 football fields every year in Brazil alone.

Worldwide, scientists estimate that nearly all the tropical rainforest ecosystems will be destroyed by the year 2030 if the current rate of deforestation continues.

Logging activities can have devastating impacts on habitats and the wildlife in those habitats. In the United States 260 threatened and endangered species live in our national forests. Poorly planned clear-cutting and building of logging roads degrade habitat by removing large stands of trees and fragmenting the remainder. Logging and the construction of timber roads also cause erosion that can clog streams with silt.

Grazing. Livestock grazing is the most widespread of the federally subsidized, private commercial practices operating on public lands. Commercial livestock grazing is allowed on 270 million acres of land managed by the federal government. Poorly managed livestock grazing (including overgrazing) can severely damage wildlife habitat by changing the species composition of native ecological communities. In addition to directly destroying habitat, overgrazing has a number of indirect impacts. For example, land users often try to kill predators or species that may compete with livestock for food.

riparian habitats in rivers and streams

Mining. Mining is the extraction of useful materials from the ground. Surface mining strips away overlying soil and rock, removing the useful material (usually coal) and then replacing the rock and soil. Properly done, surface mining can leave some habitats in good condition. Improperly managed mining significantly degrades ecosystems by degrading habitat and by polluting and degrading streams and waterways. Even well-managed mining increases road building. Poorly managed surface mining can destroy the surface ecosystem. In addition, mining requires a large amount of underground material to be brought to the surface. These materials, when exposed to rain, can create runoff that is highly acidic or has high concentrations of metal ore, both of which are highly toxic to aquatic species.

Mining for coal at this site in Pennsylvania is done using the "strip mining" method. This technique physically moves the soil back from the coal bed. Strip mining causes at least a temporary elimination of the native animals' habitat.

Water development projects. Water development projects include dams, dredging, stream channelization, flood control structures, and canals. These projects adversely affect species in a number of ways. The natural flow of rivers and streams may be disrupted. **Riparian** (stream bank) habitat may be destroyed, fragmented, or degraded. Because riparian habitat is often unique to a region, water development projects have the potential to destroy a habitat entirely. Water projects also alter water flow, which may change wetlands, marshes, and other downstream habitat. For example, in the portion of the Colorado River that flows through the Grand Canyon, the river habitat has been completely changed by the construction of Lake Powell and the Glen Canyon dam. The red, silt-laden Colorado River with its frequent floods has been replaced by a cold, clear river that never floods. Native species of fish cannot tolerate the cold water, although imported species such as rainbow trout do well. The riparian habitat has been completely changed as well. When the Colorado River flooded, it stripped vegetation from the banks and built large sandbars. Now the banks are covered with another imported species, tamarisk or salt cedar, and the sandbars are disappearing.

Introduction of non-native species. After outright habitat destruction, many biologists consider the introduction of exotic species to be the primary threat to rare and native species and even to complete ecosystems. Non-native species change the vegetation, compete with native species, and prey on native species. Hawaii, California, and Florida face particularly severe problems with exotic species. In Hawaii introduced species are now considered to be the single greatest cause of extinction of the state's native **fauna** and **flora**. For example, the introduction of cattle to the state has destroyed many plant communities. Many species in Hawaii, such as the hau hele 'ula (Hawaiian tree cotton), have been placed on the threatened or endangered species lists.

fauna animals

flora plants

Pollution. Pollution damages and degrades ecosystems in many ways. Airborne pollutants such as acid precipitation often affect natural communities miles away from the source. Acid rain and acid fog destroy northern forests, lakes, and streams hundreds or thousands of kilometers from the source of the pollutants. Acid precipitation can lower the pH of streams and lakes to the point that some fish are unable to reproduce and some die. Acid rain can cause chemical reactions in the soil that release metallic elements, such as aluminum. These elements can enter water supplies, damaging fish or other organisms. More than a billion pounds of toxic chemicals, including mercury and lead, were discharged directly into America's waters between 1990 and 1994, according to the Environmental Protection Agency. Thirty million pounds of these chemicals were known to cause cancer.

Fire suppression. For decades in the United States, we have assumed that suppression of fire was a good thing. Fire kills wildlife, destroys trees and grasslands, and damages property. Now we realize that many ecosystems depend on fire for their survival. Fire suppression allows other species to flourish, changing the species composition. For example, in Central Texas the hills are covered with Ashe juniper, a small native tree commonly called cedar. When Europeans first saw these hills, they were covered by thick, tall grass with only a few stands of cedar. Frequent wildfires swept over the hills, burning both grass and trees. However, the grass quickly recovered after the fire, whereas many trees were permanently removed. Thus the fire helped to maintain a balance between grass and trees. The suppression of fire and overgrazing disrupted that balance. Now the trees dominate and open grassy areas are rare. The distribution of animal species also changed.

Fire is an integral part of many ecosystems, maintaining the ecosystem's natural vegetation. There are many plant species that require fire to trigger the release of their seeds. Fire also clears out the underbrush in forests, and the prevention of all forest fires actually leads to fires that burn hotter and longer because of the accumulation of underbrush. Thus the suppression of all fires leads to habitat destruction and degradation. If handled judiciously to protect life and property, fires can restore an ecosystem's natural balance.

Recreation. Sometimes we love our natural areas to death. Recreation takes a great toll on wildlife and habitats, especially inappropriate recreational uses of open land. Probably the most destructive form of outdoor recreation is the improper use of off-road vehicles. These vehicles can provide access to remote areas otherwise unreachable. Improper operation of these vehicles can result in the harassment and inadvertent killing of wildlife. For example, vehicles can crush desert tortoises or the eggs of sea turtles and piping plover on beaches. These vehicles can also cause acceleration of soil compaction and erosion, pollution of water and air, and destruction of vegetation. Other forms of recreation, such as hiking and backpacking, are generally less harmful, but all recreational activities involve some harm to the environment.

Effects of Habitat Loss on Animal Species

Ecologists Curtis Flather, Linda Joyce, and Carol Bloomgarden studied the pattern of endangered species in the United States for the National Forest Service. In a report published in 1994, they concluded that habitat destruction was the leading cause of species endangerment, threatening 80 percent or more of federally listed species. They also found that habitat destruction and degradation was at least part of the reason why more than 95 percent of species listed as endangered or threatened were imperiled. In a different study of taxpayer-subsidized resource extraction, researchers found that logging affects approximately 14 to 17 percent of listed species, grazing affects 19 to 22 percent, water development affects 29 to 33 percent, recreation affects 23 to 26 percent, and mining affects 14 to 21 percent.

Habitat loss and degradation is a factor in the decline of every category of species. The decline of nearly 40 percent of migrant bird populations is directly linked to habitat destruction. For amphibians, declining populations are linked to habitat destruction, introduction of exotic species, water pollution, and ozone depletion.

Habitat Protection

The 1973 Endangered Species Act (ESA) has been a great success. Many species, such as the American alligator, have been brought back from the brink of extinction to healthy populations. However, many biologists question the species focus of the ESA. Rather, a focus on preserving extensive habitats is thought to be the best way to prevent the loss of wild species. Preservation can be achieved through a worldwide system of reserves, parks, and other protected areas. The plan put forward by biologists is ambitious, with a goal of setting aside 10 percent of Earth's land area. These preserves would conserve and manage entire ecosystems. This approach would be cheaper and more cost-effective than managing species one by one and would require less human intervention to prevent extinction. Activities in the preserves could include research and education as well as limited commercial activities such as **ecotourism**.

ecotourism tourism that involves travel to areas of ecological or natural interest usually with a naturalist guide

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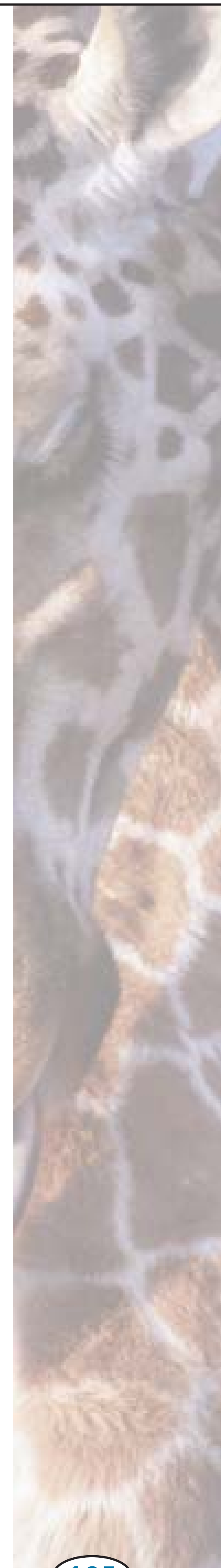

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Glossary

abiogenic: pertaining to a nonliving origin

abiotic: nonliving parts of the environment

abiotic factors: pertaining to nonliving environmental factors such as temperature, water, and nutrients

absorption: the movement of water and nutrients

acid rain: acidic precipitation in the form of rain

acidic: having the properties of an acid

acoelomate: an animal without a body cavity

acoelomates: animals without a body cavity

acoustics: a science that deals with the production, control, transmission, reception, and effects of sound

actin: a protein in muscle cells that works with myosin in muscle contractions

action potential: a rapid change in the electric charge of the cell membrane

active transport: a process requiring energy where materials are moved from an area of lower to an area of higher concentration

adaptive radiation: a type of divergent evolution where an ancestral species can evolve into an array of species that are specialized to fit different niches

adenosine triphoshate: an energy-storing molecule that releases energy when one of the phosphate bonds is broken; often referred to as ATP

aestivate: a state of lowered metabolism and activity that permits survival during hot and dry conditions

agnostic behavior: a type of behavior involving a contest of some kind that determines which competitor gains access to some resource such as food or mates

alkaline: having the properties of a base

allele: one of two or more alternate forms of a gene

alleles: two or more alternate forms of a gene

allometry: relative growth of one part of an organism with reference to another part

allopatry: populations separated by a barrier

alluvial: sediments from flowing water such as silt, sand, mud, and gravel

alpha: the dominant member of a group

altruistic behavior: the aiding of another individual at one's own risk or expense

alveoli: thin-walled sacs in the lungs where blood in capillaries and air in the lungs exchange gases

ameloblasts: cells that form dental enamel

amiote: embryo of a vertebrate that is surrounded by a fluid-filled sac

ammonites: an extinct group of cephalopods with a curled shell

amnion: the membrane that forms a sac around an embryo

amniote: a vertebrate which has a fluid-filled sac that surrounds the embryo

amniotes: vertebrates which have a fluid-filled sac that surrounds the embryo

anadromous: moving from the ocean up a river to spawn

analogous: a similarity in structures between two species that are not closely related

anemia: a condition that results from a decreased number of red blood cells

angiosperms: a flowering plant that produces seeds within an ovary

annelids: segmented worms

anoxic: an environment that lacks oxygen

anterior: referring to the head end of an organism

anterior pituitary: the front part of the pituitary gland that produces hormones that stimulate the production of sperm and testosterone in the testes

antibodies: proteins in the plasma produced by B cells and plasma cells in reaction to foreign substances or antigens

antigen: foreign substances that stimulate the production of antibodies in the blood

anurans: the order of amphibians that contains frogs and toads

aphrodisiac: a substance or object that is thought to arouse sexual desire

aphrodisiacs: substances or objects that are thought to arouse sexual desire

aposematic: a feature or signal that serves to warn

aposematic coloration: a bright coloration in animals with physical or chemical defenses that act as a warning to predators

appendicular: having to do with arms and legs

appendicular skeleton: part of the skeleton with the arms and legs

aquatic: living in water

aragonite: a mineral form of calcium carbonate

arboreal: living in trees

Archae: an ancient lineage of prokaryotes that live in extreme environments

arthropod: a phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

arthropods: members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

artificial pollination: manual pollination methods

asexual reproduction: a reproduction method with only one parent, resulting in offspring that are genetically identical to the parent

asymmetrical: lacking symmetry, having an irregular shape

aural: related to hearing

autonomic nervous system: division of the nervous system that carries nerve impulses to muscles and glands

autotroph: an organism that makes its own food

autotrophs: organisms that make their own food

axial skeleton: the skeleton that makes up the head and trunk

axon: cytoplasmic extension of a neuron that transmits impulses away from the cell body

axons: cytoplasmic extensions of a neuron that transmit impulses away from the cell body

B-lymphocytes: specialized cells produced from stem cells in the bone marrow that secrete antibodies that bind with antigens to form a pathogen fighting complex

bacterium: a member of a large group of single-celled prokaryotes

baleen: fringed filter plates that hang from the roof of a whale's mouth

Batesian mimicry: a type of mimicry in which a harmless species looks like a different species that is poisonous or otherwise harmful to predators

behavioral: relating to actions or a series of actions as a response to stimuli

benthic: living at the bottom of a water environment

bilateral symmetry: characteristic of an animal that can be separated into two identical mirror image halves

bilaterally symmetrical: describes an animal that can be separated into two identical mirror image halves

bilateria: animals with bilateral symmetry

bilipid membrane: a cell membrane that is made up of two layers of lipid or fat molecules

bio-accumulation: the build up of toxic chemicals in an organism

bioactive protein: a protein that takes part in a biological process

bioactive proteins: proteins that take part in biological processes

biodiversity: the variety of organisms found in an ecosystem

biogeography: the study of the distribution of animals over an area

biological control: the introduction of natural enemies such as parastites, predators, or pathogens as a method of controlling pests instead of using chemicals

biological controls: introduction of natural enemies such as parastites, predators, or pathogens as a method of controlling pests instead of using chemicals

biomagnification: increasing levels of toxic chemicals through each trophic level of a food chain

biomass: the dry weight of organic matter comprising a group of organisms in a particular habitat

biome: a major type of ecological community

biometry: the biological application of statistics to biology

biotic: pertaining to living organisms in an environment

biotic factors: biological or living aspects of an environment

bipedal: walking on two legs

bipedalism: describes the ability to walk on two legs

birthrate: a ratio of the number of births in an area in a year to the total population of the area

birthrates: ratios of the numbers of births in an area in a year to the total population of the area

bivalve mollusk: a mollusk with two shells such as a clam

bivalve mollusks: mollusks with two shells such as clams

bivalves: mollusks that have two shells

body plan: the overall organization of an animal's body

bone tissue: dense, hardened cells that makes up bones

botany: the scientific study of plants

bovid: a member of the family bovidae which is hoofed and horned ruminants such as cattle, sheep, goats and buffaloes

bovids: members of the family bovidae which are hoofed and horned ruminants such as cattle, sheep, goats and buffaloes

brachiopods: a phylum of marine bivalve mollusks

brackish: a mix of salt water and fresh water

brood parasites: birds who lay their eggs in another bird's nest so that the young will be raised by the other bird

buccal: mouth

budding: a type of asexual reproduction where the offspring grow off the parent

buoyancy: the tendency of a body to float when submerged in a liquid

Burgess Shale: a 550 million year old geological formation found in Canada that is known for well preserved fossils

calcified: made hard through the deposition of calcium salts

calcite: a mineral form of calcium carbonate

calcium: a soft, silvery white metal with a chemical symbol of Ca

capture-recapture method: a method of estimating populations by capturing a number of individuals, marking them, and then seeing what percentage of newly captured individuals are captured again

cardiac: relating to the heart

cardiac muscle: type of muscle found in the heart

cardiopulmonary: of or relating to the heart and lungs

carnivorous: describes animals that eat other animals

carrying capacity: the maximum population that can be supported by the resources

cartilage: a flexible connective tissue

cartilaginous: made of cartilage

catadromous: living in freshwater but moving to saltwater to spawn

character displacement: a divergence of overlapping characteristics in two species living in the same environment as a result of resource partitioning

chelicerae: the biting appendages of arachnids

chemoreceptors: a receptor that responds to a specific type of chemical molecule

chemosynthesis: obtaining energy and making food from inorganic molecules

chemosynthetic autotrophs: an organism that uses carbon dioxide as a carbon source but obtains energy by oxidizing inorganic substances

chemotrophs: animals that make energy and produce food by breaking down inorganic molecules

chitin: a complex carbohydrate found in the exoskeleton of some animals

chitinous: made of a complex carbohydrate called chitin

chloroquine: a drug commonly used to treat malaria

chromosomes: structures in the cell that carry genetic information

cilia: hair-like projections used for moving

circadian rhythm: daily, 24-hour cycle of behavior in response to internal biological cues

clades: a branching diagram that shows evolutionary relationships of organisms

Class Branchiopoda: a group of marine bivalve mollusks

Class Malacostraca: crustaceans such as lobsters, crabs, and shrimp

Class Maxillopoda: crustaceans such as barnacles, ostracods, and copepods

Class Merostomata: crustaceans such as horseshoe crabs and eurypterids

Class Pycnogonida: crustaceans such as sea spiders

cleavage: the process of cytokinesis in animal cells; as cells multiply, the plasma membrane pinches off to make two cells from one

climate: long-term weather patterns for a particular region

cnidaria: a phylum of aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

cnidarians: aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

codominance: an equal expression of two alleles in a heterozygous organism

codon: the genetic code for an amino acid that is represented by three nitrogen bases

codons: the genetic code for an amino acid that is represented by three nitrogen bases

coelom: a body cavity

coevolution: a situation in which two or more species evolve in response to each other

coexist: live together

commensal: a symbiotic relationship wherein which one species benefits and the other is neither helped nor harmed

competitive exclusion principle: the concept that when populations of two different species compete for the same limited resources, one species will use the resources more efficiently and have a reproductive edge and eventually eliminate the other species

compound eye: a multifaceted eye that is made up of thousands of simple eyes

compound eyes: multifaceted eyes that are made up of thousands of simple eyes

concentric: having the same center

conchiolin: a protein that is the organic basis of mollusk shells

coniferous, conifers: having pine trees and other conifers

connective tissue: cells that make up bones, blood, ligaments, and tendons

consumers: animals that do not make their own food but instead eat other organisms

continental drift: the movement of the continents over geologic time

contour feather: a feather that covers a bird's body and gives shape to the wings or tail

contour feathers: feathers that cover a bird's body and give shape to the wings or tail

controversy: a discussion marked by the expression of opposing views

convergence: animals that are not closely related but they evolve similar structures

copulation: the act of sexual reproduction

crinoids: an echinoderm with radial symmetry that resembles a flower

critical period: a limited time in which learning can occur

critical periods: a limited time in which learning can occur

crustaceans: arthropods with hard shells, jointed bodies, and appendages that mainly live in the water

ctenoid scale: a scale with projections on the edge like the teeth on a comb

cumbersome: awkward

cytoplasm: fluid in eukaryotes that surrounds the nucleus and organelles

cytosolic: the semifluid portions of the cytoplasm

death rate: a ratio of the number of deaths in an area in a year to the total population of the area

deciduous: having leaves that fall off at the end of the growing season

denaturing: break down into small parts

dendrites: branched extensions of a nerve cell that transmit impulses to the cell body

described: a detailed description of a species that scientists can refer to identify that species from other similar species

dessication: drying out

detritus: dead organic matter

deuterostome: animal in which the first opening does not form the mouth, but becomes the anus

deuterostomes: animals in which the first opening does not form the mouth, but becomes the anus

diadromous: animals that migrate between freshwater and saltwater

differentiation: differences in structure and function of cells in multicellular organisms as the cells become specialized

diffusion: the movement of molecules from a region of higher concentration to a region of lower concentration

dioecious: having members of the species that are either male or female

diploblastic: having two germ layers; ectoderm and endoderm

diploid cells: cells with two sets of chromosomes

direct fitness: fitness gained through personal reproduction

diurnal: active in the daytime

DNA replication: the process by which two strands of a double helix separate and form two identical DNA molecules

dominance hierarchies: the structure of the pecking order of a group of individuals of a group where the multiple levels of dominance and submission occur

dominant: an allele that is always an expressed trait

dorsal: the back surface of an animal with bilateral symmetry

dorsal root ganglia: nervous tissue located near the backbone

dorsoventrally: flattened from the top and bottom

dysentery: inflammation of the intestines that is characterized by pain, diarrhea, and the passage of mucous and blood

ecdysis: shedding the outer layer of skin or exoskeleton

ecdysone: hormone that triggers molting in arthropods

echinoderms: sea animals with radial symmetry such as starfish, sea urchins, and sea cucumbers

ecological: relating to an organism's interaction with its environment

ecology: study of how organisms interact with their environment

ecosystem: a self-sustaining collection of organisms and their environment

ecosystems: self-sustaining collections of organisms and their environments

ecotourism: tourism that involves travel to areas of ecological or natural interest usually with a naturalist guide

ectodermal: relating to the outermost of the three germ layers in animal embryos

ectoparasite: an organism that lives on the surface of another organism and derives its nutrients directly from that organism

ectoparasites: organisms that live on the surfaces of other organisms and derive their nutrients directly from those organisms

edentates: lacking teeth

El Niño: a periodic condition characterized by a warming of the central Pacific Ocean and the changes in global weather patterns that are brought about

emit: to send out or give off

endocrine system: the grouping of organs or glands that secrete hormones into the bloodstream

endoparasite: an organism that lives inside another organism and derives its nutrients directly from that organism

endoparasites: organisms that live inside other organisms and derive their nutrients directly from those organisms

endoskeleton: a skeleton that is surrounded by muscle tissue

endosymbionts: the hypothesis that certain organelles in eukaryotes are prokaryotes that have a symbiotic relationship and live within the eukaryote

endotrophic: deriving nourishment from within

enterocoelous: a cavity formed by the in-folding of the wall of the intestinal cavity in a gastrula

enzyme: a protein that acts as a catalyst to start a biochemical reaction

enzymes: proteins that act as catalysts to start biochemical reactions

epidermis: the protective portion of the outer portion of the skin found in some animals, it is composed of two layers of cells where the outer layer is continuously shed and replaced by the inner layer

epistasis: a phenomenon in which one gene alters the expression of another gene that is independently inherited

epithelial cells: cells that occur in tightly packed sheets that line organs and body cavities

epithelial lining: sheets of tightly packed cells that cover organs and body cavities

epitope: a localized region on an antigen that is recognized chemically by antibodies

equilibrium: a state of balance

erythrocytes: red blood cells, cells containing hemoglobin that carry oxygen throughout the body

estuaries: an area of brackish water where a river meets the ocean

ethology: animal behavior

eucoelomates: animals that have a true body cavity that is completely surrounded by mesoderm

eukaryota: a group of organisms containing a membrane bound-nucleus and membrane-bound organelles

eukaryotes: organisms containing a membrane-bound nucleus and membrane-bound organelles

eukaryotic cells: contains a membrane-bound nucleus and membrane-bound organelles

euryhaline: animals that can live in a wide range of salt concentrations

eusocial: animals that show a true social organization

evaporites: rocks formed from evaporation of salty and mineral-rich liquid

excrescence: an abnormal growth

excrescences: abnormal growths

exons: the coding region in a eukaryotic gene that is expressed

exoskeleton: a hard outer protective covering common in invertebrates such as insects

exoskeletons: hard outer protective coverings common in invertebrates such as insects

exponential growth: a population growing at the fastest possible rate under ideal conditions

extant: still living

facilitated diffusion: the spontaneous passing of molecules attached to a carrier protein across a membrane

facultative parasites: organisms that can survive either as a parasite or free-living

falconry: a sport where falcons are used for hunting

fascicle: a close cluster

fauna: animals

fertilization: the fusion of male and female gametes

fibroblasts: type of cells found in loose connective tissue that secretes the proteins for connective fibers

fight or flight response: an automatic, chemically controlled response to a stimulus that causes increased heart and breathing rates for increased activity

filter feeders: animals that strain small food particles out of water

fission: dividing into two parts

fixed action pattern: behaviors that are common to all members of a species

flagella (flagellum): cellular tail that allows the cell to move

flagellae: cellular tails that allow cells to move

flora: plants

fossil record: a collection of all known fossils

frequency-dependant selection: a decline in the reproductive success of a particular body type due to that body type becoming common in the population

frugivores: fruit-eating animals

functional morphology: studying form and function

fusion: coming together

gametes: reproductive cells that only have one set of chromosomes

gametocyte: cell that produces gametes through division

gametocytes: cells that produce gametes through division

ganoid scale: hard, bony, and enamel covered scales

gastropods: mollusks that are commonly known as snails

gastrovascular cavity: a single cavity where digestion occurs

gastrulation: the formation of a gastrula from a blastula

gene therapy: a process where normal genes are inserted into DNA to correct a genetic disorder

genes: segments of DNA located on chromosomes that direct protein production

genetic trait: trait related to biological inheritance

genetics: the branch of biology that studies heredity

genome: an organism's genetic material

genomes: the sum of all genes in a set of chromosomes

genotype: the genetic makeup of an organism

germ cell: an egg or sperm cell, a gamete

germ cells: egg or sperm cells, gametes

gill arches: arches of cartilage that support the gills of fishes and some amphibians

gill filaments: the site of gas exchange in aquatic animals such as fish and some amphibians

gills: site of gas exchange between the blood of aquatic animals such as fish and the water

gizzard: the muscular part of the stomach of some animals where food is ground

global warming: a slow and steady increase in the global temperature

glycoprotein: an organic molecule that contains a carbohydrate and a protein

gonad: the male and female sex organs that produce sex cells

gonads: the male and female sex organs that produce sex cells

granulocytes: a type of white blood cell where its cytoplasm contains granules

green house effect: a natural phenomenon where atmospheric gases such as carbon dioxide prevent heat from escaping through the atmosphere

habitat: the physical location where organisms live in an ecosystem

habitat loss: the destruction of habitats through natural or artificial means

habitat requirement: necessary conditions or resources needed by an organism in its habitat

habitats: physical locations where organisms live in an ecosystem

Hamilton's Rule: individuals show less agression to closely related kin than to more distantly related kin

haplodiploidy: the sharing of half the chromosomes between a parent and an offspring

haploid cells: cells with only one set of chromosomes

hemocoel: a cavity between organs in arthropods and mollusks through which blood circulates

hemocyanin: respiratory pigment found in some crustaceans, mollusks, and arachnids

hemoglobin: an iron-containing protein found in red blood cells that binds with oxygen

hemolymph: the body fluid found in invertebrates with open circulatory systems

herbivore: an animal that eats plants only

herbivores: animals that eat only plants

herbivorous: animals that eat plants

heredity: the passing on of characteristics from parents to offspring

heritability: the ability to pass characteristics from a parent to the offspring

hermaphodite: an animals with both male and female sex organs

hermaphroditic: having both male and female sex organs

heterodont: teeth differentiated for various uses

heterotrophic eukaryotes: organisms containing a membrane-bound nucleus and membrane-bound organelles and do not make their own food

heterotrophs: organisms that do not make their own food

heteroxenous: a life cycle in which more than one host individual is parasitized

heterozygote: an organism whose chromosomes contain both genes of a contrasting pair

heterozygote advantage: a condition where a heterozygous individual has a reproductive advantage over a homozygous individual

Hippocrates: a central figure in medicine in ancient Greece, he is considered the father of modern medicine

home range: the area where an animal lives and eats

homeostasis: a state of equilibrium in an animal's internal environment that maintains optimum conditions for life

homeothermic: describes animals able to maintain their body temperatures

hominid: belonging to the family of primates

hominids: belonging to the family of primates

homodont: teeth with a uniform size and shape

homologous: similar but not identical

homology: correspondence in the type of structure and its origin

homoplastic: similar but of different origins

homozygote: an animal with two identical alleles for one trait

hormone: a chemical signal secreted by glands that travel through the bloodstream to regulate the body's activities

hormones: chemical signals secreted by glands that travel through the bloodstream to regulate the body's activities

Horseshoe crabs: "living fossils" in the class of arthropods

Hox genes: also known as selector genes because their expression leads embryonic cells through specific morphologic development

Human Genome Project: a study by U.S. Department of Energy and the National Institutes of Health to map the entire human genome by 2003

hunting season: a period of time during which hunting is permited

hunting seasons: periods of time during which hunting is permited

hybrid: offspring resulting from the cross of two different species

hydrostatic skeleton: a pressurized, fluid-filled skeleton

hyperpolarizing potential: any change in membrane potential that makes the inside of the membrane more negatively charged

hypothalamus: part of the upper end of the brain stem that regulates activities in the nervous and endrocrine systems

IgA: imunoglobin A; a class of proteins that make up antibodies

IgD: imunoglobin D; a class of proteins that make up antibodies

IgE: imunoglobin E; a class of proteins that make up antibodies

IgG: imunoglobin G; a class of proteins that make up antibodies

IgM: imunoglobin M; a class of proteins that make up antibodies

inbreeding depression: loss of fitness due to breeding with close relatives

incomplete dominance: a type of inheritance where the offspring have an intermediate appearance of a trait from the parents

incus: one of three small bones in the inner ear

indirect fitness: fitness gained through aiding the survival of non-descendant kin

infrared: an invisible part of the electromagnetic spectrum where the wavelengths are shorter than red; heat is carried on infrared waves

innate behavior: behavior that develops without influence from the environment

innervate: supplied with nerves

inoculation: introduction into surroundings that support growth

insectivore: an animal that eats insects

insectivores: animals that eat insects

instars: the particular stage of an insect's or arthropod growth cycle between moltings

integument: a natural outer covering

intercalation: placing or inserting between

intraspecific: involving members of the same species

introns: a non-coding sequence of base pairs in a chromosome

invagination: a stage in embryonic development where a cell layer buckles inward

invertebrates: animals without a backbone

involuntary muscles: muscles that are not controlled by will

isthmus: a narrow strip of land

iteroparous: animals with several or many reproductive events in their lives

***k*-selected species:** a species that natural selection has favored at the carrying capacity

***k*-selecting habitat:** habitat where there is a high cost of reproduction and is sensitive to the size of the offspring

key innovation: a modification that permits an individual to exploit a resource in a new way

keystone species: a species that controls the environment and thereby determines the other species that can survive in its presence

krill: an order of crustaceans that serves as a food source for many fish, whales, and birds

lancelet: a type of primitive vertebrate

lancelets: primitive vertebrates

lateral inhibition: phenomenon that amplifies the differences between light and dark

lateral line: a row of pressure sensitive sensory cells in a line on both sides of a fish

learned behavior: behavior that develops with influence from the environment

learning: modifications to behavior motivated by experience

leukocytes: a type of white blood cells that are part of the immune system

life history strategies: methods used to overcome pressures for foraging and breeding

life history strategy: methods used to overcome pressures for foraging and breeding

lipids: fats and oils; organic compounds that are insoluble in water

logistic growth: in a population showing exponential growth the individuals are not limited by food or disease

lungs: sac-like, spongy organs where gas exchange takes place

lymphocytes: white blood cell that completes development in bone marrow

macroparsite: a parasite that is large in size

macroparasites: parasites that are large in size

macrophages: white blood cell that attacks anything foreign such as microbes

malleus: the outermost of the inner ear bones

mantle: the tissue in mollusks that drapes over the internal organs and may secrete the shell

mantles: tissues in mollusks that drape over the internal organs and may secrete the shell

matrix: the nonliving component of connective tissue

megachiroptera: fruit bats and flying foxes

meiosis: a specialized type of cell division that results in four sex cells or gametes that have half the genetic material of the parent cell

merozoite: a motile stage in some parastic protozoa

mesenchyme: the part of the mesoderm from which the connective tissues (bone, cartilage, and vascular system) arise

mesenteries: the membrane that suspends many internal organs in the fluid-filled body cavity of vertebrates

mesoderm: the middle layer of cells in embryonic tissue

messenger RNA: a type of RNA that carries protein synthesis information from the DNA in to the nucleus to the ribosomes

metamorphose: to change drastically from a larva to an adult

metamorphoses: changes drastically from its larval form to its adult form

metamorphosing: changing drastically from a larva to an adult

metamorphosis: a drastic change from a larva to an adult

metazoan: a subphylum of animals that have many cells, some of which are organized into tissues

metazoans: a subphylum of animals that have many cells, some of which are organized into tissues

microchiroptera: small bats that use echolocation

microparasite: very small parasite

microparasites: very small parasites

midoceanic ridge: a long chain of mountains found on the ocean floor where tectonic plates are pulling apart

mitochondria: organelles in eukaryotic cells that are the site of energy production for the cell

Mitochondrial DNA: DNA found within the mitochondria that control protein development in the mitochondria

mitosis: a type of cell division that results in two identical daughter cells from a single parent cell

modalities: to conform to a general pattern or belong to a particular group or category

modality: to conform to a general pattern or belong to a particular group or category

molecular clock: using the rate of mutation in DNA to determine when two genetic groups spilt off

molecular clocks: using the rate of mutation in DNA to determine when two genetic groups spilt off

mollusks: large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

molted: the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

molting: the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

monoculture: cultivation of a single crop over a large area

monocultures: cultivation of single crops over large areas

monocytes: the largest type of white blood cell

monophyletic: a taxon that derived from a single ancestral species that gave rise to no other species in any other taxa

monotremes: egg-laying mammals such as the platypus and echidna

monoxenous: a life cycle in which only a single host is used

morphogenesis: the development of body shape and organization during ontogeny

morphological: the structure and form of an organism at any stage in its life history

morphological adaptation: an adaptation in form and function for specific conditions

morphological adaptations: adaptations in form and function for specific conditions

morphologies: the forms and structures of an animal

mutation: an abrupt change in the genes of an organism

mutations: abrupt changes in the genes of an organism

mutualism: ecological relationship beneficial to all involved organisms

mutualisms: ecological relationships beneficial to all involved organisms

mutualistic relationship: symbiotic relationship where both organisms benefit

mutualistic relationships: symbiotic relationships where both organisms benefit

mutualists: a symbiotic relationship where both organisms benefit

myofibril: longitudinal bundles of muscle fibers

myofilament: any of the ultramicroscopic filaments, made up of actin and myosin, that are the structural units of a myofibril

myosin: the most common protein in muscle cells, responsible for the elastic and contractile properties of muscle; it combines with actin to form actomyosin

natural selection: the process by which organisms best suited to their environment are most likely to survive and reproduce

naturalist: a scientist who studies nature and the relationships among the organisms

naturalists: scientists who study nature and the relationships among the organisms

neuromuscular junction: the point where a nerve and muscle connect

neuron: a nerve cell

neurons: nerve cells

neurotransmitters: chemical messengers that are released from one nerve cell that cross the synapse and stimulate the next nerve cell

niche: how an organism uses the biotic and abiotic resources of its environment

nocturnal: active at night

notochord: a rod of cartilage that runs down the back of Chordates

nucleotide: the building block of a nucleic acid that is composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

nucleotide chain: a chain composed of five-carbon sugar groups that forms the basis for nucleic acid

nucleotides: building blocks of a nucleic acid that are composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

obligative mutualism: an animal that must exist as part of a mutually beneficial relationship

obligatory parasites: an animal that can only exist as a parasite

olfactory: relates to the sense of smell

omnivorous: eating both plants and animals

ontogeny: the embryonic development of an organism

oocyst: a cyst in sporozoans that contains developing sporozoites

operculum: a flap covering an opening

operculum chamber: space covered by a flap

organelles: membrane-bound structures found within a cell

ornithology: the study of birds

osmoregulatory functions: controlling the water balance within an animal

osmoregulatory system: system that regulates the water balance between an organism and its environment

osmosis: the diffusion of water across a membrane

ossification: deposition of calcium salts to form hardened tissue such as bone

osteoblasts: potential bone forming cells found in cartilage

oviparous: having offspring that hatch from eggs external to the body

ovoviparity: having offspring that hatch from eggs retained in the mother's uterus

ovoviviparous: having offspring that hatch from eggs retained in the mother's uterus

paleoanthropology: the study of ancient humans

parasitology: the study of parasites

parasympathetic division: part of the nervous system that generally enhances body activities that gain and conserve energy such as digestion and heart rate

parental imprinting: a process by which a gene's expression in a child depends on which parent donated it before development

passive diffusion: the passing of molecules across a membrane from an area of higher concentration to an area of lower concentration without any energy input

pathogens: disease-causing agents such as bacteria, fungi, and viruses

pecking order: the position of individuals of a group wherein multiple levels of dominance and submission occur

pectoral: of, in, or on the chest

pedipapls: one pair of short appendages near the mouth in some arthropods used for feeding and copulation

pericardial cavity: the space within the membrane that surrounds the heart

peripheral nervous system: the sensory and motor nerves that connect to the central nervous system

peritoneum: the thin membrane that lines the abdomen and covers the organs in it

pesticide: any substance that controls the spread of harmful or destructive organisms

pesticides: substances that control the spread of harmful or destructive organisms

pH: a measure of how acidic or basic a substance is by measuring the concentration of hydrogen ions

phalanges: bones of the fingers and toes

pharyngeal: having to do with the tube that connects the stomach and the esophagus

phenotype: physical and physiological traits of an animal

phenotypes: the physical and physiological traits of an animal

phenotypic: describes the physical and physiological traits of an animal

phenotypic trait: physical and physiological variations within a population

phenotypic variation: differences in physical and physiological traits within a population

pheromones: small, volatile chemicals that act as signals between animals that influence physiology or behavior

phlogenetic: relating to the evolutionary history

phospholipid: molecules that make up double layer membranes; one end of the molecule attracts water while the other end repels water

photoreceptors: specialized cells that detect the presence or absence of light

photosynthesis: the combination of chemical compounds in the presence of sunlight

photosynthesizing autotrophs: animals that produce their own food by converting sunlight to food

phyla: broad, principle divisions of a kingdom

phylogenetic: relating to the evolutionary history of species or group of related species

phylogeny: the evolutionary history of a species or group of related species

physiological: relating to the basic activities that occur in the cells and tissues of an animal

physiology: the study of the normal function of living things or their parts

placenta: the structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

placental: having a structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

placoid scale: a scale composed of three layers and a pulp cavity

placoid scales: scales composed of three layers and a pulp cavity

plankton: microscopic organisms that float or swim weakly near the surface of ponds, lakes, and oceans

plate tectonics: the theory that Earth's surface is divided into plates that move

platelet: cell fragment in plasma that aids clotting

platelets: cell fragments in plasma that aid in clotting

pleural cavity: the space where the lungs are found

plumose: having feathers

pluripotent: a cell in bone marrow that gives rise to any other type of cell

poaching: hunting game outside of hunting season or by using illegal means

poikilothermic: an animal that cannot regulate its internal temperature; also called cold blooded

polymer: a compound made up of many identical smaller compounds linked together

polymerase: an enzyme that links together nucleotides to form nucleic acid

polymerases: enzymes that link together nucleotides to form nucleic acid

polymodal: having many different modes or ways

polymorphic: referring to a population with two or more distinct forms present

polymorphism: having two or more distinct forms in the same population

polymorphisms: having two or more distinct forms in the same population

polyploid: having three or more sets of chromosomes

polysaccharide: a class of carbohydrates that break down into two or more single sugars

polysaccharides: carbohydrates that break down into two or more single sugars

population: a group of individuals of one species that live in the same geographic area

population density: the number of individuals of one species that live in a given area

population dynamics: changes in a population brought about by changes in resources or other factors

population parameters: a quantity that is constant for a particular distribution of a population but varies for the other distrubutions

populations: groups of individuals of one species that live in the same geographic area

posterior: behind or the back

precursor: a substance that gives rise to a useful substance

prehensile: adapted for siezing, grasping, or holding on

primer: short preexisting polynucleotide chain to which new deoxyribonucleotides can be added by DNA polymerase

producers: organisms which make up the level of an ecosystem that all other organisms ultimately depend on; usually these are plants

progeny: offspring

prokaryota: a group of organisms that lack a membrane-bound nucleus and membrane-bound organelles

prokaryotes: single-celled organisms that lack a true cell nucleus

prokaryotic endosymbionts: single-celled organisms that lack a true cell nucleus that live inside of other cells

proprioceptors: sense organs that receive signals from within the body

protostome: animal in which the initial depression that starts during gastrulation becomes the mouth

protostomes: animals in which the initial depression that starts during gastrulation becomes the mouth

protozoa: a phylum of single-celled eukaryotes

protozoan: a member of the phylum of single-celled organisms

pseudocoelom: a body cavity that is not entirely surrounded by mesoderm

pseudocoelomates: animals with a body cavity that is not entirely surrounded by mesoderm

pterylae: feather tracks

quadrupedal: describes an animal with four legs

quadrupeds: animals with four legs

quinine: substance used to treat malaria

***r*-selected species:** a species that shows the following characteristics: short lifespan; early reproduction; low biomass; and the potential to produce large numbers of usually small offspring in a short period of time

***r*-selecting habitat:** the concept where a high reproductive rate is the chief determinant of life history

radially symmetric: wheel-like symmetry in which body parts radiate out from a central point

radially symmetrical: describes an animal that features a wheel-like symmetry in which its body parts radiate out from a central point

recessive: a hidden trait that is masked by a dominant trait

recombinant DNA: DNA that is formed when a fragment of DNA is incorporated into the DNA of a plasmid or virus

regeneration: regrowing body parts that are lost due to injury

relative abundance: an estimate of population over an area

rennin: an enzyme used in coagulating cheese; is obtained from milk-fed calves

resorbed: absorption of materials already in the body

resorption: absorbing materials that are already in the body

respiratory pigments: any of the various proteins that carry oxygen

restriction enzymes: bacterial proteins that cut DNA at specific points in the nucleotide sequence

retina: a layer of rods and cones that line the inner surface of the eye

riparian: habitats in rivers and streams

ruminants: plant-eating animals with a multicompartment stomach such as cows and sheep

sagital plane: a plane that runs long-ways through the body

salamanders: four-legged amphibians with elongated bodies

sarcomere: one of the segments into which a fibril of striated muscle is divided by thin dark bands

scavengers: animals that feed on the remains of animals it did not kill

schizocoelous: the mesoderm originates from existing cell layers when the cells migrate

scleroblasts: cells that give rise to mineralized connective tissue

sedimentary rock: rock that forms when sediments are compacted and cemented together

semelparous: animals that only breed once and then die

serial homology: a rhythmic repetition

sessile: not mobile, attached

sexual reproduction: a reproduction method where two parents give rise to an offspring with a different genetic makeup from either parent

sexual selection: selection based on secondary sex characteristics that leads to greater sexual dimorphorphism or differences between the sexes

sexual size dimorphism: a noticeable difference in size between the sexes

shoals: shallow waters

single-lens eyes: an eye that has a single lens for focusing the image

skeletal muscle: muscle attached to the bones and responsible for movement

smooth muscle: muscles of internal organs which is not under conscious control

somatic: having to do with the body

somatic nervous system: part of the nervous system that controls the voluntary movement of skeletal muscles

somatosensory information: sensory information from different parts of the body except for the eyesm tongue, ears, and other primary sense organs

somites: a block of mesoderm along each side of a chordate embryo

sonar: the bouncing of sound off distant objects as a method of navigation or finding food

spinal cord: thick, whitish bundle of nerve tissue that extends from the base of the brain to the body

splicing: spliting

spongocoel: the central cavity in a sponge

sporozoa: a group of parasitic protozoa

sporozoans: parasitic protozoans

sporozoite: an infective stage in the life cycle of sporozoans

stapes: innermost of the three bones found in the inner ear

stimuli: anything that excites the body or part of the body to produce a specific response

stimulus: anything that excites the body or part of the body to produce a specific response

strata: layers of sedimentary rock consisting of approximately the same kinds of material

striated muscle: a type of muscle with fibers of cross bands usually contracted by voluntary action

striated muscles: muscles with fibers of cross bands usually contracted by voluntary actions

superposition: the order in which sedimentary layers are found with the youngest being on top

symbiosis: any prolonged association or living together of two or more organisms of different species

symbiotic relationship: close, long-term relationship where two species live together in direct contact

symbiotic relationships: close, long-term relationships where two species live together in direct contact

symmetrical: a balance in body proportions

synapse: the space between nerve cells across which impulses are chemically transmitted

systematic: study of the diversity of life

tactile: the sense of touch

tapetum: a reflective layer in the eye of nocturnal animals

taxa: named taxonomic units at any given level

taxon: named taxonomic unit at any given level

taxonomy: the science of classifying living organisms

terraria: a small enclosure or closed container in which selected living plants and sometimes small land animals, such as turtles and lizards, are kept and observed

terrariums: small enclosures or closed containers in which selected living plants and sometimes small land animals, such as turtles and lizards, are kept and observed

terrestrial: living on land

thoracic: the chest area

thromboplastin: a protein found in blood and tissues that promotes the conversion of prothrombin to thrombin

torpid: a hibernation strategy where the body temperature drops in relation to the external temperature

trachea: the tube in air-breathing vertebrates that extends from the larynx to the bronchi

transcription: process where enzymes are used to make an RNA copy of a strand of DNA

transgenic: an organism that contains genes from another species

transgenic organism: an organism that contains genes from another species

translation: process where the order of bases in messenger RNA codes for the order of amino acids in a protein

transverse plane: a plane perpendicular to the body

trilobites: an extinct class of arthropods

triploblasts: having three germ layers; ectoderm, mesoderm, and endoderm

trophic level: the division of species in an ecosystem by their main source of nutrition

trophic levels: divisions of species in an ecosystem by their main source of nutrition

ungulates: animals with hooves

urea: soluble form of nitrogenous waste excreted by many different types of animals

urethra: a tube that releases urine from the body

uric acid: insoluble form of nitrogenous waste excreted by many different types of animals

ventral: the belly surface of an animal with bilateral symmetry

vertebrates: animals with a backbone

viviparity: having young born alive after being nourished by a placenta between the mother and offspring

viviparous: having young born alive after being nourished by a placenta between the mother and offspring

vocalization: the sounds used for communications

voluntary muscles: a type of muscle with fibers of cross bands usually contracted by voluntary action

wavelength: distance between the peaks or crests of waves

zooplankton: small animals who float or weakly move through the water

zygote: a fertilized egg

zygotes: fertilized eggs

zymogens: inactive building-block of an enzyme

Topic Outline

Eukaryota
Mammalia
Metazoan
Molluska
Nematoda
Osteicthyes
Platyhelminthes
Porifera
Primates
Prokaryota
Reptilia
Rotifera
Trematoda
Turbellaria
Urochordata
Vertebrata

ANIMAL HISTORY

African Cichlid Fishes
Animal
Burgess Shale and Ediacaran Faunas
Cambrian Explosion
Coevolution
Colonization
Constraints on Animal Development
Domestic Animals
Eukaryota
Extinction
Fossil Record
Horses
Kingdoms of Life
Living Fossils
Paleontologist
Paleontology
Phylogenetic Relationships of Major Groups
Phylogenetics Systematics
Tetropods—From Water to Land
Xenopus

ANATOMY

Acoustic Signals
Biomechanics
Body Cavities
Body Plan
Bone
Cartilage
Cells
Cephalization
Comparative Biology
Echolocation
Embryology
Embryonic Development
Feeding
Functional Morphology
Gills
Growth And Differentiation of the Nervous System
Homology
Keratin
Locomotion
Mouth, Pharynx, and Teeth
Muscular System
Neuron
Scales, Feathers, and Hair
Sense Organs
Skeletons
Vision

BEHAVIOR

Acoustic Signals
Aggression
Altruism
Behavior
Behavioral Ecology
Circadian Rhythm
Courtship
Crepuscular
Diurnal
Dominance Hierarchy
Ethology
Homeostasis
Imprinting
Instinct
Learning
Migration
Nocturnal
Social Animals
Sociality
Sociobiology
Territoriality

BIOCHEMISTRY AND PHYSIOLOGY

Absorption
Allometry
Antibody

Blood
Cancer
Cell Division
Cells
Digestion
Egg
Homeostasis
Hormones
Keratin
Molecular Biologist
Molecular Biology
Molecular Systematics
Physiologist
Physiology
Respiration
Transport

BIODIVERSITY

Biodiversity
Biogeography
Biomass
Biomes
Colonization
Community Ecology
Diversity of Major Groups
Eukaryota
Habitat
Habitat Loss
Habitat Restoration
Zooplankton

CAREERS IN ANIMAL SCIENCE

Ecologist
Environmental Lawyer
Farmer
Functional Morphologist
Geneticist
Horse Trainer
Human Evolution
Livestock Manager
Marine Biologist
Medical Doctor
Molecular Biologist
Museum Curator
Paleontologist
Physiologist
Scientific Illustrator
Service Animal Trainer
Systematist
Taxonomist
Veterinarian
Wild Game Manager
Wildlife Biologist
Wildlife Photographer
Zoologist

CELL BIOLOGY

Absorption
Blood
Cell Division
Cells
Viruses

ECOLOGY

African Cichlid Fishes
Behavioral Ecology
Biotic Factors
Camouflage
Community Ecology
Competition
Competitive Exclusion
Conservation Biology
DDT
Ecologist
Ecology
Ecosystem
Evolutionary Stable Strategy
Exotic Species
Expenditure per Progeny
Feeding Strategies
Fitness
Food Web
Foraging Strategies
Growth And Differentiation of the Nervous System
Habitat
Habitat Loss
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Home Range
Human Commensals and Mutual Organisms
Interspecies Interactions
Iteroparity and Semelparity
Keystone Species
Life History Strategies

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Population Dynamics
Populations
Predation
Territoriality
Trophic Level
Zooplankton

ENVIRONMENT

Biological Pest Control
Biomass
Biomes
Biotic Factors
Carson, Rachel
DDT
Ecosystem
Endangered Species
Environment
Environmental Degradation
Environmental Impact
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Fossil Fuels
Global Warming
Human Populations
Natural Resources
Pesticide
Pollution
Silent Spring
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ETHICS

Animal Rights
Animal Testing
Bioethics

EVOLUTION

Adaptation
African Cichlid Fishes
Aposematism
Biological Evolution
Camouflage
Coevolution
Constraints on Animal Development
Continental Drift
Convergence
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Genetic Variation in a Population
Heterochrony
Homology
Human Evolution
Lamarck
Leakey, Louis and Mary
Modern Synthesis
Morphological Evolution in Whales
Morphology
Natural Selection
Peppered Moth
Sexual Dimorphism
Sexual Selection
Spontaneous Generation

FORM AND FUNCTION

Acoustic Signals
Adaptation
African Cichlid Fishes
Antlers and Horns
Aposematism
Biomechanics
Blood
Body Cavities
Body Plan
Bone
Burgess Shale and Ediacaran Faunas
Camouflage
Cell Division
Cells
Cephalization
Chitin
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Communication
Defense
Digestion
Digestive System
Echolocation
Endocrine System
Excretory and Reproductive Systems
Feeding
Flight
Gills
Gliding and Parachuting
Locomotion
Mimicry

Nervous System
Respiratory System
Sexual Selection
Shells
Vision
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GENETICS

Drosophila
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Genetic Variation in a Population
Genetically Engineered Foods
Geneticist
Genetics
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Carboniferous
Continental Drift
Cretaceous
Devonian
Geological Time Scale
Jurassic
K/T Boundary
Oligocene
Ordovician
Permian
Pleistocene
Quaternary
Silurian
Tertiary
Triassic

GROWTH AND DEVELOPMENT

Allometry
Antlers and Horns
Body Cavities
Body Plan
Bone
Cartilage
Cell Division
Cells
Comparative Biology
Constraints on Animal Development
Egg
Embryology
Embryonic Development
Haeckel's Law of Recapitulation
Heterochrony
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Metamorphosis
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Ontogeny
Serial Homology
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Bailey, Florence Augusta Merriam
Bates, Henry Walter
Carson, Rachel
Darwin, Charles
Diamond, Jared
Elton, Charles Sutherland
Fausto–Sterling, Anne
Fossey, Dian
Goodall, Jane
Gould, Steven Jay
Haldane, J. B. S.
Lamarck, Jean-Baptiste
Leakey, Louis and Mary
Linnaeus, Carolus
Lorenz, Konrad
Malthus, Thomas Robert
Mayr, Ernst
McArthur, Robert
Mendel, Gregor
Montalcini, Rita Levi
Pasteur, Louis
Simpson, George Gaylord
Stevens, Nettie Maria
Wallace, Alfred Russel
Wilson, E. O.

HUMANS AND THE ANIMAL WORLD

Cultures and Animals
Human Commensals and Mutual Organisms
Human Populations
Human–Animal Conflicts

Hunter-Gatherers
Hunting
Malaria

LIFE CYCLES

Catadromous—Diadromous and Anadromous Fishes
Cell Division
Colonization
Courtship
Endosymbiosis
Iteroparity and Semelparity
Malaria
Metamorphosis
Parasitism

REPRODUCTION

Antlers and Horns
Asexual And Sexual Reproduction
Cell Division
Excretory and Reproductive Systems
Fertilization

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Behavioral Ecology
Community Ecology
Comparative Biology
Conservation Biology
Ecology
Embryology
Entomology
Functional Morphology
Herpetology
Icthyology
Molecular Biology
Morphology
Mouth, Pharynx, and Teeth
Paleontology
Physiology
Sociobiology
Taxonomy