Pearson New International Edition

Ecology: The Experimental Analysis of Distribution and Abundance Charles J. Krebs Sixth Edition

## PEARSON

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## **Pearson New International Edition**

Ecology: The Experimental Analysis of Distribution and Abundance Charles J. Krebs Sixth Edition



#### **Pearson Education Limited**

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## Glossary

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- **abiotic factors** characterized by the absence of life; include temperature, humidity, pH, and other physical and chemical influences.
- **absolute density** the number of individuals per unit area or per unit volume.
- **abundance** the number or biomass of organisms of a particular species in a general area.
- actual evapotranspiration the actual amount of water that is used by and evaporates from a plant community over a given time period, largely dependent on the available water and the temperature.
- **adaptation** any alteration in the structure or function of an organism by which the organism becomes better able to survive and multiply in its environment.
- additive effects reproduction or mortality that simply adds or subtracts the individuals to the current population; opposite of compensatory effects.
- **aggregation** coming together of organisms into a group, as in locusts.
- **aggregative response** the response of predators or parasitoids to concentrate their foraging in an area of dense prey species.
- Allee effects population growth rates that decrease below replacement level at low population density, potentially leading to extinction.
- allele one of a pair of characters that are alternative to each other in inheritance, being governed by genes situated at the same locus in homologous chromosomes.
- **allelopathy** organisms that alter the surrounding chemical environment in such a way as to prevent other species from using it, typically with toxins or antibiotics.
- **ambient energy hypothesis** the idea that species diversity is governed by the amount of energy falling on an area.

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- **apex predator** in a food chain, it is the highest trophic level. Apex predators do not have other predators feeding on them within the food web.
- **aposematic** warning coloration, indicating to a predator that this prey is poisonous or highly defended against attack.
- apparent competition two species who do not share any resources but whose numbers change in relation to one another because of an indirect effect of a third species, typically a shared predator or natural enemy.
- **association** major unit in community ecology, characterized by essential uniformity of species composition.
- **autotroph** organism that obtains energy from the sun and materials from inorganic sources; contrast with *heterotroph*. Most plants are autotrophs.
- balance of nature the belief that natural populations and communities exist in a stable equilibrium and maintain that equilibrium in the absence of human interference.
- **barriers** any geographic feature that hinders or prevents dispersal or movement across it, producing isolation.
- basal metabolic rate the amount of energy expended by an animal while at rest in a neutral temperate environment, in the post-absorptive (fasting) state; the minimum rate of metabolism.
- **big-bang reproduction** offspring are produced in one burst rather than in a repeated manner.
- biodiversity the number of species in a community or region, which may be weighted by their relative abundances; also used as an umbrella concept for total biological diversity including genetic diversity within a species, species diversity (as used here), and ecosystem diversity at the

community or ecosystem level of organization.

- **bioelements** the chemical elements that move through living organisms.
- **biogeochemical cycles** the movement of chemical elements around an ecosystem via physical and biological processes.
- **biogeography** the study of the geographical distribution of life on Earth and the reasons for the patterns one observes on different continents, islands, or oceans.
- **biological control** the reduction of pests by the introduction of predators, parasites, or pathogens; by genetic manipulations of crops or pests; by sterilization of pests; or by mating disruption using pheromones.
- biomanipulation the management practice of using a trophic cascade to restore lakes to a clear water condition by removing herbivorous or planktivorous fishes or by adding piscivorous (predatory) fishes to a lake.
- biomass the mass or weight of living matter in an area.
- **biosphere** the whole-earth ecosystem, also called the *ecosphere*.
- **biota** species of all the plants and animals occurring within a certain area or region.
- **biotic factors** environmental influences caused by plants or animals; opposite of abiotic factors.
- **bottom-up model** the idea that community organization is set by the effects of plants on herbivores and herbivores on carnivores in the food chain.
- **bryophytes** plants in the phylum Bryophyta comprising mosses, liverworts, and hornworts.
- **Calvin-Benson cycle** the series of biochemical reactions that takes place in the stroma of chloroplasts in photosynthetic organisms and

From Ecology: The Experimental Analysis of Distribution and Abundance, Sixth Edition. Eugene Hecht.

results in the first step of carbon fixation in photosynthesis.

- **cannibalism** an animal that feeds on others of the same species.
- **carnivores** animals that eat mainly flesh from other animals; contrast with *herbivore*.
- catastrophic agents term used by Howard and Fiske (1911) to describe agents of destruction in which the percentage of destruction is not related to population density; synonymous with densityindependent factors.
- character displacement the divergence in morphology between similar species in the region where the species both occur, but this divergence is reduced or lost in regions where the species' distributions do not overlap; presumed to be caused by competition.
- climatic climax the final equilibrium vegetation for a site that is dictated by climate and toward which all successions are proceeding, according to Frederic Clements.
- climax community the final equilibrium community toward which succession moves.
- climax-pattern hypothesis the view that climax communities grade into one another and form a continuum of climax types that vary gradually along environmental gradients.
- closed population in population estimation, a population that is not changing in size during the interval of study, having no natality, mortality, immigration, or emigration.
- **coarse-grained habitat** from a particular species' point of view a habitat is coarse grained if it spends its life in one fragment of habitat and cannot move easily to another patch.
- **coevolution** the evolution of two or more species that interact closely with one another, with each species adapting to changes in the other.
- **cohort life table** a life table that follows a group of organisms from germination, birth, or hatching to the death of the last individual.
- common garden an experimental design in plant ecophysiology in which a series of plants from different areas are brought together and planted in one area, side by side, in an attempt to determine which fea-

tures of the plants are genetically controlled and which are environmentally determined.

**community** a group of populations living in the same area or habitat.

- **community structure** the species composition of an ecological community including the abundance of all the populations in the community.
- **compartment** any component of study for an analysis of nutrient cycling, such as a lake, a species of plant, or a functional group of nitrogen fixers, measured by its standing crop or amount of nutrient.
- compartment model a type of boxand-arrow model of diseases in which each compartment contains a part of the system that can be measured and the compartments are linked by flows between them; each compartment typically has an input from some compartments and an output to other compartments.
- **compensation point** for plants the equilibrium point at which photosynthesis equals respiration.
- **compensatory effects** reproduction or mortality that does not add or subtract the individuals to the current population but only replaces other individuals with no change in population size; opposite of additive effects.
- competition occurs when a number of organisms of the same or different species utilize common resources that are in short supply (exploitation) or when the organisms harm one another in the process of acquiring these resources (interference).
- **competitive exclusion principle** complete competitors cannot coexist; also called Gause's hypothesis.
- **connectance** used to describe food web complexity; the fraction of potential interactions in a food web that actually exist.
- continental climates the product of weather systems over large landmasses that result in cold winters and warm summers, not influenced by the large ocean masses, typically in temperate and polar latitudes.
- **control** in an experimental design a control is a treatment or plot in which nothing is changed so that it serves as a baseline for comparison

with the experimental treatments to which something is typically added or subtracted.

- **cost–benefit analysis** an assessment to determine whether the cost of an activity is less than the benefit that can be expected from the activity.
- crassulacean acid metabolism (CAM) a form of photosynthesis in which the two chemical parts of photosynthesis are separated in time because  $CO_2$  is taken up at night through the stomata (which are then closed during the day) and fixed to be used later in the day to complete photosynthesis carbon fixation; an adaptation used by desert plants to conserve water.
- **critical load** the amount of a nutrient such as nitrogen that can be absorbed by an ecosystem without damaging its integrity.
- cultural control the reduction of pest populations by agricultural manipulations involving crop rotation, strip cropping, burning of crop residues, staggered plantings, and other agricultural practices.
- **declining-population paradigm** the focus of this approach is on detecting, diagnosing, and halting a population decline by finding the causal factors affecting the population.
- **deme** interbreeding group in a population; also known as *local population*.
- **demographic stochasticity** the random variation in birth and death rates that can lead by chance to extinction.
- demographic transition the change in human populations from the two zero-population-growth states of high birth and high death rates to low birth and low death rates.
- **density** number of organisms per unit area or per unit volume.
- density-dependent rate as population density rises, births or immigration decrease or deaths or emigration increase, and consequently a graph of population density versus the rate will have a positive or negative slope.
- **density-independent rate** as population density rises, the rate does not change in any systematic manner, so that a graph of population

density versus the rate will have a slope of zero.

- determinate layers birds that lay a fixed number of eggs no matter what occurs.
- **deterministic extinctions** losses of species due to the removal of an essential resource.
- deterministic models mathematical models with a fixed outcome, models that give the same answer every time they are repeatedly run with a fixed set of parameters; opposite of *stochastic model*.
- **detritus** the plant production not consumed by herbivores.
- **developmental response** the increasing intake rate of prey items by an organism that is growing in size as it develops.
- dilution rate general term to describe the rate of additions to a population from birth and immigration.
- directional selection natural selection that favors traits either above or below the average of the population, so that over time the average moves in one direction.
- disease a pathological condition of an organism resulting from various causes, such as an infection, a genetic disorder, or environmental stress, with specific symptoms.
- dispersal the movement of individuals away from their place of birth or hatching or seed production into a new habitat or area to survive and reproduce.
- **disruptive selection** natural selection that favors extreme trait values rather than intermediate values so that over time extreme traits become more common.
- disturbance any short-lived strong disruption to an ecological population or community, such as a fire, flood, windstorm, or earthquake.
- dominant species common species of large biomass or numbers in a community.
- dynamic pool models a model to predict maximum sustained yield based on detailed population information on growth rates, natural mortality, and fishing mortality; contrast with *logistic-type model*.
- **dynamic stability hypothesis** for food chain length suggests that higher trophic levels are less stable than

lower trophic levels and past a certain point the longer chains go extinct.

- **dynamics** in population ecology, the study of the reasons for changes in population size; contrast with *statics*.
- ecological footprint the total land and water area that is appropriated by a nation or a city to produce all the resources it consumes and to absorb all the waste it generates.
- ecological longevity average length of life of individuals of a population under stated conditions.
- ecological specialization model a proposed explanation for Hanski's Rule, which postulates that species that exploit a wide range of resources become both widespread and common; these species are generalists; also called Brown's model.
- ecosystem biotic community and its abiotic environment; the whole Earth can be considered as one large ecosystem.
- ecosystem services all the processes through which natural ecosystems and the biodiversity they contain help sustain human life on Earth.
- ecotone transition zone between two diverse communities (e.g., the tundra-boreal forest ecotone).
- ecotype a genetic subspecies or race of a plant or animal species that is adapted to a specific set of environmental conditions such as temperature or salinity.
- edaphic pertaining to the soil. effective population size a population genetic concept of the number of breeding individuals in an idealized population that would maintain the existing genetic variability; it is typically much less than the observed population size.
- Eltonian pyramid abundance or biomass of successive trophic levels of an ecosystem, illustrating the impact of energy flows through successive trophic transfers.
- emigration the movement of individuals out of an area occupied by the population, typically the site of birth or hatching.
- endemic phase for locusts and other organisms that show outbreaks, the phase of low numbers when indi-

viduals are difficult to find in the field.

- endemic species species that occur in one restricted area but in no other.
- energetic hypothesis for food chain length, postulates that higher trophic levels are restricted by the limited efficiency of energy transfer along the chain.
- **environment** all the biotic and abiotic factors that actually affect an individual organism at any point in its life cycle.
- environmental heterogeneity variation in space in any environmental parameter such as soil pH or tree cover.
- environmental stochasticity variation in population growth rates imposed by changes in weather and biotic factors, as well as natural catastrophes such as floods and hurricanes.
- epidemic phase for locusts and other species that show rapid increases to high density, the phase of high numbers and maximum damage; contrast with *endemic phase*.
- **epidemiology** branch of medicine dealing with epidemic diseases.
- epipelic algae algae living in or on the sediments of a body of water.
- equilibrium model of community organization the global view that ecological communities are relatively constant in composition and are resilient to disturbances.
- equitability evenness of distribution of species abundance patterns; maximum equitability occurs when all species are represented by the same number of individuals.
- **eutrophic lake** a highly productive lake with dense phytoplankton, typically with green water.
- **eutrophic soils** soils with high nutrient levels, mostly recent and often volcanic in origin.
- eutrophication the process by which lakes are changed from clear water lakes dominated by green algae into murky lakes dominated by bluegreen algae, typically caused by nutrient runoffs from cities or agriculture.
- **evapotranspiration** sum total of water lost from the land by evaporation and plant transpiration.

- **experiment** test of a hypothesis. It can be observational (observe the system) or manipulative (perturb the system). The experimental method is the scientific method.
- experimental analysis an approach to studying population regulation that relies on the manipulation of populations rather than simple observation of changes used in key factor analysis.
- **facilitation** helping another organism, providing positive feedback in a population interaction.
- facilitation model the classic view that succession proceeds via one species helping the next species in the sequence to establish.
- fact particular truth of the natural world. Philosophers endlessly discuss what a fact is. Ecologists make observations, which may be faulty; consequently, every observation is not automatically a fact.
- facultative agents term used by Howard and Fiske (1911) to describe agents of destruction that increase their percentage of destruction as population density rises; synonymous with *densitydependent factors*.
- **fecundity** an organism's potential reproductive capacity over a period of time, measured by the number of gametes produced.
- feeding guilds organisms that eat the same general foods, such as seed-eaters.
- fertility the actual number of viable offspring produced by an organism over a period of time, equivalent to realized *fecundity*.
- **fertility schedule** the age-specific reproductive output per individual.
- **field metabolic rate** the amount of energy used per unit of time by an organism under normal conditions of life in a natural ecosystem.
- **fine-grained habitat** from a particular species' point of view, a habitat is fine grained if it moves freely from one patch to another at no cost.
- First Principle of Population Regulation no closed population stops increasing unless either the per capita birth rate or death rate is density dependent.

- fitness the ability of a particular genotype or phenotype to leave descendants in future generations, relative to other organisms.
- **flux rate** the rate of flow of nutrients or biomass from one compartment to another.
- food chain the transfer of energy and materials from plants to herbivores to carnivores.
- **food web** a linked set of *food chains* that most often resemble a web.
- frost drought for plants a shortage of water in winter when the ground is frozen so no water can be taken up by the roots and yet air temperature is high enough that plants attempt to photosynthesize.
- **functional group** a group of species that perform the same function in a community.
- functional response the change in the intake rate of a predator in relation to the density of its prey species.
- **fundamental niche** the ecological space occupied by a species in the absence of competition and other biotic interactions from other species.
- Gause's hypothesis complete competitors cannot coexist; also called the competitive exclusion principle.
- **gene flow** the movement of alleles of genes in space and time from one population to another.
- genecology study of population genetics in relation to the habitat conditions; the study of species and other taxa by the combined methods and concepts of ecology and genetics.
- **generalist predators** predators that eat a great variety of prey species.
- generalists species that eat a variety of foods or live in a variety of habitats; contrast to *specialists*.
- **genet** a unit of genetically identical individuals, derived by asexual reproduction from a single original zygote.
- genetic stochasticity any potential loss of genetic variation due to inbreeding or genetic drift (the nonrandom assortment of genes during reproduction).
- **genotype** entire genetic constitution of an organism; contrast with *phenotype*.
- **genotypic** under the control of the genetic endowment of an individual.

- global nutrient cycles nutrient cycles that operate at very large scales over much of the Earth because the nutrients are volatile, such as oxygen.
- global stability occurs when a community can recover from any disturbance, large or small, and go back to its initial configuration of species composition and abundances; compare with *neighborhood stability*.
- **gradocoen** totality of all factors that impinge on a population, including *biotic* agents and *abiotic* factors.
- grazing facilitation the process of one herbivore creating attractive feeding conditions for another herbivore so there is a benefit provided to the second herbivore.
- green world hypothesis the proposed explanation for the simple observation that the world is green, that herbivores are held in check by their predators, parasites, and diseases, although other explanations have been suggested.
- greenhouse effect the process in which the emission of infrared (long-wave) radiation by the atmosphere warms a planet's surface.
- greenhouse gases gases present in the Earth's atmosphere that reflect infrared radiation back to Earth, thus warming it. The most important ones affected by humans are carbon dioxide, methane, nitrous oxide, and chlorofluorocarbons. Water vapor also acts as a greenhouse gas.
- gross primary production the energy or carbon fixed via photosynthesis per unit time.
- **gross production** production before respiration losses are subtracted; photosynthetic production for plants and metabolizable production for animals.
- **gross productivity** the assimilation rate of an animal, which includes all the digested energy less the urinary waste.
- **group selection** natural selection for traits that favor groups within a species irrespective of whether the traits favor individuals or not.
- growth form morphological categories of plants, such as trees, shrubs, and vines.
- guild a group of species that exploit a common resource base in a similar fashion.

- habitat a particular environment in which a species lives, or broadly speaking the biotic environment occupied by an individual or population.
- habitat selection the behavioral actions of organisms (typically animals) in choosing the areas in which they live and breed.
- handling time the time utilized by a predator to consume an individual prey item.
- Hanski's Rule the generalization that there is a positive relationship between distribution and abundance, such that abundant species have wide geographical ranges.
- **harvest method** the measurement of primary production by clipping the vegetation at two successive times.
- **herbivore** an animal that eats plants or parts of plants; contrast with *carnivore*.
- **herbivory** the eating of parts of plants by animals, not typically resulting in plant death.
- **heterogeneity** the distribution of relative abundance among the species.
- **heterotroph** organism that obtains energy and materials by eating other organisms; contrast with *autotroph*.
- homeostasis maintenance of constancy or a high degree of uniformity in an organism's functions or interactions of individuals in a population or community under changing conditions; results from the capabilities of organisms to make adjustments.
- **homeothermic** pertaining to warmblooded animals that regulate their body temperature; contrast with *poikilothermic*.
- **host** organism that furnishes food, shelter, or other benefits to another organism of a different species.
- hotspots of biodiversity areas of the Earth that contain many endemic species (typically 1500) and as such are of important conservation value.
- **hydrophyte** plant that grows wholly or partly immersed in water; compare with *xerophyte* and *mesophyte*.
- hypothesis universal proposition that suggests an explanation for some observed ecological situation.
- **hypoxia** lack of oxygen, typically in lakes or parts of an ocean basin in which excessive primary production

is broken down by bacteria and other decomposers, using up all the oxygen in the water.

- ideal despotic distribution a theoretical spatial spread of members of a population in which the competitive dominant "aggressive" individuals take up the best resources or territories, and less competitive individuals take up areas or resources in direct relationship to their dominance status.
- ideal free distribution a theoretical spatial spread of members of a population in which individuals take up areas with equal amounts of resources in relation to their needs, so all individuals do equally well (the polar opposite to the ideal despotic distribution).
- **immigration** the movement of organisms into an area.
- immunocontraception the use of genetic engineering to insert genes that stimulate the immune system of a vertebrate to reject sperm or eggs, thus causing infertility.
- **incidence functions** the fraction of patches of a given size occupied by a breeding population of a particular species.
- indeterminate layers birds that continue to lay eggs until the nest is full, thus compensating for any egg removals.
- index of similarity ratio of the number of species found in common in two communities to the total number of species that are present in both.
- indifferent species species occurring in many different communities; are poor species for community classification.
- individual optimization hypothesis that each individual in a population has its own optimal clutch size, so that not all individuals are identical.
- inducible defenses plant defense methods that are called into action once herbivore attack occurs and are nearly absent during periods of no herbivory.
- inhibition model succession proceeds via one species trying to stop the next species in the sequence from establishing.
- initial floristic composition the model of succession of who-getsthere-first wins, part of the inhibition model.

- **insect parasitoids** insects that lay their eggs in or on the host species, so that the larvae enter the host and kill it by consuming it from the inside.
- **integrated pest management (IPM)** the use of all techniques of control in an optimal mix to minimize pesticide use and maximize natural controls of pest numbers.
- interactive herbivore system plantherbivore interactions in which there is feedback from the herbivores to the plants so that herbivores affect plant production and fitness.
- intermediate disturbance hypothesis the idea that biodiversity will be maximal in habitats that are subject to disturbances at a moderate level, rather than at a low or high level.
- interspecific between two or more different species.
- interspecific competition competition between members of different species.
- **intransitive competition** a competitive network that never reaches a fixed endpoint because A replaces B and B replaces C but C can replace A.
- **intraspecific** between individuals of the same species.
- intrinsic capacity for increase (r) measure of the rate of increase of a population under controlled conditions, with fixed birth and death rates; also called *innate capacity for increase*.
- **irruption** a rapid increase in a population, often after being introduced to a new area, followed by a collapse that may be rapid or prolonged and may result in a convergent oscillation to a lower equilibrium density.
- **isocline** a contour line in graphical presentations of mathematical models in which some parameter is equal all along the line.
- **isotherm** line drawn on a map or chart connecting points with the same temperature at a particular time or over a certain period.
- key factor analysis a systematic approach using life tables to determine the factors responsible for the regulation and fluctuation of populations.
- **keystone species** relatively rare species in a community whose removal causes a large shift in the structure

of the community and the extinction of some species.

- kin selection the evolution of traits that increase the survival, and ultimately the reproductive success, of one's relatives.
- **Krantz anatomy** the particular type of leaf anatomy that characterizes C<sub>4</sub> plants; plant veins are encased by thick-walled photosynthetic bundlesheath cells that are surrounded by thin-walled mesophyll cells.
- *K*-selection the type of natural selection experienced by organisms that live at carrying capacity or maximal density in a relatively stable environment.
- Lack clutch size the clutch size at which productivity is maximal for the population.
- Lack's hypothesis that clutch size in birds is determined by the number of young that parents can provide with food.
- Leslie matrix model a method of casting the age-specific reproductive schedule and the age-specific mortality schedule of a population in matrix form so that predictions of future population change can be made.
- Liebig's law of the minimum the generalization first stated by Justus von Liebig that the rate of any biological process is limited by that factor in least amount relative to requirements, so there is a single limiting factor.
- **life table** the age-specific mortality schedule of a population.
- **limiting factor** a factor is defined as limiting if a change in the factor produces a change in average or equilibrium density.
- **littoral** shallow-water zone of lakes or the sea, with light penetration to the bottom; often occupied by rooted aquatic plants.
- **local nutrient cycles** nutrient cycles that are confined to small regions because the elements are nonvolatile, such as the phosphorus cycle.
- local population see *deme*. local population model a proposed explanation for Hanski's Rule, which assumes that species differ in their capacity to disperse, and if the environment is divided into patches, some species will occupy

more local patches than others as a function of their dispersal powers.

- **local stability** occurs when communities recover from only small disturbances and return to their former configuration of species composition and abundances.
- **logistic equation** model of population growth described by a symmetrical S-shaped curve with an upper asymptote.
- **logistic-type model** type of optimumyield model in which the yield is predicted from an overall descriptive function of population growth without a separate analysis of the components of mortality, recruitment, and growth; contrast with *dynamic pool model*.
- **log-normal distribution** the statistical distribution that has the shape of a normal, bell-shaped curve when the *x*-axis is expressed in a logarithmic scale rather than an arithmetic scale.
- **loss rate** general term to describe the rate of removal of organisms from a population by death and emigration.
- Lotka-Volterra equations the set of equations that describe competition between organisms for food or space; another set of equations describes predator-prev interactions
- **lottery competition** a type of interference competition in which an individual's chances of winning or losing are determined by who gets access to the resource first.
- macroparasites large multicellular organisms, typically arthropods or helminths, which do not multiply within their definitive hosts but instead produce transmission stages (eggs and larvae) that pass into the external environment.
- marine protected area a national park in the ocean where fishing is restricted or eliminated for the purpose of protecting populations from overharvesting.
- match-mismatch hypothesis the idea that population regulation in many fish is determined in the early juvenile stages by food supplies, so that if eggs hatch at the same time that food is abundant, many will survive, but if eggs hatch when food is scarce, many will die.

- **matrix models** a family of models of population change based on matrix algebra, with the Leslie matrix model being the best known.
- maximum economic rent the desired economic goal of any exploited resource, measured by total revenues – total costs.
- maximum reproduction the theory that natural selection will maximize reproductive rate, subject to the constraints imposed by feeding and predator avoidance.
- maximum sustained yield (MSY) the predicted yield that can be taken from a population without the resource collapsing in the short or long term.
- **mean length of a generation** the average length of time between the birth of a female and her offspring.
- **mechanism** a biological process that explains some phenomenon.
- mesic moderately moist.
- mesophyte plant that grows in environmental conditions that include moderate moisture conditions.
- mesopredators secondary consumers (e.g., carnivores) in a food chain that are fed upon by tertiary consumers such as apex predators.
- metabolic theory of ecology an attempt to derive patterns of individual performance, population, and ecosystem dynamics from the fundamental observation that the metabolic rate of individuals is related to body size and temperature.
- **metapopulations** local *populations* in patches that are linked together by dispersal among the patches, driven by colonization and extinction dynamics.
- **microparasites** small pathogenic organisms, typically protozoa, fungi, bacteria, or viruses, that can cause disease.
- minimum viable population (MVP) the size of a population in terms of breeding individuals that will ensure at some specified level of risk continued existence with ecological and genetic integrity.
- **model** verbal or mathematical statement of a hypothesis.
- **modular organisms** organisms that have an indefinite growth form, such as plants or corals.
- **monoclimax hypothesis** the classic view of Frederic Clements that all

vegetation in a region converges ultimately to a single climax plant community.

- **monogamy** mating of an animal with only one member of the opposite sex.
- **morphology** study of the form, structure, and development of organisms.
- **mortality** the death of organisms in a population.
- **multivoltine** refers to an organism that has several generations during a single season; contrast with *univoltine*.
- **mutualism** a relationship between two organisms of different species that benefits both and harms neither.
- mycorrhizae a mutually beneficial association of a fungus and the roots of a plant in which the plant's mineral absorption is enhanced and the fungus obtains nutrients from the plant.
- **natality** birth or germination or hatching; reproductive output of a population.
- **natural control** the limitation of pest populations by predators, parasitoids, parasites, diseases, and weather in the absence of chemical control.
- natural selection the process in nature by which only the organisms best adapted to their environment tend to survive and transmit their genetic characteristics to succeeding generations while those less adapted tend to be eliminated.
- **neighborhood stability** also called *local stability*, the ability of a community to return to its former configuration after a small disturbance.
- **nested subsets** a sequence of habitat patches, ordered by size, is nested if all the species in the smaller patches are also included in the larger patches.
- net primary production the energy (or carbon) fixed in photosynthesis minus the energy (or carbon) lost via respiration per unit time.
- **net production** production after respiration losses are subtracted.
- **net reproductive rate** ( $R_0$ ) the average number of offspring produced per female or reproductive unit.
- **niche** the ecological space occupied by a species, and the occupation of the species in a community.

- **niche breadth** a measurement of the range of resources utilized by a species.
- **niche overlap** a measure of how much species overlap with one another in the use of resources.
- nonequilibrium model of community organization the global view that ecological communities are not constant in their composition because they are always recovering from *biotic* and *abiotic* disturbances, never reaching an equilibrium.
- noninteractive herbivore system plant-herbivore interactions in which there is no feedback from the herbivores to the plants.
- **numerical response** the change in the numbers or density of a predator in relation to changes in the density of its prey species.
- **obligate** predator or parasite that is restricted to eating a single species of prey.
- oligochaetes any of a class or order (Oligochaeta) of hermaphroditic terrestrial or aquatic annelids lacking a specialized head; includes earthworms.
- oligotrophic lake an unproductive, clear-water lake with a low density of phytoplankton.
- oligotrophic pattern soils of very low nutrient levels that are common in tropical areas and regions with geologically old, highly eroded soils with most of the nutrients in the litter layer.
- **omnivore** an animal that feeds on both plants and animals in a food chain.
- **open population** in population estimation, a population that has natality, mortality, immigration, or emigration during the interval of study.
- **optimal defense hypothesis** the idea that plants allocate defenses against herbivores in a manner that maximizes individual plant fitness, and that defenses are costly to produce.
- **optimal foraging** any method of searching for and obtaining food that maximizes the relative benefit. **optimal foraging theory** a detailed
- model of how animals should forage to maximize their fitness. **optimal group size** the size that re
  - sults in the largest relative benefit.

- **optimality models** models that assume natural selection will achieve adaptations that are the best possible for each trait in terms of survival and reproduction.
- optimum yield amount of material that can be removed from a population to maximize biomass (or numbers, or profit, or any other type of "optimum") on a sustained basis.
- **ordination** process by which plant or animal communities are ordered along a gradient.
- overcompensation hypothesis the idea that a small amount of grazing will increase plant growth and fitness rather than cause harm to the plant.
- **paradox of the plankton** the problem of understanding how many phytoplankton species that have the same basic requirements can coexist in a community without competitive exclusion.
- **parasite** an organism that grows, feeds, or is sheltered on or in a different organism while harming its host.
- parasitoid an insect that completes larval development in another insect host.
- **parthenogenesis** development of the egg of an organism into an embryo without fertilization.
- **patch** any discrete area, regardless of size.
- **pesticide** any chemical that kills a plant or animal pest.
- **pesticide suppression** the reduction of pest populations with herbicides, fungicides, insecticides, or other chemical poisons.
- **Petersen method** a population estimation procedure based on two periods of mark-and-recapture.
- **phenology** study of the periodic (seasonal) phenomena of animal and plant life and their relations to the weather and climate (e.g., the time of flowering in plants).
- **phenotype** expression of the characteristics of an organism as determined by the interaction of its genic constitution and the environment; contrast with *genotype*.
- **photoperiodism** the physiological responses of plants and animals to the length of day.
- photosynthesis the series of chemical reactions in plants that results in

the fixation of carbon from  $CO_2$  into some form of carbohydrate.

- photosynthetically active radiation (PAR) that part of the solar radiation spectrum in the range 0.4 to  $0.7 \ \mu m$  that can be used for photosynthesis by green leaves.
- physiological ecology the subdiscipline of ecology that studies the biochemical, physical, and mechanical adaptations and limitations of plants and animals to their physical and chemical environments.
- **physiological longevity** maximum life span of individuals in a population under specified conditions; the organisms die of senescence.
- phytoplankton plant portion of the plankton; the plant community in marine and freshwater environments that floats free in the water and contains many species of algae and diatoms.
- **Plant Apparency Theory** the hypothesis that herbivores attack plants that are highly visible and common, and the more apparent a plant is to herbivores, the more it must invest in defensive chemicals and structures.
- **plant stress hypothesis** the idea that herbivores prefer to attack stressed plants, which produce leaves that are higher in nitrogen.
- **plant vigor hypothesis** the idea that herbivores prefer to attack fastgrowing, vigorous plants rather than slow-growing, stressed plants.
- **poikilothermic** of or pertaining to cold-blooded animals, organisms that have no rapidly operating heatregulatory mechanism; contrast with *homeothermic*.
- **polyandry** mating of a single female animal with several males.
- polyclimax hypothesis the view of Whittaker that there are several different climax vegetation communities in a region governed by many environmental factors.
- **polygyny** mating of one male animal with several females.
- **pool** the amount of nutrient or biomass in a compartment.
- **population** a group of organisms of the same species occupying a particular space at a particular time.
- **population regulation** the general problem of what prevents populations from growing without limit,

and what determines the average abundance of a species.

- potential evapotranspiration the theoretical depth of water that would evaporate from a standard flat pan over a given time period if water is not limiting, largely dependent on temperature.
- **precipitation** rainfall and snowfall over a specified time period.
- **predation** the action of one organism killing and eating another.
- preemptive initial floristics model the first species at a site take over and prevent others from colonizing the site, emphasizing inhibition as the main mechanism of succession.
- **prey isocline** the contour line of densities of predator and prey at which the prey are in equilibrium; the impact of a predator exactly balances the prey's rate of population growth, so the prey population growth rate is zero.
- **primary production** production by green plants.
- **primary succession** succession occurring on a landscape that has no biological legacy.
- principle universal statement that we all accept because they are mostly definitions, or are ecological translations of physical-chemical laws. For example, "no population increases without limit" is an important ecological principle that must be correct in view of the finite size of the planet Earth.
- **probabilistic models** in contrast to deterministic models, including an element of probability so that repeated runs of the models do not produce exactly the same outcome.
- **production** amount of energy (or material) formed by an individual, population, or community in a specific time period; includes growth and reproduction only; see *primary production, secondary production, gross production, net production.*
- **productivity** a general term that covers all processes involved in ecological *production* studies—carbon fixation, consumption, rejection, leakage, and respiration.
- promiscuity a general term for multiple matings in organisms, called polyandry if multiple males are involved, or polygyny if multiple females; opposite of *monogamy*.

- proximate factors the mechanisms responsible for regulating a particular trait in a physiological or biochemical manner; opposite of *ultimate factors*.
- **push-pull strategies** management strategies that manipulate the behavior of insect pests to make the crop resource unattractive (push) and lure the pests toward an attractive source (pull) where the pests are destroyed.
- **quadrat** a sampling frame for stationary organisms; a square, circle, or rectangle of a specified size.
- ramet an individual derived by asexual reproduction from a single original zygote, which is able to live independently if separated from the parent organism. Compare with genet.
- random colonization model succession proceeds completely randomly with no fixed sequence or fixed end point.
- **Rapoport's Rule** the generalization that geographic range sizes decrease as one moves from polar to equatorial latitudes, such that range sizes are smaller in the tropics.
- **realized niche** the observed resource use of a species in the presence of competition and other biotic interactions; contrast with *fundamental niche*.
- **reciprocal replacement** two codominant plants retain their presence in the climax community by A replacing B while B replaces A.
- **recruitment** increment to a natural population, usually from young animals or plants entering the adult population.
- Red Queen Hypothesis the coevolution of parasites and their hosts, or predators and their prey, in which improvements in one of the species is countered by evolutionary improvements in the partner species, so that an evolutionary arms race occurs but neither species gains an advantage in the interaction.
- **Redfield ratio** the observed 16:1 atomic ratio of nitrogen to phosphorus found in organisms in the open ocean by A. C. Redfield in  $1934-C_{106}N_{16}P_1$ .
- **regulating factor** a factor is defined as potentially regulating if the percentage of mortality caused by the factor

increases with population density or if per capita reproductive rate decreases with population density.

- **Reid's paradox** the observed large discrepancy between the rapid rate of movement of trees recolonizing areas at the end of the Ice Age and the observed slow dispersal rate of tree seeds spreading by diffusion.
- relative benefit the difference between
  the costs and benefits (= net
  benefit).
- relative density the density of a population in relation to another, specified in terms of larger/smaller without knowing the absolute density.
- **relay floristics** the classical view of succession as specified in the facilitation model.
- **repeated reproduction** organisms that reproduce several times over their life span.
- replacement series an experimental design involving two or more species in competition in which a series of ratios are set out (such as 20:80 or 50:50) and some measure of performance is measured.
- **reproductive value** the contribution an individual female will make to the future population.
- residence time the time a nutrient spends in a given compartment of an ecosystem; equivalent to turnover time.
- resilience magnitude of disturbance that can be absorbed before an ecosystem changes its structure; one aspect of ecosystem stability.
- **Resource Availability Hypothesis** a theory of plant defense that predicts higher plant growth rates will result in less investment in defensive chemicals and structures.
- resource concentration hypothesis the idea that agricultural pests are able to cause serious damage because crops are planted as monocultures at high densities.
- **respiration** complex series of chemical reactions in all organisms by which energy is made available for use; carbon dioxide, water, and energy are the end products.
- *r*-selection the type of natural selection experienced by populations that are undergoing rapid population increase in a relatively empty environment.

- **safe sites** for animals, sites where prey individuals are able to avoid predation; for plants, sites where seeds can germinate and plants can grow.
- sampling model one proposed explanation for Hanski's Rule that the observed relationship between distribution and abundance is an artifact of the difficulty of sampling rare species and does not therefore require a biological explanation.
- **saprophyte** plant that obtains food from dead or decaying organic matter.
- scientific law universal statement that is deterministic and so well corroborated that everyone accepts it as part of the scientific background of knowledge. There are laws in physics, chemistry, and genetics, but not yet in ecology.
- Second Principle of Population Regulation differences between two populations in equilibrium density can be caused by variation in either density-dependent or densityindependent per capita birth and death rates.
- secondary plant substances chemicals produced by plants that are not directly involved in the primary metabolic pathways and whose main function is to repel herbivores.
- secondary production production by herbivores, carnivores, or detritus feeders; contrast with *primary production*.
- secondary succession succession occurring on a landscape that has a biological legacy in the form of seeds, roots, and some live plants.
- self-regulation process of population regulation in which population increase is prevented by a deterioration in the quality of individuals that make up the population; population regulation by adjustments in behavior and physiology within the population rather than by external forces such as predators.
- self-thinning rule the prediction that the regression of organism size versus population density has a slope of -1.5 for plants and animals that have plastic growth rates and variable adult size.

senescence process of aging.

- seral referring to a series of stages that follow one another in an ecological succession.
- serotinous cones cones of some pine trees that remain on the trees for several years without opening and require a fire to open and release the seeds.
- **sessile** attached to an object or fixed in place (e.g., barnacles).
- **shade-intolerant plants** plants that cannot survive and grow in the shade of another plant, requiring open habitats for survival.
- **shade-tolerant plants** plants that can live and grow in the shade of other plants.
- Shelford's law of tolerance the ecological rule first described by Victor Shelford that the geographical distribution of a species will be controlled by that environmental factor for which the organism has the narrowest range of tolerance.
- **sigmoid curve** S-shaped curve; in ecology, often a plot of time (*x*-axis) against population size (*γ*-axis); an example is the logistic curve.
- sink populations local populations in which the rate of production is below replacement level so that extinction is inevitable without a source of immigrants.
- **small-population paradigm** the focus of this approach is on rare species and on the population consequences of rareness, and the abilities of small populations to deal with rarity.
- **soil drought** the lack of water in the soil, less than what is needed for plant survival and growth, caused by a lack of precipitation.
- source populations local populations in which the rate of production exceeds replacement so that individuals emigrate to surrounding populations.
- **specialist predators** predators that eat only one or a very few prey species.
- specialists species that eat only a few foods or live in only one or two habitats; contrast to *generalists*.species richness the number of
- species in a community. species-area curve a plot of the area
- of an island or habitat on the *x*-axis and the number of species in that island or habitat on the

*y*-axis, typically done as a log-log plot and typically restricted to one taxonomic group such as plants or reptiles.

- **stability** absence of fluctuations in populations; ability to withstand perturbations without large changes in composition.
- stabilizing selection natural selection that favors the norm, the most common or average trait in a population, so the population mean stays constant.

**stable age distribution** the age distribution reached by a population growing at a constant rate.

stable point an equilibrium in a mathematical model to which the system converges and remains.

- stage-based matrix model a type of matrix model not based on organism ages but on life history stages, such as larva, pupa, and adult.
- **standard error** a statistical estimate of the precision of an estimate such as the mean.

**static life table** a life table constructed at a single point in time by doing a cross section of a population.

- **statics** in population ecology, the study of the reasons of equilibrium conditions or average values; contrast with *dynamics*.
- stationary age distribution the age distribution that is reached in a population that is constant in size over time because the birth rate equals the death rate.

steppe extensive area of natural, dry grassland; usually used in reference to grasslands in southwestern Asia and southeastern Europe; equivalent to prairie in North American usage.

- sterile-insect technique the release of large numbers of sterilized males to mate with wild females and prevent the fertilization of eggs and production of viable young.
- sterol any of a group of solid, mostly unsaturated polycyclic alcohols, such as cholesterol or ergosterol, derived from plants and animals.
- **stochastic** based on probability, as in coin-flipping.
- stochastic model mathematical model based on probabilities; the prediction of the model is not a single fixed number but a range of possible numbers; opposite of *deterministic model*.

**stock** the harvestable part of the population being exploited.

- **stock-recruit relationship** a key graph relating how many recruits come into the exploited population from a given population of adults.
- stress a condition occurring in response to adverse external influences and capable of affecting the performance of an organism, for example, in plants in a drought.
- **sublethal effects** any pathogenic effects that reduce the well-being of an individual without causing death.
- **sublittoral** lower division in the sea from a depth of 40 to 60 meters to about 200 meters; below the littoral zone.
- **succession** replacement of one kind of community by another kind; the progressive changes in vegetation and animal life that may culminate in the *climax state*.
- supply-side ecology the view that population dynamics are driven by immigration of seeds or juveniles from sources extrinsic to the local population, so there is no local control of recruitment processes.
- sustainability the characteristic of a process that can be maintained at a certain level indefinitely, often used in an economic and environmental context. Many definitions have been suggested. The original one of the Bruntland Commission of 1987 defined sustainable development as development that meets the needs of the present without compromising the ability of future generations to meet their own needs.
- **symbiosis** in a broad sense, the living together of two or more organisms of different species; in a narrow sense, synonymous with *mutualism*.
- synecology study of groups of organisms in relation to their environment; includes population, community, and ecosystem ecology.
- taiga the northern boreal forest zone, a broad band of coniferous forest south of the arctic tundra.
- tannins a class of secondary compounds produced by plants (and present in tea and coffee) that reduce the digestibility of plant tissues eaten by herbivores; tannins have been used for centuries to tan animal hides.

- **tens rule** the rule of thumb that 1 species in 10 alien species imported into a country becomes introduced, 1 in 10 of the introduced species becomes established, and 1 in 10 of the established species becomes a pest.
- territory any defended area.
- theory an integrated and hierarchical set of empirical hypotheses that together explain a significant fraction of scientific observations. The theory of evolution is perhaps the most frequently used theory in ecology.
- **thermoregulation** maintenance or regulation of temperature, specifically the maintenance of a particular temperature of the living body.
- theta-logistic model the modification of the original logistic equation to permit curved relationships between population density and the rate of population increase.
- tillers ramets, the modular unit of construction, for example, in grasses.
- time lags in population models, basing a parameter on past events, such as basing population growth rate on the density of the population last year or the year before.
- **tolerance model** the view that plants in a successional sequence do not interact with one another in either a negative or a positive manner.
- **top-down model** the idea that community organization is set by the effects of carnivores on herbivores and herbivores on plants in the food chain.
- total fertility rate number of children a woman could expect to produce in her lifetime if the birth rate were held constant at current conditions.
- total response the total losses imposed on a prey species by a combination of the numerical, functional, aggregative, and developmental responses of a predator species.
- trace element chemical element used by organisms in minute quantities and essential to their physiology.
- trade-offs compromises between two desirable but incompatible activities.
- tragedy of the commons the inherent tendency for overexploitation of resources that have free access and unlimited demand, so that it pays

the individual to continue harvesting beyond the limits dictated by the common good of sustainability.

- transitive competition a linear competitive network in which A wins over B and B wins over C, so that the results of competition reach a final state of competitive exclusion.
- treeline the altitude on a mountain above which no trees can survive, equivalent of timberline.
- trophic cascade model the idea that a strict top-down model applies to community organization so that impacts flow down the food chain as a series of + and – impacts on successive trophic levels.
- **trophic efficiency** net production at one trophic level as a fraction of net production of the next lower trophic level.
- trophic levels classification of organisms based on their source of energy—i.e., primary producers, herbivores, carnivores, and higher carnivores.

- tundra treeless area in arctic and alpine regions, varying from a bare area to various types of vegetation consisting of grasses, sedges, forbs, dwarf shrubs, lichens, and mosses.
  ultimate factors the evolutionary reason for an adaptation or why a trait is maintained in a population; op-
- posite of *proximate factors*. **umbrella species** in conservation biology, species that serve as a proxy for entire communities and ecosystems, so that the entire system is con-
- so that the entire system is conserved if they are conserved. unitary organisms organisms appear as individual units with a definite
- growth form, like most animals. **univoltine** refers to an organism that
- has only one generation per year. **unstable point** an equilibrium in a mathematical model from which the system diverges and does not remain.
- vector organism organism (often an insect) that transmits a pathogenic virus, bacterium, protozoan, or fungus from one organism to another.

- virulence the degree or ability of a pathogenic organism to cause disease; often measured by the host death rate.
- wilting point measure of soil water; the water remaining in the soil (expressed as percentage of dry weight of the soil) when the plants are in a state of permanent wilting from water shortage.
- **xeric** deficient in available moisture for the support of life (e.g., desert environments).
- **xerophyte** plant that can grow in dry places (e.g., cactus).
- yield amount of usable material taken from a harvested population, measured in numbers or biomass.
- zooplankton animal portion of the plankton; the animal community in marine and freshwater environments that floats free in the water, independent of the shore and the bottom, moving passively with the currents.

# Introduction to the Science of Ecology

## Key Concepts

- Ecology is the scientific study of the interactions that determine the distribution and abundance of organisms.
- Descriptive ecology forms the essential foundation for functional ecology, which asks *how* systems work, and for evolutionary ecology, which asks *why* natural selection has favored this particular solution.
- Ecological problems can be analyzed using a theoretical approach, a laboratory approach, or a field approach.
- Like other scientists, ecologists observe problems, make hypotheses, and test the predictions of each hypothesis by field or laboratory observations.
- Ecological systems are complex, and simple cause–effect relationships are rare.



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## KEY TERMS

**experiment** Test of a hypothesis. It can be observational (observe the system) or manipulative (perturb the system). The experimental method is the scientific method.

**hypothesis** Universal proposition that suggests explanations for some observed ecological situation. Ecology abounds with hypotheses.

**model** Verbal or mathematical statement of a hypothesis.

**principle** Universal statement that we all accept because they are mostly definitions, or are ecological translations of physical–chemical laws.

**scientific law** Universal statement that is deterministic and so well corroborated that everyone accepts it as part of the scientific background of knowledge. There are laws in physics, chemistry, and genetics, but not yet in ecology.

**theory** An integrated and hierarchical set of empirical hypotheses that together explain a significant fraction of scientific observations. The theory of evolution is perhaps the most frequently used theory in ecology.

## Introduction to the Science of Ecology

You are embarking on a study of ecology, the most integrative discipline in the biological sciences. The purpose of this chapter is to get you started by defining the subject, providing a small amount of background history, and introducing the broad concepts that will serve as a road map for the details to come.

## **Definition of Ecology**

The word *ecology* came into use in the second half of the nineteenth century. Ernst Haeckel in 1869 defined ecology as the total relations of the animal to both its organic and its inorganic environment. This very broad definition has provoked some authors to point out that if this is ecology, there is very little that is *not* ecology. Four biological disciplines are closely related to ecology—genetics, evolution, physiology, and behavior (**Figure 1**). Broadly interpreted, ecology overlaps each of these four subjects; hence, we need a more restrictive definition.



Figure 1 The four biological disciplines closely related to ecology.

Charles Elton in his pioneering book Animal Ecology (1927) defined ecology as scientific natural history. Although this definition points out the origin of many of our ecological problems, it is again uncomfortably vague. In 1963 Eugene Odum defined ecology as the study of the structure and function of nature. This statement emphasizes the form-and-function idea that permeates biology, but it is still not a completely clear definition. A clear but restrictive definition of ecology is this: Ecology is the scientific study of the distribution and abundance of organisms (Andrewartha 1961). This definition is static and leaves out the important idea of relationships. Because ecology is about relationships, we can modify Andrewartha's definition to make a precise definition of **ecology**: Ecology is the scientific study of the interactions that determine the distribution and abundance of organisms.

This definition of ecology appropriately constrains the scope of our quest, and is the meaning that will be adopted in this chapter. To better understand what ecology is, we need to know what is special about scientific studies, and what is meant by distribution and abundance. **Distribution**—where organisms are found—and **abundance**—how many organisms are found in a given area—are key facts that must be determined before we can address the most difficult question: *Why* this particular distribution, *why* this abundance? We seek the causeand-effect relationships that govern distribution and abundance.

## History of Ecology

The historical roots of ecology are varied, and in this section we will explore briefly some of the origins of ecological ideas. We are not the first humans to think about ecological problems. The roots of ecology lie in natural history. Primitive tribes, for example—who depended on hunting, fishing, and food gathering—needed detailed knowledge of where and when their quarry might be found. The establishment of agriculture also increased the need to learn about the ecology of plants and domestic animals. Agriculture today is a special form of applied ecology.

Outbreaks of pests such as locusts in the Middle East and North Africa or rats in rice crops in Asia are not new problems in agriculture. Spectacular plagues of animals attracted the attention of the earliest writers. The Egyptians and Babylonians feared locust plagues (Figure 2), often attributing them to supernatural powers (Exodus 7:14-12:30). In the fourth century B.C., Aristotle tried to explain plagues of field mice and locusts in Historia Animalium. He pointed out that the high reproductive rate of field mice could produce more mice than could be reduced by their natural predators, such as foxes and ferrets, or by the control efforts of humans. Nothing succeeded in reducing these mouse plagues, Aristotle stated, except the rain, and after heavy rains the mice disappeared rapidly. And even today, Australian wheat farmers face plagues of house mice, and ask the same question: How can we get rid of these pests?

Pests are a problem for people because they violate our feeling of harmony or balance in the environment. Ecological harmony was a guiding principle basic to the Greeks' understanding of nature. The historian Frank Egerton (1968a) has traced this concept from ancient times to the modern term *balance of nature*. The concept of *providential ecology*, in which nature is designed to benefit and preserve each species, was implicit in the writings of Herodotus and Plato. A major assumption of this concept was that the number of every species remained essentially constant. Outbreaks of some populations were acknowledged, but were usually attributed to divine punishment. And since each species had a special place in nature, extinction could not occur because it would disrupt the balance and harmony in nature.



Figure 2 A young girl looks at a dense swarm of the desert locust in North Africa.

How did we get from these early Greek and Roman ideas about harmony to our modern understanding? A combination of mathematics and natural history paved the way. By the seventeenth century students of natural history and human ecology began to focus on population ecology and to construct a quantitative framework. Graunt, who in 1662 described human population change in quantitative terms, can be called the "father of demography"1 (Cole 1958). He recognized the importance of measuring birth rates, death rates, and age structure of human populations, and he complained about the inadequate census data available in England in the seventeenth century. Graunt estimated the potential rate of population growth for London, and concluded that even without immigration, London's population would double in 64 years.

Today, human population growth is an increasing concern, but population growth was not always measured quantitatively for animals and plants. Leeuwenhoek made one of the first attempts to calculate theoretical rates of increase for an animal species (Egerton 1968b). He studied the reproductive rate of grain beetles, carrion flies, and human lice, counting the number of eggs laid by female carrion flies and calculating that one pair of flies could produce 746,496 flies in three months.

By the eighteenth century, natural history had become an important cultural occupation. Buffon, who authored Natural History (1756), touched on many of our modern ecological problems and recognized that populations of humans, other animals, and plants are subjected to the same processes. Buffon discussed, for example, how the great fertility of every species was counterbalanced by innumerable agents of destruction. He believed that plague populations of field mice were checked partly by diseases and scarcity of food. Buffon did not accept Aristotle's idea that heavy rains caused the decline of dense mouse populations, but thought instead that control was achieved by biological agents. Rabbits, he stated, would reduce the countryside to a desert if it were not for their predators. If the Australians had listened to Buffon before they introduced rabbits to their environment in 1859, they could have saved their rangelands from destruction (Figure 3). Buffon in 1756 was dealing with problems of population regulation that are still unsolved today.

Malthus, the most famous of the early demographers, published one of the earliest controversial books on demography, *Essay on Population* (1798). He calculated that although the number of organisms can increase geometrically (1, 2, 4, 8, 16, ...), food supply can

<sup>&</sup>lt;sup>1</sup>Demography originated as the study of human population growth and decline. It is now used as a more general term that includes plant and animal population changes.



**Figure 3 European rabbit overpopulation in eastern Australia.** Rabbits were introduced to Australia in 1859 and have become a serious pest because of their abundance. Their burrowing increased soil erosion, and they competed with sheep and cattle for forage.

never increase faster than arithmetically  $(1, 2, 3, 4, \ldots)$ . The arithmetic rate of increase in food production seems to be somewhat arbitrary. The great disproportion between these two powers of increase led Malthus to infer that reproduction must eventually be checked by food production. What prevents populations from reaching the point at which they deplete their food supply? What checks operate against the tendency toward a geometric rate of increase? Two centuries later we still ask these questions. These ideas were not new; Machiavelli had said much the same thing around 1525, as did Buffon in 1751, and several others had anticipated Malthus. It was Malthus, however, who brought these ideas to general attention. Darwin used the reasoning of Malthus as one of the bases for his theory of natural selection. The struggle for existence results from the high reproductive output of species.

Other workers questioned the ideas of Malthus and made different predictions for human populations. For example, in 1841 Doubleday put forward the True Law of Population. He believed that whenever a species was threatened, nature made a corresponding effort to preserve it by increasing the fertility of its members. Human populations that were undernourished had the highest fertility; those that were well fed had the lowest fertility. You can make the same observations by looking around the world today (**Table 1**). Doubleday explained these effects by the oversupply of mineral nutrients in well-fed populations. Doubleday observed a basic fact that we recognize today: low birth rates occur in wealthy countries although his explanations were completely wrong.

Interest in the mathematical aspects of demography increased after Malthus. Can we describe a mathemati-

# Table 1Total fertility rate of human<br/>populations and gross national<br/>income per person in selected<br/>countries of the globe in 2007.

Country	Total fertility rate	Gross national income per person
Sudan	4.5	2160
Gambia	5.1	1970
Niger	7.1	830
Tanzania	5.4	740
Botswana	3.1	12,240
South Africa	2.7	11,710
Canada	1.5	34,610
United States	2.1	44,260
Costa Rica	1.9	10,770
Mexico	2.4	11,330
Haiti	4.0	1490
Brazil	2.3	8800
Peru	2.5	6070
Turkey	2.2	9060
India	2.9	3800
Pakistan	4.1	2500
Indonesia	2.4	3950
China	1.6	7730
Japan	1.3	33,730
Sweden	1.9	34,780
Switzerland	1.4	40,630
Russia	1.3	11,620
Italy	1.4	29,840
Solomon Islands	4.5	2170

The total fertility rate is the average number of children a woman would have, assuming no change in birth rates. The gross national income (GNI) is in U.S. dollars per person. (Data from 2007 World Population Data Sheet.)

cal law of population growth? Quetelet, a Belgian statistician, suggested in 1835 that the growth of a population was checked by factors opposing population growth. In 1838 his student Pierre-François Verhulst derived an equation describing the initial rapid growth and eventual leveling off of a population over time. This S-shaped curve he called the logistic curve. His work was overlooked until modern times, but it is fundamentally important, and we will return to it later in detail.

Until the nineteenth century, philosophical thinking had not changed from the idea of Plato's day that there was harmony in nature. Providential design was still the guiding light. In the late eighteenth and early nineteenth centuries, two ideas that undermined the idea of the balance of nature gradually gained support: (1) that many species had become extinct and (2) that resources are limited and competition caused by population pressure is important in nature. The consequences of these two ideas became clear with the work of Malthus, Lyell, Spencer, and Darwin in the nineteenth century. Providential ecology and the balance of nature were replaced by natural selection and the struggle for existence (Egerton 1968c).

The balance of nature idea, redefined after Darwin, has continued to persist in modern ecology (Pimm 1991). The idea that natural systems are stable and in equilibrium with their environments unless humans disturb them is still accepted by many ecologists and theoreticians.

Humans must eat, and many of the early developments in ecology came from the applied fields of agriculture and fisheries. Insect pests of crops have been one focus of work. Before the advent of modern chemistry, biological control was the only feasible approach. In 1762 the mynah bird was introduced from India to the island of Mauritius to control the red locust; by 1770 the locust threat was a negligible problem (Moutia and Mamet 1946). Forskål wrote in 1775 about the introduction of predatory ants from nearby mountains into date-palm orchards to control other species of ants feeding on the palms in southwestern Arabia. In subsequent years, an increasing knowledge of insect parasitism and predation led to many such introductions all over the world in the hope of controlling nonnative and native agricultural pests (De Bach 1974).

Medical work on infectious diseases such as malaria in the late 1800s gave rise to the study of epidemiology and interest in the spread of disease through a population. Malaria is still one of the great scourges of humans. In 1900 no one even knew the cause of the disease. Once mosquitoes were pinpointed as the vectors, medical workers realized that it was necessary to know in detail the ecology of mosquitoes. The pioneering work of Robert Ross (1911) attempted to describe in mathematical terms the propagation of malaria, which is transmitted by mosquitoes. In an infected area, the propagation of malaria is determined by two continuous and simultaneous processes: (1) The number of new infections among people depends on the number and infectivity of mosquitoes, and (2) the infectivity of mosquitoes depends on the number of people in the locality and the frequency of malaria among them. Ross

could write these two processes as two simultaneous differential equations:

$\begin{pmatrix} \text{Rate of increase of} \\ \text{infected humans} \end{pmatrix} = \begin{pmatrix} \text{New infections} \\ \text{per unit time} \end{pmatrix} - \begin{pmatrix} \text{Recoveries per} \\ \text{unit time} \end{pmatrix}$
$\downarrow$
(Depends on number of infected mosquitoes)
$\begin{pmatrix} \text{Rate of increase of} \\ \text{infected mosquitoes} \end{pmatrix} = \begin{pmatrix} \text{New infections} \\ \text{per unit time} \end{pmatrix} - \begin{pmatrix} \text{Death of infected} \\ \text{per unit time} \end{pmatrix}$
(Depends on number of infected humans)

Ross had described an ecological process with a mathematical model, and his work represents a pioneering parasite-host model of species interactions. Such models can help us to clarify the problem—we can analyze the components of the model—and predict the spread of malaria or other diseases.

Production ecology, the study of the harvestable yields of plants and animals, had its beginnings in agriculture, and Egerton (1969) traced this back to the eighteenthcentury botanist Richard Bradley. Bradley recognized the fundamental similarities of animal and plant production, and he proposed methods of maximizing agricultural yields (and hence profits) for wine grapes, trees, poultry, rabbits, and fish. The conceptual framework that Bradley used—monetary investment versus profit—is now called the "optimum-yield problem" and is a central issue in applied ecology.

Individual species do not exist in a vacuum, but instead in a matrix of other species with which they interact. Recognition of communities of living organisms in nature is very old, but specific recognition of the interrelations of the organisms in a community is relatively recent. Edward Forbes in 1844 described the distribution of animals in British coastal waters and part of the Mediterranean Sea, and he wrote of zones of differing depths that were distinguished by the associations of species they contained. Forbes noted that some species are found only in one zone, and that other species have a maximum of development in one zone but occur sparsely in other adjacent zones. Mingled in are stragglers that do not fit the zonation pattern. Forbes recognized the dynamic aspect of the interrelations between these organisms and their environment. As the environment changed, one species might die out, and another might increase in abundance. Karl Möbius expressed similar ideas in 1877 in a classic essay on the oyster-bed community as a unified collection of species.

Studies of communities were greatly influenced by the Danish botanist J. E. B. Warming (1895, 1909), one of the fathers of plant ecology. Warming was the first plant ecologist to ask questions about the composition of plant communities and the associations of species that made up these communities. The dynamics of vegetation change was emphasized first by North American plant ecologists. In 1899 H. C. Cowles described plant succession on the sand dunes at the southern end of Lake Michigan. The development of vegetation was analyzed by the American ecologist Frederick Clements (1916) in a classic book that began a long controversy about the nature of the community.

With the recognition of the broad problems of populations and communities, ecology was by 1900 on the road to becoming a science. Its roots lay in natural history, human demography, biometry (statistical approach), and applied problems of agriculture and medicine.

The development of ecology during the twentieth century followed the lines developed by naturalists during the nineteenth century. The struggle to understand how nature works has been carried on by a collection of colorful characters quite unlike the mythical stereotypes of scientists. From Alfred Lotka, who worked for the Metropolitan Life Insurance Company in New York while laying the groundwork of mathematical ecology (Kingsland 1995), to Charles Elton, the British ecologist who wrote the first animal ecology textbook in 1927 and founded the Bureau of Animal Population at Oxford (Crowcroft 1991), ecology has blossomed with an increasing understanding of our world and how we humans affect its ecological systems (McIntosh 1985).

Until the 1970s ecology was not considered by society to be an important science. The continuing increase of the human population and the associated destruction of natural environments with pesticides and pollutants awakened the public to the world of ecology. Much of this recent interest centers on the human environment and human ecology, and is called environmentalism. Unfortunately, the word *ecology* became identified in the public mind with the much narrower problems of the human environment, and came to mean everything and anything about the environment, especially human impact on the environment and its social ramifications. It is important to distinguish ecology from environmental studies.

Ecology is focused on the natural world of animals and plants, and includes humans as a very significant species by virtue of its impact. Environmental studies is the analysis of human impact on the environment of the Earth-physical, chemical, and biological. Environmental studies as a discipline is much broader than ecology because it deals with many natural sciencesincluding ecology, geology, and climatology—as well as with social sciences, such as sociology, economics, anthropology, political science, and philosophy. The science of ecology is not solely concerned with human impact on the environment but with the interrelations of all plants and animals. As such, ecology has much to contribute to some of the broad questions about humans and their environment that are an important scientific component of environmental studies.

Environmental studies have led to "environmentalism" and "deep ecology," social movements with an important agenda for political and social change intended to minimize human impact on the Earth. These social and political movements are indeed important and are supported by many ecologists, but they are not the science of ecology. Ecology should be to environmental science as physics is to engineering. Just as we humans are constrained by the laws of physics when we build airplanes and bridges, so also are we constrained by the principles of ecology when altering the environment.

Ecological research can shed light on what will happen when global temperatures increase as a result of increasing  $CO_2$  emissions, but it will not tell us what we *ought* to do about these emissions, or whether increased global temperature is good or bad. Ecological scientists are not policy makers or moral authorities, and should not as scientists make ethical or political recommendations. However, on a personal level, most ecologists are concerned about the extinction of species and would like to prevent extinctions. Many ecologists work hard in the political arena to achieve the social goals of environmentalism.

## Basic Problems and Approaches to Ecology

We can approach the study of ecology from three points of view: descriptive, functional, or evolutionary. The descriptive point of view is mainly natural history and describes the vegetation groups of the world-such as the temperate deciduous forests, tropical rain forests, grasslands, and tundra-and the animals and plants and their interactions within each of these ecosystems. The descriptive approach is the foundation of all of ecological science, and while much of the world has been reasonably described in terms of its vegetation and animal life, some areas are still poorly studied and poorly described. The functional point of view, on the other hand, is oriented more toward dynamics and relationships, and seeks to identify and analyze general problems common to most or all of the different ecosystems. Functional studies deal with populations and communities as they exist and can be measured now. Functional ecology studies proximate causes—the dynamic responses of populations and communities to immediate factors of the environment. Evolutionary ecology studies ultimate causes-the historical reasons why natural selection has favored the particular adaptations we now see. The evolutionary point of view considers organisms and relationships between organisms as historical products of evolution. Functional ecologists ask how: How does the system operate? Evolutionary ecologists ask *why*: Why does natural selection favor this particular ecological solution? Since evolution not only has occurred in the past but is also going on in the present, the evolutionary ecologist must work closely with the functional ecologist to understand ecological systems (Pianka 1994). Because the environment of an organism contains all the selective forces

## ESSAY

## Science and Values in Ecology

Science is thought by many people to be value free, but this is certainly not the case. Values are woven all through the tapestry of science. All applied science is done because of value judgments. Medical research is a good example of basic research applied to human health that virtually everyone supports. Weapons research is carried out because countries wish to be able to defend themselves against military aggression.

In ecology the strongest discussions about values have involved conservation biology. Should conservation biologists be objective scientists studying biodiversity, or should they be public advocates for preserving biodiversity? The preservation of biodiversity is a value that often conflicts with other values—for example, clear-cut logging that produces jobs and wood products. The pages of the journal *Conservation Biology* are peppered with this discussion about advocacy (see, for example, *Conservation* 

There will always be a healthy tension between scientific knowledge and public policy in environmental matters . . .

*Biology* February 2007 issue, Brussard and Tull 2007, Scott et al. 2007).

Scientists in fact have a dual role. First, they carry out objective science that both obtains data and tests hypotheses about ecological systems. They can also be advocates for particular policies that attempt to change society, such as the use of electric cars to reduce air pollution. But it is crucial to separate these two kinds of activities.

Science is a way of knowing, a method for determining the principles by which systems like ecological systems operate. The key scientific virtues are honesty and objectivity in the search for truth. Scientists assume that once we know these scientific principles we can devise effective policies to achieve social goals. All members of society collectively decide on what social goals we will pursue, and civic responsibility is part of the job of everyone, scientists included. There will always be a healthy tension between scientific knowledge and public policy in environmental matters because there are always several ways of reaching a particular policy goal. The debates over public policy in research funding and environmental matters will continue, so please join in.

that shape its evolution, ecology and evolution are two viewpoints of the same reality.

All three approaches to ecology have their strengths, but the important point is that we need all three to produce good science. The descriptive approach is absolutely fundamental because unless we have a good description of nature, we cannot construct good theories or good explanations. The descriptive approach provides us maps of geographical distributions and estimates of relative abundances of different species. With the functional approach, we need the detailed biological knowledge that natural history brings if we are to discover how ecological systems operate. The evolutionary approach needs good natural history and good functional ecology to speculate about past events and to suggest hypotheses that can be tested in the real world. No single approach can encompass all ecological questions. This chapter uses a mixture of all three approaches and emphasizes the general problems ecologists try to understand.

The basic problem of ecology is to determine the causes of the distribution and abundance of organisms. Every organism lives in a matrix of space and time. Consequently, the concepts of distribution and abundance are closely related, although at first glance they may seem

quite distinct. What we observe for many species is that the numbers of individuals in an area vary in space, so if we make a contour map of a species' geographical distribution, we might get something similar to **Figure 4**.



Figure 4 Schematic contour map of the abundance of a plant or animal species.



**Figure 5** Abundance of the horned lark in North America from 1994 to 2003. Data are from the Breeding Bird Survey (BBS). Maximal abundance of this bird is reached in the short grass prairie of western Kansas and Nebraska and eastern Colorado. (From Sauer et al. 2005.)

**Figure 5** illustrates this idea for the horned lark of North America. Horned larks are most common in the prairies of eastern Colorado and in western Kansas and Nebraska, and are absent altogether in Florida. Why should these patterns of abundance occur? Why does abundance decline as one approaches the edge of a species' geographic range? What limits the eastern and northern extension of the horned lark's range? These are examples of the fundamental questions an ecologist must ask of nature.

Similarly, the red kangaroo occurs throughout the arid zone of Australia (**Figure 6**). It is absent from the tropical areas of northern Australia and most common in western New South Wales and central Queensland. Why

are there no red kangaroos in tropical Australia? Why is this species absent from Victoria in southern Australia and from Tasmania? We can view the average density of any species as a contour map, with the provision that the contour map may change with time. Throughout the area of distribution, the abundance of an organism must be greater than zero, and the limit of distribution equals the contour of zero abundance. Distribution may be considered a facet of abundance, and distribution and abundance may be said to be reverse sides of the same coin (Andrewartha and Birch 1954). The factors that affect the distribution of a species may also affect its abundance.

The problems of distribution and abundance can be analyzed at the level of the population of a single



**Figure 6 Distribution and abundance of the red kangaroo in Australia.** Data from aerial surveys, 1980–1982. (From Caughley et al. 1987.)

species or at the level of a community, which contains many species. The complexity of the analysis may increase as more and more species are considered in a community; consequently, we will first consider the simpler problems involving single-species populations.

Considerable overlap exists between ecology and its related disciplines. Environmental physiology has developed a wealth of information that is needed to analyze problems of distribution and abundance. Population genetics and ecological genetics are two additional foci of interest that we touch on only peripherally. Behavioral ecology is another interdisciplinary area that has implications for the study of distribution and abundance. Evolutionary ecology is an important focus for problems of adaptation and studies of natural selection in populations. Each of these disciplines can become an area of study entirely on its own.

## Levels of Integration

In ecology we are dealing primarily with the five starred (\*) levels of integration, as shown in **Figure 7**. At one end of the spectrum, ecology overlaps with environmental physiology and behavioral studies of individual organisms, and at the other end, ecology merges into meteorology, geology, and geochemistry as we consider landscapes. Landscapes can be aggregated to include the whole-Earth ecosystem, which is called the **ecosphere** or the **biosphere**. The important message is that the boundaries of the sciences are not sharp but diffuse, and nature does not come in discrete packages.

Each level of integration involves a separate and distinct series of attributes and problems. For example, a population has a density (e.g., number of deer per square kilometer), a property that cannot be attributed



Figure 7 Levels of integration studied in biology.

to an individual organism. A community has biodiversity (or species richness), an attribute without meaning at the population level. In general, a scientist dealing with a particular level of integration seeks explanatory mechanisms from lower levels of integration and biological significance from higher levels. For example, to understand mechanisms of changes in a population, an ecologist might study mechanisms that operate on the behavior and physiology of individual organisms, and might try to view the significance of these population events within a community and ecosystem framework.

Much of modern biology is highly reductionistic, as it attempts to work out the physical-chemical basis of life. A good example is the Human Genome Project, an expensive and highly targeted research program to sequence all the genes on human chromosomes. The Human Genome Project is now completed, yet we do not know how many species of beetles live on the Earth, or how many species of trees there are in the Amazon basin. It should not surprise you that the amount of scientific understanding varies with the level of integration. We know an enormous amount about the molecular and cellular levels of organisms, organs and organ systems, and whole organisms, but we know relatively little about populations and even less about communities and ecosystems. This point is illustrated by looking at the levels of integration: Ecology constitutes more than one-third of the levels of biology, but no biology curriculum can be one-third ecology and do justice to current biological knowledge. The reasons for this are not hard to find; they include the increasing complexity of these higher levels and the difficulties involved in dealing with them in the laboratory.

This decrease in understanding at the higher levels has serious implications. You will not find in ecology the strong theoretical framework that you find in physics, chemistry, molecular biology, or genetics. It is not always easy to see where the pieces fit in ecology, and we will encounter many isolated parts of ecology that are well developed theoretically but are not clearly connected to anything else. This is typical of a young science. Many students unfortunately think of science as a monumental pile of facts that must be memorized. But science is more than a pile of precise facts; it is a search for systematic relations, for explanations to problems in the physical world, and for unifying concepts. This is the growing end of science, so evident in a young science like ecology. It involves many unanswered questions and much more controversy.

The theoretical framework of ecology may be weaker than we would like at the present time, but this must not be interpreted as a terminal condition. Chemistry in the eighteenth century was perhaps in a comparable state of theoretical development as ecology at the present time. Sciences are not static, and ecology is in a strong growth phase.

## Methods of Approach to Ecology

Ecology has been approached on three broad fronts: the theoretical, the laboratory, and the field. These three approaches are interrelated, but some problems have arisen when the results of one approach fail to verify those of another. For example, theoretical predictions may not be borne out by field data. We are primarily interested in understanding the distribution and abundance of organisms in nature—that is, in the field. Consequently, the descriptive ecology of populations, communities, and ecosystems will always be our basis for comparison, our basic standard.

Plant and animal ecology have tended to develop along separate paths. Historically, plant ecology got off to a faster start than animal ecology, despite the early interest in human demography. Because animals are highly dependent on plants, many of the concepts of animal ecology are patterned on those of plant ecology. Succession is one example. Also, since plants are the source of energy for many animals, to understand animal ecology we must also know a good deal of plant ecology. This is illustrated particularly well in the study of community relationships.

Some important differences, however, separate plant and animal ecology. First, because animals tend to be highly mobile whereas plants are stationary, a whole series of new techniques and ideas must be applied to animals—for example, to determine population density. Second, animals fulfill a greater variety of functional roles in nature—some are herbivores, some are carnivores, some are parasites. This distinction is not complete because there are carnivorous plants and parasitic plants, but the possible interactions are on average more numerous for animals than for plants. During the 1960s population ecology was stimulated by the experimental field approach in which natural populations were manipulated to test specific predictions arising from controversial ecological theory. During these years ecology was transformed from a static, descriptive science to a dynamic, experimental one in which theoretical predictions and field experiments were linked. At the same time, ecologists realized that populations were only parts of larger ecosystems, and that we needed to study communities and ecosystems in the same experimental way as populations. To study a complex ecosystem, teams of ecologists had to be organized and integrated, which was first attempted during the late 1960s and the 1970s.

Modern ecology is advancing particularly strongly in three major areas. First, communities and ecosystems are being studied with experimental techniques and analyzed as systems of interacting species that process nutrients and energy. Insights into ecosystems have been provided by the comparative studies of communities on different continents. Second, modern evolutionary thinking is being combined with ecological studies to provide an explanation of how evolution by natural selection has molded the ecological patterns we observe today. Behavioral ecology is a particularly strong and expanding area combining evolutionary insights with the ecology of individual animals. Third, conservation biology is becoming a dominant theme in scientific and political arenas, and this has increased the need for ecological input in habitat management. All of these developments are providing excitement for students of ecology in this century.

## Application of the Scientific Method to Ecology

The essential features of the scientific method are the same in ecology as in other sciences (Figure 8). An ecologist begins with a problem, often based on natural history observations. For example, pine tree seedlings do not occur in mature hardwood forests on the Piedmont of North Carolina. If the problem is not based on correct observations, all subsequent stages will be useless; thus, accurate natural history is a prerequisite for all ecological studies. Given a problem, an ecologist suggests a possible answer, which is called a **hypothesis**—a statement of cause and effect. In many cases, several answers might be possible, and several different hypotheses can be proposed to explain the observations. Hypotheses arise from previous research, intuition, or inspiration. The origin of a hypothesis tells us nothing about its likelihood of being correct.

A hypothesis makes predictions, and the more precise predictions it makes the better. Predictions follow logically from the hypothesis, and mathematical reason-



Figure 8 Schematic illustration of the scientific method as applied to ecological questions.

ing is the most useful way to check on the logic of predictions. An example of a hypothesis is that pines do not grow under hardwoods because of a shortage of light. Alternative hypotheses might be that the cause is a shortage of pine seeds, or a shortage of soil water. Predictions from simple hypotheses like these are often straightforward: If you provide more light, pine seedlings will grow (under the light hypothesis). A hypothesis is tested by making observations to check the predictions—an experiment. An **experiment** is defined as any set of observations that test a hypothesis. Experiments can be manipulative or natural. We could provide light artificially under the mature forest canopy, or we could look for natural gaps in the forest canopy. The protocol for the experiments and the data to be obtained are called

#### ESSAY

## **On Ecological Truth**

We wish our scientists to speak the truth, and when politicians bend the truth they lose credibility. What is truth, and what in particular is the hallmark of ecological truth? The notion of truth is a profound one that philosophers discuss in detail and scientists just assume is simple.

Truth consists of correspondence with the facts. If we say that there are 23 elephants in a particular herd in the Serengeti, we are stating an ecological truth because we assume that if another person counted the elephants, he or she would get the same number. These kinds of facts are relatively simple, and scientists rarely get into arguments about them. Where arguments start is in the inferences that are drawn from whole sets of facts. For example, if we had counts of the same elephant herd over 20 years, and numbers were continually falling, we could say that this elephant population is declining in size. This statement is also an ecological truth if we have done our counting well and recorded all the data correctly.

But now suppose we wish to state that the elephant population is declining and that a disease is the cause of this decline. Is this statement an ecological truth? It is better to consider it an ecological hypothesis and to outline the predictions it makes about what we will find if we search for a disease organism in elephants dying in this particular area. We now enter a gray zone in which ecological truth is approximately equivalent to a supported hypothesis, one in which we checked the predictions and found them to be correct. But if a scientist wished to extend this argument to state that elephant populations all over east Africa are collapsing because of this disease, this is a more general hypothesis, and before we can consider it an ecological truth we would need to test its predictions by studying many more populations of elephants and their diseases. Many of our ecological ideas are in this incomplete stage because we lack the time, money, or personnel to gather the data to decide whether the general hypothesis is correct. So ecologists, like other scientists, must then face the key question of how to deal with uncertainty when we do not know if we have an ecological truth or not.

The central idea of this principle is to do no harm to the environment, to take no action that is not reversible, and to avoid risk.

The key resolution to this dilemma for environmental management has been the precautionary principle: "Look before you leap," or "An ounce of prevention is worth a pound of cure." The precautionary principle is the ecological equivalent of part of the Hippocratic Oath in medicine: "Physician, do no harm." The central idea of this principle is to do no harm to the environment, to take no action that is not reversible, and to avoid risk. Ecological truth is never obvious in complex environmental issues and emerges more slowly than we might like, so we cannot wait for truth or certainty before deciding what to do about emerging problems in the environment, whether they concern declining elephant populations or introduced pest species.

the experimental design. Using the data that result from the experiments, we either accept or reject the hypothesis. And so the cycle begins again (Figure 8).

Many qualifications need to be attached to this simple scheme. Popper (1963) pointed out that we should always look for evidence that falsifies a hypothesis, and that progress in science consists of getting rid of incorrect ideas. In practice, we cannot achieve this ideal. We should also prefer simple hypotheses over complex ones, according to Popper, because we can reject simple hypotheses more quickly. This does not mean that we must be simpleminded. On the contrary, in ecology we must deal with complex hypotheses because the natural world is not simple. Every hypothesis must predict something and forbid other things from happening. The predictions of a hypothesis must say exactly what it allows and what it forbids. If a hypothesis predicts everything and forbids nothing, it is quite useless in science. The light hypothesis for pine seedlings both predicts more seedlings if you add more light and forbids more seedlings if you add more water.

Ecological systems are complex, and this causes difficulty in applying the simple method outlined in Figure 8. In some cases factors operate together, so it may not be a situation of light *or* water for pine seedlings but one of light *and* water. Systems in which many factors operate together are most difficult to analyze, and ecologists must be alert for their presence (Quinn and Dunham 1983). The principle, however, remains—no matter how complex the hypothesis, it must make some predictions that we can check in the physical world.

All ecological systems have an evolutionary history, and this provides another fertile source of possible explanations. There is controversy in ecology about whether one needs to invoke evolutionary history to explain present-day population and community dynamics. Evolutionary hypotheses can be tested as Darwin did, by comparative methods but not by manipulative experiments (Diamond 1986).

Ecological hypotheses may be statistical in nature, but they do not fall into the "either A or B" category of hypotheses. Statistical hypotheses postulate quantitative relationships. For example, in North Carolina forests, pine seedling abundance (per m<sup>2</sup>) is linearly related to incident light in summer. Tests of statistical hypotheses are well understood and are discussed in all statistics textbooks. They are tested in the same way indicated in Figure 8.

Some ecological hypotheses have been very fruitful in stimulating work, even though they are known to be incorrect. The progress of ecology, and of science in general, occurs in many ways, using mathematical models, laboratory experiments, and field studies.

#### **Review Questions and Problems**

- 1 Discuss the connotation of the words *ecologist* and *environmentalist*. Would you like to be labeled either of these names? Where in a public ranking of preferred professions would these two fall?
- 2 Look up the definition of *environment* in several standard dictionaries and in the *Oxford Dictionary of Ecology* (2006), and compare them. Is it possible to measure the environment of an individual? Are other individuals part of the environment of an individual?
- 3 Is it necessary to define a scientific subject before one can begin to discuss it? Contrast the introduction to several ecology textbooks with those of some areas of physics and chemistry, as well as other biological areas such as genetics and physiology.
- 4 A plant ecologist proposed the following hypothesis to explain the absence of trees from a grassland area: Periodic fires may prevent tree seedlings from becoming established in grassland. Is this a suitable hypothesis? How could you improve it?
- 5 Is it necessary to study the scientific method and the philosophy of science in order to understand how science works? Consider this question before and after reading the essays by Popper (1963) and Platt (1964).
- 6 Discuss the application of the distribution and abundance model to microbes and viruses.

- 7 Quinn and Dunham (1983) argue that the conventional methods of science cannot be applied to ecological questions because there is not just one cause; one effect and many factors act together to produce ecological changes. Discuss the problem of "multiple causes" and how scientists can deal with complex systems that have multiple causes.
- 8 A wildlife ecologist interested in protecting large mammals by means of wolf control analyzed data from six sites at which wolves had been removed for five consecutive years. On three of the sites, the prey species (moose and caribou) had increased, and on three of the sites prey populations did not change. How would you interpret these data in light of Figure 8?
- 9 Plot the data in Table 1 graphically, with gross national product (*x*-axis) versus total fertility rate (*y*-axis). How tight is the relationship between these two variables? Discuss the reasons for the overall form of this relationship, and the reasons why there might be variation or spread in the data.

#### **Overview Question**

Does ecology progress as rapidly as physics? How can we measure progress in the sciences, and what might limit the rate of progress in different sciences? Will there be an "end to science"?

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# Evolution and Ecology

## Key Concepts

- Evolution is the genetic adaptation of organisms to the environment.
- Ecology and evolution are intricately connected because evolution operates through natural selection, which is ecology in action.
- Natural selection may act by directional selection, stabilizing selection, or disruptive selection.
- Evolution results from directional selection, but for most ecological situations, stabilizing selection is most common.
- Natural selection may operate on four different levels: gametic, individual, kin, or group. Individual or Darwinian selection is probably most important in nature.



From Chapter 2 of *Ecology: The Experimental Analysis of Distribution and Abundance,* Sixth Edition. Eugene Hecht. Copyright © 2009 by Pearson Education, Inc. Published by Pearson Benjamin Cummings. All rights reserved.

## KEY TERMS

**coevolution** The evolution of two or more species that interact closely with one another, with each species adapting to changes in the other.

**individual optimization hypothesis** That each individual in a population has its own optimal clutch size, so that not all individuals are identical.

**Lack clutch size** The clutch size at which productivity is maximal for the population.

**Lack's hypothesis** That clutch size in birds is determined by the number of young that parents can provide with food.

**maximum reproduction** The theory that natural selection will maximize reproductive rate, subject to the constraints imposed by feeding and predator avoidance.

**natural selection** The process in nature by which only the organisms best adapted to their environment tend to survive and transmit their genetic characteristics to succeeding generations while those less adapted tend to be eliminated.

**optimality models** Models that assume natural selection will achieve adaptations that are the best possible for each trait in terms of survival and reproduction.

**phenotype** The observable physical characteristics of an organism.

**proximate factors** How a particular trait is regulated by an individual in a physiological or biochemical manner.

**ultimate factors** The evolutionary reason for an adaptation or why a trait is maintained in a population; opposite of *proximate factors*.

Charles Darwin was an ecologist before the term had even been coined, and is an appropriate patron for the science of ecology because he recognized the intricate connection between ecology and evolution. As we discuss ecological ideas, we will use evolutionary concepts. This chapter provides a brief survey of the basic principles of evolution that are important in evolutionary ecology. We will not discuss all aspects of evolution, which are covered in detail in books devoted to evolutionary biology (e.g., Futuyma 2005), but only those aspects that intersect directly with ecological questions of distribution and abundance.

## What Is Evolution?

Evolution is change, and biological evolution might be defined as changes in any attribute of a population over time. But we must be more specific than this. Evolutionary changes often lead to adaptation and must involve a change in the frequency of individual genes in a population from generation to generation. What produces evolutionary changes?

**Natural selection**, said Charles Darwin and Alfred Wallace independently in 1858, is the mechanism that drives adaptive evolution. Natural selection operates through the following steps:

- Variation occurs in every group of plant and animal. Individuals of the same species are not identical in any population, as was observed in the breeding of domestic animals.
- Every population of organism produces an excess of offspring. (The high reproductive capacity of plants and animals was well known to Malthus and Buffon long before Darwin.)
- Life is difficult, and not all individuals will survive and reproduce.
- Among all the offspring competing for limited resources, only those individuals best able to obtain and use these resources will survive and reproduce.
- If the characteristics of these organisms are inherited, the favored traits will be more frequent in the next generation.

Natural selection will favor traits that allow individuals possessing those traits to leave more descendants. These individuals are said to be fitter, and evolution in general maximizes fitness. The process of natural selection is the end result of the processes of ecology in action. The environments that organisms inhabit shape the evolution that occurs. The present distribution, abundance, and diversity of animals and plants are set by the evolutionary processes of the past impinging on the environment of the present.

A simple example of natural selection is shown in **Figure 1**. The moth *Biston betularia* shows variation in the amount of black color on the wings. The typical moth is white with black speckling on the wings. The black form, *carbonaria*, was first described near Manchester in central England in 1848, and it spread over most of England during the next 50 years. When industrial pollution in central England caused lichens on tree bark to die, black-colored moths survived better because bird predators could not see them against this dark background (see Figure 1). Black wing color is in-

## ESSAY

## What Is Fitness?

Evolutionary ecologists discuss fitness in many forms, and we need to have a clear idea of what fitness means. **Fitness** is a measure of the contribution of an individual to future generations and can also be called **adaptive value**. Individuals have higher fitness if they leave more descendants. Individuals can be fitter for three reasons: They may reproduce at a high rate, they may survive longer, or both. A fish that reproduces rapidly and dies young may be fitter than another fish of the same species that lives a long time but reproduces slowly. From this definition, it should be clear that fitness is a relative term and applies to individual organisms within the same species. One individual may be fitter than another of the same species, or less fit. Ecologists tend to assume that there are traits that allow greater fitness, and that these traits have a genetic basis. Evolution will act to maximize fitness.

We should also be clear about what fitness is not:

• Fitness is not absolute. Measures of fitness are specific for a given environment. Individuals with genes that make them fit for cold environments may

not be fit if the climate changes and they must live in warm environments.

- Fitness cannot be compared across species. We cannot compare the fitness of an elephant with that of an oak tree. Fitness is a measure that is defined only within a single species.
- Fitness is not only about reproduction. High reproductive rates may not by themselves confer high fitness if survival rates of these young are poor.
- Fitness is not a short-term measure. Fitness should be measured across several generations, although this is difficult for studies of long-lived plants and animals. Ecologists often study short-term measures that they hope will correlate with fitness in the long term.
- Fitness is not about individual traits. Evolution is a whole-organism affair. Individual traits such as large body size or fast growth rates may be components of fitness, but the test of fitness is the test of wholeorganism survival and reproduction.





**Figure 1 Evolution in the peppered moth** *B. betularia* **in England and North America.** The photo shows both phenotypes of the peppered moth. The black form, *carbonaria*, has been declining in abundance since 1950 with the decline in industrial pollution in central England. The same change has occurred in eastern North America. Differential bird predation is believed to be the major mechanism of selection. (Photo: H. B. D. Kettlewell; data from Majerus 1998.)

herited in these moths, and the result was an increase in the frequency of black moths during industrialization (Majerus 1998, Grant 2005). Because industrial pollution has decreased in England during the past 50 years, this process of natural selection is reversing (see Figure 1). The same changes have occurred in the American form of the peppered moth as air quality has improved in the eastern United States (Grant and Wiseman 2002).

Evolution through natural selection results in adaptation, and under appropriate conditions produces new species (speciation). **Adaptation** has important ecological implications because it sets limits to the life cycle traits that determine distribution and abundance.

## Adaptation

Natural selection acts on **phenotypes**, the observable attributes of individuals. Different genotypes give rise to different phenotypes, but because embryological and subsequent development is affected in many ways by environmental factors, such as temperature, it is often not a direct translation. Consequently, it is simpler to observe the effect of natural selection directly on the phenotype and to ignore the underlying genotype. Ecologists, like plant and animal breeders, are primarily interested in phenotypic characters such as seed numbers or body size.

Three types of selection can operate on phenotypic characters (Figure 2). The simplest form is directional selection, in which phenotypes at one extreme are selected against. Directional selection produces genotypic changes more rapidly than any other form, so most artificial selection is of this type. Darwin's finches on the Galápagos Islands have been the best-studied example of directional selection. Peter and Rosemary Grant from Princeton University have spent more than 30 years studying these finches on the Galápagos. Figure 3 illustrates directional selection in one of Darwin's finches, the Galápagos ground finch Geospiza fortis. During a prolonged drought, the birds that survived were predominantly those with large beaks that could crack large seeds (Grant and Weiner 2000). Birds with large beaks can eat both large and small seeds, while birds with small beaks can eat only small seeds. Directional selection probably accounts for many of the phenotypic changes that occur during evolution. In wild populations, resistance of pests to insecticides or herbicides is produced by directional selection.

**Stabilizing selection** (see Figure 2) is very common in present-day populations. In stabilizing selection, phenotypes near the mean of the population are fitter than those at either extreme; thus, the population mean value does not change. **Figure 4** illustrates stabi-



Figure 2 Three types of selection on phenotypic characters. Individuals in the colored areas are selected against. (Tamarin 1999)



Figure 3 Directional selection for beak size in the Galápagos ground finch *Geospiza fortis.* From 1976 to 1978, a severe drought in the Galápagos Islands caused an 85 percent drop in the population, and birds with larger beaks survived better because they could crack larger, harder seeds. (Grant 1986)

lizing selection for birth weight in humans in the United States. Early mortality is lowest for babies weighing about 4.2 kilograms (kg), slightly above the observed mean birth weight of 3.4 kg for the population. Very small babies die more frequently, and very large babies are at increased risk even with modern medical care.

Figure 5 shows another example of stabilizing selection in lesser snow geese *Anser caerulescens*. Snow geese



**Figure 4 Stabilizing selection for birth weight in humans.** Data from United States for infants, 1990 and 2002. The optimal birth weight (red arrow) is 4.25 kg, with a broad range of minimal mortality between 3.2 kg and 4.8 kg. Because of medical advances, infant mortality has been falling steadily, so the 1990 curve is higher than the 2002 curve. (Data from National Center for Health Statistics 2006).



Figure 5 Stabilizing selection for hatching synchrony in lesser snow geese (Anser caerulescens) at La Perouse Bay in northern Manitoba, Canada. Relative hatch date is the number of days a female's eggs hatched before or after the mean date for the colony. (From Cooke and Findlay 1982.)

nest in colonies in northern Canada, and clutches hatch over a two-week period in early summer. Because predation is concentrated on whole colonies, eggs hatching synchronously confer a "safety-in-numbers" advantage against predators such as foxes. Females whose eggs hatch synchronously on or near the mean date for the colony are more likely to raise their young successfully. Nests that hatch early suffer greater predation loss, as do nests that hatch later. The result is natural selection favoring an optimum hatching time (Cooke and Findlay 1982).

In the third type of selection, **disruptive selection** (see Figure 2), the extremes are favored over the mean. But because the extreme forms breed with one another, every generation will produce many intermediate forms doomed to be eliminated. In any environment favoring the extremes, any mechanism that would prevent the opposite extremes from breeding with one another would be advantageous. Isolating mechanisms are thus an important adjunct of disruptive selection. Disruptive selection has been suggested to be important in speciation (Rueffler et al. 2006). A good illustration of how disruptive selection operates is found in three-spine sticklebacks (Gasterosteus aculeatus) in coastal lakes of British Columbia. Don McPhail, Dolph Schluter, and their students have shown that two forms of this small fish live in some coastal freshwater lakes (Figure 6). The two forms are so distinct they are effectively species. The small form lives in the open water of the lake and feeds on small plankton, while the large form lives on the bottom of the lake and feeds on insects and crustaceans that live on the bottom of the lake. These two forms seem to have originated from two separate invasions of the lakes as the sea level rose and fell during glacial periods. Competition between the earlier and the later invaders and disruptive selection have produced the two existing species that are closely related to the plankton-feeding marine ancestor species (Rundle et al. 2000).

The net result of all this selection is that organisms are adapted to their environment, and the great diversity of biological forms is a graphic essay on the power of adaptation by natural selection. But we must be careful to note that adaptation does not produce the "best" phenotypes or "optimal" phenotypes (defined as phenotypes that are theoretically the most efficient in surviving and reproducing). The "better" survive, not the "best," and the biological world can never be described as "the best of all possible worlds."

Adaptation is constrained in populations by four major forces. First, genetic forces prevent perfect adaptation because of mutation and gene flow. Mutation is always occurring, generating variation in populations, and most mutations are detrimental to organisms rather than adaptive. The immigration of individuals into an area where local environments differ will add



(a)



(b)

Figure 6 Two males of the three-spine stickleback in

**Paxton Lake, British Columbia.** (a) The smaller male ("limnetic" species) has evolved to feed in the open water of the lake, while (b) the larger form ("benthic" species) lives and feeds on the bottom. The two forms are reproductively isolated and thus are effectively two new species that have originated from the marine ancestor species by invading coastal freshwater lakes. Both males are shown in courtship coloration. (Photos: Todd Hatfield and Ernie Taylor.)

other alleles to the gene pool and act to smooth out local adaptations. Second, environments are continually changing, and this is the most significant shortterm constraint on adaptation. Third, adaptation is always a compromise because organisms have at their disposal only a limited amount of time and energy. There are trade-offs between adaptations such as wing shape in birds. A loon's wings are efficient for diving but not so efficient for flying. Fourth, historical constraints are always present because organisms have a history and change in small increments. Let us look in detail at one example of adaptation to illustrate some of these principles.

## **Clutch Size in Birds**

Each year, Emperor penguins lay one egg; pigeons, one or two eggs; gulls, typically, three eggs; the Canada goose, four to six eggs; and the American merganser, 10 or 11 eggs. What determines clutch size in birds? We must distinguish two different aspects of this question: proximate and ultimate.

**Proximate factors** explain *how* a trait is regulated by an individual. Proximate factors that determine clutch size are the physiological factors that control ovulation and egg laying. Ultimate factors are selective factors, and ultimate explanations for clutch size differences involve evolutionary arguments about adaptations. Proximate factors affecting clutch size have to do with how an individual bird decodes its genetic information on egg laying; ultimate factors have to do with changes in this genetic program through time and with the reason for these changes (Mayr 1982). Clutch size may be modified by the age of the female, spring weather, population density, and habitat suitability. The ultimate factors that determine clutch size are the requirements for long-term (evolutionary) survival. Clutch size is viewed as an adaptation under the control of natural selection, and we seek the selective forces that have shaped the reproductive rates of birds. We shall not be concerned here with the proximate factors determining clutch size, which are reviewed by Carey (1996).

Natural selection will favor those birds that leave the most descendants to future generations. At first thought, we might hypothesize that natural selection favors a clutch size that is the physiological maximum the bird can lay. We can test this hypothesis by taking eggs from nests as they are laid. When we do this, we find that some birds, such as the common pigeon, are determinate layers; they lay a given number of eggs, no matter what. The pigeon lays two eggs; if you take away the first, it will incubate the second egg only. If you add a third egg, it will incubate all three. But many other birds are indeterminate layers; they will continue to lay eggs until the nest is "full." If eggs are removed once they are laid, these birds will continue laying. When this subterfuge was used on a mallard female, she continued to lay one egg per day until she had laid 100 of them. In other experiments, herring gull females laid up to 16 eggs (normal clutch: 2-3); a yellow-shafted flicker female, 71 eggs (normal clutch: 6-8); and a house sparrow, 50 eggs (normal clutch: 3-5) (Klomp 1970; Carey 1996). This evidence suggests that most birds under normal circumstances do not lay their physiological limit of eggs but that ovulation is stopped long before this limit is reached.

The British ornithologist David Lack was one of the first ecologists to recognize the importance of evolutionary thinking in understanding adaptations in life history traits. In 1947 Lack put forward the idea that clutch size in birds was determined ultimately by the number of young that parents can provide with food. This hypothesis stimulated much research on birds because it immediately suggested experimental manipulations. If this hypothesis is correct, the total production of young ought to be highest at the normal clutch size, and if one experimentally increased clutch size by adding eggs to nests, increased clutches should suffer greater losses because the parents could not feed the extra young in the nest.

One way to think about this problem of optimum clutch size is to use a simple economic approach. Everything an organism does has costs and benefits. Organisms integrate these costs and benefits in evolutionary time. The benefits of laying more eggs are very clearmore descendants in the next generation. The costs are less clear. There is an energy cost to make each additional egg, and there is a further cost to feeding each additional nestling. If the adult birds must work harder to feed their young, there is also a potential cost in adult survival-the adults may not live until the next breeding season. If adults are unable to work harder, there is a potential reduction in offspring quality. A cost-benefit model of this general type is shown in **Figure 7**. Models of this type are called **optimality models**. They are useful because they help us think about what the costs and benefits are for a particular ecological strategy.

No organism has an infinite amount of energy to spend on its activities. The reproductive rate of birds can



Figure 7 A cost-benefit model for the evolution of clutch size in birds. An individual benefits from laying more eggs because it will have more descendants, but it incurs costs because of increasing parental care required for larger clutches. The clutch size with the maximum difference between benefits and costs is the optimal clutch size for that individual. (The Lack clutch size, named after David Lack.)

be viewed as one sector of a bird's energy balance, and the needs of reproduction must be maximized within the constraints of other energy requirements. The total requirements involve metabolic maintenance, growth, and energy used for predator avoidance, competitive interactions, and reproduction. Lack's hypothesis (1947)that the clutch size of birds that feed their young in the nest was adapted by natural selection to correspond to the largest number of young for which the parents can provide enough food—has been a very fertile hypothesis in evolutionary ecology because it has stimulated a variety of experiments. According to this idea, if enough additional eggs are placed in a bird's nest, the whole brood will suffer from starvation so that, in fact, fewer young birds will fledge from nests containing larger numbers of eggs. In other words, clutch size is postulated to be under stabilizing selection (see Figure 2). Let us look at a few examples to test this idea.

In England, the blue tit normally lays a clutch of 9 to 11 eggs. What would happen if blue tits had a brood of 12 or 13? Pettifor (1993) artificially manipulated broods at hatching by adding or subtracting chicks, and found that the survival of the young blue tits in manipulated broods was poor (**Figure 8**). Blue tits feed on insects and apparently cannot feed additional young adequately, so more of the young starve. Consequently, it would not benefit a blue tit in the evolutionary sense to lay more eggs, and the results are consistent with Lack's hypothesis. Individual birds appear to produce the clutch size that maximizes their reproductive potential.

Tropical birds usually lay small clutches, and Skutch (1967) argued that this was an adaptation against nest predators. If the intensity of nest predation increases with the number of parental feeding trips away from the nest, natural selection would favor a reduced clutch size. Low clutch size and low predation rates are associated. Parents would leave more descendants if they had smaller broods and did not need to feed them as often. Exactly the same argument was used by Martin (1995) to explain the pattern of clutch size in hole-nesting birds. Hole-nesting passerine birds lay fewer eggs than comparable species that nest in the open, and predation rates are much lower for hole-nesting species (Martin 1995). So again, low clutch size and low predation rates are correlated. This suggests that a high risk of predation on the whole brood in the nest is a strong selective factor that increased clutch size in open-nesting birds. This factor also favors a shortened nesting period, independent of the ability of the parents to provide food to the nestlings. Open nesting is a gamble because of high predation rates, and passerine birds gamble on large clutches and short nesting periods.

Natural selection would seem to operate to maximize reproductive rate, subject to the constraints imposed by feeding and predator avoidance. This is called the theory

#### **Evolution and Ecology**



removed added 0.0 0 2 4 6 8 10 12 14 Clutch size

Figure 8 Production of young blue tits (Parus caeruleus) in relation to clutch size in Wytham Wood, Oxford, England. Only females that had laid 11 eggs in previous years are shown here, because we expect these individuals to have their highest fitness at a clutch size of 11. These results fit Lack's hypothesis because adding more chicks just after hatching does not increase fitness. (Data from Pettifor 1993, p. 136.)

of maximum reproduction, and Lack's hypothesis is part of this theory. It is a good example of how stabilizing selection can operate on a phenotypic trait such as reproductive rate. The maximum clutch size is called the Lack **clutch size** (see Figure 7), after David Lack.

Not all manipulation experiments confirm Lack's hypothesis. Young (1996) manipulated clutch size in tropical house wrens (Troglodytes aedon) in Costa Rica to produce clutches ranging from one to six. House wrens in the tropics typically lay three or four eggs. Figure 9 shows the resulting offspring produced. The number of surviving offspring per brood was maximized for broods of six eggs. Since mean brood size was 3.5, the most common clutch size was smaller than the most productive clutch size. Vanderwerf (1992) surveyed 77 experiments in which clutches had been manipulated and



Figure 9 Number of house wren chicks fledged from broods manipulated to have larger and smaller than average brood size. These results do not agree with the predictions from Lack's hypothesis that larger broods should fledge fewer young than average-sized broods. (After Young 1996.)

found that 69 percent of these were like the house wren-the most productive clutch size was larger than the most common clutch size. Why should this be?

The presence of trade-offs is one explanation of why clutches are smaller than the Lack clutch size. Clutch size may affect the chances of the adult birds surviving to breed again. Birds may become exhausted by rearing large clutches; such exhaustion is a delayed cost of reproduction. Alternatively, laying a large clutch may postpone the next breeding attempt, leading to reduced lifetime reproduction. Laying a large clutch is energetically costly for birds, and this cost is not usually measured in brood manipulation experiments (Monaghan and Nager 1997).

The Lack clutch size may not be a constant for a species, and different individuals may vary in their parenting abilities and have a personal Lack clutch size. Clutch size is under strong genetic control in birds. One female may consistently lay three eggs and this may be best for her, while another female in the same population may consistently lay five eggs and this may be best for her. This is called the individual optimization hypothesis, and it explains why there is considerable variation in clutch size within a population. The individual optimization hypothesis has been the subject of several experimental tests (Pettifor et al. 2001). This hypothesis predicts that any manipulation of clutch size will reduce the fitness of the parent birds because they rear fewer young or survive less well. It also predicts that in natural broods there

should be more young recruited as clutch size increases, coupled with no impairment of fitness of the parent birds. Tinbergen and Sanz (2004) did not find these predictions to be correct for a population of great tits in the Netherlands (**Figure 10**). Artificially enlarged first clutches produced more recruits, and adult survival was not affected by the manipulations either in the same year or in the following year. They rejected the individual optimization hypothesis for



Figure 10 Test of the Individual Optimization Hypothesis for clutch size variation in the great tit (*Parus major*) in the Netherlands. These results do not agree with the predictions from this hypothesis that larger manipulated broods should fledge fewer young than unmanipulated (control) broods. The combined measure of fitness includes the number of young produced that live to the next breeding season and the survival of their parents to the next breeding season. These results would predict directional selection for increased clutch size. (Data from Tinbergen and Sanz 2004.) this bird population. Individual birds may not be able to predict environmental variation in any given year, and food supplies may fluctuate so much that individuals cannot predict the optimal clutch size for any particular year (Török et al. 2004).

An alternative explanation of why the average clutch may be smaller than the Lack clutch size is that observed clutch sizes are a nonadaptive compromise. If gene flow occurs between two habitats, one good and one poor, clutches may be larger than optimal in poor habitats and smaller than optimal in good habitats. Blue tits and great tits in Belgium rarely breed in woodlands where they were born and show this nonadaptive compromise (Dhondt et al. 1990).

Recent work on bird reproduction investigates how individual parents adjust their reproductive costs in relation to environmental conditions to maximize the output of young. The proximate controls of reproduction operate through the energy available to reproducing birds, and the role of female condition is critical in determining reproductive effort. Reproductive effort this year may affect the chances of surviving until next year, and parents must balance the short-term and longterm costs of breeding.

## Coevolution

The term *coevolution* was popularized by Paul Ehrlich and Peter Raven (1964) to describe the reciprocal evolutionary influences that plants and plant-eating insects have had on each other. **Coevolution** occurs when a trait of species *A* has evolved in response to a trait of species *B*, which has in turn evolved in response to the trait in species *A*. Coevolution is specific and reciprocal. In the more general case, several species may be involved instead of just two, and this is called diffuse coevolution (Thompson 1994).

Coevolution is simply a part of evolution, and it provides important linkages to ecology. The interactions between herbivores and their food plants have been emphasized as a critical coevolutionary interaction. Predator–prey interactions can also be coevolutionary, and in some cases can lead to "arms races" between species.

Coevolution shapes the characteristics of coevolving pairs of species, while diffuse coevolution might also occur in communities of many species. There is considerable doubt about whether whole communities of plants and animals could coevolve, and most ecologists believe that coevolution is restricted to interactions between only a few species that interact tightly (Benkman et al. 2001).

## **Evolution and "Arms Races"**

If you look up "arms race" on the Web, you will find much discussion of military strategies and little of biological evolution. An arms race is tit-for-tat evolution a reciprocal interaction between species—in which as species A evolves better adaptations to exploit species B, the latter fights back by evolving adaptations to thwart the improvements in species A. The best examples of arms races occur between hosts and parasites. The brown-headed cowbird in North America and the European cuckoo in Britain are good examples of parasitic birds that lay their eggs in the nests of other species (**Figure 11**). The host species then raise the cowbird or cuckoo chick, often to the detriment of its own young.

The brown-headed cowbird has greatly expanded its geographic range in North America because of agriculture and is invading new areas and utilizing new host species, so it has become a major conservation problem. Parasitic birds such as the cowbird often lay eggs that have the same color and pattern as the host species in order to avoid detection and the possibility that the host species will remove the parasite's eggs from their nests. The host species on the other hand should evolve the ability to discriminate cowbird eggs from its own eggs. Host individuals that discriminate more will leave more offspring (and raise fewer cow-



**Figure 11 Arms race.** Schematic illustration of the arms race between the parasitic cowbird, which lays its eggs in other birds' nests, and the parasitized species that try to defend against this kind of parasitism by ejecting the cowbird eggs.

birds). Consequently, an evolutionary arms race can develop in which both the parasite and the host are continually evolving counterstrategies in a tit-for-tat manner (Takasu 1998).

Deadly toxins and resistance to them are an evolutionary enigma and illustrate a potential difficulty in the evolution of arms races between predators and prey (Brodie and Brodie 1999). Some snakes, for example, can feed on prey that are poisonous to most other animals. There can be no natural selection for increased resistance if predators do not survive encounters with toxic prey. Similarly, deadly toxins are of no advantage to individual prey if the prey dies delivering the toxins (Williams et al. 2003). For natural selection to drive an arms race between resistant predators and lethal prey, the survivorship of individual predators must vary with their resistance. One example is the extreme toxicity of some populations of the rough-skinned newt (Taricha granulosa) that appear to have coevolved with resistance in its predator, the common garter snake (Thamnophis sirtalis) in North America (Figure 12). The rough-skinned newt is one of the most toxic animals known. Its skin contains a neurotoxin that is fatal to most animals in small doses. But some garter snakes feed on these newts, and have evolved resistance to their toxins. For example, San Francisco populations of garter snakes are nearly 100 times more resistant to newt neurotoxins than are garter snakes from Oregon (Brodie and Brodie 1999). There is a geographical mosaic in the amount of poison carried by the newts in their skin and the resistance shown by garter snakes, so that coevolution of this arms race has not reached the same point in all populations.

## **Units of Selection**

Darwin conceived natural selection as operating through the reproduction and survival of individuals who differ in their genetic constitution. Most discussion of natural selection operates at this level of Darwinian selection, or individual selection.

But natural selection is not restricted to individuals. It can act on any biological units so long as these units meet the following criteria: (1) They have the ability to replicate; (2) they produce an excess number of units above replacement needs; (3) survival depends on some attribute (size, color, behavior); and (4) a mechanism exists for the transmission of these attributes. Three units of selection other than the individual can fulfill these criteria: gametic, kin, and group selection.

#### **Evolution and Ecology**



(a)



(b)

**Figure 12** (a) The rough-skinned newt (*Taricha granulosa*) from western North America, an extremely toxic salamander, and (b) the garter snake (*Thamnophis sirtalis*) that preys on these newts.

## **Gametic Selection**

Gametes (eggs and sperm) have a genetic composition that differs from the diploid organisms that produce them. Gametes are produced in vast excess and may have characteristics that they transmit through the zygote and adult organism to the next generation of gametes. Consequently, natural selection can act on a population of gametes independently from the natural selection that operates on the parent organisms. Many different characteristics of gametes could be under natural selection. Sperm mobility, for example, may be under strong selection. In plants, pollen grains that produce a faster-growing pollen tube have a better chance of releasing their sperm nuclei and fertilizing an egg. Gametic selection is an interesting and important aspect of natural selection, but it does not directly impinge on ecological relationships.

## **Kin Selection**

If an individual is able to increase the survival or reproduction of its relatives with whom it shares some of the same genes, natural selection can operate through kin selection. Kin selection and individual selection may act together, and this action is described by the concept of inclusive fitness. Natural selection favors not only alleles that benefit an individual but also alleles that benefit close relatives of that individual because close relatives share many alleles. All relatives can help pass copies of an individual's genes to future generations.

Kin selection was recognized as one way of explaining the existence of altruistic traits such as the sounding of alarm calls. When ground squirrels sight a predator, they give an alarm call. As a result, the individual calling (1) draws attention to itself and thus may be attacked by the predator (detrimental to the individual) and (2) warns nearby squirrels to run for cover (beneficial to relatives nearby).

Kin selection has important consequences for ecological relationships because of its effects on social organization and population dynamics. Competition between individual organisms will be affected by the proximity of close relatives; thus, it can be important for an ecologist to know the degree of kinship among members of a population.

## **Group Selection**

Group selection can occur when populations of a species are broken up into discrete groups more or less isolated from other such groups. Groups that contain less adaptive genes can become extinct, and the conditions for natural selection could occur at the level of the group, as well as at the level of the individual organism.

Group selection is highly controversial, and most biologists consider it to be rare in nature. Most of the characteristics of organisms that are favorable to groups can also be explained by individual or kin selection. Controversy erupts over traits that appear to be good for the group but bad for the individual. A classic example is the evolution of reproductive rates in birds. Group selectionists argue that many birds reproduce at less-thanmaximal rates because populations with low reproductive rates will not overpopulate their habitats. Any populations with higher reproductive rates will overpopulate their habitats and become extinct, so restraint is selected for at the group level. But low reproductive rates are bad for the individual, and individual selection will act to favor higher reproductive rates, so group selection and individual selection are operating at cross purposes. In a group in which all members restrain themselves, a cheater will always be favored.

The alternative argument is that all reproductive rates are in fact maximal and have responded only to individual selection favoring individuals that leave the most offspring for future generations. Restraint does not exist, according to this view. Group selection may occur, but at present it is not believed to be an important force shaping the adaptations that ecologists observe while trying to understand the distribution and abundance of organisms.

#### Summary

Organisms survive and reproduce, and because not all individuals are equally successful at these activities, natural selection occurs. The fitter individuals leave more descendants to future generations because of either higher survival or higher reproductive rates. Natural selection is ecology in action, and the ecologist asks which traits of individuals improve their chances of survival or reproduction.

The clutch size of birds is a classic problem in evolutionary ecology—why don't birds lay more eggs? David Lack suggested in 1947 that clutch size was limited by the number of chicks the adults could feed successfully. Experimental additions of eggs and chicks to nests have often shown that bird parents can in fact rear more nestlings than they usually do. This anomaly is probably due to the higher costs of reproduction for birds rearing large broods, and adults may die or lay fewer eggs in subsequent years as a cost of breeding performance in the current year. Clutch size is thus expected to be under stabilizing selection in most cases. Coevolution can occur between interacting species. Coevolution occurs when a trait of a particular species has evolved in response to a trait of a second species, which has in turn evolved in response to the trait in the first species. Many examples of coevolution occur in plant-herbivore interactions and in predator-prey interactions. Arms races between species are a particular kind of coevolution. The best examples of arms races occur between hosts and parasites.

Individual, or Darwinian, selection is the classic form of selection on individual phenotypes, and it is the level of selection responsible for most of the adaptations we see in nature. Some adaptations may evolve by kin selection for actions that favor the survival or reproduction of close relatives carrying the same genes. Group selection might also occur if whole groups or populations become extinct because of genetic characteristics present in the group. Group selection is probably uncommon in nature.

### **Review Questions and Problems**

- Birds living on oceanic islands tend to have a smaller clutch size than the same species (or close relatives) breeding on the mainland (Klomp 1970, p. 85). Explain this on the basis of Lack's hypothesis.
- 2 Cane toads have been introduced to Australia and many of the Pacific islands. Their skin contains glands that secrete poisons that are toxic to most vertebrates. Discuss how evolution might operate on potential predators of cane toads in areas like Australia in which the predators have no prior evolutionary history of interactions with these toads. Phillips and Shine (2006) discuss this issue.
- 3 Ladybird beetles are distasteful to predators because of toxic chemicals they secrete, yet they also have

dark melanic forms (Majerus 1998, p. 221). Melanic ladybirds have declined in frequency in central England along with the peppered moth during the past 50 years as air quality has improved. If ladybirds are not eaten by predators, how might you explain these changes in melanic frequency?

4 Figure 10 provides data that appear to contradict the Individual Optimization Hypothesis for the evolution of clutch size in birds. Are there any components of fitness in these birds that are ignored in Figure 10 and that might change the interpretation from an example of directional selection to one of stabilizing selection? Read de Heij et al. (2006) for a discussion. 5 Royama (1970, pp. 641–642) states:

Natural selection favors those individuals in a population with the most efficient reproductive capacity (in terms of the number of offspring contributed to the next generation), which means that the present-day generations consist of those individuals with the highest level of reproduction possible in their environment.

Is this correct? Discuss.

- 6 In many temperate zone birds, those individuals that breed earlier in the season have higher reproductive success than those that breed later in the season. If climate change is making spring weather occur at earlier dates, will this lead to directional selection for earlier breeding dates in these birds? What constraints might affect this type of directional selection?
- 7 Some birds such as grouse and geese have young that are mobile and able to feed themselves at hatching (precocial chicks). Discuss which factors might limit clutch size in these bird species. Winkler and Walters (1983) have reviewed studies on clutch size in precocial birds.
- 8 In arctic ground squirrels, adult females are more likely to give alarm calls than adult males. If alarm calls are favored by kin selection, why might this difference occur? Could alarm calls be explained by group selection? Why or why not?
- 9 Apply the cost–benefit model in Figure 7 to seed production in a herbaceous plant. Discuss biological reasons for the general shape of these curves. Can you apply this model to both annual and perennial plants in the same way?
- 10 A research scientist obtained the following data on the fitness of seven females in a small population of house sparrows:

Year	Variable		Fe	ema nu	ile imł	ba: ver	nd	
		A	B	С	D	E	F	G
1999	No. eggs laid	8	5	4	5	7	6	7
	No. young fledged	5	1	3	4	2	4	3
2000	No. eggs laid	5	6	4	5	7	7	9
	No. young fledged	4	2	3	5	3	3	0
2001	No. eggs laid	6	10	5	5	8	10	10
	No. young fledged	4	8	5	4	6	8	9
2002	No. eggs laid	6	6	3	5	7	8	10
	No. young fledged	2	5	3	5	3	4	4

Rank the fitness of these seven female sparrows. What data might you collect to improve on this measure of fitness for these birds?

- 11 Discuss how the concept of time applies to evolutionary changes and to ecological situations. Do ecological time and evolutionary time ever correspond?
- 12 A hypothetical population of frogs consists of 50 individuals in each of two ponds. In one pond, all of the individuals are green; in the other pond, half are green and half are brown. During a drought, the first pond dries up, and all the frogs in it die. In the population as a whole, the frequency of the brown phenotype has gone from 25 percent to 50 percent. Has evolution occurred? Has there been natural selection for the brown color morph?

#### **Overview Question**

Humans in industrialized countries increased in average body size during the twentieth century. List several possible explanations for this change, and discuss how you could decide if an evolutionary explanation is needed to interpret it. How does a physiological explanation for this change differ from an evolutionary explanation?

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# Behavioral Ecology

## Key Concepts

- Behavioral ecology asks how individual animals interact with other animals, plants, and their physical environments to maximize fitness.
- The consequences of decisions individual animals make will affect their survival and reproduction.
- Natural selection is assumed to have optimized the behavior of individuals to achieve maximal fitness, and the job of the behavioral ecologists is to find the mechanisms by which this is achieved.
- Foraging, antipredator, social, and mating behaviors are four critical foci of study in behavioral ecology that can be analyzed by cost-benefit models.
- Behavioral ecology is a bridge not only to evolutionary biology but also to animal population and community ecology because mechanisms driving population and community dynamics all result from the behavior of individuals.



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#### **Behavioral Ecology**

#### KEY TERMS

**cost-benefit analysis** An assessment to determine whether the cost of an activity is less than the benefit that can be expected from the activity.

**group selection** Natural selection for traits that favor groups within a species irrespective of whether the traits favor individuals or not.

**kin selection** The evolution of traits that increase the survival, and ultimately the reproductive success, of one's relatives.

**optimal foraging** Any method of searching for and obtaining food that maximizes the relative benefit.

**optimal group size** The size that results in the largest relative benefit.

**promiscuity** A general term for multiple matings in organisms, called polyandry if multiple males are involved, or polygyny if multiple females.

**relative benefit** The difference between the costs and benefits (= net benefit).

territory Any defended area.

**trade-offs** Compromises between two desirable but incompatible activities.

The ecology of a species is ultimately determined by interactions between individuals and their environment. The environment includes other individuals of the same species as well as members of other species, such as predators. The environment also includes physical factors, such as temperature, rainfall, and wind. The ways that organisms respond to each other and to particular cues in the environment are called **behaviors**. In this chapter, we will focus on the behaviors of animals as they interact with their food resources, mates, and other members of their social group. How does a rabbit decide where to feed? How does a male lion achieve reproductive success? These are some of the questions we will address.

Behavioral ecology is a strong subdiscipline in animal ecology dealing with the ecology of individuals. Like evolutionary ecology, behavioral ecology has strong links to other sciences, in this case psychology, physiology, and developmental biology. As such, it forms an important link to understanding how populations and communities change. It is unique within ecology in that it deals almost solely with animals and largely ignores plants and microbes. Of course, plants as well as animals respond to changes in their environment, and we shall discuss these plant responses.

All animal behaviors are generated through a complex set of physiological and neurological reactions triggered by environmental stimuli. Four questions can be asked about any behavior (Tinbergen 1963): (1) How is a behavior produced? (2) How does a behavior develop? (3) What is the adaptive value of a behavior? and (4) What is the evolutionary history of a behavior?

The first two questions are "how" questions (or "proximate" questions) that refer to the mechanisms of behavior, and the second two questions are "why" questions (or "ultimate" questions) that examine the function of behavior. The behavioral ecologist is interested in answering the last two questions, while the physiologist, neurobiologist, and developmental biologist study the first two questions. Behavioral ecologists want to understand the ecological and evolutionary contexts of behavior. They want to learn how an individual's behavior is shaped by its social and physical environment, both past and present, and how specific behaviors affect its chances of surviving and reproducing. Evolutionary questions are key to behavioral ecology.

The following is an example of the kind of questions behavioral ecologists commonly ask: "Why is promiscuity common among mammals?" Monogamy occurs in less than 3 percent of mammalian species (Kleiman 1977). Promiscuity, or multiple-male or multiple-female mating, is very common in mammals, and has been described in many species of mammals (Wolff and Macdonald 2004). Figure 1 shows the frequency of multiple-male mating in the Ethiopian wolf (Canis simiensis). These wolves live in packs and the males within each pack can be ranked as alpha (top male), beta, or other (lower ranking) within their pack social system. Female wolves decide which males they will copulate with, and typically solicit multiple-male matings from males that live in adjacent packs and reject matings from subordinate males within their own pack (Sillero-Zubiri et al. 1996). Why might they do this?

The basic assumption is that animals are well adapted to their environment, and hence there must be some advantage to them to behave in certain ways. Promiscuity in mammals is often an attempt to confuse paternity. For Ethiopian wolves, males from packs can attack juveniles in adjacent packs if they are not genetically related. By soliciting copulations from adjacent pack males, a female can reduce the probability of infanticide occurring because none of the males can determine the father of a litter. Much of this promiscuity seems to be an adaptation for paternity confusion (Wolff and Macdonald 2004).

#### **Behavioral Ecology**



Figure 1 Percentage of copulations achieved by males of different social rank from (a) the resident pack of the female and from males in (b) adjacent packs. Wolves live in packs with well-defined territories. Alpha males are dominant males; beta males are subordinate. Female wolves copulate many times when they are in heat. (Data from Sillero-Zubiri et al. 1996.)

## All Behaviors Have Costs and Benefits

We begin with the assumption that observed behaviors are beneficial, and that evolution through natural selection has molded animals to their environment. We can rarely observe the evolution of behavior because behavioral changes occur slowly in evolutionary time. And even though we can sequence the DNA in individuals, this technology will not help us understand the adaptive value of behavior because no complex behavior is under the control of a single gene. Instead, we must adopt an indirect approach to analyze why a particular kind of behavior is adaptive.

What benefits do individuals gain from behaving in certain ways? To answer this question, behavioral ecologists must examine the decisions that animals make when faced with environmental options such as where to feed, what to eat, where to live, and which individuals to mate with. An animal's decisions translate into differences in survival, fecundity, or mating success, and therefore are shaped by natural selection. Consider parental care, which is a major investment in many vertebrates. Mammals and birds in particular must divide limited resources between reproduction and other activities such as feeding. The choices involved require **trade-offs**, which are compromises between two desirable but incompatible activities.

All organisms are constrained by time, energy, and risk of injury. Time spent engaged in one activity cannot be spent on another, and energy expended in doing one thing will not be available to do something else. We can analyze some of the choices made by individuals of a given species by comparing the costs and the benefits of alternative activities. This kind of assessment, called a **cost-benefit analysis**, is commonly used in economics to determine whether the financial cost of a project is less than the economic benefit that can be expected from the project. In behavioral ecology, costs are typically measured in terms of energy consumed, the probability of injury, or the probability of being killed by a predator. Benefits are usually measured in terms of a net gain in energy or an increase in reproductive success.

Behavioral ecologists assume that natural selection favors aspects of an individual's behavior that maximize the net benefit. For example, individuals that make better decisions about where to feed should have a higher net energy intake and be in better condition. Therefore, they should be better able to avoid predators and diseases, attract mates, and produce many young. Thus, natural selection should favor any behavioral attribute that consistently leads to good feeding decisions.

Given a set of assumptions, we can construct an optimality model to predict which combination of be-

haviors will maximize an individual's reproductive success in a given environment. Optimality models make explicit the relationships between costs and benefits of behaviors under various conditions. They are most useful in circumstances where it is clear that making the right decision maximizes some payoff, such as survival rate, reproductive success (number of young produced), feeding efficiency (energy gained per unit time), or mating success (number of matings per unit time). The following three sections are examples of optimality models.

### **Territorial Defense**

We can examine how an optimality model works by considering territorial defense in animals. An animal's territory is any defended area. Many mammals, birds, lizards, and fishes defend a feeding area against other individuals of the same species. How large a territory should an individual defend? To answer this question, we need to think about the costs and benefits of defending a territory. The costs are time, energy, and risk of injury. The total cost will increase with the size of the territory, and for simplicity, we will assume that the relationship between cost and territory size is a rising curve because larger areas are more expensive to defend (Figure 2). The benefit of defending a territory is exclusive access to food, and it also increases with the size of the territory but suffers from diminishing returns.

Since an individual can consume only a certain amount of food, however, the benefit curve gradually levels off as the territory becomes larger. Above a certain territory size, there is no further increase in benefit (see Figure 2). The optimal territory size is the one that maximizes the **relative benefit** or profitability, which is the difference between the costs and benefits. In the hypothetical example shown in Figure 2, the relative benefit would be greatest at the territory size indicated by the arrow. Clearly, the optimal territory size is determined by the shapes of the cost and benefit curves, which vary with the species, habitat, and an individual's age or mating status.

The benefits of defending a territory are typically thought of as obtaining exclusive use of food resources, but for some species it may be the benefit of obtaining mates, avoiding predators, or defending juvenile animals from infanticide. Typically, for birds, the main considerations seem to be food and mates. Hummingbirds that migrate defend territories even during the nonbreeding period, and the assumption is that these territories are solely about food. Hummingbirds obtain most of their food energy from the nectar in flowers. Nectar is a resource that occurs in tiny amounts in individual flowers, consists mostly of water and some dissolved sugars, and



Figure 2 Hypothetical cost-benefit model for territory size in animals.

varies highly in availability. Hummingbirds have very high energy requirements for their body weight due to their small size, high body temperature, and use of hovering flight.

Rufous hummingbirds (*Selasphorus rufus*) live in western North America and migrate along the mountain chains—north to breed and south to overwinter. During their migration, they stop temporarily in mountain meadows to feed, and then move to a new site after refueling. They respond very quickly to changes in food resources—i.e., the nectar contained in flowers. Kodric-Brown and Brown (1978) showed that rufous hummingbirds adjusted their territory size to the available food supply (**Figure 3**), so that individuals always defended the same number of flowers regardless of the size of territory.

But why don't these hummingbirds defend a larger territory with more flowers? The implication is that the cost of defending a larger territory would exceed the benefits of having more food available. Carpenter et al. (1983) showed that if a hummingbird defended too large a territory, its rate of energy intake decreased because it spent too much time defending the territory and less time feeding (**Figure 4**). Diminishing returns are caused by high locomotion costs to defend more space, and a higher frequency of intrusions that reduce feeding time.

Hummingbirds are useful animals for the study of the costs and benefits of territorial defense because they can change their behavior daily and territories can change quickly in size. In many species, however, we cannot measure the costs and benefits of territorial defense at the same time, so we can see only part of the behavioral picture.



**Figure 3 Territories defended by rufous hummingbirds** *(S.rufus)* in relation to flower density. In this study, hummingbirds in the White Mountains of Arizona in both years defended territories with a constant number of flowers, indicating a constant food amount (indicated by the dashed line) regardless of the territory size. (Data from Kodric-Brown and Brown 1978.)

If an animal does not behave as predicted by an optimality model, we should ask if the costs and benefits of the behavior have been correctly assessed or if additional factors should be considered. For example, the optimality model in Figure 2 assumes that cost and benefit curves are constant over time. Suppose instead that the shape of the cost curve varies from year to year. Should an animal change its territory size each year in response to these variations, or should it maintain a territory size that is optimal in average years? In ecosystems in which territories are occupied and defended year round, and the prey base fluctuates in size from year to year, individuals may adopt a territorial defense strategy that is suited to times of scarcity rather than change territory size every year. In many predators, such as the great horned owl, individuals defend territories that are larger than necessary on the basis of their food requirements (Rohner 1997).

One difficulty with optimality models is that they consider only one or two behaviors at a time, whereas individuals must simultaneously optimize all aspects of their behavior in order to survive and reproduce. We assume, however, that if a behavior such as territorial defense is directly linked to survival or reproductive success, then we should be able to detect how an individual organizes that behavior in a way consistent with the predictions of an optimality model.

Not all animals defend territories all the time, and some never defend any space. But all animals must eat



**Figure 4** Daily weight change of one marked rufous hummingbird in the Sierra Nevada of California. This individual stayed in the mountain meadow for five days on its migration south. It showed the ability to adjust its territory size to an optimum in order to maximize the rate of gain of fuel for migration. (Data from Carpenter et al. 1983.)

and we turn now to a more general question of foraging and how behavior can be organized to allow individuals to forage in an optimal manner.

## **Optimal Foraging**

For all animals, food is not evenly distributed in time or in space. Consequently, acquiring food involves many behavioral decisions such as what type of food to consume, where and how to search for food, and once food is located, how much to eat and how long to keep foraging. Since animals must acquire food at a certain rate to maintain their physiological functions, the efficiency with which they can find and eat food is also important. Thus, we can assume that natural selection favors optimal foraging, which is any method of searching for and obtaining food that maximizes the relative benefit (the difference between costs and benefits, typically the net caloric gain per unit of time). Foraging provides an excellent opportunity to examine the factors that influence behavioral decisions because its benefits and costs are relatively easy to define, measure, and manipulate. Much of the research on foraging has been done on mammals and birds, and we begin our discussion with a simple model of optimal foraging.

Consider a predator such as an owl hunting for two kinds of prey. The prey are encountered at rates  $\lambda_1$ and  $\lambda_2$  prey per second during a specified time of searching,  $T_s$  seconds of searching. The two prey types yield  $E_1$  and  $E_2$  units of energy (measured in joules or calories), and take  $h_1$  and  $h_2$  seconds to handle each prey item. We define:

Profitability of prey type 
$$1 = E_1/h_1$$
 (1)  
Profitability of prey type  $2 = E_1/h_1$  (2)

Profitability of prey type  $2 = E_2/h_2$  (2)

If the predator forages completely at random in  $T_s$  seconds, it will obtain on average this amount of food:

$$E = T_s(\lambda_1 E_1 + \lambda_2 E_2) \tag{3}$$

And this foraging will take the following total amount of time (T) for searching and then handling the prey items:

$$T = T_s + T_s \left(\lambda_1 h_1 + \lambda_2 h_2\right) \tag{4}$$

The overall rate of food intake of the predator is thus defined by the following equation:

$$\frac{E}{T} = \frac{(\lambda_1 E_1 + \lambda_2 E_2)}{(1 + \lambda_1 h_1 + \lambda_2 h_2)}$$
(5)

Now we ask what happens if prey type 1 is more profitable to eat than prey type 2. In order to maximize the food intake (E/T), the predator should eat only prey type 1 if the rate of energy gain from prey type 1 is greater than the energy gained from eating both prey types:

$$\frac{\lambda_1 E_1}{1 + \lambda_1 h_1} > \frac{\lambda_1 E_1 + \lambda_2 E_2}{1 + \lambda_1 h_1 + \lambda_2 h_2} \tag{6}$$

If we rearrange this equation, we obtain the following prediction: *The predator should specialize in eating only prey 1 if the equation below is true.* 

$$\frac{1}{\lambda_1} < \frac{E_1}{E_2} (h_2 - h_1)$$
 (7)

This prediction is a threshold—eat only prey type 1 if the abundance of prey 1 exceeds this density, and eat both prey types if this inequality does not hold.

This simple model assumes there is some criterion to maximize (intake rate), some constraints to maximization (handling time), and alternative strategies (eat only prey 1 or eat both types of prey). **Table 1** lists the assumptions and the predictions of this simple optimal foraging model.

This simple optimal diet model has been very effective in stimulating research on foraging behavior in a variety of animals. In general, the results of empirical studies do not follow the model in observing a threshold change in diet. Instead, animals show partial preferences and eat the less preferred prey to some extent even when the model predicts they should eat only prey type 1 (Krebs and Davies 1993). **Figure 5** shows one example of this for the great tit. The data do not fit the model exactly because in nature birds must monitor the environment to estimate the relative abundances of the prey items, and in the process of doing this they encounter the less preferred prey occasionally and eat them in addition to the preferred prey. Animals do not

|--|

Assumptions	Predictions
Prey value is measured in net energy of some single dimension	The highest-ranking prey in terms of profitability should never be ignored
Handling time is fixed for a given prey type	Low-ranking prey should be ignored according to Equation 6 above
Handling and searching cannot be done at the same time	Low-ranking prey are all or nothing in the diet, according to Equation 7 above
Prey are recognized instantly with no errors	The exclusion of low-ranking prey does not depend on their abundance (measured by $\lambda_2$ )
Prey are encountered sequentially and randomly	
All prey individuals of a given prey type are identical	
Energetic costs of handling are similar for the two prey items	
Predators are maximizing the rate of energy intake	



Figure 5 Test of the simple optimal foraging model for the great tit (*Parus major*). Two sizes of worms were the prey choice in the laboratory. As more and more large prey are presented, the bird should stop eating small prey at the threshold and eat only large prey (red dashed line), according to the model. In reality the birds switch to large prey but always take some small prey (blue points). (Data from Krebs et al. 1977.)

have the perfect knowledge assumed in the simple models of foraging. Nevertheless, simple models are useful because they highlight the key processes that need studying and further analysis.

For many animals, food is distributed in a series of discrete patches across the landscape, some patches containing more food than others. If an animal is engaging in optimal foraging, it should preferentially forage in patches where the difference between benefits and costs is high. The benefits of foraging can be measured in terms of the amount of food obtained in each patch, and the costs can be measured in terms of the time taken and the probability of injury or predation. How will a forager respond when the costs of feeding in different patches are varied? We can answer this question by providing the same amount of food (a fixed benefit) in experimental patches that differ in their risk of predation or level of competition (varied costs). We can then determine how animals respond to changes in the costs of foraging by measuring how much food they eat in each patch. This approach was first used by Joel Brown in 1988 to investigate the foraging behavior of small mammals in desert habitats. He predicted that if the food levels are equal in two patches, a forager should stay longer and eat more food in the patch where the costs of foraging are lower.

One animal on which Brown's hypothesis has been tested is the gerbil (*Gerbillus* spp.). Gerbils are nocturnal, seed-eating rodents that live in sandy burrows. Their major predator is the barn owl, a rodent



Figure 6 Proportion of seeds eaten by gerbils under bushes (green bars) and in the open (red bars) in the Negev Desert. Trays of seeds were set out in experimental enclosures in which the presence of moonlight and the presence of a predator, the barn owl, varied. Not all the seeds in the trays were eaten even in the best of circumstances in these overnight experiments. (Data from Kotler et al. 1991.)

specialist. Ecologists studied the foraging behavior of gerbils by placing seed trays in open areas and under bushes in experimental enclosures. Some enclosures were illuminated; others were dark. Captive, trained barn owls were released into some enclosures and not into others. If predation is the major cost of foraging by gerbils, they should eat more seeds under bushes and spend more time foraging there, especially in enclosures that are illuminated or that contain predators. This is exactly what the researchers found. As Figure 6 shows, gerbils fed primarily at trays under bushes and reduced their overall feeding on bright nights, particularly when owls were present. They fed in open areas only when owls were absent. The results indicate that these desert rodents make choices based on the benefits of easily available food and the costs due to predation, and that the risk of predation influences their foraging behavior. If we were managing populations of gerbils, this study could tell us what kinds of habitat alterations might improve or decrease their survival and breeding success.

Simple optimal foraging models fit the observed data on many animals quite well but not perfectly, and this highlights some of the rigid assumptions of these quantitative models. Foraging models may be only partially correct (e.g., see Figure 6) because of discrimination errors (animals may confuse a prey 1 for a prey 2), simultaneous encounters (animals may see two different prey at the same time), or runs of bad luck in which animals do not encounter prey in a reasonably random manner. In spite of these problems, optimal foraging models have helped to instill quantitative rigor into studies of foraging in animals.

Optimal foraging studies support the conclusion that animals are finely adapted to searching for food in ways that achieve maximum relative benefit. Natural selection continues to favor efficient foraging traits.

## **Optimal Migration**

Animals need information in order to make decisions, and optimality models often assume that animals are fully informed about their environment when foraging or mating. Migrating birds are a special case of the problem of decision making. Migrating animals must choose how far to move in one step, and if they cannot feed while migrating, how much fuel to carry en route. Migrating birds are a special case in decision making because they incur large locomotory costs in flight, and the strategies migratory birds use have been extensively studied (Alerstam 1990).

Migrating birds have three potential migration strategies:

- Time minimization (complete migration in the minimum possible time). The birds should optimize the overall speed of migration, which means that the birds will waste energy to achieve this goal. This would be a desirable strategy if early arrival at the destination is an important fitness advantage for the birds.
- Energy minimization (complete migration with the least energy cost). This strategy will be selected for when the risks associated with migration are relatively high and the use of energy during migration is high. This strategy would also be advantageous if energy resources along the migratory route are sparse. The net result from adopting this strategy will be some waste of energy on an annual basis. The birds are expected to minimize stopover times and increase migration speed.
- Cost of transport minimization. This is a second energy minimization strategy but focuses on the overall goal of minimizing total energy use over the entire annual cycle. The energy used in migration is only one part of the annual energy use for migratory birds, and minimizing energy in migration typically results in using more energy

over the whole annual cycle. This model optimizes migration cost but within the whole annual cycle rather than only the restricted migration period.

Because the aerodynamics and energetics of bird flight have been so well investigated, it is possible to construct optimal migration models for these three strategies (Hedenström and Alerstam 1997). We consider here only the simple case for many passerine migrants that migrate in a series of hops rather than in one long flight. At each stopover point, the birds must refuel, and there is an energy cost to finding the necessary food at the stopover points. Two variables are critical for the birds: (1) fuel deposition rate-the rate of energy accumulation by feeding before migration begins and during stopovers-which is measured by the fraction of lean body mass accumulated per day; and (2) departure load-the amount of fat and protein expressed as a fraction of lean body mass. The predicted relationship between these two variables under the three optimality models is shown in Figure 7. The key prediction of the third model is that the departure load of a bird will be constant and independent of the rate at which fuel can be accumulated. Both the time and the energy minimization models show an increasing relationship so that when more fuel can be accumulated, the departure load will increase.



(fraction of body mass accumulated per day)

Figure 7 Relation between fuel deposition rate and departure load for birds migrating in a series of flights with stopovers en route. Three migration strategies are possible to minimize time or energy, and the graph shows the predictions of these three models. The costs of transport model is energy minimization on an annual basis, while the energy minimization model is energy minimization for the migratory period only. (Modified from Bayly 2006.)

#### **Behavioral Ecology**

We can test the models by measuring fuel deposition rate and departure loads for migrating birds. Bayly (2006) did this with reed warblers (Acrocephalus scirpaceus), a trans-Saharan migrant. These birds must cross over 2500 km of desert, a feat that requires a large fuel load. Much of the migration in this species and other birds is spent in a series of fuelling phases, and migratory flight will occupy a relatively short amount of time overall. Bayly (2006) provided reed warblers with supplementary food at a site in southern England, and was able to record fuel deposition rate and departure loads, with the results shown in Figure 8. There is considerable variation among individual birds, but the time minimization model fit the data best. So far, most of the tests of the optimal migration model have supported the time minimization model.

The amount of energy small birds use in stopovers is typically two to three times the amount of energy used in actual migratory flights (Hedenström and Alerstam 1997). The time spent in stopovers is about 7 times that spent on flight for small birds, and much more for larger birds. These surprising results suggest that more studies need to be undertaken at stopover points for migratory birds to measure the energetics of individual birds during stopovers. Critical habitats for migratory birds are



**Figure 8 Optimal migration strategy for the reed warbler.** The best fit to the observed data is given by the time minimization model with 3 days stopover costs. The cost of transport model, which predicts a horizontal relationship, is not supported for this species. High variability among the individual birds could be due to birds making errors when calculating the correct departure load. (Modified from Bayly 2006.)

not just the endpoints (breeding and wintering areas), but also the stopover localities in between.

Many large mammals undertake seasonal migrations typically associated with seasonal food resources (Fryxell and Sinclair 1988). These migrations can have important consequences for population dynamics.

## **Group Living**

Many animals live in groups. Grazing herbivores form large herds, fish school together, carnivores form hunting groups, birds breed in large colonies, and some animals live in extended family groups. If natural selection favors individual interests over group interests, why should animals ever associate, much less cooperate with others to hunt or raise young? We can start to understand the factors that drive the evolution of group living by evaluating its benefits and costs (Table 2).

## Benefits of Group Living

The two main factors affecting group size are food and predators. If food is sparsely distributed and difficult to locate, living in a group can increase an individual's foraging success by allowing it to obtain information about the location of food from successful foragers. This idea, which was first proposed by Paul Ward and Amotz Zahavi in 1973, explains why some birds nest in colonies.

Social insects are the classic example of cooperation for food gathering. Karl von Frisch discovered more than 80 years ago that when successful bee foragers returned

## Table 2Potential benefits and costs<br/>of group living in animals.

Potential benefits	Potential costs
Increased foraging efficiency	Competition for food Increased risk of disease or parasites
Reduced predation	Attraction of predators
Increased access to mates	Loss of paternity Brood parasitism
Help from kin	Loss of individual reproduction

#### Behavioral Ecology

to the hive, they communicate the location of a rich food source using a waggle dance (**Figure 9**). This dance involves running through a small figure-eight pattern—a straight run followed by a turn to the right to circle back to the starting point, and then another straight run followed by a turn and circle to the left. The straight section of the dance is the most striking and the most informative part of the signaling bee's dance. While walking straight ahead, the bee waggles or vibrates its body back and forth, side to side. At the same time, the bee emits a buzzing sound. Typically, several workers cluster closely around the dancing bee, trying to maintain contact and to obtain information (von Frisch 1967).

The direction and duration of straight runs in the dance are closely correlated with the direction and distance of the patch of flowers just visited by the dancing forager (see Figure 9). The farther away the target, the longer the straight-run part of the dance. In addition to information on the direction and distance of the flower food source, the dancing bee also communicates the odor of the flowers. This communication is typically given by the pollen it carries back on its hind legs, or in the nectar it regurgitates to the surrounding bees.

There is no question that the dance of the returning honeybees gives information to the recruits, but how precise is it and over what range can it operate. Bees routinely forage up to 12 km from their nest (Seeley 1985), and it is clear that bees can recruit nestmates to forage in patches up to 10 km from home. But how precise is this recruitment? Only a small percentage of bees that closely follow the waggle dance actually find the food source. Gould (1975) described one study in which the precision of recruitment to a food source 315 m distant had an error of about 60 m in either direction. Successful recruits in several studies needed two to seven trips to find the exact food source. One suggestion is that once in the general area of a food source, bees use odors to find flowers. But it has been shown that bees in hives that are allowed to carry out dances with directional light had improved food collection compared with bees in colonies that had diffused light in the hives (which does not permit the correct dance orientation). Sherman and Visscher (2002) found that this advantage from the properly oriented dances was effective in increasing colony food collection only in those seasons of the year when the sun was at its highest.

A second potential benefit of group living is a reduced risk of predation. Group living may appear to be a benefit to the group, but it is the advantage it gives to individual animals that is the driving force in the evolution of group living. If a predator takes a single individual as prey, each individual's risk of predation would drop from 10 percent in a group of 10 to 1 percent in a group of 100, if all other factors are equal. This "dilution effect" is a passive benefit



(a)





(c)

1000

2000

**Figure 9** The waggle dance of the honey bee. (a) The patch of flowers lies 1500 m out along a line 40° to the right of the sun as the bee leaves the colony nest in the tree. (b) To advertise this target when the forager returns to the nest, the bee runs through a figure-eight pattern, vibrating her body laterally as she passes down the straight run. The straight run is oriented on the vertical honeycomb by transposing the angle shown in (a) to the angle between the straight run and the vertical. (c) Distance to the flowers is coded by the duration of the straight run. (Data from Seeley 1985.)

3000

Distance to the food source (m)

4000

5000

6000

of larger groups. But this benefit must be balanced against the higher probability that a predator will find a large group than a small group or an individual. Animals in a group can also actively lower their risk of predation by being vigilant for predators. Increasing group size can make vigilance more effective and less costly, since many eyes increase the probability of predator detection and reduce the time each individual must spend being vigilant. Less time spent in vigilance should translate into more time for other activities, such as foraging.

Guppies (*Poecilia reticulata*) in Trinidad live in streams with differing predator densities. When predators are abundant, guppies school in more tightly spaced groups (**Figure 10**). But predators prefer to attack larger schools of guppies, which challenges the idea that it is safer in a group. The key question is whether an individual guppy is safer in a larger group. Krause and Godin (1995) tested the safety of group living in the laboratory where they could expose groups of guppies to cichlid predators for short time periods. **Figure 11** shows that predators attack larger schools more often if given a choice between a small school of guppies and a large school, but that for each individual guppy the likelihood of being captured by the predator is much higher in small groups.

From an evolutionary point of view, success is measured in terms of the number of copies of one's genes in future generations. An individual can increase its evolutionary success, or fitness, directly by producing its own young, and indirectly by increasing the survival or reproductive success of close relatives, which have some of the same genes. Helping relatives and being helped by relatives is one benefit of group living in some animals, so cooperation in these animals has an evolutionary explanation.

Belding's ground squirrels (Spermophilus beldingi) provide an example of apparent cooperation in groupliving animals. These rodents live in burrows in alpine and subalpine meadows in western North America. Although both sexes disperse from the burrow where they were born, males move much farther than females. This difference in dispersal distance leads to neighborhoods where females are closely related but males are not. Belding's ground squirrels produce loud alarm calls when predators-chiefly coyotes, pine martens, and long-tailed weasels-are in the area. Alarm calls serve as an early warning for other ground squirrels living nearby, but they provide no immediate benefit to the caller. In fact, they may increase costs for the caller by attracting predators to it. Why then should any individual produce alarm calls? Paul Sherman addressed this question by studying a population of individually tagged Belding's ground squirrels over several years. He found that females were far more



Figure 10 Guppies in Trinidad streams live in tighter schools in streams in which predators are more abundant. Each point represents a different stream, and the cohesion score is based on how much individual fish spaced from one another (with 95 percent confidence). (Data from Seghers 1974.)



**Figure 11 Experimental analysis of predation risk in guppy schools.** The cichlid fish *Aequidens pulcher* was used as the predator in these experiments. The overall result is that an individual guppy always benefited by joining a large school, even though large schools are attacked more often. (Data from Krause and Godin 1995.)

### ESSAY

## Do Individuals Act for the Good of the Species?

atural selection occurs because of the reproductive advantages of some individuals. This view of the world implies that all individuals are in competition with each other and will behave to further their own interests. From a philosophical viewpoint, the idea that the world is full of selfish individuals clashes with many of the values we hold for human societies, such as cooperation, community spirit, and selflessness. Does the variety of behaviors that we observe in animals, even the apparently cooperative ones, really arise from the interactions of selfish individuals? Can traits evolve that favor the larger interests of a group or society? Does evolution lead only to selfishness? These are key questions that interest social scientists, philosophers, and biologists. Biologists do not think that individuals ever act for the good of the species, but there are many situations in which what appear to be selfish individual behaviors operate to benefit a group.

It is easy to imagine that populations of selfish individuals might overexploit the available resources and become extinct, whereas populations that have evolved social behaviors preventing overexploitation of resources might have better long-term survival prospects. Natural selection for traits that favor groups rather than individuals is termed **group selection**. The idea that groups of animals could evolve self-regulating mechanisms that prevent overexploitation of their food resources was first argued in detail in 1962 by V. C. Wynne Edwards, an ecologist at the University of Aberdeen in Scotland. Despite its intuitive appeal, group selection is not considered very important in producing changes in species traits. Group selection operates much more slowly than individual selection, making it a much weaker selective force in most circumstances.

To understand apparently cooperative behaviors that benefit the group or society, we need to look for benefits accruing to individuals.

Imagine, for example, a species of bird, such as the puffin that lives in large colonies and lays only a single egg. Could laying a single egg have evolved in puffins by group selection to limit population growth and maintain an adequate food supply for the long-term good of the puffin



colony? The answer is no, because any mutation that increased the number of eggs laid would be favored only if individuals laying two eggs leave more copies of their genes to the next generation, compared with birds laying a single egg. But ecologically speaking, costs would increase as well as benefits. A puffin with two eggs would have to collect more calcium to lay two eggs and would have to fly more to feed two young. There are ecological costs to increasing the clutch size in puffins. Consequently, genes for laying two eggs would not spread through the population unless the benefits would exceed the costs. Individual selection favors the small clutch size in puffins. Short-term advantages to selfish individuals will accrue much more guickly than long-term advantages to the group, so it is difficult to see how traits favored by group selection can be maintained in a population unless they are also favored by individual selection.

But this does not mean that all behavior must be selfish and that altruism does not exist. To understand apparently cooperative behaviors that benefit the group or society, we need to look for benefits accruing to individuals. Individual selection can produce behaviors that are a benefit for the group.

Some of the best examples of individuals working for the good of the group come from the social insects. Ants and many bees live in colonies in which the individuals cooperate to rear young and defend the hive. Natural selection in the social insects operates through kin selection, and individuals in these insect colonies cooperate to further the interests of the entire colony (Queller and Strassmann 1998).

#### **Behavioral Ecology**

likely to give alarm calls than males (Figure 12a). However, females differed in the frequency with which they called: Females with nearby relatives, even young females that had no offspring of their own, called more often than females that had no relatives in the area (Figure 12b). Thus, Belding's ground squirrels are more likely to call when doing so may benefit the survival of their close relatives. The evolution of traits that increase the survival, and ultimately the reproductive success, of one's relatives rather than oneself is termed kin selection.

## Costs of Group Living

Living in a group has costs, as well as benefits (see Table 2). The magnitude of these costs limits the extent to which a species forms groups and explains why some groups are larger than others. Not surprisingly, living in large groups leads to competition for resources, such as food or mates. For example, Magellanic penguins *(Spheniscus magellanicus)* form breeding colonies of up to 200,000 birds on subantarctic islands. Colony size in this species appears to be limited by competition for food,

100 80 Proportion of times they respond 80 60 60 40 40 20 20 0 0 Male Female No Sister Daughters relatives or only mother only (b) (a)

**Figure 12 Patterns of alarm calling by Belding's ground squirrels.** (a) Effect of sex on frequency of calling. (b) Effect of type of nearby relatives on frequency of calling by females. In both (a) and (b), the vertical axis is the percentage of time that squirrels produced alarm calls when a predator approached. (Data from Sherman 1977.)

which consists of squid and pelagic schooling fishes including anchovy. Adults and chicks in small colonies ingest more prey of high-energy content than do individuals in large colonies (**Figure 13**), and fledglings in small colonies are healthier and therefore more likely to reach adulthood. The costs of group living are related to colony size, and one of the consequences of this is population regulation by food shortage.

Breeding in large colonies can also increase the transmission of diseases and parasites, which have population consequences. Another species of penguin, the king penguin (*Aptenodytes patagonicus*), breeds in Antarctica in colonies of up to 500,000 individuals. In large colonies, adults and chicks become infested with ticks (*Ixodes uriae*). High rates of tick infestation reduce the incubation success of adults (**Figure 14**).



Figure 13 Relationship between nitrogen index and colony size in Magellanic penguins. The nitrogen index is based on the ratio of stable nitrogen isotopes in blood samples and is an indicator of food quality. A higher nitrogen index reflects a diet of more nutritious prey, such as anchovies. All age and sex groups suffer a poorer diet in large colonies. (Data from Forero et al. 2002.)





Another important cost of group living is loss of parentage. Breeding in a group increases the chance that an animal will raise another individual's offspring. This problem is well illustrated in cooperatively breeding birds. Splendid fairy wrens (Malurus splendens) in southern Australia are small songbirds that live in cooperative groups of a dominant male, a single female, and one or more auxiliaries (almost always males). All individuals in the territorial group cooperate in feeding and caring for young, and this is why dominant males tolerate auxiliary males in the group. But females engage in extra-pair copulations, both with males from another group and with auxiliary males within the group, so that about 40 percent to 70 percent of the offspring are sired by males who are not the dominant territory holder (Rowley and Russell 1997; Webster et al. 2004). The frequency of extra-pair copulations increases with the size of the cooperative group (Figure 15). Extra-pair copulations help to prevent inbreeding in cooperative breeders, and they explain in part the advantage that auxiliary males may gain from helping raise broods. Webster et al. (2004) found that 75 percent of the extra-pair young were fathered by the dominant male in another group, 10 percent by auxiliary males in the same group, and 14 percent by auxiliary males in another group. The potential costs and benefits of group living can vary among breeding groups with different levels of relatedness. If all members of the group are closely related, individuals will gain by helping their relatives. But if few members of the group are related, individual selection will be stronger than kin selection and the ratio of costs and benefits for an individual bird will be less favorable.

## Group Living in African Lions

Ecologists have been studying the social behavior of lions (Panthera leo) for more than 40 years in eastern



Figure 15 Percentage of offspring that were sired by extra-pair males as a function of the number of auxiliary males in the splendid fairy wren in South Australia. Bars indicate upper 95 percent confidence limits. The larger the cooperative breeding group, the less the reproductive success for the dominant male. (Data from Webster et al. 2004.)

#### **Behavioral Ecology**

and southern Africa, and they are now a classic example of the costs and benefits of group living. Lions are the most social member of the cat family, forming groups called prides composed of one to seven males, 2 to 18 females, and their young. Prides are relatively small in arid areas such as the Kalahari, and relatively large in areas such as the Serengeti Plains that have more abundant large prey (Packer et al. 1988). In this section, we will examine the costs and benefits of different pride sizes and try to understand the benefits of group living for lions. Why do lions live in prides, and why do pride sizes vary from place to place?

Male and female lions behave in very different ways, and these differences influence the costs and benefits of group living for each sex. Females almost never leave the pride in which they were born. They cooperate with their mothers, sisters, and other female relatives in hunting, raising young, and defending territory. In contrast, male lions are highly transient. They leave their pride of birth when two to three years old and roam widely in search of a new pride. Males that do not belong to a pride often group with related or unrelated males, forming coalitions that challenge males in existing prides for breeding positions. These challenges may result in the death of one or more of the participants. Once in a pride, the males do little hunting, and instead spend most of their time defending their territory by patrolling, scent marking, and roaring. Because of frequent challenges, males rarely retain control of a pride for more than two years.

Because of the behavioral differences between male and female lions, we will consider the benefits of male-male groups and female-female groups separately. For males, the major benefit of grouping is straightforward. Single males rarely succeed in obtaining a breeding position within a pride. Large coalitions are more likely to take over a pride and are more effective at repelling challenges from other males. Males that take over a pride kill unrelated cubs, and thus challenges must be repelled. Consequently, an individual male's reproductive success increases with the number of males in a coalition (Figure 16). The longer a coalition can remain in control of a pride, the more cubs those males can produce, and the greater the cubs' chances of survival. Although male reproductive success increases with coalition size, individual breeding success becomes more variable in the largest coalitions: Some males mate often, whereas others rarely mate. As a result, male-male competition for mating can act to set an upper limit on coalition size.

For female lions, the benefit of group living—as measured by reproductive success—is greatest in groups of 3 to 10 females (**Figure 17**). This appears to be the **optimal group size**, the size that results in the



**Figure 16 Benefit of group living in male lions.** Males in larger coalitions have increased reproductive success. (Data from Packer et al. 1988.)



**Figure 17** Reproductive success of female lions in prides of differing size. The production of cubs is maximal when prides contain 3 to 10 females. (Data from Packer et al. 1988.)

Table 3 Specific benefits and costs of forming male or female groups in African lions.				
Sex	Benefits of grouping	Costs of grouping		
Male	Increased ability to gain control of a pride (access to mates)	Sharing of paternity with coalition members		
	Increased ability to maintain control of a pride (higher survival of offspring)			
Female	Preferential feeding of close kin (help from kin)	Lower rate of food intake		
	Territorial defense (increased female and offspring survival)			

largest relative benefit. How can we explain this observation? Careful calculations have shown that very small prides (and even solitary lionesses) have the highest rates of food intake. Thus, hunting success seems to decrease as group size increases. In contrast, larger groups facilitate territorial defense, which is important in preventing male takeovers. When new males take over a pride, they typically kill all the young cubs. That causes the females in the pride to rapidly enter estrus, allowing the new males to father offspring quickly. Cub survival is higher in larger female groups because larger groups are better able to save young cubs from infanticide. Thus, the optimal group size in female lions may represent a balance between hunting success and territorial defense. As this example of African lions illustrates, understanding which factors favor group living in a species can be complex (**Table 3**). Although we can easily identify potential costs or benefits of group living, to single out the important factors, we must determine how this behavior affects the survival and reproductive success of an individual. Doing this successfully requires detailed data on individuals from groups of different sizes, carefully designed field experiments, or both. The relative benefit of group living may vary with habitat type and other environmental conditions, making long-term studies especially important. In many species, the costs and benefits of group living differ between the sexes, which can lead to conflict between males and females over the optimal group size.

#### Summary

If a population is to persist, its members must obtain food, avoid predators and disease, and produce offspring. They achieve these goals through a variety of behaviors, which must be appropriate for their particular environment. Many animals must make decisions about where to forage, which individuals to mate with, how large a territory to defend, and which habitat to select for nesting. Natural selection is the force that achieves the fit between how individuals behave and their subsequent survival.

The key to understanding the behavior of individuals is to determine the costs and benefits of these decisions in terms of the number of offspring an individual produces. Optimality models assist us in understanding animal behaviors by forcing us to quantify the costs and benefits of decisions. This approach has been particularly successful for foraging behavior, and we can identify foraging rules by which animals optimize their food intake rates. A cost–benefit analysis can also help us identify the factors that affect the social structure of a species, such as its optimal group size and how large a territory it defends. Understanding the factors that influence the behavior of individuals may allow us to predict how different species will respond to conservation problems such as habitat loss.

Behavioral ecology forms a bridge to understanding the dynamics of populations and communities. Mechanisms such as climate change that affect populations and communities must ultimately relate to how individual animals adapt their behavior to a changing environment.

#### **Review Questions and Problems**

- 1 In 1957 Carl Haskins moved 200 guppies from a river with high predator abundance to the predatorfree upper headwaters of the Oropuche River in Trinidad. What predictions would you make for the guppies moved in this transplant experiment? How would you test experimentally whether the antipredator behaviors are under genetic control or under environmental control? State two or more hypotheses for this experiment and discuss how you might test their predictions. Magurran et al. (1992) discuss this transplant experiment.
- 2 What assumptions underlie the cost–benefit approach to optimality models? Is it possible to test whether or not an animal is acting optimally? Could there be cases in which animals might not be well adapted? Krebs and Davies (1993) discuss these questions.
- 3 Altruism—personal sacrifice on behalf of others—is difficult for behavioral ecologists and evolutionary biologists to explain because natural selection favors the interests of individuals. Nevertheless, altruistic behaviors toward relatives are observed in many animal societies. Is there any way that altruism among nonrelatives can evolve in animal societies? How might altruism arise in human societies if it is based on selfinterest? Gintis et al. (2003) discuss this question.

## **Suggested Readings**

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- Dornhaus, A., and L. Chittka. 2004. Why do honey bees dance? *Behavioral Ecology and Sociobiology* 55:395–401.
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- Hamilton, W. D. 1971. Geometry of the selfish herd. *Journal of Theoretical Biology* 31:295–311.
- Hedenström, A., and T. Alerstam. 1997. Optimum fuel loads in migratory birds: Distinguishing between time and energy minimization. *Journal of Theoretical Biology* 189:227–234.

- 4 Many birds form groups in which only one female breeds and other birds act as helpers at the nest. Discuss the relative benefits of males and females for being a helper in such breeding groups. Why might an individual choose to stay as a helper in a group rather than move away and breed elsewhere? Heinsohn and Legge (1999) discuss this problem of cooperative breeding.
- 5 In Scotland, female offspring of red grouse disperse to surrounding areas, while male offspring take up a territory next to their father, if they survive. A male's territory is always occupied exclusively by one bird. Describe how the aggression associated with territorial defense might differ if a male is surrounded by his sons or by unrelated males. Mougeot et al. (2003) describe this system and some experiments on this issue.
- 6 Infanticide is observed in many mammals, birds, and insects. Female infanticide is surprisingly common in human cultures. Using the approaches discussed in this chapter, (a) formulate two hypotheses to explain infanticide in humans, (b) describe the data you would collect to test your hypotheses, and (c) discuss the proposition that infanticide is adaptive in humans.
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