CHAPTER 11

Natural Selection and Adaptation

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Adapting an adaptation. Nudibranchs such as *Flabellina iodinea* are marine gastropod molluscs that lack shells. Many nudibranchs are unpalatable or dangerous because of stinging nematocysts they acquire by feeding on coral tissue and storing the noxious structures in their own bodies as a defense against predators. Bright "warning coloration" like this individual's is adaptive in toxic animal species, a signal to would-be predators that consuming this particular prey is not a good idea. (Photo © Ralph A. Clevenger/Photolibrary.com.)

The theory of natural selection is the centerpiece of *The Origin of Species* and of evolutionary theory. It is this theory that accounts for the adaptations of organisms, those innumerable features that so wonderfully equip them for survival and reproduction; it is this theory that accounts for the divergence of species from common ancestors and thus for the endless diversity of life. Natural selection is a simple concept, but it is perhaps the most important idea in biology. It is also one of the most important ideas in the history of human thought—"Darwin's dangerous idea," as the philosopher Daniel Dennett (1995) has called it—for it explains the apparent design of the living world without recourse to a supernatural, omnipotent designer.

An **adaptation** is a characteristic that enhances the survival or reproduction of organisms that bear it, relative to alternative character states (especially the ancestral condition in the population in which the adaptation evolved). Natural selection is the only mechanism known to cause the evolution of adaptations, so many biologists would simply define an adaptation as a characteristic that has evolved by natural selection. The word "adaptation" also refers to the process whereby the members of a population become better suited to some feature of their environment through change in a characteristic that affects their survival or reproduction. These definitions, however, do not fully incorporate the complex issue of just how adaptations (or the process of adaptation) should be defined or measured. We will touch on some of these complexities later in this chapter.

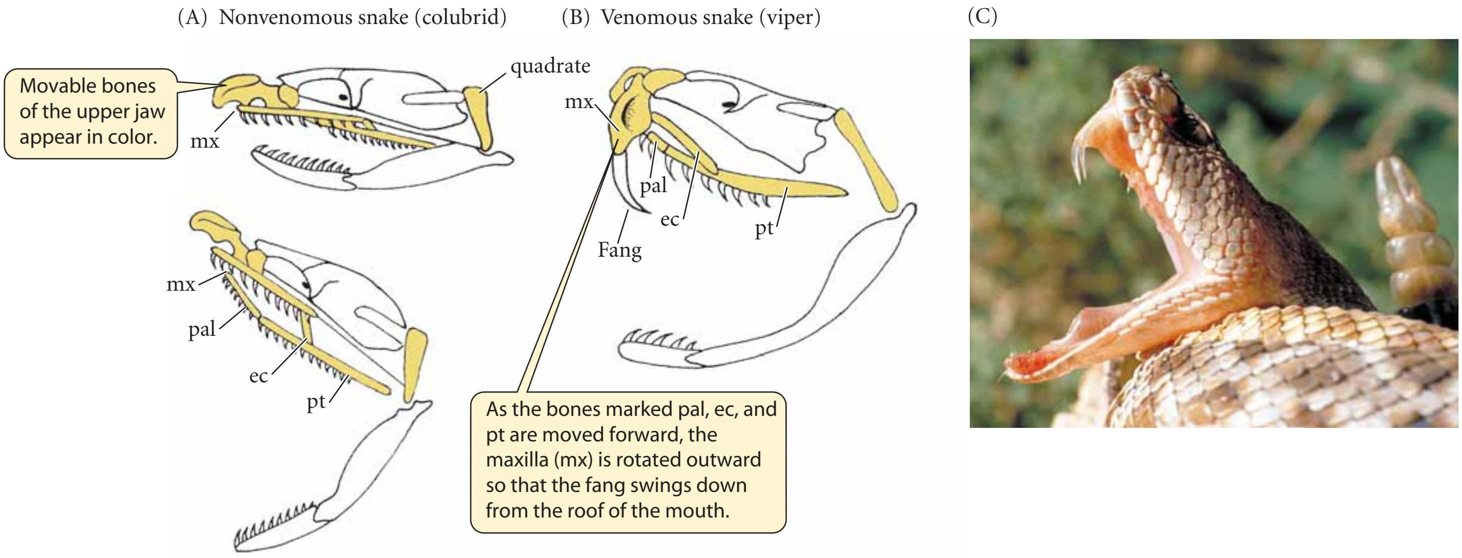


Figure 11.1 The kinetic skull of snakes. The movable bones of the upper jaw are shown in gold. (A) The skull of a nonvenomous snake with jaws closed (top) and open (bottom). (B) A viper's skull. (C) The head of a red diamondback rattlesnake (*Crotalus ruber*) in strike mode. (A, B after Porter 1972; C © Tom McHugh/Photo Researchers, Inc.)

Adaptations in Action: Some Examples

We can establish a few important points about adaptations by looking at some striking examples.

- In most terrestrial vertebrates, the skull bones are rather rigidly attached to one another, but in snakes they are loosely joined. Most snakes can swallow prey much larger than their heads, manipulating them with astonishing versatility. The lower jawbones (mandibles) articulate to a long, movable quadrate bone that can be rotated downward so that the mandibles drop away from the skull; the front ends of the two mandibles are not fused (as they are in almost all other vertebrates), but are joined by a stretchable ligament. Thus the mouth opening is greatly increased (Figure 11.1A). Both the mandibles and the tooth-bearing maxillary bones, which are suspended from the skull, independently move forward and backward to pull the prey into the throat. In rattlesnakes and other vipers, the maxilla is short and bears only a long, hollow fang, to which a duct leads from the massive poison gland (a modified salivary gland). The fang lies against the roof of the mouth when the mouth is closed. When the snake opens its mouth, the same lever system that moves the maxilla in nonvenomous snakes rotates the maxilla 90 degrees (Figure 11.1B), so that the fang is fully erected. Snakes' skulls, then, are complex mechanisms, "designed" in ways that an engineer can readily analyze. Their features have been achieved by modifications of the same bones that are found in other reptiles.
- Among the 18,000 to 25,000 species of orchids, many have extraordinary modifications of flower structure and astonishing mechanisms of pollination. In pseudocopulatory pollination, for example (Figure 11.2), part of the flower is modified to look somewhat like a female insect, and the flower emits a scent that mimics the attractive sex pheromone (scent) of a female bee, fly, or thynnine wasp, depending on the orchid species. As a male insect "mates" with the flower, pollen is deposited precisely on that part of the insect's body that will contact the stigma of the next flower visited. Several points are of interest. First, adaptations are found among plants as well as animals. For Darwin, this was an important point, because Lamarck's theory, according to which animals inherit characteristics altered by their parents' behavior, could not explain the adaptations of plants. Second, the floral form and scent are adaptations to promote reproduction rather than survival. Third, the plant achieves reproduction by deceiving, or exploiting, another organism; the insect gains nothing from its interaction with the flower. In fact, it would surely be advantageous to resist the flower's deceptive allure, since copulating with a flower probably reduces the insect's opportunity to find proper mates. So organisms are not necesssarily as well adapted as they could be.

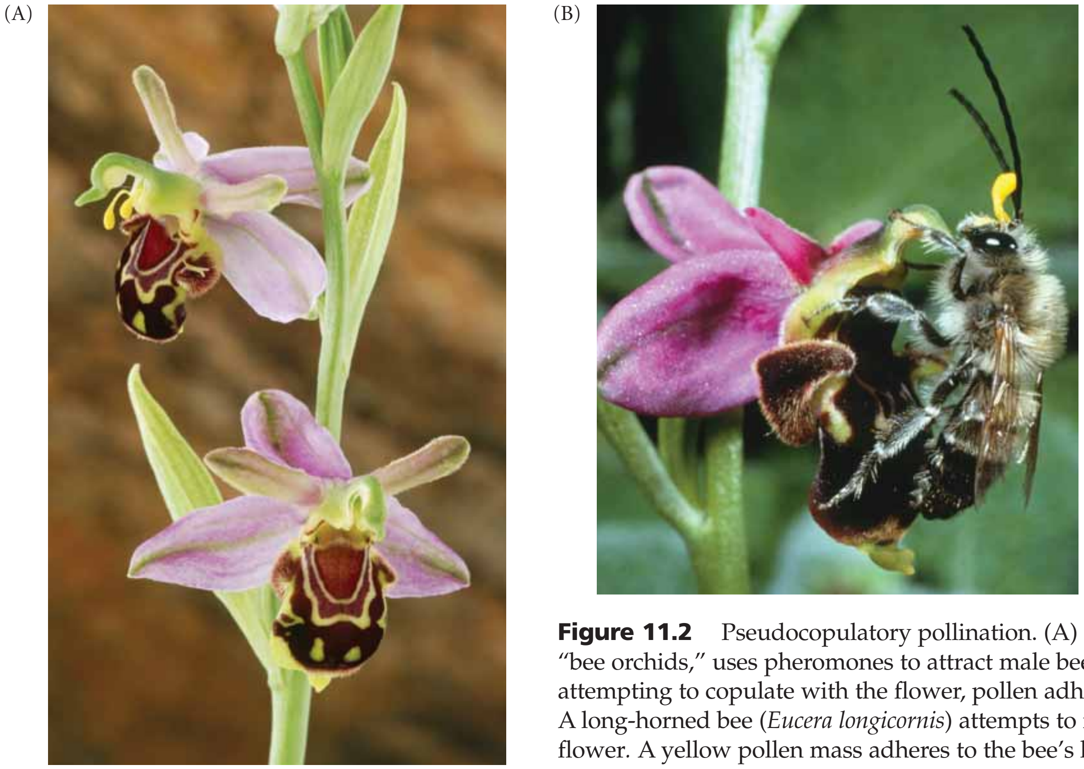
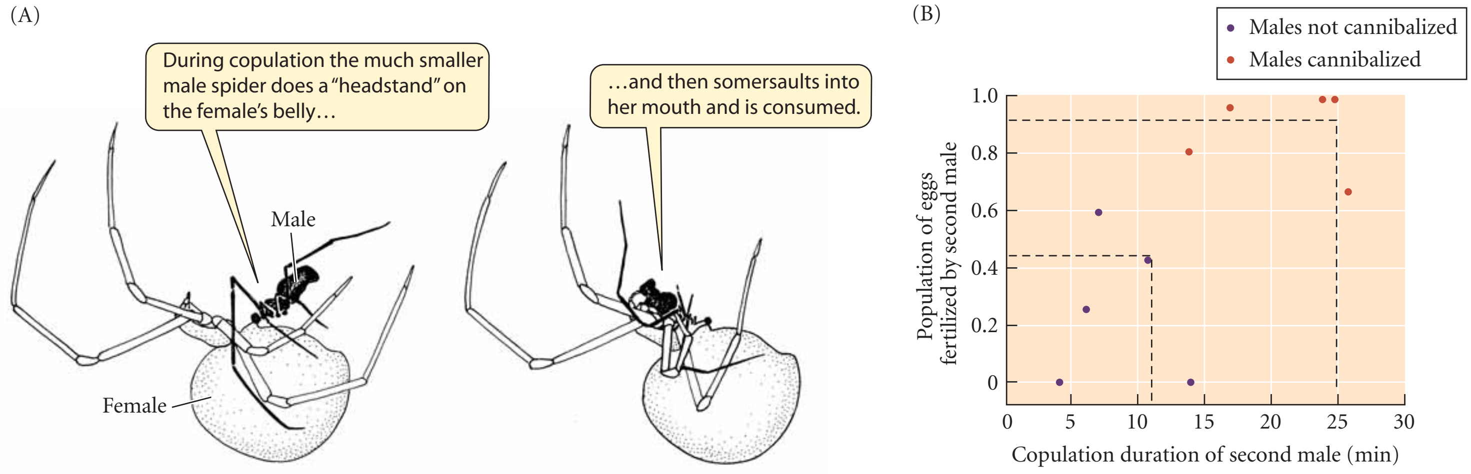


Figure 11.2 Pseudocopulatory pollination. (A) *Ophrys apifera*, one of the "bee orchids," uses pheromones to attract male bees and is shaped such that, in attempting to copulate with the flower, pollen adheres to the insect's body. (B) A long-horned bee (*Eucera longicornis*) attempts to mate with an *Ophrys scolopax* flower. A yellow pollen mass adheres to the bee's head. (A © E. A. Janes/Photolibrary.com; B © Perennou Nuridsany/Photo Researchers, Inc.)

- After copulation, male redback spiders (*Latrodectus hasselti*; relatives of the "black widow" spider), often somersault into the female's mouthparts and are eaten (Figure 11.3A). This suicidal behavior might be adaptive, because males seldom have the opportunity to mate more than once, and it is possible that a cannibalized male fathers more offspring. Maydianne Andrade (1996) tested this hypothesis by presenting females with two males in succession, recording the duration of copulation, and using genetic markers to determine the paternity of the females' offspring. She found that females that ate the first male with whom they copulated were less likely to mate a second time, so these cannibalized males fertilized all the eggs. Furthermore, among females that did mate with both males, the percentage of offspring that were fathered by the second male was greater if he was eaten than if he survived. (Figure 11.3B). Both outcomes support the

Figure 11.3 (A) The small male redback spider somersaults into the large female's mouthparts after copulation. (B) The proportion of eggs fertilized by the second male that copulated with a female was correlated with the duration of his copulation. On average, copulation by cannibalized males lasted longer than that by noncannibalized males. (A after Forster 1992; B after Andrade 1996.)



hypothesis that sexual suicide enhances reproductive success. This example suggests that prolonged survival is not necessarily advantageous, and illustrates how hypotheses of adaptation may be formulated and tested.

- Many species of animals engage in cooperative behavior, but it reaches extremes in some social insects. An ant colony, for example, includes one or more inseminated queens and a number of sterile females, the workers. Australian arboreal weaver ants (genus *Oecophylla*) construct nests of living leaves by the intricately coordinated action of numerous workers, groups of which draw together the edges of leaves by grasping one leaf in their mandibles while clinging to another (Figure 11.4). Sometimes several ants form a chain to collectively draw together distant leaf edges. The leaves are attached to one another by the action of other workers carrying larvae that emit silk from their labial glands. (The adult ants cannot produce silk.) The workers move the larvae back and forth between the leaf edges, forming silk strands that hold the leaves together. In contrast to the larvae of other ants, which spin a silk cocoon in which to pupate, *Oecophylla* larvae produce silk only when used by the workers in this fashion. These genetically determined behaviors are adaptations that enhance the reproductive success not of the worker ants that perform them, since the workers do not reproduce, but rather of their mother, the queen, whose offspring include both workers and reproductive daughters and sons. In some species, then, individuals have features that benefit other members of the same species. How such features evolve is a topic of special interest.

Figure 11.4 Weaver ants (*Oecophylla*) constructing a nest. Chains of workers, each seizing another's waist with her mandibles, pull leaves together. (Photo from Hölldobler and Wilson 1983, courtesy of Bert Hölldobler.)

The Nature of Natural Selection

Design and mechanism

Most adaptations, such as a snake's skull, are *complex*, and most have the appearance of *design*—that is, they are constructed or arranged so as to accomplish some *function*, such as growth, feeding, or pollination, that appears likely to promote survival or reproduction. In inanimate nature, we see nothing comparable—we would not be inclined to think of erosion, for example, as a process designed to shape mountains.

The complexity and evident function of organisms' adaptations cannot conceivably arise from the random action of physical forces. For hundreds of years, it seemed that adaptive design could be explained only by an intelligent designer; in fact, this "argument from design" was considered one of the strongest proofs of the existence of God. For example, the Reverend William Paley wrote in *Natural Theology* (1802) that, just as the intricacy of a watch implies an intelligent, purposeful watchmaker, so every aspect of living nature, such as the human eye, displays "every indication of contrivance, every manifestation of design, which exists in the watch," and must, likewise, have had a Designer.

Supernatural processes cannot be the subject of science, so when Darwin offered a purely natural, materialistic alternative to the argument from design, he not only shook the foundations of theology and philosophy, but brought every aspect of the study of life into the realm of science. His alternative to intelligent design was design by the completely mindless process of natural selection, according to which organisms possessing variations that enhance survival or reproduction replace those less suitably endowed, which therefore survive or reproduce in lesser degree. This process cannot have a goal, any more than erosion has the goal of forming canyons, for *the future cannot cause material events in the present*. Thus the concepts of goals or purposes have no place in biology (or in any other of the natural sciences), except in studies of human behavior. According to Darwin and contemporary evolutionary theory, the weaver ants' behavior has the appearance of design because among many random genetic variations (mutations) affecting the behavior of an ancestral ant species, those displayed by *Oecophylla* enhanced survival and reproduction under its particular ecological circumstances.

Adaptive biological processes *appear* to have goals: weaver ants act as if they have the goal of constructing a nest; an orchid's flower develops toward a suitable shape and stops developing when that shape is attained. We may loosely describe such features by TELEOLOGICAL statements, which express goals (e.g., "She studied *in order* to pass the exam"). But no conscious anticipation of the future resides in the cell divisions that shape a flower or, as far as we can tell, in the behavior of weaver ants. Rather, the apparent goal-directedness is caused by the operation of a program—coded or prearranged information, residing in DNA sequences—that controls a process (Mayr 1988). A program likewise resides in a computer chip, but whereas that program has been shaped by an intelligent designer, the information in DNA has been shaped by a historical process of natural selection. Modern biology views the development, physiology, and behavior of organisms as the results of purely mechanical processes, resulting from interactions between programmed instructions and environmental conditions or triggers.

Definitions of natural selection

It is important to recognize that *"natural selection" is not synonymous with "evolution."* Evolution can occur by processes other than natural selection, especially genetic drift. And natural selection can occur without any evolutionary change, as when natural selection maintains the status quo by eliminating deviants from the optimal phenotype.

Many definitions of natural selection have been proposed (Endler 1986). For our purposes, we will define natural selection as *any consistent difference in fitness among phenotypically different classes of biological entities*. Let us explore this definition in more detail.

The **fitness**—often called the **reproductive success**—of a biological entity is its average per capita rate of increase in numbers. When we speak of natural selection among genotypes or organisms, the components of fitness generally consist of (1) the probability of survival to the various reproductive ages, (2) the average number of offspring (e.g., eggs, seeds) produced via female function, and (3) the average number of offspring produced via male function. "Reproductive success" has the same components, since survival is a prerequisite for reproduction.

Variation in the number of offspring produced as a consequence of competition for mates is often referred to as **sexual selection**, which some authors distinguish from natural selection. We will follow the more common practice of regarding sexual selection as a kind of natural selection.

Because the *probability* of survival and the *average* number of offspring enter into the definition of fitness, and because these concepts apply only to *groups* of events or objects, fitness is defined for a *set* of like entities, such as all the individuals with a particular genotype. That is, natural selection exists if there is an average (i.e., statistically consistent) difference in reproductive success. It is not meaningful to refer to the fitness of a single individual, since its history of reproduction and survival may have been affected by chance to an unknown degree, as we will see shortly.

Differences in survival and reproduction obviously exist among individual organisms, but they also exist below the organismal level, among genes, and above the organismal level, among populations and species. In other words, different kinds of biological entities may vary in fitness, resulting in different **levels of selection**. The most commonly discussed levels of selection are genes, individual organisms that differ in genotype or phenotype, populations within species, and species. Of these, selection among individual organisms (**individual selection**) and among genes (**genic selection**) are by far the most important.

Natural selection can exist only if different classes of entities differ in one or more features, or traits, that affect fitness. Evolutionary biologists differ on whether or not the definition of natural selection should require that these differences be inherited. We will adopt the position taken by those (e.g., Lande and Arnold 1983) who define selection among individual organisms as a consistent difference in fitness among phenotypes. Whether or not this variation in fitness alters the frequencies of genotypes in subsequent generations depends on whether and how the phenotypes are inherited—but that determines the *response to selection*, not the process of selection itself. Although we adopt the phenotypic perspective, we will almost always discuss natural selection among heritable phenotypes because selection seldom has a lasting evolutionary effect unless there is inheritance. Most of our discussion will assume that inheritance of a trait is based on genes. However, many of the principles of evolution by natural selection also apply if inheritance is epigenetic (based on, for example, differences in DNA methylation; see Chapter 9) or is based on cultural transmission, especially from parents to offspring. CULTURE has been defined as "information capable of affecting individuals' behavior that they acquire from other members of their species through teaching, imitation, and other forms of social transmission" (Richerson and Boyd 2005, p. 5).

Notice that according to our definition, natural selection exists whenever there is variation in fitness. Natural selection is not an external force or agent, and certainly not a purposeful one. It is a name for statistical differences in reproductive success among genes, organisms, or populations, and nothing more.

Natural selection and chance

If one neutral allele replaces another in a population by random genetic drift (see Chapter 10), then the bearers of the first allele had a greater rate of increase than the bearers of the other. However, natural selection has not occurred, because the genotypes do not differ *consistently* in fitness: the alternative allele could just as well have been the one to increase. There is no *average* difference between the alleles, no *bias* toward the increase of one relative to the other. Fitness differences, in contrast, are *average* differences, *biases*, differences in the *probability* of reproductive success. This does not mean that every individual of a fitter genotype (or phenotype) survives and reproduces prolifically while every individual of an inferior genotype perishes; some variation in survival and reproduction occurs independent of—that is, at random with respect to—phenotypic differences. But natural selection resides in the difference in rates of increase among biological entities that is *not* due to chance. *Natural selection is the antithesis of chance.*

If fitness and natural selection are defined by consistent, or average, differences, then we cannot tell whether a difference in reproductive success between two *individuals* is due to chance or to a difference in fitness. We cannot say that one identical twin had lower fitness than the other because she was struck by lightning (Sober 1984), or that the genotype of the Russian composer Tchaikovsky, who had no children, was less fit than the genotype of Johann Sebastian Bach, who had many. We can ascribe genetic changes to natural selection rather than random genetic drift only if we observe consistent, nonrandom changes in replicate populations, or measure numerous individuals of each phenotype and find an average difference in reproductive success.

Selection of and selection for

In the child's "selection toy" pictured in Figure 11.5, balls of several sizes, when placed in the top compartment, fall through holes in partitions, the holes in each partition being smaller than in the one above. If the smallest balls in the toy are all red, and the larger ones are all other colors, the toy will select the small, red balls. Thus we must distinguish *selection of objects* from *selection for properties* (Sober 1984). Balls are selected *for* the property of small size—that is, *because of* their small size. They are not selected for their color, or because of their color; nonetheless, here there is selection *of* red balls. Natural selection may similarly be considered a sieve that selects *for* a certain body size, mating behavior, or other feature. There may be incidental selection *of* other features that are correlated with those features.

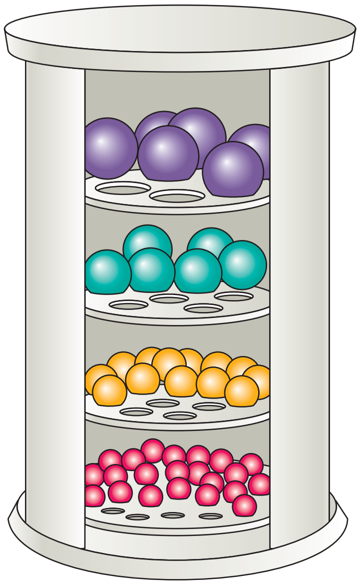
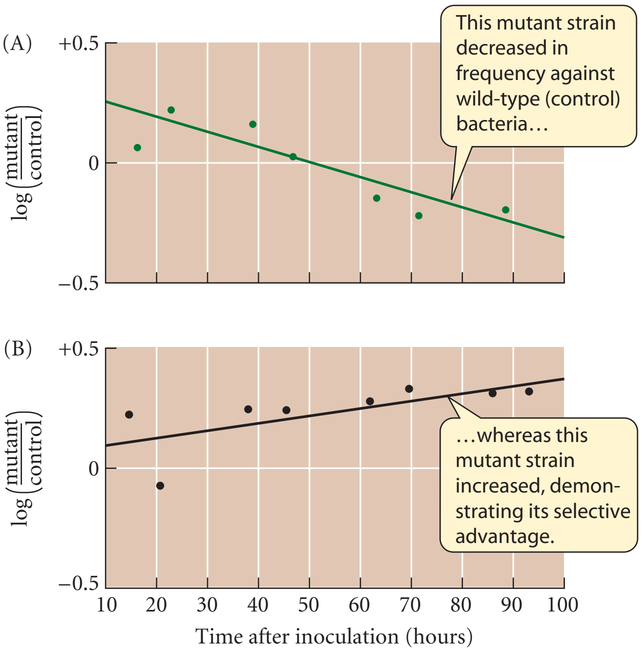


Figure 11.5 A child's toy that selects small balls, which drop through smaller and smaller holes from top to bottom. In this case there is selection *of* red balls, which happen to be the smallest, but selection is *for* small size. (After Sober 1984.)

The importance of this semantic point is that when we speak of the **function** of a feature, we imply that there has been natural selection *of* organisms with that feature and *of* genes that program it, but selection *for* the feature itself. We suppose that the feature *caused* its bearers to have higher fitness. The feature may have other **effects**, or conse-



This mutant strain decreased in frequency against wild-type (control) bacteria…

…whereas this mutant strain increased, demonstrating its selective advantage.

Figure 11.6 Natural selection on mutations in the β-galactosidase gene of *Escherichia coli* in laboratory populations maintained on lactose. In each case, a strain bearing a mutation competed with a control strain bearing the wild-type allele. Populations were initiated with equal numbers of cells of each genotype; i.e., with log (ratio of mutant/control) initially equal to zero. Without selection, no change in the log ratio would be expected. (A) One mutant strain decreased in frequency, showing a selective disadvantage. (B) Another mutant strain increased in frequency, demonstrating its selective (adaptive) advantage. (After Dean et al. 1986.)

quences, that were not its function, and *for* which there was no selection. For instance, there was selection for an opposable thumb and digital dexterity in early hominins, with the incidental effect, millions of years later, that we can play the piano. Similarly, a fish species may be selected for coloration that makes it less conspicuous to predators. The *function* of the coloration, then, is predator avoidance. An *effect* of this evolutionary change might well be a lower likelihood that the population will become extinct, but *avoidance of extinction is not a cause of evolution* of the coloration.

Examples of Natural Selection

We can illustrate the foregoing rather abstract points by several examples of natural selection, some of which show how natural selection can be studied.

Bacterial populations

Bacteria and other microbes are useful for experimental evolutionary studies because of their very rapid population growth. Anthony Dean and colleagues (1986) studied competition between a wild-type strain of *Escherichia coli* and each of several strains that differed from the wild type only by mutations of the gene that codes for β-galactosidase, the enzyme that breaks down lactose. Pairs of genotypes, each consisting of the wild type and a mutant, were cultured together in vessels with lactose as their sole source of energy. The populations were so large that changes in genotype frequencies attributable to genetic drift alone would be almost undetectably slow. Indeed, in certain populations the ratio of mutant to wild type did not change for many generations, indicating that these mutations were selectively neutral. One mutant strain, however, decreased in frequency, and so had lower fitness than the wild type, apparently because of its lower enzyme activity. Another mutant strain, with higher enzyme activity, increased in frequency, displaying a greater rate of increase than the wild type (Figure 11.6).

This experiment conveys the essence of natural selection: it is a completely mindless process without forethought or goal. Adaptation—evolution of a bacterial population with a higher average ability to metabolize lactose—resulted from a difference in the rates of reproduction of different genotypes caused by a phenotypic difference (enzyme activity).

Another experiment with bacteria illustrates *the distinction between "selection of" and "selection for."* In *E. coli*, the wild-type allele his^+ codes for an enzyme that synthesizes histidine, an essential amino acid, whereas his^- alleles are nonfunctional. The his^- alleles are selectively neutral if histidine is supplied so that cells with the mutant allele can grow. Atwood and colleagues (1951) observed, to their surprise, that every few hundred generations, the allele frequencies changed rapidly and drastically in experimental cultures that were supplied with histidine (Figure 11.7). The experimenters showed that the *his* alleles were **hitchhiking** with advantageous mutations at other loci—a phenomenon readily observed in bacteria because their rate of recombination is extremely low. Occasionally, a genotype (say, his^-) would increase rapidly in frequency because of linkage to an advantageous mutation that had occurred at another locus. Subsequently, the alternative allele (his^+) might increase because of linkage to a new advantageous mutation at another locus

The his^- allele, which is neutral, fluctuates in frequency by "hitchhiking" with advantageous mutations.

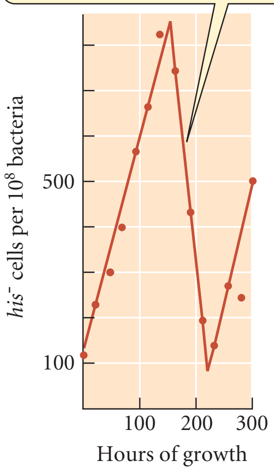


Figure 11.7 Allele frequency fluctuates because of hitchhiking in a laboratory population of *Escherichia coli*. The *y*-axis represents the frequency of the selectively neutral his^- allele compared with that of the wild-type his^+ allele. The frequency of the his^- allele increases if a cell bearing it experiences an advantageous mutation at another locus, then decreases if a different, more advantageous mutation occurs in a wild-type cell. (After Nestmann and Hill 1973.)

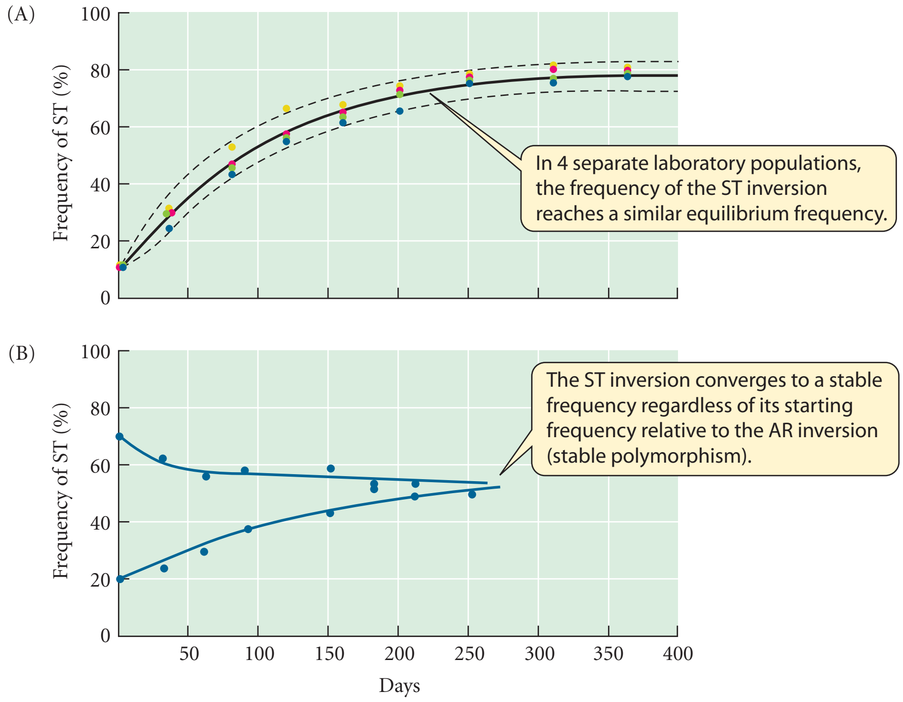


Figure 11.8 Changes in the frequencies of chromosome inversions in laboratory populations of *Drosophila pseudoobscura*. (A) The frequency of the ST inversion increased in much the same way in four laboratory populations, leveling off at an equilibrium frequency. (B) The frequency of ST arrived at about the same equilibrium level irrespective of starting frequencies of ST and AR. The convergence of the populations toward the same frequency shows that the ST and AR inversions affect fitness, and that natural selection maintains both in a population in a stable, or balanced, polymorphism. (A after Dobzhansky and Pavlovsky 1953; B after Dobzhansky 1948.)

altogether. Thus there was selection *for* new advantageous mutations in these bacterial populations, and selection *of* neutral alleles at the linked *his* locus.

Inversion polymorphism in *Drosophila*

Natural populations of *Drosophila pseudoobscura* are highly polymorphic for inversions—that is, differences in the arrangement of genes along a chromosome resulting from 180 degree reversals in the orientation of chromosome segments (see Chapter 8). Theodosius Dobzhansky suspected that these inversions affected fitness when he observed that the frequencies of several such arrangements in natural populations displayed a regular seasonal cycle that suggested changes in their relative fitnesses as a consequence of environmental changes, perhaps in temperature. He followed these observations with several experiments using POPULATION CAGES: boxes in which populations of several thousand flies are maintained by periodically providing cups of food in which larvae develop. In one such experiment, Dobzhansky and Pavlovsky (1953) used flies with two inversions, called Standard (ST) and Chiricahua (CH), that can be distinguished under the microscope by their banding patterns. They set up four populations, each with 20 percent ST and 80 percent CH chromosome copies (Figure 11.8A). In all the populations, the ST chromosome increased in frequency and leveled off at about 80 per cent. In another experiment (Figure 11.8B), Dobzhansky (1948) initiated one cage with 1119 ST and 485 AR (Arrowhead inversion) chromosome copies (i.e., frequencies of 0.70 and 0.30, respectively). A second cage was initiated with ST and AR frequencies of 0.19 and 0.81, respectively. Within about 15 generations, the frequency of ST had dropped to and leveled off at about 0.54 in the first cage, and it had risen to almost the same frequency (0.50) in the second cage.

The important feature of these experiments is that the chromosome frequencies changed consistently in different populations, approaching a *stable equilibrium.* Replicate populations followed the same trajectory in the first experiment, and different populations approached the same equilibrium in the second experiment, despite different initial frequencies. These results can only be due to natural selection, for random genetic drift would not show such consistency. Moreover, natural selection must be acting in such a way as to *maintain variation* (polymorphism); it does not necessarily cause fixation of a single best genotype. When the genotype frequencies reach equilibrium, natural selection continues to occur, but evolutionary change does not.

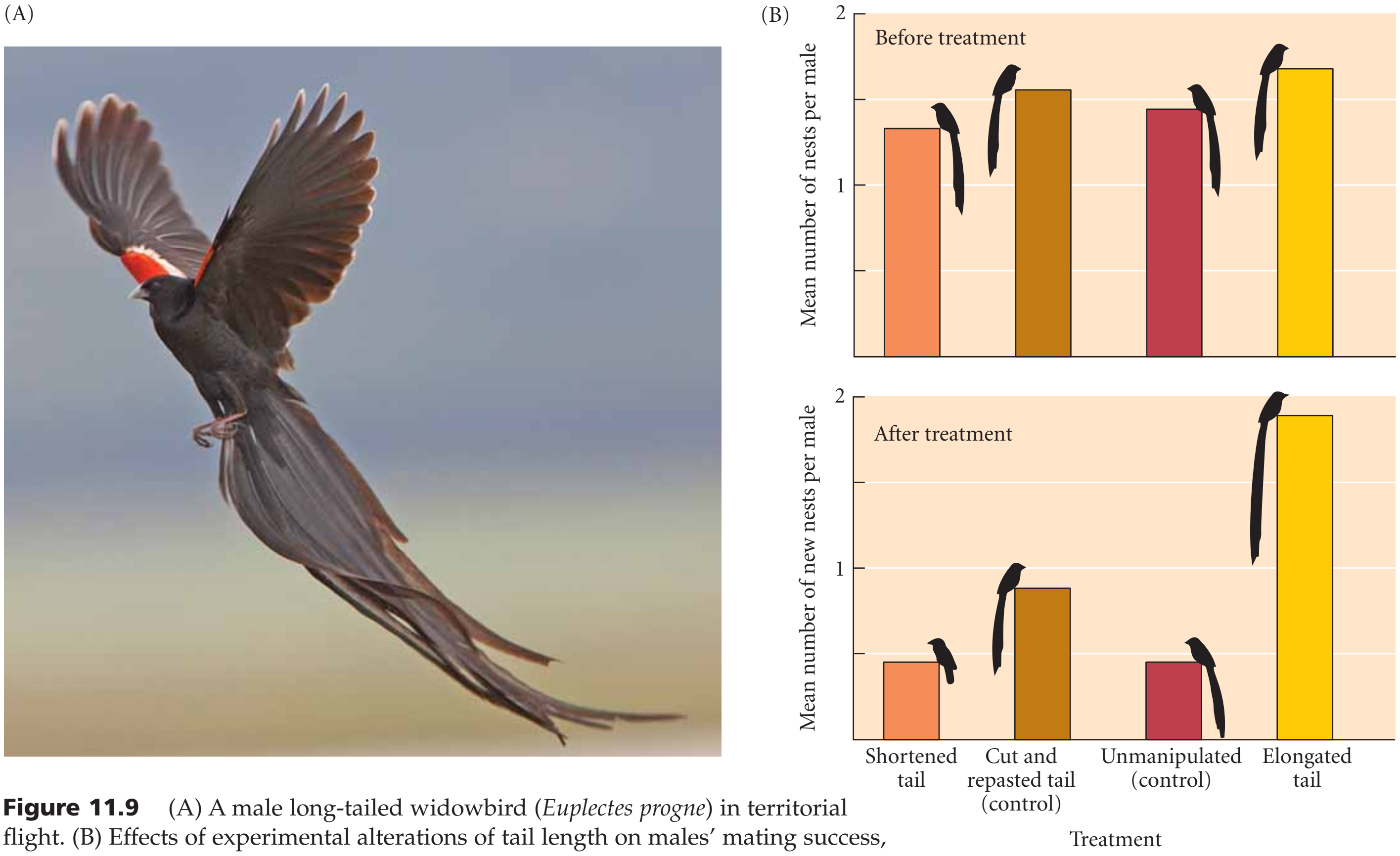


Figure 11.9 (A) A male long-tailed widowbird (*Euplectes progne*) in territorial flight. (B) Effects of experimental alterations of tail length on males' mating success, measured by the number of nests in each male's territory. Nine birds were chosen for each of four treatments: shortening or elongating the tail feathers, or controls of two types: one in which the tail feathers were cut and repasted, and one in which the tail was not manipulated. (A © Jason Gallier/Alamy; B after Andersson 1982.)

Male reproductive success

The courting males of many species of animals have elaborate morphological features and engage in conspicuous displays; roosters provide a familiar example. Some such features appear to have evolved through female choice of males with conspicuous features, which therefore enjoy higher reproductive success than less elaborate males (see Chapter 15). For example, male long-tailed widowbirds (*Euplectes progne*) have extremely long tail feathers. Malte Andersson (1982) shortened the tail feathers of some wild males and attached the clippings to the tail feathers of others, thus elongating them well beyond the natural length. He then observed that males with shortened tails mated with fewer females than did normal males, and that males with elongated tails mated with more females (Figure 11.9).

Male guppies (*Poecilia reticulata*) have a highly variable pattern of colorful spots. In Trinidad, males have smaller, less contrasting spots in streams inhabited by their major predator, the fish *Crenicichla*, than in streams without this predator. John Endler (1980) moved 200 guppies from a *Crenicichla*-inhabited stream to a site that lacked the predator. About two years (15 generations) later, he found that the newly established population had larger spots and a greater diversity of color patterns, so that the population now resembled those that naturally inhabit *Crenicichla*-free streams. Endler also set up populations in large artificial ponds in a greenhouse. After six months of population growth, he introduced *Crenicichla* into four ponds, released a less dangerous predatory fish (*Rivulus*) into four others, and maintained two control populations free of predators. In censuses after four and ten generations, the number and brightness of spots per fish had increased in the ponds without *Crenicichla* and had declined in those with it (Figure 11.10).

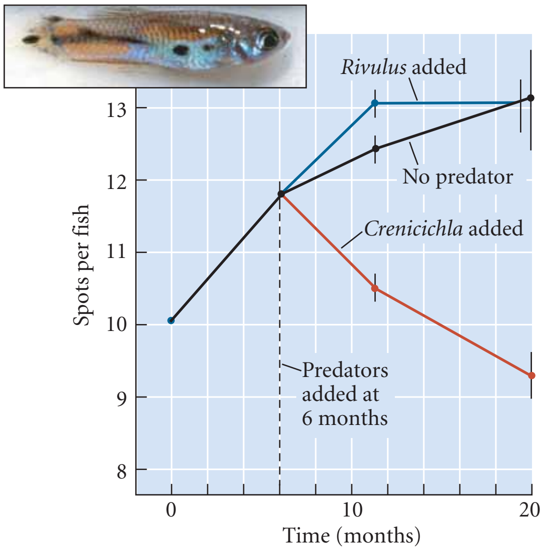


Figure 11.10 Evolution of male color pattern in experimental populations of guppies. Six months after the populations were established, some were exposed to a major predator of adult guppies (*Crenicichla*), some to a less effective predator that feeds mainly on juvenile guppies (*Rivulus*), and some were left free of predators (controls). Numbers of spots were counted after 4 and 10 generations. The vertical bars measure the variation among males. (After Endler 1980; photo courtesy of Anne Houde.)

Males with more and brighter spots have greater mating success, but they are also more susceptible to being seen and captured by *Crenicichla*.

These experiments show that natural selection may consist of differences in reproductive rate, not survival. Differences in mating success, which Darwin called *sexual selection*, result in adaptations for obtaining mates, rather than adaptations for survival. *The guppy experiments also show that a feature may be subjected to conflicting selection pressures* (such as sexual selection and predation), and that the direction of evolution may then depend on which is stronger. Many advantageous characters, in fact, carry corresponding disadvantages, often called COSTS or TRADE-OFFS: the evolution of male coloration in guppies is governed by a trade-off between mating success and avoidance of predation.

Population size in flour beetles

The small beetle *Tribolium castaneum* breeds in stored grains and can be reared in containers of flour. Larvae and adults feed on flour but also eat (cannibalize) eggs and pupae. Michael Wade (1977, 1979) set up 48 experimental populations under each of three treatments. Each population was propagated from 16 adult beetles each generation. The control populations (treatment C) were propagated simply by moving beetles to a new vial of flour: each population in one generation gave rise to one population in the next. In treatment A, Wade deliberately selected for high population size by initiating each generation's 48 populations with sets of 16 beetles taken only from those few populations (out of the 48) in which the greatest number of beetles had developed. In treatment B, low population size was selected in the same way, by propagating beetles only from the smallest populations (Figure 11.11A).

Over the course of nine generations, the average population size declined in all three treatments, most markedly in treatment B and least in

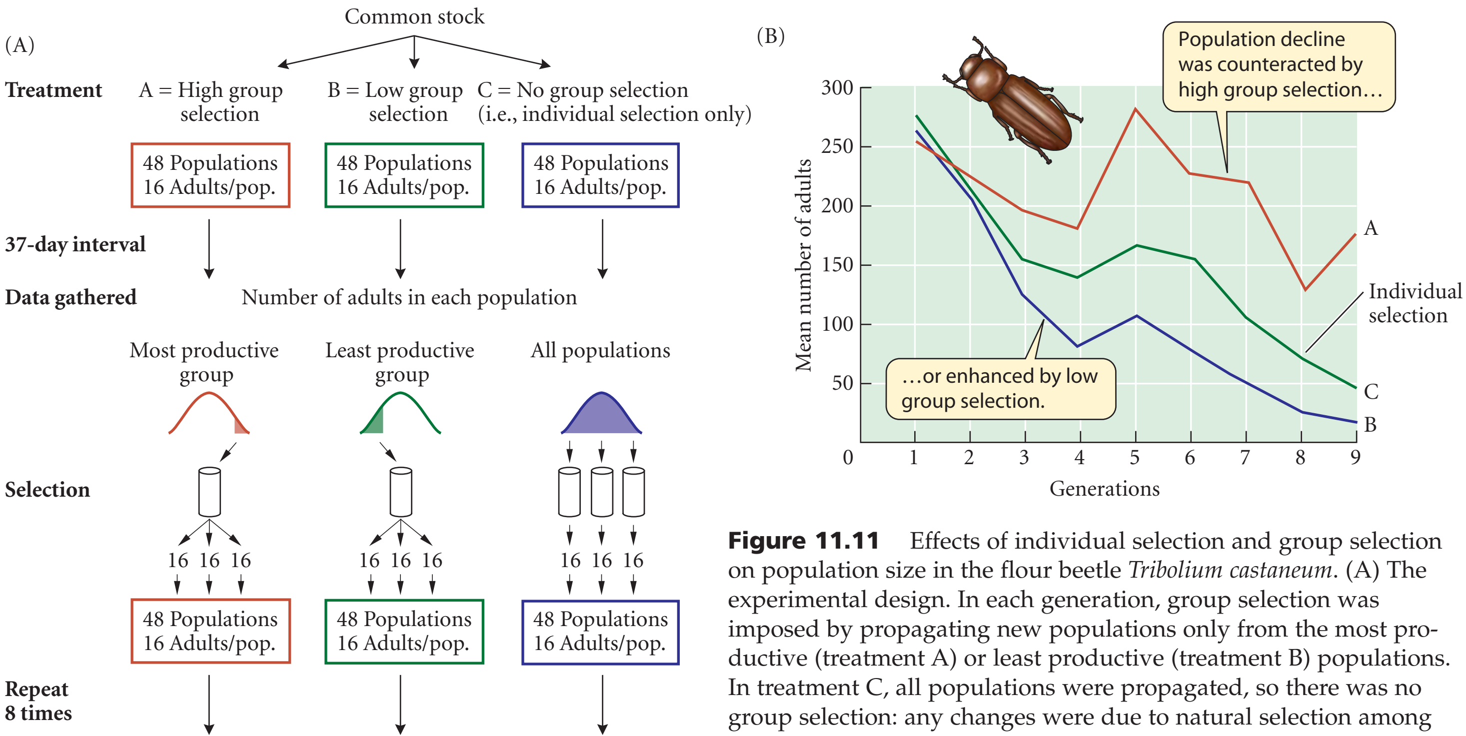


Figure 11.11 Effects of individual selection and group selection on population size in the flour beetle *Tribolium castaneum*. (A) The experimental design. In each generation, group selection was imposed by propagating new populations only from the most productive (treatment A) or least productive (treatment B) populations. In treatment C, all populations were propagated, so there was no group selection: any changes were due to natural selection among individuals within populations. (B) Changes in the mean number of adult beetles in the three treatments. (After Wade 1977.)

treatment A (Figure 11.11B). The net reproductive rate also declined. In treatment C, these declines must have been due to evolution *within* each population, with natural selection acting on the genotypes of individual beetles within a population. This process is *individual selection*, of the same kind we have assumed to operate on, say, the color patterns of guppies. But in treatments A and B, Wade imposed another level of selection by allowing some populations, or groups, but not others, to persist based on a phenotypic characteristic of each *group*—namely, its size. This process, called **group selection**, or **interdemic selection**, operates *in addition to* individual selection among genotypes within populations. We must distinguish selection *within* populations from selection *among* populations.

The decline of population size in the control (C) populations seems like the very antithesis of adaptation. Wade discovered, however, that compared with the foundation stock from which the experimental populations had been derived, adults in the C populations had become more likely to cannibalize pupae, and females were prone to lay fewer eggs when confined with other beetles. For an individual beetle, cannibalism is an advantageous way of obtaining protein, and it may be advantageous for a female not to lay eggs if she perceives the presence of other beetles that may eat them. But although these features are advantageous to the individual, they are disadvantageous to the population, whose growth rate declines.

By selecting groups for low population size (treatment B), Wade *reinforced* these same tendencies. In treatment A, however, selection at the group level for large population size *opposed* the consequences of individual selection within populations. Compared with the C populations, beetles from treatment A had higher fecundity in the presence of other beetles, and they were less likely to cannibalize eggs and pupae. Thus selection among groups had affected the course of evolution.

This experiment shows that the size or growth rate of a population may decline as a result of natural selection even as individual organisms become fitter. *It also illustrates that selection might operate at two levels*: among individuals and among populations. In this case, selection at the group level was imposed by the investigator, so the experiment shows that it is possible, but whether or not it occurs in nature is an open question.

Kin discrimination in cannibalistic salamanders

To continue the cannibal theme: aquatic larvae of the tiger salamander (*Ambystoma tigrinum*) often develop into a distinctive phenotype that eats smaller larvae. Most, although not all, cannibals tend to avoid eating close relatives, such as siblings. One hypothesis for the evolution of such kin discrimination is that an allele that influences its bearer to spare its siblings' lives will increase in frequency, because the siblings are likely to carry other copies of that same allele, which are identical by descent. This is the concept of *kin selection*, to which we will soon return. There are alternative hypotheses, however, of which the most likely is that cannibals are at risk of contracting infectious diseases, especially if they share with their relatives a genetic susceptibility to certain pathogens—in which case it would be advantageous not to eat kin.

David Pfennig and colleagues (1999) tested these and other hypotheses. They reasoned that if the disease hypothesis were correct, cannibals ought to avoid eating diseased larvae, and that non-kin prey would be more likely to transmit disease to a cannibal than would kin prey. But when they offfered cannibals a choice between diseased and healthy prey, or exposed them to diseased kin versus diseased non-kin, neither of the predictions was confirmed. However, the kin selection hypothesis holds (see Chapter 16) that a behavior is advantageous if its genetic benefit/cost ratio is greater than the coefficient of relationship between the actor (cannibal) and the subject of the action (e.g., a sibling whose coefficient of relationship is 0.5). Pfennig et al. compared discriminating and nondiscriminating cannibals, each of which was presented with several related and unrelated prey. They found that discriminators suffered no reduction in growth rate (i.e., no evident cost), whereas sparing their siblings' lives results in a high genetic benefit, i.e., survival of copies of the cannibal's own genes (Figure 11.12). They

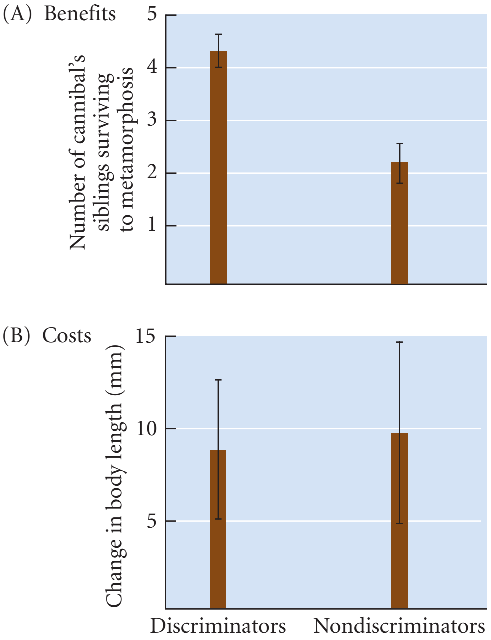


Figure 11.12 Genetic benefit and cost of kin discrimination in cannibalistic tiger salamanders (*Ambystoma tigrinum*). (A) Discriminators benefit by sparing their siblings' lives, since siblings share half of their genes. (B) At least as indicated by the rate of growth in length, discriminators suffer no reduction in fitness, or cost. (After Pfennig et al. 1999.)

concluded that kin selection explains the discriminatory behavior. Notice that the concept of natural selection invoked here is that *a gene may change in frequency because of its effect on the survival of copies of itself*, even if these copies are carried by other individuals of the species.

Selfish genetic elements

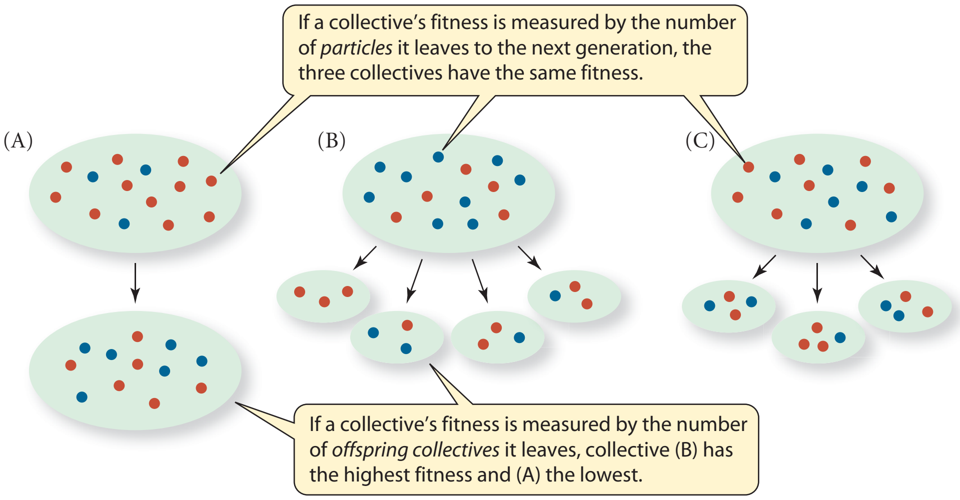
In many species of animals and plants, there exist **"selfish" genetic elements**, which are transmitted at a higher rate than the rest of an individual's genome and are detrimental (or at least not advantageous) to the organism (Hurst and Werren 2001; Burt and Trivers 2006). Many of these elements exhibit **meiotic drive**, or **segregation distortion**, meaning that the element is carried by more than half of the gametes of a heterozygote. For example, the *t* locus of the house mouse (*Mus musculus*) has several alleles that, in a male heterozygous for one of these alleles and for the normal allele *T*, are carried by more than 90 percent of the sperm. In the homozygous condition, certain of the *t* alleles are lethal, and others cause males to be sterile. Despite these disadvantages to the individual, the meiotic drive of the *t* alleles is so great that they reach a high frequency in many populations. Another selfish element is a small chromosome called *psr* (which stands for "paternal sex ratio") in the parasitic wasp *Nasonia vitripennis*. It is transmitted mostly through sperm rather than eggs. When an egg is fertilized by a sperm containing this genetic element, it causes the destruction of all the other paternal chromosomes, leaving only the maternal set. In *Nasonia*, as in all Hymenoptera, diploid eggs become females and haploid eggs become males. The *psr* element thus converts female eggs into male eggs, thereby ensuring its own future propagation through sperm, even though this could possibly so skew the sex ratio of a population as to threaten its survival.

Selfish genetic elements forcefully illustrate the nature of natural selection: it is nothing more than differential reproductive success (of genes in this case), which need not result in adaptation or improvement in any sense. These elements also exemplify different levels of selection: in these cases, genic selection acts in opposition to individual selection. Selection among genes may not only be harmful to individual organisms, but might also cause the extinction of populations or species.

Levels of Selection

The last three examples introduced the idea of different levels of selection, corresponding to levels of biological organization. The philosopher of science Samir Okasha (2006) refers to higher-level units as collectives, and the included units as particles. Thus collective/particle pairs might be clade/species, species/population, population/individual organism, organismal genotype/gene. If the particles (e.g., genotypes) in a collective (e.g., population) vary in some character, then collectives will differ in their mean (average) character. Sometimes this is a straightforward relationship: the distribution of body sizes among individuals determines the mean body size in a population, which is therefore an "aggregate" property of its members. But there may also be features of a population (e.g., its abundance or geographic distribution) that cannot be measured on an individual, even if they are the consequences of individual organisms' properties. Such features, sometimes called "emergent" or "relational" characteristics (Damuth and Heisler 1988), may affect the rates at which populations become extinct or give rise to new populations. Note, then, that we might distinguish two measures of fitness of a collective: the mean reproductive success of its constituent members, or the rate at which collectives produce "offspring collectives" (Figure 11.13).

Conceptualizing the level at which selection acts is a philosophically complex issue, on which a great deal has been written. If, for instance, alleles *A* and *a* determine dark versus pale color in an insect, and populations of dark insects have a lower extinction rate than populations of pale insects, does this represent selection at the level of populations, of individual insects, or of genes? Okasha suggests that we can take a "gene's-eye view," in which allele *A* increases as a consequence of both the extinction of populations and the reproductive success of individuals. This "view," though, is not the same as genic selec-



If a collective's fitness is measured by the number of *particles* it leaves to the next generation, the three collectives have the same fitness.

If a collective's fitness is measured by the number of *offspring collectives* it leaves, collective (B) has the highest fitness and (A) the lowest.

Figure 11.13 Concepts of the fitness of "particles" and "collectives." The small circles represent individual particles, such as two different asexual genotypes. Each of the three ovals represents a collective of individuals. In collective (A), the fitness (per capita rate of increase) of blue particles is greater than the fitness of red particles. In collective (B), red particles have higher fitness. In collective (C), the fitness of blue and red particles is equal. Collectives (B) and (C) both produce "offspring collectives" by colonization, but (B) has more offspring collectives than (C). (After Okasha 2006, in part.)

tion, which requires that the cause of gene frequency change operate at the level of the gene, not at the level of individual genotypes (such as greater susceptibility of pale insects to predators) or of the population. In contrast, an "outlaw gene," such as the *t* allele in mice, increases because of the activity of the gene itself, not of the collective (the genotype of the mouse) of which the gene is a part, and so it exhibits genic selection.

Evolutionary biologists have extensively discussed selection at the level of gene, genotype of the individual organism, population, and species (Sober 1984; Okasha 2006). Selection can occur at other levels, such as among cell lineages within a multicellular organism, which is the basis of cancer. Evolutionary biologists have begun to study this topic as well (Michor et al. 2003).

Selection of organisms and groups

By "natural selection," both Darwin and contemporary evolutionary biologists usually mean consistent differences in fitness among genetically different organisms within populations. However, it is common to read statements to the effect that oysters have a high reproductive rate "to ensure the survival of the species," or that antelopes with sharp horns refrain from physical combat because combat would lead to the species' extinction. These statements betray a misunderstanding of natural selection as it is usually conceived. If traits evolve by individual selection—by the replacement of less fit by more fit individuals, generation by generation—then the possibility of future extinction cannot possibly affect the course of evolution. Moreover, an **altruistic trait**—a feature that reduces the fitness of an individual that bears it for the benefit of the population or species—cannot evolve by individual selection. An altruistic genotype amid other genotypes that were not altruistic would necessarily decline in frequency, simply because it would leave fewer offspring per capita than the others. Conversely, if a population were to consist of altruistic genotypes, a selfish mutant—a "cheater"—would increase to fixation, even if a population of such selfish organisms had a higher risk of extinction (Figure 11.14).

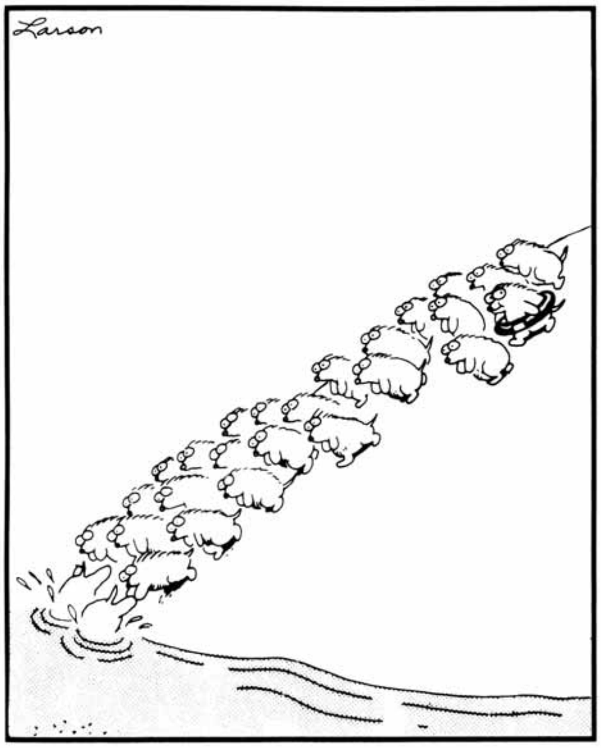
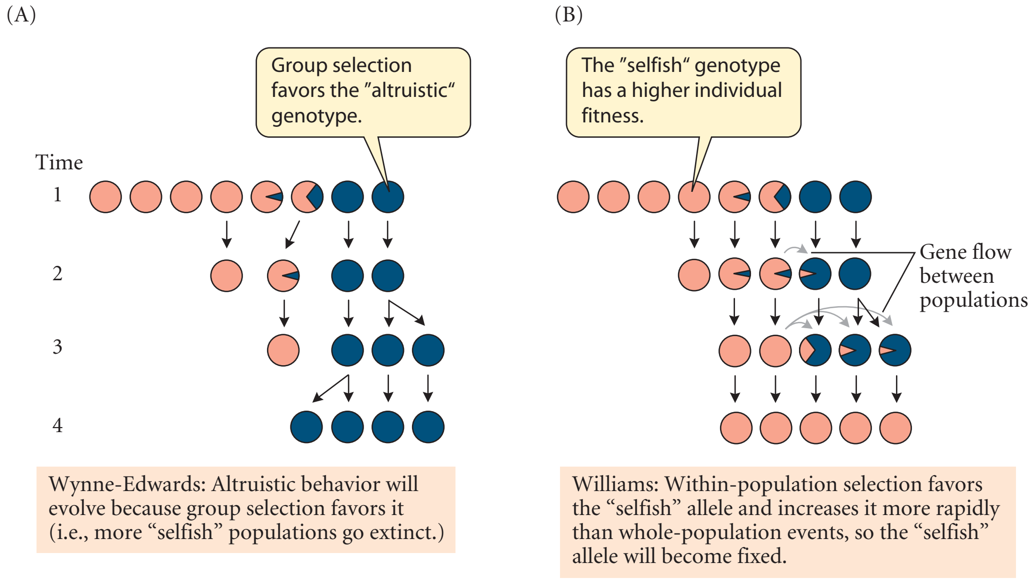


Figure 11.14 The mythical self-sacrificial behavior of lemmings, which (according to popular belief) rush en masse into the sea to prevent overpopulation. Cartoonist Gary Larson, in *The Far Side*, illustrates the "cheater" principle, and why such altruistic behavior would not be expected to evolve. (Reprinted with permission of Chronicle Features, San Francisco.)

There is a way, however, in which traits that benefit the population at a cost to the individual might evolve, which is by group selection: differential production or survival of groups that differ in genetic composition. For instance, populations made up of selfish genotypes, such as those with high reproductive rates that exhaust their food supply, might have a higher extinction rate than populations made up of altruistic



Group selection favors the "altruistic" genotype.

Wynne-Edwards: Altruistic behavior will evolve because group selection favors it (i.e., more "selfish" populations go extinct.)

The "selfish" genotype has a higher individual fitness.

Williams: Within-population selection favors the "selfish" allele and increases it more rapidly than whole-population events, so the "selfish" allele will become fixed.

Figure 11.15 Conflict between group and individual selection. Each circle represents a population of a species, traced through four time periods. Some new populations are founded by colonists from established populations, and some populations become extinct. The proportions of blue and pink areas in each circle represent the proportions of an "altruistic" and a "selfish" genotype in the population, the selfish genotype having a higher reproductive rate (individual fitness). Lateral arrows indicate gene flow between populations. (A) An altruistic trait may evolve by group selection if the rate of extinction of populations of the selfish genotype is very high. (B) Williams's argument: because individual selection operates so much more rapidly than group selection, the selfish genotype increases rapidly within populations and may spread by gene flow into populations of altruists. Thus the selfish genotype becomes fixed, even if it increases the rate of population extinction.

genotypes that have lower reproductive rates. If so, then the species as a whole might evolve altruism through the greater survival of groups of altruistic individuals, even though individual selection within each group would act in the opposite direction (Figure 11.15A).

The hypothesis of group selection was criticized by George Williams (1966) in an influential book, *Adaptation and Natural Selection*. Williams argued that supposed adaptations that benefit the population or species, rather than the individual, do not exist: either the feature in question is not an adaptation at all, or it can be plausibly explained by benefit to the individual or the individual's genes. For example, females of many species lay fewer eggs when population densities are high, but not to ensure a sufficient food supply for the good of the species. At high densities, when food is scarce, a female simply cannot form as many eggs, so her reduced fecundity may be a physiological necessity, not an adaptation. Moreover, an individual female may indeed be more fit if she forms fewer eggs in these circumstances and allocates the energy to surviving until food becomes more abundant, when she may reproduce more prolifically.

Williams based his opposition to group selection on a simple argument. Individual organisms are much more numerous than the populations into which they are aggregated, and they turn over—are born and die—much more rapidly than populations, which are born (formed by colonization) and die (become extinct) at relatively low rates. Selection at either level requires differences—among individuals or among populations—in rates of birth or death. Thus the rate of replacement of less fit by more fit individuals is potentially much greater than the rate of replacement of less fit by more fit populations, so individual selection will generally prevail over group selection (Figure 11.15B). Among evolutionary biologists, the majority view is that *few characteristics have evolved because they benefit the population or species*. We will consider an alternative position, that group selection is important in evolution, in Chapter 16.

If adaptations that benefit the population are so rare, how do we explain worker ants that labor for the colony and do not reproduce, or birds that emit a warning cry when they see a predator approaching the flock? Among the possible explanations is one posited by William Hamilton (1964): such seemingly altruistic behaviors have evolved by **kin selection**, which is best understood from the "viewpoint" of a gene (see Chapter 16). An allele for altruistic behavior can increase in frequency in a population if the beneficiaries of the behavior are usually related to the individual performing it. Since the altruist's relatives are more likely to carry copies of the altruistic allele than are members of the population at random, when the altruist enhances the fitness of its relatives, even at some cost to its

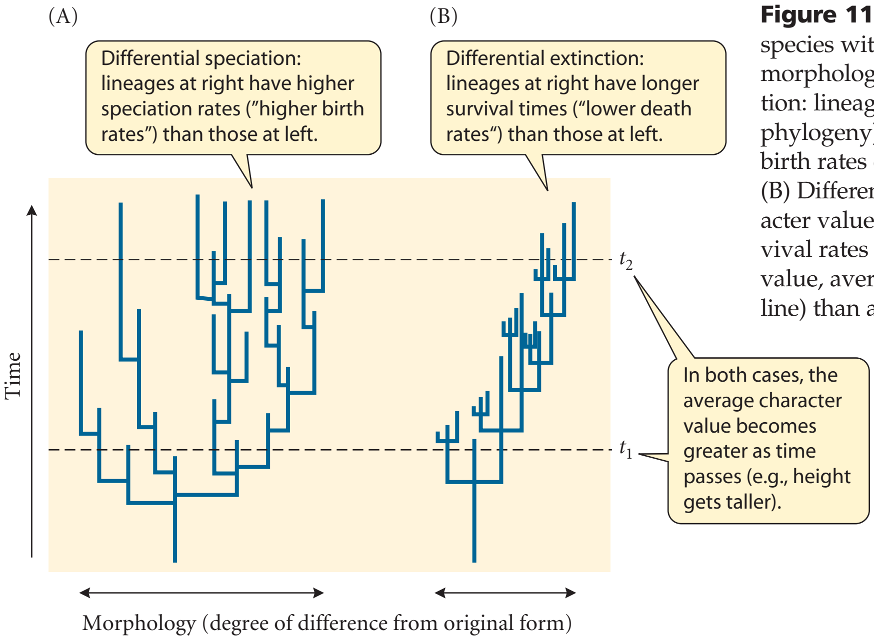


Figure 11.16 Species selection (differential proliferation of species with different character states). The *x*-axis represents a morphological character, such as body size. (A) Differential speciation: lineages with higher character values (toward the right of the phylogeny) have higher rates of speciation—analogous to higher birth rates of individual organisms—than those with lower values. (B) Differential extinction and survival: lineages with higher character values have longer survival times—analogous to higher survival rates of individual organisms. In both cases, the character value, averaged across species, is greater at time t_2 (upper dashed line) than at time t_1 (lower dashed line). (After Gould 1982.)

own fitness, it can increase the frequency of the allele. We may therefore define kin selection as a form of selection in which alleles differ in fitness by influencing the effect of their bearers on the reproductive success of individuals (kin) who carry the same allele by common descent.

Species selection

Selection among groups of organisms is called **species selection** when the groups involved are species and there is a correlation between some characteristic and the rate of speciation or extinction. Species selection became a major topic of interest when Niles Eldredge and Stephen Jay Gould (1972), in their theory of punctuated equilibria (Chapter 4), proposed that most characteristics are static within species lineages, and evolve mostly or entirely in "daughter" species that arise as small, localized populations (see Figure 4.19C). A consequence of this view, they said, is that long-term trends in a feature, such as body size in horses (see Figure 4.17B), may be attributed to differences in rates of speciation (Figure 11.16A) or extinction (Figure 11.16B), so that the mean character among the species that make up a clade changes over time (see also Stanley 1979). Some authors use "species selection" to refer to both "aggregate" and "emergent" collective features, whereas others restrict it to the few "emergent" characteristics of a species. The size of a species' geographic range, which might be considered an emergent property, is correlated with the species' geological duration in late Cretaceous molluscs (Figure 11.17A). Moreover, related species have a similar range size, which therefore is "heritable" at the species level (Figure 11.17B; Jablonski 1987; Jablonski and Hunt 2006). The combination of species selection and species-level heritability might have resulted in a long-term increase in the average range size of species, but the K-T mass extinction event cut short any possible trend, and range size did not affect the chance of species' survival at that time.

Another likely example of the effects of species selection is the prevalence of sexual species compared with closely related asexual forms. Many groups of plants and animals have given rise to asexually reproducing lineages, but almost all such lineages are very young, as indicated by their very close genetic similarity to sexual forms. This observation implies that asexual forms have a higher rate of extinction than sexual populations, since asexuals that arose long ago have not persisted (Normark et al. 2003; see Figure 15.2).

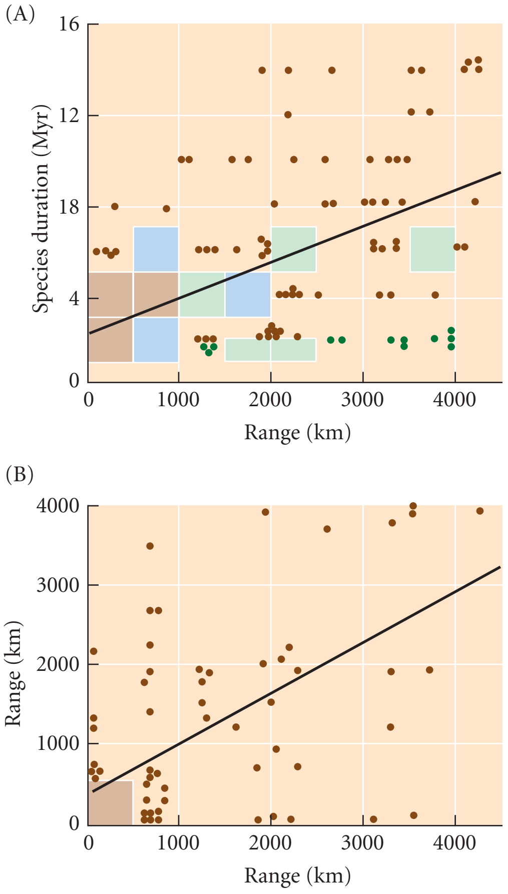


Figure 11.17 An example of species selection. (A) The geological duration of species of late Cretaceous gastropods is correlated with the size of their geographic range (kilometers of coastline). Points represent single species; green, blue, and beige squares represent groups of 6–10, 11–20, and >20 species, respectively. (B) Geographic range size is correlated between pairs of closely related species, so range size is a highly "heritable" species-level trait. Each point represents a pair of species. (After Jablonski 1987.)

The Nature of Adaptations

Definitions of adaptation

All biologists agree that an adaptive trait is one that enhances fitness compared with at least some alternative traits. However, some authors include a historical perspective in their definition of adaptations, and others do not.

An ahistorical definition was provided by Kern Reeve and Paul Sherman (1993): "An adaptation is a phenotypic variant that results in the highest fitness among a specified set of variants in a given environment." This definition refers only to the current effects of the trait on reproductive success, compared with those of other variants. At the other extreme, Paul Harvey and Mark Pagel (1991) hold that "for a character to be regarded as an adaptation, it must be a derived character that evolved in response to a specific selective agent." This history-based definition requires that we compare a character's effects on fitness with those of a specific variant; namely, the ancestral character state from which it evolved. Phylogenetic or paleontological data may provide information about the ancestral state.

One reason for this emphasis on history is that a character state may be a simple consequence of phylogenetic history, rather than an adaptation. Darwin saw clearly that a feature might be beneficial, yet not have evolved for the function it serves today, or for any function at all: "The sutures in the skulls of young mammals have been advanced as a beautiful adaptation for aiding parturition [birth], and no doubt they facilitate, or may be indispensable for this act; but as sutures occur in the skulls of young birds and reptiles, which have only to escape from a broken egg, we may infer that this structure has arisen from the laws of growth, and has been taken advantage of in the parturition of the higher animals" (*The Origin of Species*, chapter 6). Whether or not we should postulate that a trait is an adaptation depends on such insights. For example, we know that pigmentation varies in many species of birds (see Figure 9.1A), so it makes sense to ask whether there is an adaptive reason for color differences among closely related species. But it is not sensible to ask whether it is adaptive for a goose to have four toes rather than five, because the ancestor of birds lost the fifth toe and it has never been regained in any bird since. Five toes are probably not an option for birds because of genetic developmental constraints. Thus, if we ask why a species has one feature rather than another, the answer may be adaptation, or it may be phylogenetic history.

A **preadaptation** is a feature that fortuitously serves a new function. For instance, parrots have strong, sharp beaks, used for feeding on fruits and seeds. When domesticated sheep were introduced into New Zealand, some were attacked by an indigenous parrot, the kea (*Nestor notabilis*), which pierced the skin and fed on the sheep's fat. The kea's beak was fortuitously suitable for a new function and may be viewed as a preadaptation for slicing skin.

Preadaptations that have been co-opted to serve a new function have been termed **exaptations** (Gould and Vrba 1982). For example, the wings of alcids (birds in the auk family) may be considered exaptations for swimming: these birds "fly" underwater as well as in air (Figure 11.18A). An exaptation may be further modified by selection so that the modifications are adaptations for the feature's new function: the wings of penguins have been modified into flippers and cannot support flight in air (Figure 11.18B). Some proteins have been "exapted" to serve new functions, and some play a dual role (Piatigorsky 2007). For instance, the diverse crystallin proteins of animal eye lenses have been co-opted from several phylogenetically widespread proteins, such as stress proteins that stabilize cellular function, lactate dehydrogenase, and other enzymes (Figure 11.19). In some cases, exactly the same protein serves both its ancestral and new roles, such as the τ-crystallin of reptiles and birds which doubles as α-enolase; in other cases, the ancestral gene was duplicated, and the crystallin encoded by one of the duplicates has undergone some amino acid substitutions.

Recognizing adaptations

Not all the traits of organisms are adaptations. There are several other possible explanations of organisms' characteristics. First, a trait may be a necessary consequence of physics or chemistry. Hemoglobin gives blood a red color, but there is no reason to think that red-

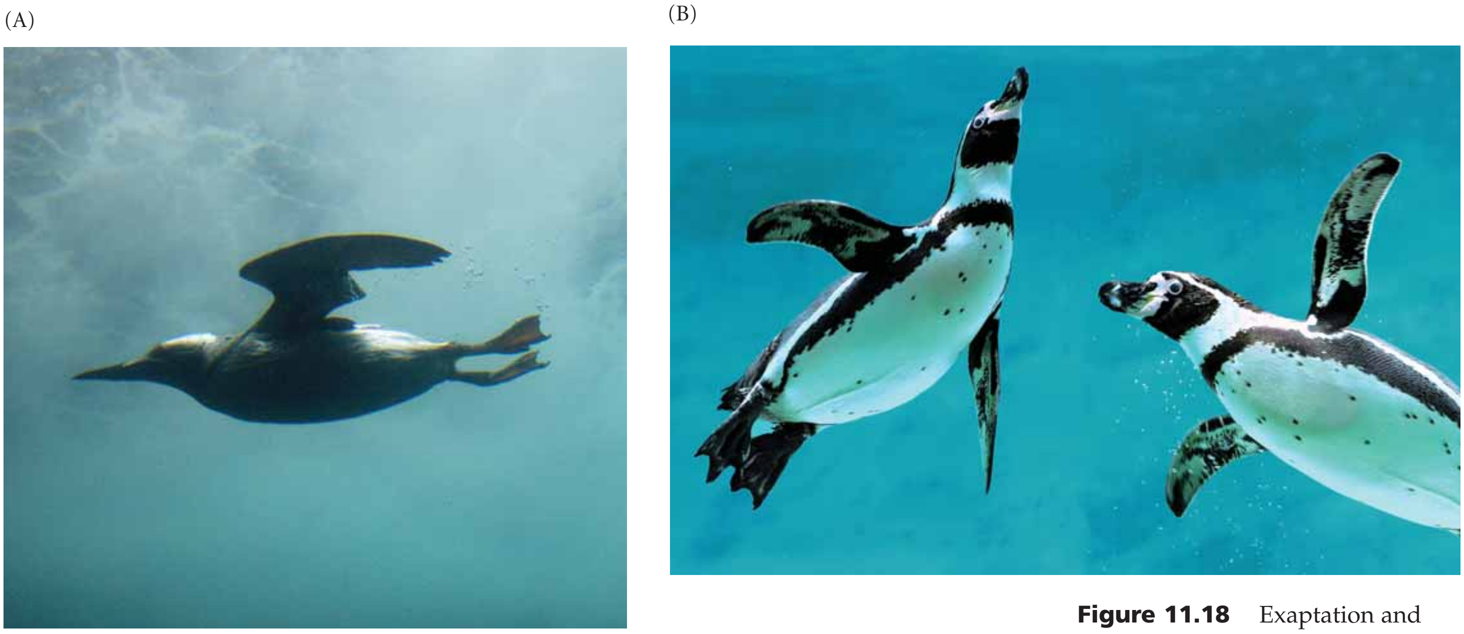
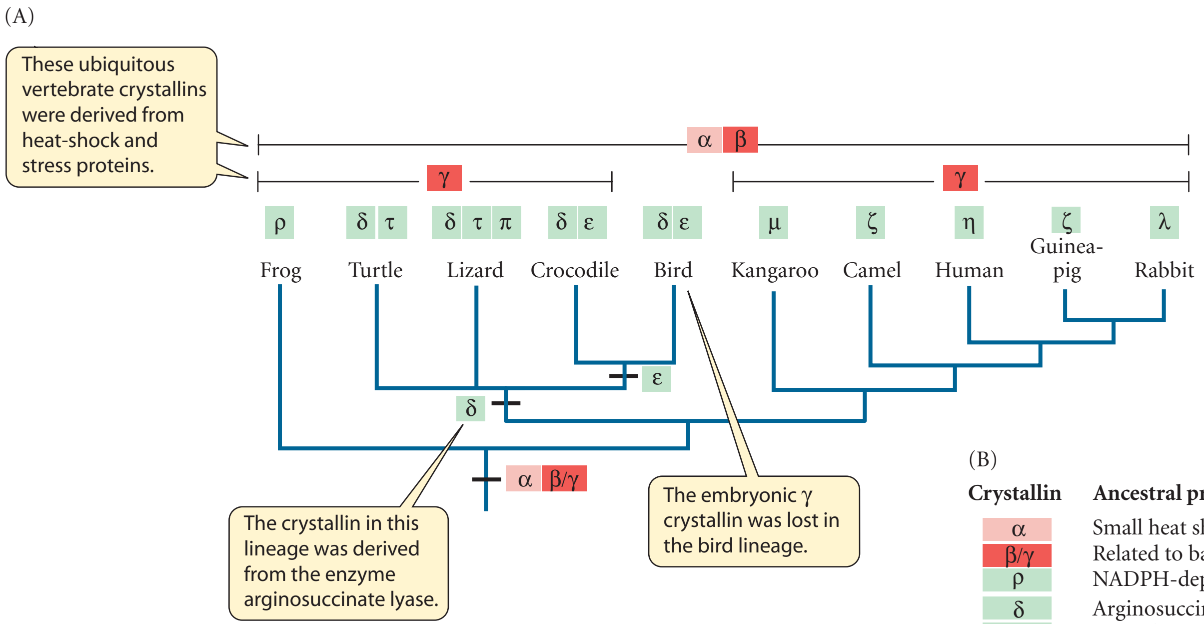


Figure 11.18 Exaptation and adaptation. (A) The wing might be called an exaptation for underwater "flight" in members of the auk family, such as this common murre (*Uria aalge*). (B) The modifications of the wing for efficient underwater locomotion in penguins (these are Humboldt penguins, *Spheniscus humboldti*) may be considered adaptations. (A © Chris Gomersall/Alamy; B © Christian Musat/ShutterStock.)

ness is an adaptation; it is a by-product of the structure of hemoglobin. Second, the trait may have evolved by random genetic drift rather than by natural selection. Third, the feature may have evolved not because it conferred an adaptive advantage, but because it was correlated with another feature that did. (Genetic hitchhiking, as exemplified in the bacterial experiment by Atwood et al. described on page 285, is one cause of such correlation; pleiotropy—the phenotypic effect of a gene on multiple characters—is another.) Fourth, as we saw in the previous section, a character state may be a consequence of phylogenet-



These ubiquitous vertebrate crystallins were derived from heat-shock and stress proteins.

The crystallin in this lineage was derived from the enzyme arginosuccinate lyase.

The embryonic γ crystallin was lost in the bird lineage.

(B)

Crystallin	Ancestral protein function
α	Small heat shock proteins
β/γ	Related to bacterial stress protein
ρ	NADPH-dependent reductase
δ	Arginosuccinate lyase
τ	α-Enolase
π	Glyceraldehyde phosphate dehydogenase
ε	Lactate dehydrogenase
μ	Similar to bacterial ornithine deaminase
η	Aldehyde dehydrogenase
ζ	Alcohol dehydrogenase
λ	Hydroxyacyl-CoA dehydrogenase

Figure 11.19 Diversity of crystallin proteins in the eye lens of some vertebrates. (A) Taxon-specific crystallins are shown for taxa in which they have been found; their complete taxonomic distributions are not necessarily indicated or known. (B) The ancestral protein from which each crystallin was derived, with or without further modification. (After True and Carroll 2002.)

ic history. For instance, it may be an ancestral character state, as Darwin recognized in his analysis of skull sutures.

Because there are so many alternative hypotheses, many authors believe that we should not assume that a feature is an adaptation unless the evidence favors this interpretation (Williams 1966). This is not to deny that a great many of an organism's features, perhaps the majority, are adaptations. Several methods are used to infer that a feature is an adaptation for some particular function. We shall note these methods only briefly and incompletely at this point, exemplifying them more extensively in later chapters. The approaches described here apply to phenotypic characters; in the next chapter, we will describe how selection can be inferred from DNA sequence data.

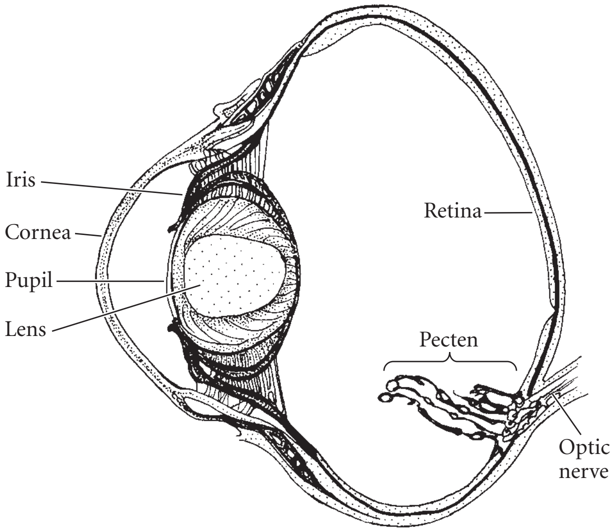


Figure 11.20 Sagittal section of a bird's eye, showing the pecten. Among the 30 or so hypotheses that have been proposed for the function of the pecten, the most likely is that it supplies oxygen to the retina. (After Gill 1995.)

COMPLEXITY. Even if we cannot immediately guess the function of a feature, *we often suspect it has an adaptive function if it is complex*, for complexity cannot evolve except by natural selection. For example, a peculiar, highly vascularized structure called a pecten projects in front of the retina in the eyes of birds (Figure 11.20). Only recently has evidence been developed to show that the pecten supplies oxygen to the retina, but it has always been assumed to play some important functional role because of its complexity and because it is ubiquitous among bird species.

DESIGN. The function of a character is often inferred from its *correspondence with the design* an engineer might use to accomplish some task, or with the *predictions of a model* about its function. For instance, many plants that grow in hot environments have leaves that are finely divided into leaflets, or which tear along fracture lines (Figure 11.21). These features conform to a model in which the thin, hot "boundary layer" of air at the surface of a leaf is more readily dissipated by wind passing over a small rather than a large surface, so that the leaf's temperature is more effectively reduced. The fields of functional morphology and ecological physiology are concerned with analyses of this kind.

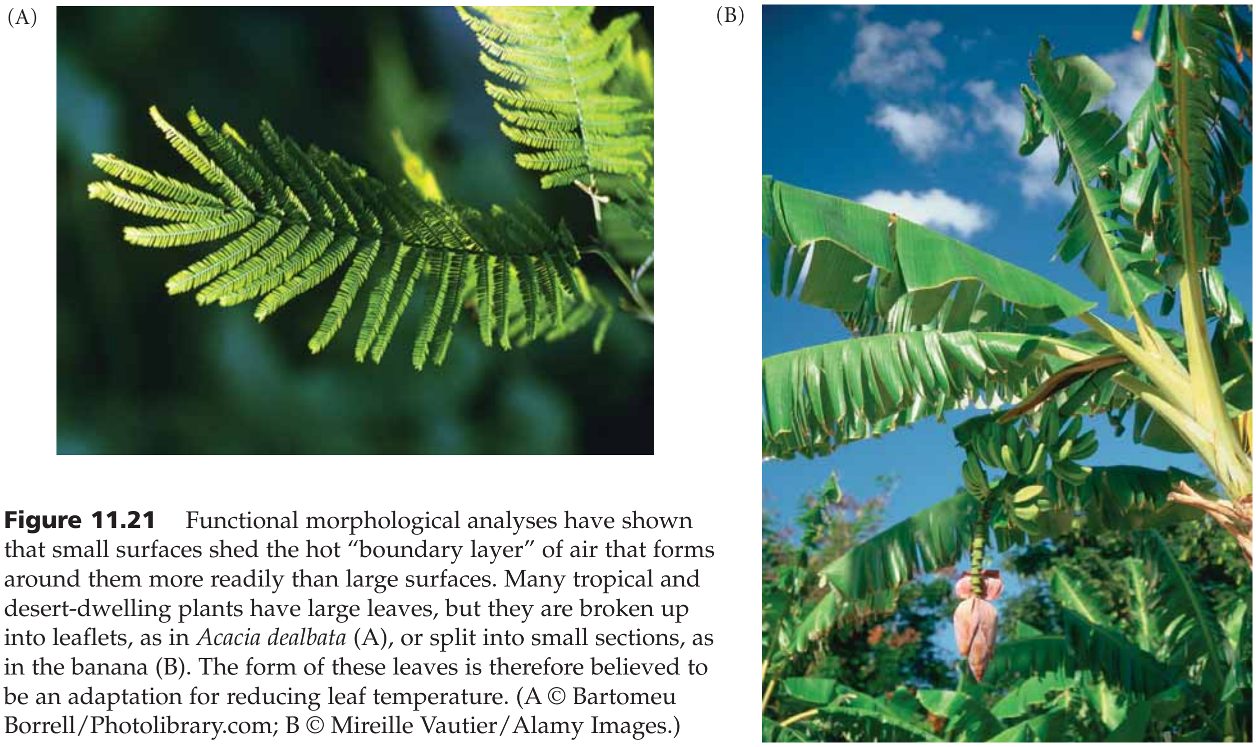


Figure 11.21 Functional morphological analyses have shown that small surfaces shed the hot "boundary layer" of air that forms around them more readily than large surfaces. Many tropical and desert-dwelling plants have large leaves, but they are broken up into leaflets, as in *Acacia dealbata* (A), or split into small sections, as in the banana (B). The form of these leaves is therefore believed to be an adaptation for reducing leaf temperature. (A © Bartomeu Borrell/Photolibrary.com; B © Mireille Vautier/Alamy Images.)

EXPERIMENTS. Experiments may show that a feature enhances survival or reproduction, or enhances performance (e.g., locomotion or defense) in a way that is likely to increase fitness, relative to individuals in which the feature is modified or absent. Andersson's (1982) alteration of the tail length of male widowbirds (see Figure 11.9) illustrates how artificially created variation may be used to demonstrate a feature's adaptive function—in this case, its role in mating success.

THE COMPARATIVE METHOD. A powerful means of inferring the adaptive significance of a feature is the **comparative method**, which consists of *comparing sets of species to pose or test hypotheses on adaptation and other evolutionary phenomena*. This method takes advantage of "natural evolutionary experiments" provided by convergent evolution. If a feature evolves independently in many lineages because of a similar selection pressure, we can often infer the function of that feature by determining the ecological or other selective factor with which it is correlated.

For instance, a long, slender beak has evolved in at least six lineages of birds that feed on nectar (see Figure 3.10). Human digestion of milk provides another example. Most adult humans are sickened by lactose, the principal carbohydrate in milk, and cannot digest it because the digestive enzyme lactase-phloridzin hydrolase (LPH) is regulated at low levels. However, people in several populations around the world have persistently high LPH levels in adulthood, especially in northern Europe and in certain populations in Africa. Milk and milk products have traditionally been an important part of the diet of all these populations. Adult lactose digestion has evolved at least three times in different populations (Holden and Mace 1997; Tishkoff et al. 2007), based on three different mutations, marked by different SNPs, in a DNA sequence upstream of the gene for LPH. DNA sequence evidence suggests that these evolutionary changes occurred after dairying was adopted. That a similar feature arose independently in a similar ecological context—a diet of dairy products—strongly suggests that it is an adaptation to that context.

Biologists often predict such correlations by postulating, perhaps on the basis of a model, the adaptive features we would expect to evolve repeatedly in response to a given selective factor. For example, in species in which a female mates with multiple males, the several males' sperm compete to fertilize eggs. Males that produce more abundant sperm should therefore have a reproductive advantage. In primates, the quantity of sperm produced is correlated with the size of the testes, so large testes should be expected to provide a greater reproductive advantage in polygamous than in monogamous species. Paul Harvey and collaborators compiled data from prior publications on the mating behavior and testes size of various primates and confirmed that, as predicted, the weight of the testes, relative to body weight, is significantly higher among polygamous than monogamous taxa (Figure 11.22).

This example raises several important points. First, although all the data needed to test this hypothesis already existed, the relationship between the two variables was not known until Harvey and collaborators compiled the data, because no one had had any reason to do so until an adaptive hypothesis had been formulated. Hypotheses about adaptation can be fruitful because they suggest investigations that would not otherwise occur to us.

Second, because the consistent relationship between testes size and mating system was not known a priori, the hypothesis generated a prediction. The predictions made by evolutionary theory, as in many other scientific disciplines, are usually predictions of what we will find when we collect data. Prediction in evolutionary theory does *not* usually mean that we predict the future course of evolution of a species. Predictions of what we will find, deduced from hypotheses, constitute the **hypothetico-deductive method**, of which Darwin was one of the first effective exponents (Ghiselin 1969; Ruse 1979).

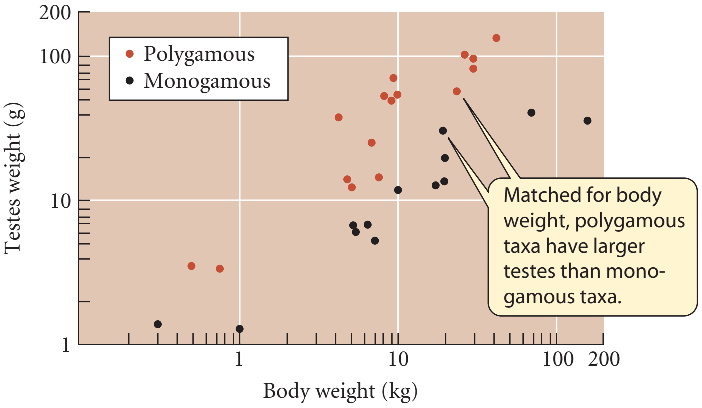
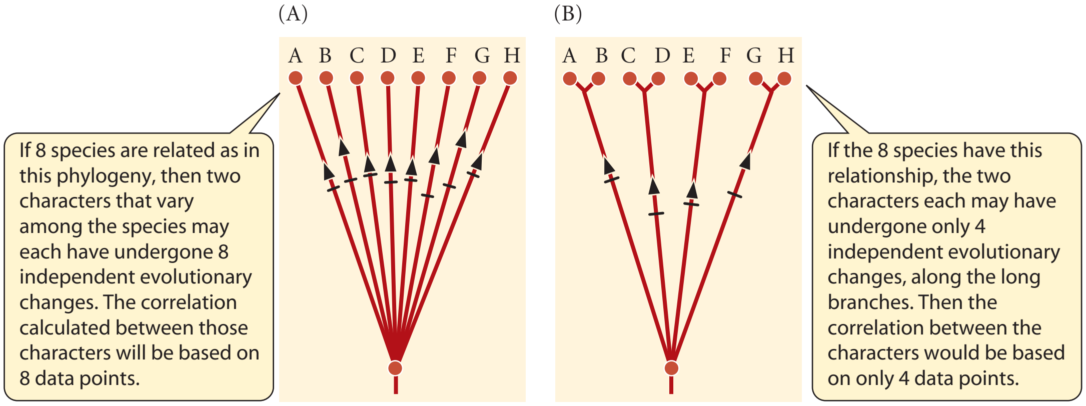


Figure 11.22 The relationship between weight of the testes and body weight among polygamous and monogamous primate taxa. (After Harvey and Pagel 1991.)



If 8 species are related as in this phylogeny, then two characters that vary among the species may each have undergone 8 independent evolutionary changes. The correlation calculated between those characters will be based on 8 data points.

If the 8 species have this relationship, the two characters each may have undergone only 4 independent evolutionary changes, along the long branches. Then the correlation between the characters would be based on only 4 data points.

Figure 11.23 The problem of phylogenetic correlation in employing the comparative method. Suppose we test a hypothesis about adaptation by calculating the correlation between two characters, such as testes size (arrowheads) and mating system (ticks), in eight species (A–H). (A) If the species are related as shown in this phylogenetic tree, the character states in each species have evolved independently, as shown by ticks and arrowheads, and we have a sample of eight. (B) If the species are related as shown in this phylogenetic tree, the states of both characters may be similar in each pair of closely related species because of their common ancestry, rather than independent adaptive evolution. Some authors maintain that the two species in each pair are not independent tests of the hypothesis; we would have four samples in this case. (After Felsenstein 1985.)

Third, the hypothesis was supported by demonstrating that the average testes sizes of polygamous and monogamous taxa show a STATISTICALLY SIGNIFICANT difference. To do this, it is necessary to have a sufficient number of data points—that is, a large enough sample size. For a statistical test to be valid, each data point must be INDEPENDENT of all others. Harvey et al. could have had a larger sample size if they had included, say, 30 species of marmosets and tamarins (Callithricidae) as separate data points, rather than using only one. All the members of this family are monogamous. That suggests that monogamy evolved only once, and has been retained by all callithricids for unknown reasons: perhaps monogamy is advantageous for all the species, or perhaps an internal constraint of some kind prevents the evolution of polygamy even if it would be adaptive. Because our hypothesis is that testes size *evolves* in response to the mating system, we must suspect that the different species of callithricids represent only one evolutionary change, and so provide only one data point (Figure 11.23). Therefore, if we use convergent evolution (i.e., the comparative method) to test hypotheses of adaptation, we should count the *number of independent convergent evolutionary events* by which a character state evolved in the presence of one selective factor versus another (Ridley 1983; Felsenstein 1985; Harvey and Pagel 1991). Consequently, methods that employ PHYLOGENETICALLY INDEPENDENT CONTRASTS (Felsenstein 1985) are usually used in comparative studies of adaptation. Often, this approach confirms a conclusion reached by a simple correlation among all species, and some biologists argue that counting only phylogenetically independent character changes may not be necessary if the characters are genetically variable, because the characters should be unconstrained and able to evolve to a different adaptive optimum quite rapidly (Westoby et al. 1997). However, the more "conservative" method of phylogenetically independent contrasts sometimes calls into question conclusions from the simpler approach. For example, the temperature preferred by 12 species of Australian skinks is correlated with the temperature at which these lizards run fastest, but this correlation proved to be statistically nonsignificant when the data were analyzed by the method of phylogenetically independent contrasts (Garland et al. 1991).

What Not to Expect of Natural Selection and Adaptation

We conclude this discussion of the general properties of natural selection and adaptation by considering a few common misconceptions of, and misguided inferences from, the theory of adaptive evolution.

The necessity of adaptation

It is naïve to think that if a species' environment changes, the species must adapt or else become extinct. Not all environmental changes reduce population size. Nonetheless, an environmental change that does not threaten extinction may set up selection for change in some characteristics. Thus white fur in polar bears may be advantageous, but it is not necessary for survival (Williams 1966). Just as a changed environment need not set in motion selection for new adaptations, new adaptations may evolve in an unchanging environment if new mutations arise that are superior to any pre-existing genetic variations. We have already stressed that the probability of future extinction of a population or species does not in itself constitute selection on individual organisms, and so cannot cause the evolution of adaptations.

Perfection

Darwin noted that "natural selection will not produce absolute perfection, nor do we always meet, as far as we can judge, with this high standard in nature" (*The Origin of Species*, Chapter 6). Selection may fix only those genetic variants with a higher fitness than other genetic variants in that population at that time. It cannot fix the best of all conceivable variants if they do not arise, or have not yet arisen, and the best possible variants often fall short of perfection because of various constraints. For example, with a fixed amount of available energy or nutrients, a plant might evolve higher seed numbers, but only by reducing the size of its seeds or some other part of its structure (see Chapter 14).

Progress

Whether or not evolution is "progressive" is a complicated question (Nitecki 1988; Ruse 1996). The word "progress" has the connotation of a goal, and as we have seen, evolution does not have goals. But even if we strip away this connotation and hold only that progress means "betterment," the possible criteria for "better" depend on the kind of organism. Better learning ability or greater brain complexity has no more evident adaptive advantage for most animals—for example, rattlesnakes—than an effective poison delivery system would have for humans. Measurements of "improvement" or "efficiency" must be relevant to each species' special niche or task. There are, of course, many examples of adaptive trends, each of which might be viewed as progressive within its special context. We will consider this topic in depth in Chapter 22.

Harmony and the balance of nature

As we have seen, selection at the level of genes and individual organisms is inherently "selfish": the gene or genotype with the highest rate of increase increases at the expense of other individuals. The variety of selfish behaviors that organisms inflict on conspecific individuals, ranging from territory defense to parasitism and infanticide, is truly stunning. Indeed, cooperation among organisms requires special explanations. For example, a parent that forages for food for her offspring, at the risk of exposing herself to predators, is cooperative, but for an obvious reason: her own genes, including those coding for this parental behavior, are carried by her offspring, and the genes of individuals that do not forage for their offspring are less likely to survive than the genes of individuals that do. This is an example of kin selection, an important basis for the evolution of cooperation within species (see Chapter 16).

Because the principle of kin selection cannot operate across species, "natural selection cannot possibly produce any modification in a species exclusively for the good of another species" (*The Origin of Species*, Chapter 6). If a species exhibits behavior that benefits another species, either the behavior is profitable to the individuals performing it (as in bees that obtain food from the flowers they pollinate), or they have been duped or manipulated by the species that profits (as are insects that copulate with orchids). Most mutualistic interactions between species consist of reciprocal exploitation (see Chapter 19).

The equilibrium we may observe in ecological communities—the so-called balance of nature—likewise does not reflect any striving for harmony. We observe coexistence of predators and prey not because predators restrain themselves, but because prey species are well enough defended to persist, or because the abundance of predators is limited by some factor other than food supply. Nitrogen and mineral nutrients are rapidly and "efficiently" recycled within tropical wet forests not because ecosystems are selected for or strive for efficiency, but because under competition for sparse nutrients, microorganisms have evolved to decompose litter rapidly, while plants have evolved to capture the nutrients released by decomposition. Selection of individual organisms for their ability to capture nutrients has the *effect*, in aggregate, of a dynamic that we measure as ecosystem "efficiency." There is no scientific foundation for the notion that ecosystems evolve toward harmony and balance (Williams 1992a).

Morality and ethics

Natural selection is just a name for differences among organisms or genes in reproductive success. Therefore, it cannot be described as moral or immoral, just or unjust, kind or cruel, any more than wind, erosion, or entropy can. Hence it cannot be used as a justification or model for human morality or ethics. Nevertheless, evolutionary theory has often been misused in just this way. Darwin expressed distress over an article "showing that I have proved 'might is right,' and therefore that Napoleon is right, and every cheating tradesman is also right." In the late nineteenth and early twentieth century, Social Darwinism, promulgated by the philosopher Herbert Spencer, considered natural selection to be a beneficent law of nature that would produce social progress as a result of untrammeled struggle among individuals, races, and nations. Evolutionary theory has likewise been used to justify eugenics and racism, most perniciously by the Nazis. But neither evolutionary theory nor any other field of science can speak of or find evidence of morality or immorality. These precepts do not exist in nonhuman nature, and science describes only what *is*, not what *ought to be*. The **naturalistic fallacy**, the supposition that what is "natural" is necessarily "good," has no legitimate philosophical foundation.

Summary

1. A feature is an adaptation for a particular function if it has evolved by natural selection for that function by enhancing the relative rate of increase—the fitness—of biological entities with that feature.
2. Natural selection is a consistent difference in fitness among phenotypically different biological entities, and is the antithesis of chance. Natural selection may occur at different levels, such as genes, individual organisms, populations, and species.
3. Selection at the level of genes or organisms is likely to be the most important because the numbers and turnover rates of these entities are greater than those of populations or species. Therefore, most features are unlikely to have evolved by group selection, the one form of selection that could in theory promote the evolution of features that benefit the species even though they are disadvantageous to the individual organism.
4. Not all features are adaptations. Methods for identifying and elucidating adaptations include studies of function and design, experimental studies of the correspondence between fitness and variation within species, and correlations between the traits of species and environmental or other features (the comparative method). Phylogenetic information may be necessary for proper use of the comparative method.
5. Natural selection does not necessarily produce anything that we can justly call evolutionary progress. It need not promote harmony or balance in nature, and, utterly lacking any moral content, it provides no foundation for morality or ethics in human behavior.

Terms and Concepts

adaptation
altruistic trait
comparative method
exaptation
fitness
function (vs. effect)
genic selection
group selection (= interdemic selection)
hitchhiking
hypothetico-deductive method
individual selection
kin selection
levels of selection
meiotic drive (= segregation distortion)
naturalistic fallacy
preadaptation
reproductive success
selfish genetic elements
sexual selection
species selection

Suggestions for Further Reading

Adaptation and Natural Selection by G. C. Williams (Princeton University Press, Princeton, NJ, 1966) is a classic: a clear, insightful, and influential essay on the nature of individual and group selection. See also the same author's *Natural Selection: Domains, Levels, and Challenges* (Oxford University Press, New York, 1992).

Two books by R. Dawkins, *The Selfish Gene* (Oxford University Press, Oxford, 1989) and *The Blind Watchmaker* (W. W. Norton, New York, 1986), explore the nature of natural selection in depth, as well as treating many other topics in a vivid style for general audiences. Levels of selection and related issues are treated in *The Nature of Selection: Evolutionary Theory in Philosophical Focus* by E. Sober (MIT Press, Cambridge, MA, 1984), *Evolution and the Levels of Selection* by S. Okasha (Oxford University Press, Oxford, 2006), and *Levels of Selection in Evolution*, edited by L. Keller (Princeton University Press, Princeton, NJ, 1999). *The Comparative Method in Evolutionary Biology* by P. H. Harvey and M. D. Pagel (Oxford University Press, Oxford, 1991) treats the use and phylogenetic foundations of the comparative method.

Problems and Discussion Topics

1. Discuss criteria or measurements by which you might conclude that a population is better adapted after a certain evolutionary change than before.
2. Consider the first copy of an allele for insecticide resistance that arises by mutation in a population of insects exposed to an insecticide. Is this mutation an adaptation? If, after some generations, we find that most of the population is resistant, is the resistance an adaptation? If we discover genetic variation for insecticide resistance in a population that has had no experience of insecticides, is the variation an adaptation? If an insect population is polymorphic for two alleles, each of which confers resistance against one of two pesticides that are alternately applied, is the variation an adaptation? Or is each of the two resistance traits an adaptation?
3. Adaptations are features that have evolved because they enhance the fitness of their carriers. It has sometimes been claimed that fitness is a tautological, and hence meaningless, concept. According to this argument, adaptation arises from the "survival of the fittest," and the fittest are recognized as those that survive; consequently there is no independent measure of fitness or adaptiveness. Evaluate this claim. (See Sober 1984.)
4. It is often proposed that a feature that is advantageous to individual organisms is the reason for the great number of species in certain clades. For example, wings have been postulated to be a cause of the great diversity of winged insects compared with the few species of primitively wingless insects. How could an individually advantageous feature cause greater species diversity? How can one test a hypothesis that a certain feature has caused the great diversity of certain groups of organisms?
5. Provide an adaptive and a nonadaptive hypothesis for the evolutionary loss of useless organs, such as eyes in many cave-dwelling animals. How might these hypotheses be tested?
6. Could natural selection, at any level of organization, ever cause the extinction of a population or species?
7. If natural selection has no foresight, how can it explain features that seem to prepare organisms for future events? For example, deciduous trees at high latitudes drop their leaves before winter arrives, male birds establish territories before females arrive in the spring, and animals such as squirrels and jays store food as winter approaches.
8. List the possible criteria by which evolution by natural selection might be supposed to result in "progress," and search the biological literature for evidence bearing on one or more of these criteria.