8 The size of beaks of Darwin's finches on the Galápagos Islands is influenced by natural selection.

Natural Selection

Empirical Studies in the Wild

Learning Objectives

- Describe the differences between directional selection and stabilizing selection.
- Demonstrate how predators can act as agents of selection.
- Explain how scarlet kingsnakes can exhibit a colorful pattern in one part of their range and be much redder in another.
- Define extended phenotypes.
- Explain how replicated natural experiments can be used to examine evolutionary change in response to selection.
- Analyze how selective sweeps can be detected within genomes.
- Describe three genetic changes that have been identified in the evolution of maize.
- Explain how Bt resistance came about in insects.
- Explain how body size and gape width could have evolved in Australian snakes in response to the invasion of cane toads.
- Discuss how fishing regulations could affect growth rates of fish populations.

Charles Darwin managed to visit only a handful of the Galápagos Islands in 1835 while on his journey aboard the *Beagle.* Among the many islands he passed by was a tiny volcanic cone known as Daphne Major. Even today, it is not an easy place to visit. To set foot on Daphne Major, you have to approach a steep cliff in a small boat and then take an acrobatic leap onto a tiny ledge. There are no houses on Daphne Major and no supply of water. In fact, just about the only things to see on Daphne Major are low scrubby plants and the little birds that eat their seeds.

In 1973, a British-born couple named Peter and Rosemary Grant came to Daphne Major and lived on the island for months. They've returned every year since, for four decades, bringing with them a team of students and all the supplies they need for a lengthy stay: tents, coolers, jugs of water, cooking fuel, clothes, radios, binoculars, and notebooks. This dedication has allowed the Grants—who are now biologists at Princeton University—to make one of the most extensive studies of natural selection in the wild.

As we saw in the last chapter, some scientists study natural selection by conducting laboratory experiments. Richard Lenski, for example,
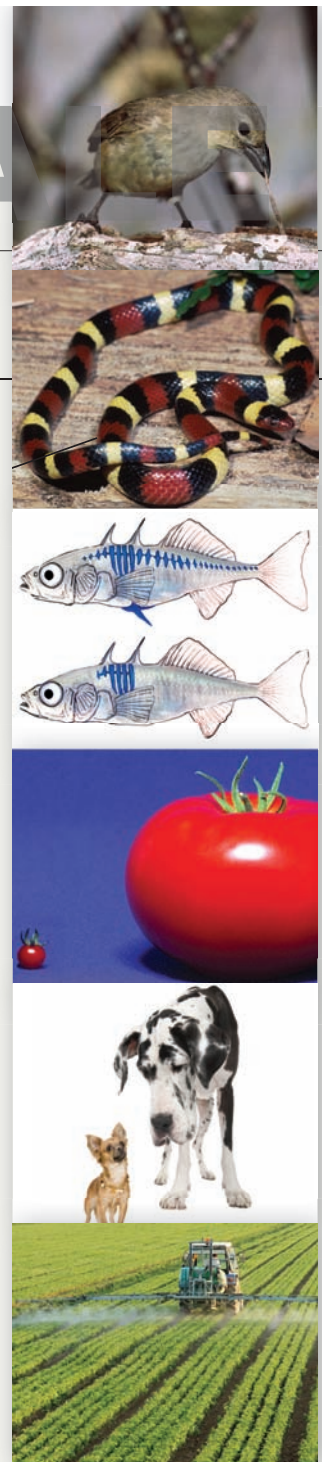
Figure 8.1 Peter and Rosemary Grant collect body measurements and place colored leg bands on wild-caught birds (A). The tiny island of Daphne Major (B), which is accessible only by scrambling up the surrounding cliffs (C), provides an isolated and unusually pristine environment for this study.

has tracked 50,000 generations of evolution in *Escherichia coli*. Thanks to his carefully designed experiments, he and his colleagues can measure natural selection in the bacteria with great precision. He knows that all 12 lines of *E. coli* that he rears descend from a common ancestor, and that they all have experienced precisely the same controlled conditions ever since. He can even thaw out frozen ancestors to compare them to their evolved descendants.

Scientists who study organisms in the wild do not have these luxuries. To study the birds of Daphne Major, the Grants can't consult a perfect genealogy of all the birds that ever lived on the island. They cannot thaw out birds that lived thousands of generations ago to compare them to their living descendants. Nevertheless, with enough tenacity and patience, they can document the process that Darwin and Wallace first proposed over 150 years ago.

In this chapter we'll consider a wide range of studies on natural selection in wild populations. These studies are not just important for documenting that natural selection exists. They also reveal some of the marvelous complexity of natural selection's effects on species. ●

8.1 Evolution in a Bird's Beak

The Grants study Darwin's finches, the birds that Darwin himself collected on his visit to the Galápagos Islands. The ancestors of these 13 species arrived on the islands approximately 3 million years ago, according to studies on their DNA. (We'll explore these studies in more detail in Chapter 9.) The birds then rapidly diversified into many different forms, adapting to the many different opportunities the islands offered for finding food. There are cactus finches that nest in cactus, sleep in cactus, mate in cactus, drink cactus nectar, and eat the flowers, pollen, and seeds of cactus. There are two species of finches that use tools: they pick up a twig or a cactus spine, trim it to shape with their beaks, and then poke into bark on dead branches to pry out larvae. There are finches that eat green leaves, which is practically unheard of for birds to do. Still other finches perch on the backs of Nazca boobies and peck at their wings and tails, drawing blood, which they then drink. There are finches that ride on the backs of iguanas and eat their ticks.

The bird that captured most of the Grants' attention is the medium ground finch (*Geospiza fortis*), a species that primarily eats seeds on Daphne Major. Despite the inaccessibility of the island—indeed, precisely because of it—Daphne Major is an ideal place to measure selection in the wild. It remains relatively pristine. No one has ever tried to farm on the island. No one introduced goats or other invasive species. As far as the Grants can tell, no species on Daphne Major have become extinct since the arrival of humans.

The island also has the added advantage of being ecologically simple. There aren't very many plant species on Daphne Major, so the Grants were able to identify and measure every type of seed that the island's finches eat. The island is small, and so is its population of birds. On Daphne Major only a few hundred ground finches may be born in a given year, and most spend their entire lives there, thus permitting

Figure 8.2 Diversity in Darwin's finches. Over the past 3 million years, these birds have specialized for feeding on cactus flowers (A); for using twigs as tools to pry insects from bark (B); and for eating eggs (C), leaves (D), blood (E), and ticks (F).

the Grants to mark and follow every individual in the population. Emigrant finches rarely leave the island, and immigrants rarely arrive. As a result, the Grants can be confident that migrations have a negligible effect at best on the changes in the allele frequencies of the island population.

The Grants survey every bird on Daphne Major, measuring vital statistics such as their body mass and beak width. They trace families, determining how many offspring each bird had, and how many offspring their offspring had. From year to year, the Grants also compare individual finches to their offspring to determine how strongly inherited each kind of variation was.

The Grants' team has found that beak size is heritable. Roughly 65 percent of the phenotypic variance in beak length, and as much as 90 percent of the variance in beak depth, is attributable to additive genetic effects of alleles ($h^2 = 0.65$ and 0.90, respectively; Boag 1983, Grant and Grant 1993). In other words, big-beaked birds tend to produce chicks with big beaks, and small-beaked birds tend to produce chicks with small beaks. With such high heritability, we can use the breeder's equation ($R = h^2 \times S$) to find that the average beak size on Daphne Major has the potential to evolve rapidly in response to natural selection (Chapter 7).

But how much natural selection do the birds actually experience? The Grants reasoned that the size of a bird's beak could affect how it ate seeds, so they investigated the kinds of food available to the birds on Daphne Major. They measured the sizes and hardness of each of the seeds produced by two dozen species of plants on the island. They took samples of the seeds to see when and where they were available to the birds. They dug up soil samples and counted all of the seeds that they contained. Thanks to the small size of the island and the simplicity of its ecosystem, the Grants were able to measure precisely how much food was available to the birds, including the relative amounts of each kind of seed. The Grants and their colleagues also closely observed the birds as they ate, noting which kinds of seeds they chose, and the time it took birds to process seeds of each type. During that first season alone, they observed over four thousand meals.
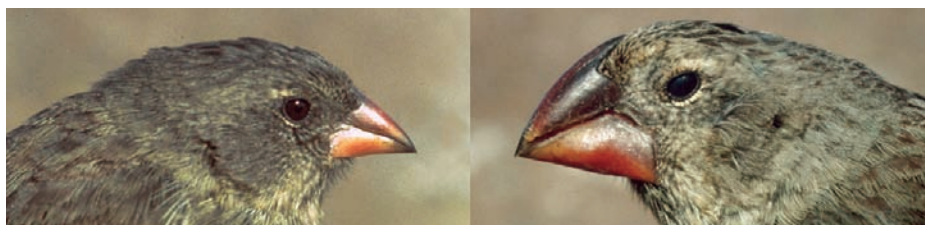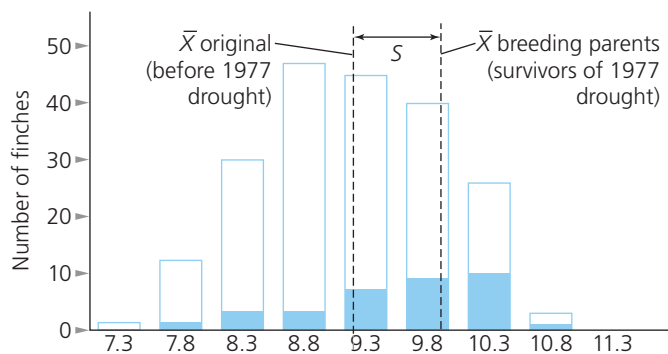

Figure 8.3 Ground finches on Daphne Major differ in the thickness of their bills, and this variation causes some individuals to be more efficient at processing hard seeds.
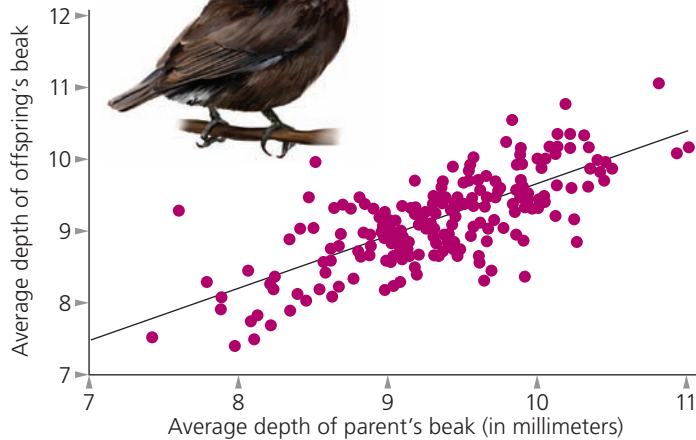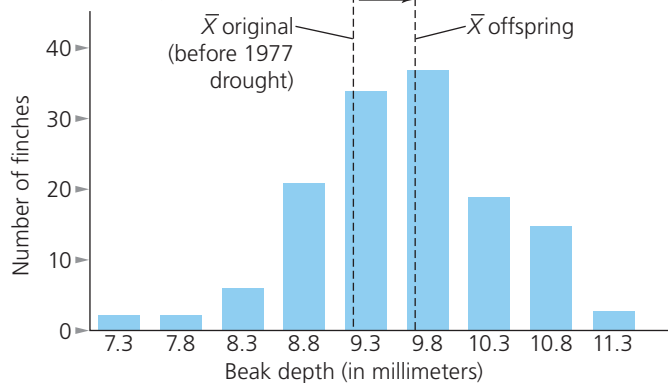
Figure 8.4 Top: The size of beaks is heritable in medium ground finches. Middle: During a drought in 1977, birds with large, deep beaks had more chicks than birds with small, narrow beaks. (The white bars show the total number of medium ground finches on Daphne Major with beaks in each size class, before the drought. The blue bars show the number of birds with beaks in each size class that survived the drought and subsequently reproduced.) Bottom: The average beak size increased in the offspring produced by birds surviving the drought. The dashed vertical lines show the average bill size from one year to the next. (Adapted from Grant and Grant 2002.)

When the Grants started their historic study, they were surprised to find that different species did not specialize on different kinds of seeds. In addition to the medium ground finch, Daphne Major is also home to the small ground finch (*Geospiza fuliginosa*), which has a narrower, pointier bill. Despite the different shapes of their beaks, both species of birds fed on the same soft, small seeds that were abundant on the island. Even species that weren't seed specialists, such as cactus finches, were eating the seeds.

When the Grants returned six months later, however, the island was transformed. The dry season had begun, and the island had not gotten a drop of rain for four months. Many of the plants on Daphne Major had died, leaving behind a barren landscape. The small, soft seeds were all gone. Now the birds were no longer all eating the same kind of food. They had become specialists. The Grants discovered that even within each species, individuals selected different kinds of seeds. Their choice, it turned out, depended on subtle differences in the shapes of their beaks.

The medium ground finches could choose from two kinds of seeds: small seeds from a plant known as spurge (*Chamaesyce amplexicaulis*) and hard, woody seeds from the plant *Tribulus cistoides,* commonly called caltrop. Finches with big beaks (11 millimeters deep) could crack open the caltrop seeds in 10 seconds. Finches with beaks 10.5 mm deep needed 15 seconds. If a bird's beak was 8 mm deep or less, it took so long to crack caltrop seeds that the bird gave up on it altogether. Instead, it ate only small spurge seeds.

The Grants found that the size of a finch's beak could make the difference between life and death. In 1977, Daphne Major was hit by a major drought. Most of the spurge plants died, leaving the medium ground finches without any small seeds to eat. Many of the birds died, most likely because they couldn't crack open the big seeds from caltrop. The Grants discovered that within a few years, the population of finches had recovered. But now the average size of their beaks was deeper. Before the drought, the population ranged in beak size from 8 to 11 mm with an average depth of 9.2 mm. After the drought, the average beak size had shifted half a millimeter to 9.7 mm, or about 15 percent of the range of variation (Grant 1986). The shift occurred because finches with bigger beaks had a better chance of surviving the drought. They could therefore produce a bigger fraction of the next generation. In other words, natural selection caused the average size of the beaks of medium ground finches to increase within the population (**Figure 8.4**).

Figure 8.5 The Grants have measured natural selection on finch beaks for almost 40 years. During this period, the strength and direction of selection fluctuated. The Grants plotted the difference between the mean beak size of the population and the mean beak size of the individuals producing offspring in the next generation (the selection differential) for each year (A). In some years, birds with large beaks were favored (bars above the horizontal line); in other years, birds with small beaks were (bars below horizontal line). In still other years, selection on beak size was minimal. The finch population evolved in response to these episodes of selection, with the result that beak size fluctuated in tandem with the directions of selection (B). (Modified from Grant and Grant 2002.)

A   Selection on beak size

B   Evolution of beak size

Five years later, the Grants were able to observe natural selection at work again. At the end of 1982, heavy rains came to the islands. Spurge bloomed, producing lots of small seeds. Now small-beaked birds had the advantage. They could eat small seeds more efficiently than the big-beaked birds, allowing them to grow faster and have more energy for producing offspring. In just a few generations, the average size of beaks decreased by 2.5 percent (about a tenth of a millimeter).

The Grants had made an historic observation. It was the first time scientists had measured the effects of natural selection in a wild population as they were unfolding. The Grants had measured the heritability of beak size (h^2), they had measured the strength and direction of several episodes of natural selection acting on beak size (S), and they had measured what happened to the population for several generations after the episode of selection (the evolutionary response, R). They documented how, precisely, selection caused evolution in the finches ($R = h^2 \times S$; Chapter 7).

But the Grants did not abandon Daphne Major after their initial observations. They've continued coming back for nearly 40 years (**Figure 8.5**). That persistence has paid off impressively. Their research now offers many deep insights into how natural selection works (Grant and Grant 2002).
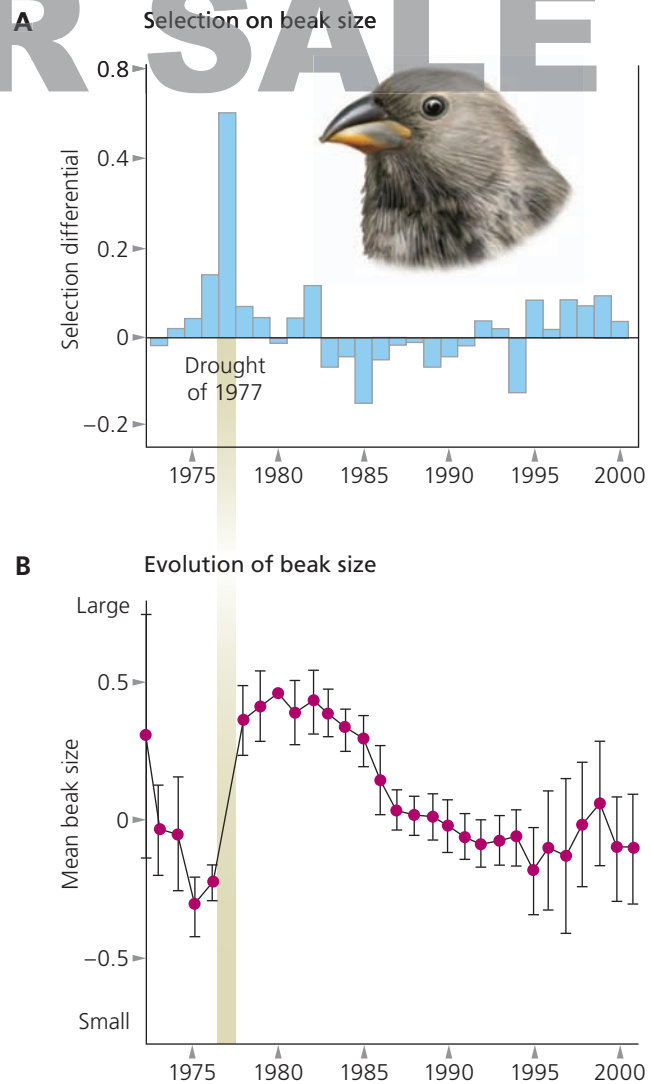
The first lesson is that natural selection may itself be variable. Had the Grants sampled Daphne Major only during the wet seasons, they would have missed important episodes of directional selection. It was during the dry seasons—and in particular, the dry seasons of drought years—when selection favored big beaks.

The second lesson is that evolution can occur with surprising speed. Before the Grants conducted their research, many evolutionary biologists maintained that evolution likely occurred over very long timescales. Gradual changes in the fossil record unfolded over millions of years, suggesting that the strength of natural selection was probably very weak—weaker, for example, than the artificial selection imposed on populations of domesticated plants and animals. But the Grants were able to observe evolutionary changes in a natural population that were every bit as fast as those resulting from **artificial selection**. The selection they measured was strong, and their populations evolved in a matter of generations.

Finally, and perhaps most important, the nature of selection can change over time. The Grants measured selection favoring big, deep beaks in some years and small, narrow beaks in others. Both the strength of selection, and its direction, fluctuated several times over the course of their study.

Artificial selection: Similar to natural selection, except that it results from human activity. When breeders nonrandomly choose individuals with economically favorable traits to use as breeding stock, they impose strong artificial selection on those traits.

Key Concepts

During a severe drought on Daphne Major, subtle differences in beak thickness among medium ground finches affected who lived and who died. Because beak depth is highly heritable, natural selection could lead to rapid evolution of beak size.

8.1 EVOLUTION IN A BIRD'S BEAK   **223**

Natural selection is directional if it favors increases, or decreases, in the size or dimensions of a trait. It is stabilizing or balancing if it favors the current value for the trait.

Long-term studies of natural selection often show fluctuations in the direction and magnitude of selection.

8.2 Mice in Black and White

The studies of Peter and Rosemary Grant are still exceptional for their 40-year span. But they are now just one of hundreds of studies documenting selection in wild populations. These studies reveal different aspects of selection's complexity. And in some cases, researchers are even able to zero in on the specific genes that selection is altering.

In Chapter 7, we met Hopi Hoekstra, who studies oldfield mice (*Peromyscus polionotus*) in the southeastern United States. As we saw, Hoekstra and her colleagues are interested in the variation in coat color in different populations. Hoekstra and her colleagues used quantitative trait locus (QTL) mapping to identify a few key genes involved in determining the color on the coats of the mice. This discovery raises the possibility that the difference in coloration between the beach mice and the mainland mice is the result of selection. It shows us that the trait possesses two of the three requirements for natural selection to operate—variation and a genetic basis that can be passed down from parents to offspring.

The third requirement is that variation in the trait leads to differential survival or fecundity in a population. To explore this possibility, Hoekstra and her colleagues studied how the color of the mice affects their chances of getting killed by predators. To catch a mouse, a bird or another predator has to see it. The oldfield mice make themselves difficult to see by foraging mainly on dark, cloudy nights. It was possible that the color of the mice also helped them become harder to see (Kaufman 1974). Oldfield mice that live on the mainland tend to be dark, matching the dark, loamy soils they walk on. Beach mice, which live on white sand, are much lighter.

To test the hypothesis that natural selection produced this variation, Hoekstra and her colleague, Sacha Vignieri, then at Harvard, conducted a simple field experiment. They made hundreds of life-sized clay models of mice and put them in each type of habitat. Half of the imitation mice were dark and half were light. Hoekstra and Vignieri then waited for predators to attack the models.

The predatory birds and mammals attacked some of the imitation mice, but then quickly discarded them once they realized their prey wasn't real. Hoekstra and Vignieri then gathered all the models and tallied the ones that had been damaged by predators. They discovered that predators are much more likely to attack mismatched phenotypes. In the light-colored sands of the beach habitats, predators attack primarily dark individuals, whereas in the more complex and darker backgrounds of inland habitats, they attack primarily light individuals (Vignieri et al. 2010).

Experiments like these have allowed Hoekstra and her colleagues to develop a detailed hypothesis for the evolution of coat color in oldfield mice—a hypothesis that can address both the ecological factors driving natural selection and the genetic basis that makes it possible. In mainland populations, there is genetic variation for coat color, based on different alleles for genes involved in pigmentation. Predators are quick to kill off mice with alleles that produce light coats, keeping the frequency of those alleles very low in the population. As a result, a disproportionate number of brown mice survive long enough to breed. Later generations will also tend to be brown.

Several thousand years ago, some oldfield mice colonized Gulf Coast beaches and barrier islands. Now the dark mice stood out and were more likely to be killed. Natural selection favored genetic variants that produce pale coats, leading to a drastic shift in the average phenotype of the beach population. On the Gulf Coast, it turns out, these lighter coats were the results of mutations to several genes involved in the pathway for pigmentation. One mutation changed a single amino acid in the mela-
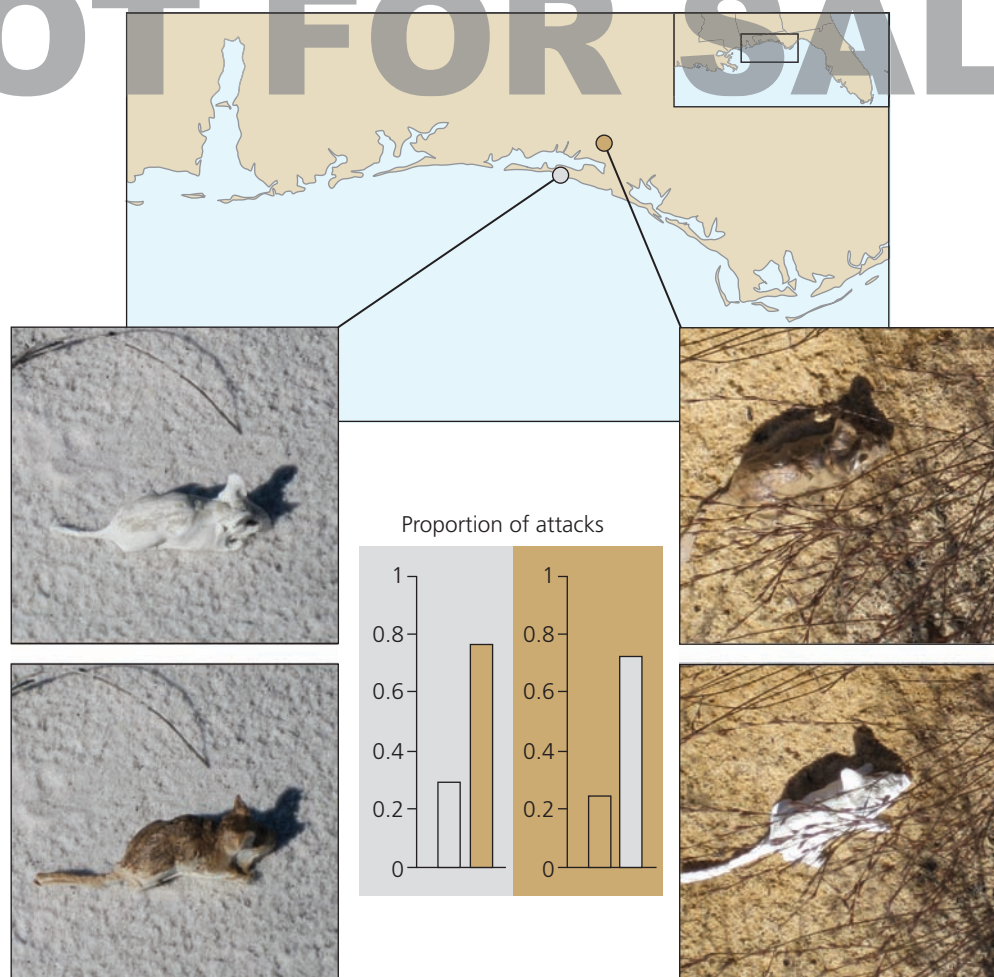
Figure 8.6 Hopi Hoekstra and her colleagues set up an experiment to measure natural selection on coat color in oldfield mice. Clay models of mice were painted to resemble beach or mainland forms and placed in either mainland or beach habitat in Florida. Blending into the background effectively reduced predation rate in both the beach and mainland habitat. Predation rates of dark clay models in beach habitats (left) were much higher relative to white models, and predation rates of light models in mainland habitats (right) were much higher relative to dark models. Photos: Sacha Vignieri. (Modified from Vignieri et al. 2010.)

nocortin-1 receptor (*Mc1r*), decreasing the sensitivity of the receptor to signals that would otherwise lead to the production of dark pigmentation. A second mutation increased expression of a gene known as *Agouti,* which interferes with the signaling of *Mc1r*. Combined, these two genetic changes resulted in reduced levels of melanin synthesis and lighter overall coat color (Chapter 7).
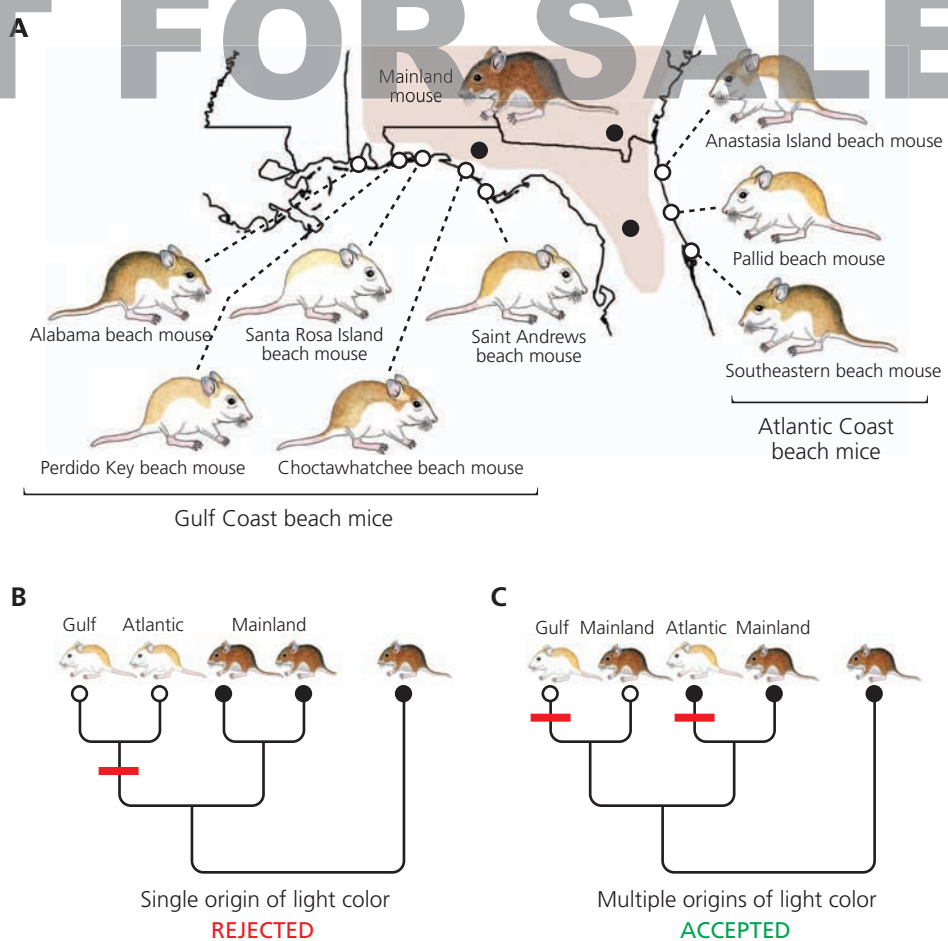
The Gulf Coast is not the only place where one can find white oldfield mice. On Florida's Atlantic coast, they exist as well. It's unlikely that one population descended from the other, since that would have required white mice traveling across 300 kilometers of dark soils. Instead, it's much more likely that the two populations evolved from mainland mice independently. Hoekstra and her colleagues compared the genetic basis of coat color in the two coastal populations and got an intriguing result: the light-colored mice on the Atlantic Coast lacked the Gulf Coast alleles of *Mc1r.*

The altered phenotype of the Atlantic Coast mice appears to be produced by mutations to other genes—genes for which Hoekstra and her colleagues are now searching (Steiner et al. 2009). This turns out to be a common pattern in natural selection: closely related populations under the same selective pressures often evolve the same phenotype in parallel. But different populations can reach that phenotype through different mutations.

The evolution of color is a richly complex phenomenon that biologists are only beginning to decipher. In New Hampshire, for example, Hoekstra and her colleagues

Figure 8.7 A: Pale beach mouse subspecies occur along both the Gulf Coast and the Atlantic coast of Florida. B: Possible relationship among subspecies. Based on DNA data, the hypothesis that light pigmentation evolved only once in the lineage can be rejected. C: Light coloration in beach mice likely evolved twice independently—once in the Gulf Coast and a second time in Atlantic populations. This phylogenetic hypothesis is supported by mapping of the mutations responsible for pale coat coloration (see text). (Modified from Hoekstra 2010.)

A

Mainland mouse

Anastasia Island beach mouse

Pallid beach mouse

Southeastern beach mouse

Atlantic Coast beach mice

Alabama beach mouse

Santa Rosa Island beach mouse

Saint Andrews beach mouse

Perdido Key beach mouse

Choctawhatchee beach mouse

Gulf Coast beach mice

B

Gulf Atlantic Mainland

Single origin of light color
REJECTED

C

Gulf Mainland Atlantic Mainland

Multiple origins of light color
ACCEPTED

have studied black deer mice (*Peromyscus maniculatus*), the sister species to oldfield mice. They discovered that the black deer mice carry yet another mutation to *Agouti*—this time a deletion of genetic material that reduces its activity (Kingsley et al. 2009). This genetic change has the opposite effect of the mutation in the Gulf Coast mice. Instead of *increasing* the activity of *Mc1r,* it *decreases* its activity and therefore leads to an increase in melanin production. Mutations that increase melanin synthesis (by reducing activity of the antagonist *Agouti*) result in darker fur.

Key Concepts

Evolution in response to natural selection is the inevitable outcome whenever three conditions are met: individuals differ in their expression of a trait; this variation is at least partially heritable; and, because of these differences, some individuals survive and reproduce more effectively than others.

Specific features of the environment can generate natural selection on a trait. These agents of selection can be events, such as storms or droughts, or environmental factors like predators or diet.

8.3 The Geography of Fitness

Natural selection can produce variation in time, but it can also create variation in space—across the geographical range of a population. As an allele spreads through a population, it also spreads through space. If a giraffe carrying a beneficial allele strolls across the Serengeti and joins a new herd, the allele may then become common over a few generations in the new herd as well. Another giraffe can then carry it on to an even more distant herd. The rate at which alleles move between populations (a process known as **gene flow**) is controlled by many variables. The amount of gene flow depends on how far individual organisms move, for example, and how far their gametes move. A tree obviously will not pull up its roots and go for a stroll, but its pollen can drift far and wide. Seeds can get stuck to the feet of birds and cross entire oceans.

Gene flow: The transfer of alleles from one population to another. It occurs when organisms or their gametes move from one location to another.

Scarlet kingsnake
(not venomous)

Mimic kingsnake

Eastern coral snake
(venomous)
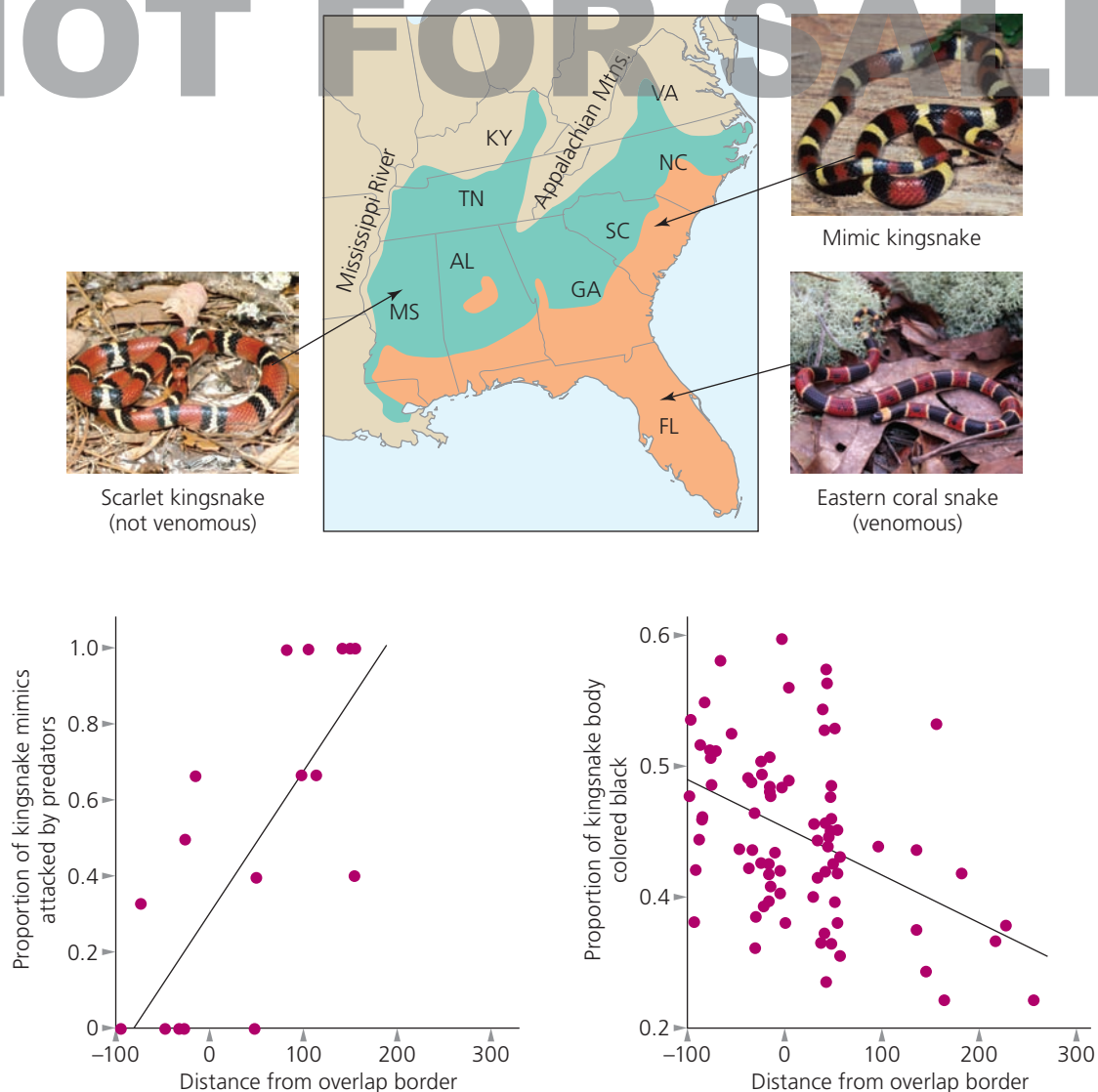
Figure 8.8 Scarlet kingsnakes mimic the venomous coral snakes where the ranges of the two species overlap. But farther away from these regions, the kingsnakes look less like the coral snakes. Natural selection favors genes for mimicry in the regions of overlap, but as these genes flow to other regions they get eliminated. Predators that live in the coral snake's territory learn to avoid the bright color pattern. But in other regions, they are more likely to attack kingsnakes with this pattern because it's easy to spot. (Adapted from Harper and Pfennig 2008.)

Many of the alleles that flow between populations are neutral. They don't raise or lower the fitness of organisms, no matter where those organisms live. But gene flow also carries beneficial and deleterious alleles between populations. Once in a new population, an allele that previously raised fitness may actually lower it, if the agents of selection are different in the new location. In this way, new copies of alleles may arise in one population, only to disappear in another—like water coming out of a faucet and going down a drain.

This complex movement of genes accounts for many patterns in nature. Take, for example, the scarlet kingsnake (*Lampropeltis triangulum elapsoides*), which lives in the eastern United States. In the southeastern part of their range, in such states as Florida and Georgia, scarlet kingsnakes have a colorful pattern of red, yellow, and black rings. But in the northern part of their range (in Tennessee, Kentucky, and Virginia), scarlet kingsnakes are much redder.

In 2008, George Harper and David Pfennig, two biologists at the University of North Carolina, discovered why the same species of snake looks so different in different places (**Figure 8.8**; Harper and Pfenning 2008). In the southeastern portion of

Aposematism: An antipredator strategy used by a potential prey item to signal danger or a lack of palatability. The most commonly known form of aposematism is warning coloration, in which the bright coloration of prey that are potentially dangerous can act as a deterrent to potential predators.

their range, scarlet kingsnakes live alongside eastern coral snakes (*Micrurus fulvius*). Eastern coral snakes have a potentially fatal bite, and, like many species of venomous animals, have a bright color pattern as a defense mechanism. Predators, such as carnivorous mammals, recognize the pattern on the coral snakes and avoid them. (This type of warning coloration is called **aposematism**.) Scarlet kingsnakes are not venomous, but the ones that live alongside coral snakes have an aposematic-like coloration. As a result, predators avoid the scarlet kingsnakes even though they're harmless.

Scarlet kingsnakes have a much larger range than coral snakes. In the northern part of their range, where scarlet kingsnakes don't live alongside coral snakes, their pattern is different from that of coral snakes. However, the variation between the northern and southern populations of kingsnakes is not a result of their being genetically isolated from each other. Collecting DNA from scarlet kingsnakes throughout their range, Harper and Pfennig documented gene flow across the entire range of the snakes. Scarlet kingsnakes from the southern part of the range migrate to other populations, bringing their alleles for mimicking coral snakes.

So why don't all scarlet kingsnakes look like coral snakes? Because, it turns out, mimicking a coral snake provides protection only from predators that live in the range of the coral snake. Predators outside the coral snake's range are more willing to attack snakes with an aposematic-like pattern. An adaptation that serves as an effective warning in one place becomes a way to draw the attention of predators in another. The farther away scarlet kingsnakes are from the overlap zone, Harper and Pfennig found, the more strongly natural selection works against coral snake mimics. As a result, the farther you move from the overlap zone, the less the kingsnakes look like coral snakes.

Key Concept

Natural selection can lead to variation in space—across habitats or environments—just as dramatically as it can lead to variation in a single habitat over time.

8.4 Predators versus Parasitoids: When Agents of Selection Act in Opposing Directions

More than one agent of selection can act on a trait. And sometimes, scientists have found, those agents drive a population in two different directions at once. At first it can be hard to see these multiple agents at work, just as a rope may become motionless during a game of tug-of-war as two teams are pulling in opposite directions. It takes careful experiments to tease apart the effects of the different agents. One of the most striking cases of this evolutionary tug-of-war has been documented in the gallfly (*Eurosta solidaginis*; **Figure 8.9**).

Female gallflies lay eggs into the growing tips of goldenrod (*Solidago* spp.), a plant that thrives in old farm fields. After the eggs hatch, each larva bores into the

Figure 8.9 The gallfly (*Eurosta solidaginis*) lays her eggs into the stems of goldenrod (A). When the fly larvae hatch, they secrete chemicals that induce the plant to form a gall (B), which serves as both a food source and protection for the developing larva (C). Photos courtesy of Warren Abrahamson.
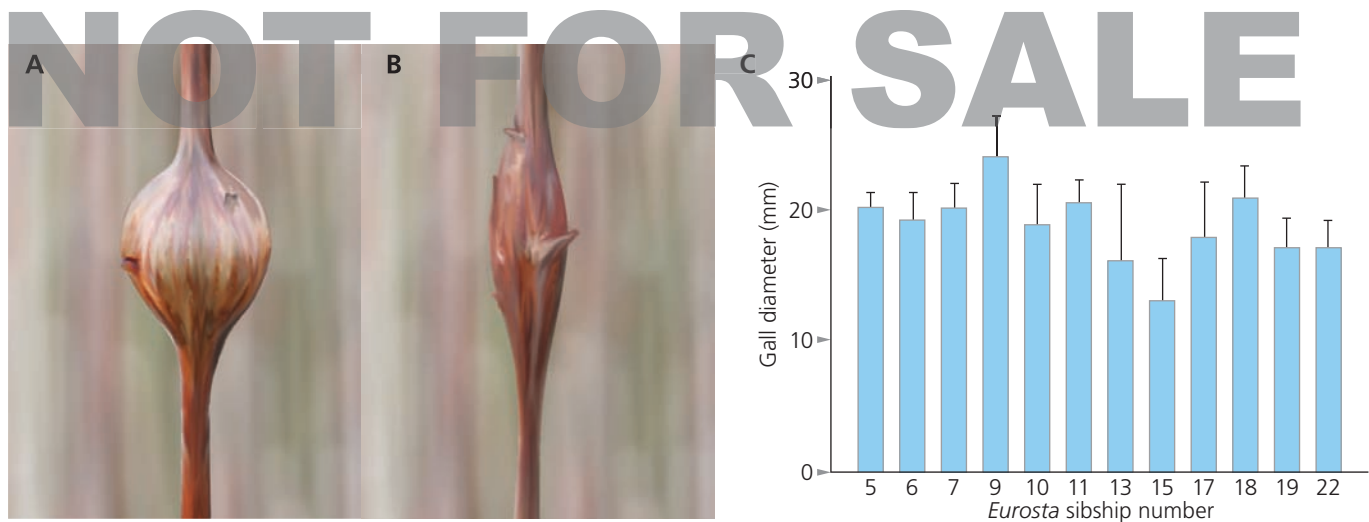
Figure 8.10 Fly larvae differ in the diameter of the galls they produce (A, B), and some of this variation is heritable. Larvae from the same mother produce similar-sized galls, and some families produce much larger galls than others (C). (Modified from Abrahamson and Weis 1997.)

bud tissues to feed. The larva secretes fluids containing proteins and other molecules that change the gene expression of cells in the plant. The plant cells grow into a bulbous, tumor-like structure, known as a gall, that is hard on the outside and soft on the inside. Cradled at the center of the gall, the gallfly larva can feed on the plant's fluids.

The gall is made of plant cells, and yet its growth is controlled by the flies. It can thus be considered an **extended phenotype** of the flies. Biologists Arthur Weis and Warren Abrahamson found that the final size of galls varies, and at least some of the variation is due to inherited differences among the fly larvae, not the plants. The scientists were able to demonstrate this link with a two-part experiment: they allowed several different female gallflies to lay eggs on goldenrod, and they let each female lay eggs on several different plants. (To remove the effects of genetic differences among the plants, they had all of the females oviposit on clones—plants with the same genotype.) Abrahamson and Weis let all of the offspring of each female make galls, and they compared the average sizes of the galls that were produced. They found that fly families differed significantly in the gall sizes that they produced (**Figure 8.10**).

This difference pointed to an inherited component to the variation in how the flies induced galls to form in their host plants. These studies revealed that galls met two of the conditions for natural selection—variation in populations and an inherited component of that variation (Weis and Abrahamson 1986).

The scientists then considered the third condition for evolution by natural selection: whether an inherited phenotypic trait influenced survivorship. They investigated whether the size of galls had an effect on the survivorship of gallflies in natural populations. Their size turned out to matter a lot. Galls provide physical protection for the larvae from two major sources of mortality: predatory birds and parasitoid wasps. Predatory birds tear into the galls and pull out the larvae, but parasitoid wasps pose a different problem. Female parasitoid wasps drill their ovipositors into the galls to lay eggs beside the fly larvae. Once the parasitoid egg hatches, the wasp larva develops very fast—faster than the fly larva—and it eats both the gall tissues and the fly as it grows.

The likelihood of each of these sources of mortality is influenced by the size of the gall, but in different ways. Bird predation, Abrahamson and Weis found, selects very strongly for small gall sizes. During the winter, when vegetation has died back, bigger galls are easier for the birds to find. As a result, large galls get eaten more often than smaller galls. Abrahamson and Weis observed this same pattern of selection at several different sites and during multiple years. In all these cases, predation by birds favored the evolution of small, inconspicuous gall sizes.

The parasitoids also cause strong selection on the galls, but their effect is opposite that of bird predators. Parasitoid female wasps must reach into the center of the

Extended phenotypes: Structures constructed by organisms that can influence their performance or success. Although they are not part of the organism itself, their properties nevertheless reflect the genotype of each individual. Animal examples include the nests constructed by birds and the galls of flies.

Figure 8.11 Downy woodpeckers feed on goldenrod galls during the winter, when oldfield vegetation has died back and the galls are most visible (A). They find primarily large galls (B). Tiny parasitic wasps inject their eggs into galls (C) and kill larvae in the smallest galls (D). The result is a balance: natural selection favors flies that produce intermediate gall sizes. (Modified from Weis et al. 1992.)
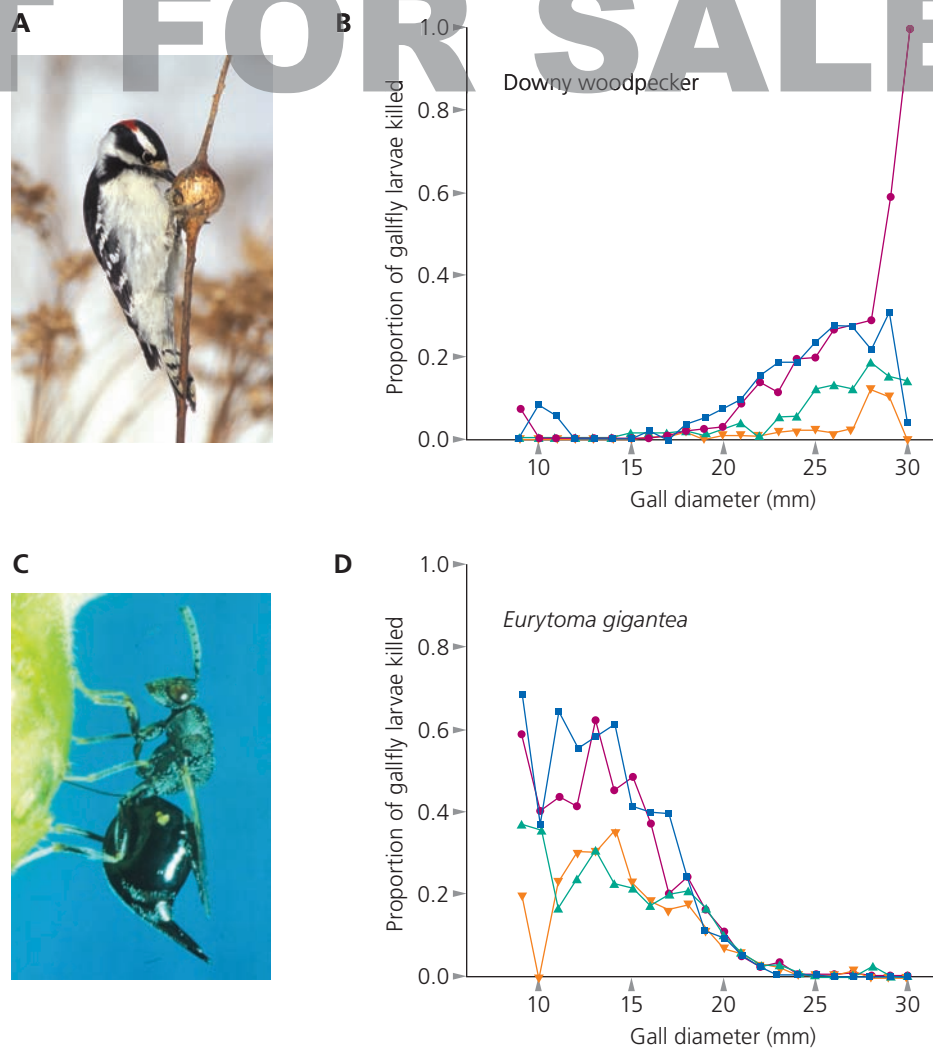
gall to place their eggs on the surface of the gallfly larvae. Although the wasps have unusually long ovipositors, some galls in a population are too big for them to reach the larva inside. As a result, the larvae in the largest galls often escape being parasitized. Parasitoid wasps thus favor the evolution of large galls, and this pattern, too, was observed across multiple populations and many years.

Taken together, the studies of Abrahamson and Weis reveal a balance. When galls are too large, larvae are likely to be eaten by birds. When galls are too small, larvae are likely to die from parasitoids. The result is a trade-off with stabilizing selection for intermediate-sized galls (Weis, Abrahamson, and Andersen 1992).

Key Concept

When agents of selection act in opposition, the net effect can be a balance: stabilizing selection for an intermediate trait value.

8.5 Replicated Natural Experiments

Three-spined sticklebacks (*Gasterosteus aculeatus*) are small fish that live across much of the Northern Hemisphere. Some populations live as adults off the coasts of North America, Europe, and Asia. They swim inland to spawn in freshwater, and their offspring swim back to the sea. Other stickleback populations live their entire lives in lakes. Their ancestors reached the lakes before the end of the last ice age 11,000 years ago, and when the glaciers retreated, the land rebounded and created barriers that cut

Box 8.1   Mapping the Fitness Landscape

To represent the fitness of a single trait within a population, we can draw a two-dimensional curve, with the value of the trait along one axis, and the fitness for trait values on the other. But it can also be enlightening to see how the reproductive success of a population is related to more than one trait at a time (Schluter and Nychka, 1994). Imagine, for example, a species of bird in which the survival of young depends strongly on both body mass and running speed. The probability that a particular individual survives is a function of both traits.

If we are studying two such traits at once, we can trade in our two-dimensional curve for a three-dimensional surface. Think of a range of hills, where each point is represented by three coordinates: latitude, longitude, and elevation. On a fitness surface, latitude and longitude are the values of two phenotypic traits, and the elevation is the corresponding fitness.

As we saw in Chapter 7, a fitness graph for a single trait can assume many shapes: it may have a peak at the mean value in the population or at one end of a range of values; it may even form a saddle shape if the mean value of a trait has the lowest fitness. Likewise, a fitness surface for two traits can potentially assume many different topographies. It may be dominated by a single peak or several; it may have a complex network of valleys representing combinations of trait values that are associated with low fitness. The slopes of these peaks and valleys may be steep in some places and gentle in others.

To estimate the fitness surface for a real population, we must take measurements of the two traits in a large sample of individuals and then find the topography that best fits the data. There are a number of methods for doing so; one of the most influential was developed in 1994 by Dolph Schluter and Douglas Nychka, based on a curve-fitting technique known as cubic splines. In one example, they examined medical records from 7307 babies. For each child, Schluter and Nychka compared two traits—birth weight and maternal gestation period—and also noted whether the child survived the first two weeks after birth.

Box Figure 8.1.1 shows their result: a dome-shaped topography. The steepness of the dome shows the strength of selection. Selection acts most strongly against small babies with short gestation periods. But babies could have different combinations of intermediate values of the two traits and still have the same odds of surviving. A baby with low birth weight and a gestation of moderate length had the same fitness as a heavier baby that was born sooner. The topog-
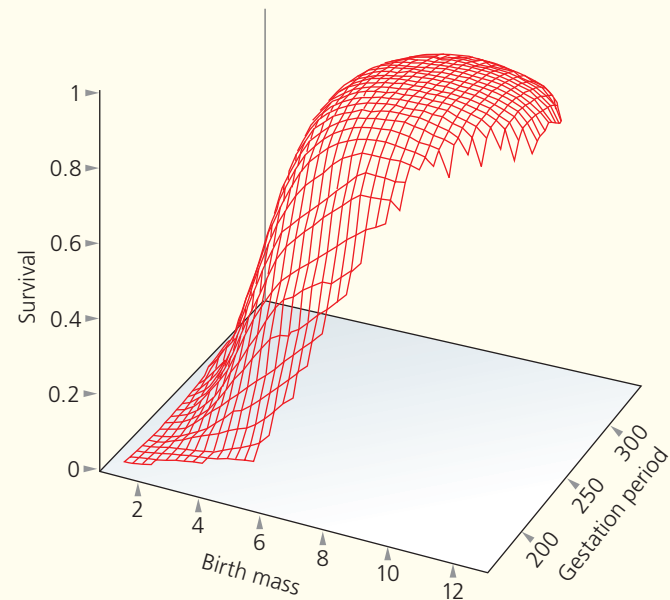
Box Figure 8.1.1 This three-dimensional graph shows how birth weight and gestation period combine to determine how likely a baby is to survive to 2 weeks of age. (Adapted from Schluter and Nychka 1994.)

raphy gains a dome shape because babies with the greatest body size and longest gestation periods were less likely to survive. Thus, this topography reveals that the selection human babies experience is mainly directional selection but also weakly stabilizing (Schluter and Nychka 1994).

Of course, it's also possible for more than two traits to be strongly selected in a population. Unfortunately, our brains cannot visualize graphs in four or more dimensions, but it is possible to use the same methods we've considered here to analyze these more complex interactions. The notion of an evolutionary landscape can also be a useful metaphor for thinking about how populations change over time. For extensive discussions of these issues, see Schluter (2000) and Pigliucci and Kaplan (2006).

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the lakes off from the ocean. The sticklebacks living in them could no longer return to the ocean. In each of these lakes, the isolated sticklebacks experienced a new set of selection pressures. Scientists can treat the lakes like a natural evolutionary experiment with replicate populations, analogous to Richard Lenski's flasks of *E. coli.* The lake sticklebacks are now measurably different from marine populations in a number of different ways. Here we'll focus on one change in particular: how the sticklebacks lost their armor.

Marine sticklebacks grow spines and bony plates that protect them from predators. If a cutthroat trout tries to swallow a stickleback with spines, the attack will fail almost 90 percent of the time and the trout will eject its prey from its mouth. Even these failed attacks can be harmful to a stickleback, but bony plates that grow along its flanks can shield it against injury (Reimchen 1992).

The amount of armor plating varies from one stickleback to another. David Kingsley, of Stanford University, and his colleagues have investigated the source of this variation and discovered that it originates from inherited differences (Colosimo et al. 2005).

Figure 8.12 Marine three-spined sticklebacks protect themselves from predators with long dorsal and pelvic spines and with a row of tough lateral plates (A). In freshwater lakes, the expression of these defensive structures can be greatly reduced (B).
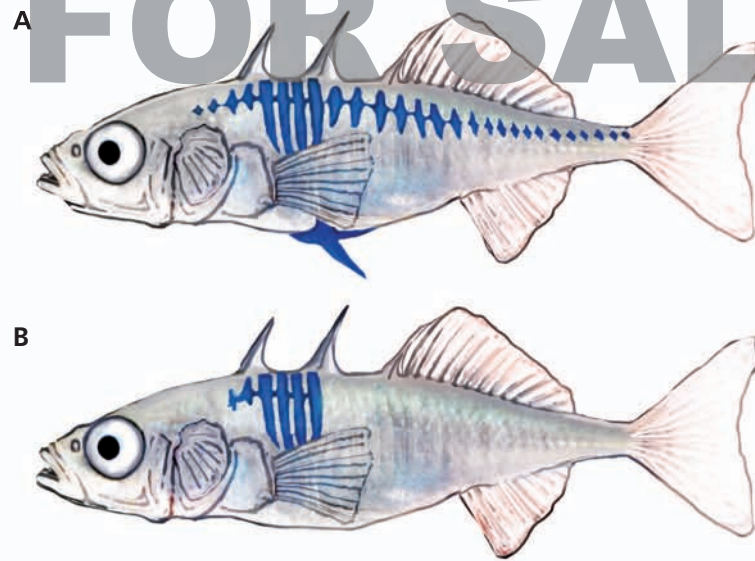
The scientists used QTL mapping to analyze the source of this variation in the stickleback genome. They determined that alternative alleles for the *ectodysplasin* (*Eda*) gene underlie much of the variation in the number of lateral plates each stickleback grows.

Eda signaling is involved with the development of adult integument and dental structures in vertebrates. In sticklebacks, *Eda* appears to regulate the growth of lateral armor plates. Fish inheriting two copies of a recessive "low" *Eda* allele develop with fewer lateral plates (low armor). The low allele Kingsley and his colleagues discovered differs from normal *Eda* alleles at four locations. At each site, a base-pair mutation changes an amino acid in the final protein.

These studies on sticklebacks reveal all three of the necessary conditions for evolution by natural selection: the functional importance of armor for survival, extensive among-individual differences in phenotype (e.g., armor plate numbers), and inherited genetic variation underlying these differences. In the ocean, the presence of predators selects for *Eda* alleles that are associated with heavy armor. But whenever stickleback fishes became isolated in lakes with few predators or none, the selection pressures they experience changed. Elaborate defenses no longer raised their fitness.

Sticklebacks have made the transition from the ocean to freshwater lakes for millions of years, as sea level has risen and fallen. Michael Bell, of Stony Brook University, and his colleagues have found a remarkable set of freshwater stickleback fossils from a geological formation in Nevada dating back 10 million years (Bell, Travis, and Blouw 2006). The fossil record is so dense that they have reconstructed 110,000 years of evolutionary history in 10-year slices. Bell and his colleagues measured the armor on the stickleback fossils in order to estimate the long-term history of selection on the animals.

For the first 93,000 years, Bell found sticklebacks with just a few small spines and few armor plates. But then this ancestral phenotype was joined by fully armored sticklebacks with full plates and long spines. Bell suspects that this influx was the result of marine fish being carried into the lake by a flood. For 100 years, the two stickleback forms coexisted in the fossil record. But then the early fish with few spines and armor plates disappeared.

Over the next 17,000 years, the defensive structures in the new fish regressed (**Figure 8.13**). Step by step, its spines got shorter and disappeared. The lateral plates receded. By the end of this period, the new stickleback had come to resemble the earlier form that it had replaced.

The same pattern has occurred among sticklebacks that became isolated in lakes after the last ice age. Heavily armored individuals spread into the freshwater lakes, but then their less armored descendants had more offspring than the heavily armored
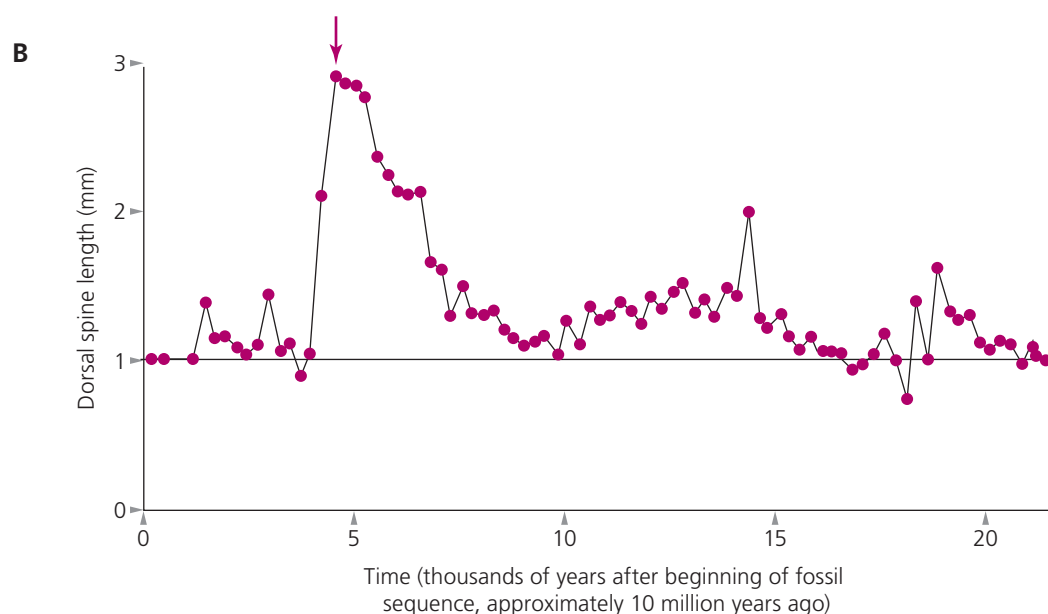
Figure 8.13 A: Sticklebacks have an unusually comprehensive fossil record, and this has let biologists reconstruct the gradual evolution of their form. B: A site in Nevada preserves over 100,000 years of stickleback evolution in a lake from 10 million years ago. This graph shows the size of the dorsal spines on fossils from the last 20,000 years of the sequence. The arrow indicates the sudden arrival of highly armored fish, which most likely came from the ocean where predators favored the selection of armor. These fish replaced the earlier population of sticklebacks in the lake and then gradually lost their spines as well. The same trend occurred in the extent of their armor (data not shown). (Redrawn from Bell et al. 2006.)

ones. The mean level of armor plating thus dropped over time. Today, the sticklebacks in freshwater lakes have fewer spines and drastically reduced lateral plating compared to their closest marine relatives. This evolutionary reduction of defensive weaponry occurred repeatedly in lake after lake.

Dolph Schluter, of the University of British Columbia, and his colleagues study living populations of sticklebacks in Canadian lakes to better understand how natural selection can erode defenses. Without predatory fish in the lakes, growing armor no longer benefits the fish. In fact, it turns out to be very expensive to produce armor in lakes because freshwater has low concentrations of the ions necessary for bone growth. As a result, fish with low-*Eda* alleles have an advantage in freshwater. They

grow to be larger as juveniles, have higher overwinter survival, and begin breeding sooner than fish that have the "complete armor" version of the *Eda* allele.

Taken together, these studies allow scientists to reconstruct the recent history of natural selection in freshwater lakes. The low allele for the *Eda* gene is rare in populations of marine sticklebacks because heavily armored fishes are more likely to survive in an environment with many predators. When marine sticklebacks moved into freshwater lakes, however, their environment changed: it now lacked high densities of predatory fish. Heavily armored fish no longer had a survival advantage, and the cost of growing spines and plates meant that they could not grow as fast as other fish. The low allele for the *Eda* gene, which once lowered fitness in marine sticklebacks, now raised it in the predator-free lakes. The allele spread, and the average number of lateral armor plates dropped.

By comparing the low-*Eda* allele in different stickleback populations, Schluter found that it is quite old. (We'll discuss how scientists can estimate the age of alleles in the next chapter.) At least 2 million years ago, the low-*Eda* allele arose in the marine ancestors of freshwater sticklebacks. It managed to linger in the stickleback population at low frequency until some fishes colonized lakes. Once the sticklebacks were in the new habitat, the allele was strongly favored by natural selection. (We saw in Chapter 6 that when recessive alleles are rare in a population, they are largely invisible to selection, enabling them to persist for a very long time.)

One final piece completes this story: an exception that, in effect, proves the rule. The sticklebacks in Lake Washington, near Seattle, have full armor. Daniel Bolnick, a University of Texas biologist, and his colleagues wondered why these sticklebacks should differ so much from those in other lakes (Kitano et al. 2008). They discovered that this shift in armor happened very recently. Fish collected in the late 1950s had the reduced armor typical of other lake sticklebacks. Within the following 40 years, the sticklebacks in Lake Washington changed. They rapidly evolved back toward a fully armored form.

Bolnick argues that the solution to this paradox lies in the government regulations that have reduced pollution in Lake Washington over the past few decades. Trout that have been introduced into the lake can now see the sticklebacks more easily in the clear water and can attack them. This increase in predation can be dated to the 1970s. It also coincides with the beginning of the evolutionary reversal in stickleback morphology.

Key Concept

Sometimes multiple populations independently experience the same change in their selection environment. These populations are ideal for evolutionary studies because they act like replicated natural experiments. The nature of the evolutionary response can be observed for each population and compared across the different populations.

8. 6 Drinking Milk: A Fingerprint of Natural Selection

If your ancestors hail from Western Europe, chances are you can digest milk. If you're Chinese, chances are you can't. It turns out that the difference is in part the result of natural selection on humans over the past few thousand years.

Humans are mammals, and one of the hallmarks of living mammals is the production of milk. Milk is rich in a sugar called lactose, and young mammals produce an enzyme called lactase to break it down into simpler sugars they can digest. Around the time young mammals are weaned, they typically stop producing lactase in their guts because they stop drinking milk. Natural selection should favor this shift, since it means that mammals don't waste energy making an enzyme with no advantage.

About 70 percent of humans also stop producing lactase in their intestinal cells during childhood. As a result, they can digest milk when they're young, but they have a difficult time with it when they're adults. Lactose builds up in their guts, spur-

A

North West → South East

Frequency of lactose persistence allele (*L/CT*P*) in population

Swedish, Danes, Irish, British, Finland Swedish spkers, Germans-NW, Czechs, Swiss, Finland Finnish spkers, Austrians, Germans-SW, French-north, Spanish, Estonians, Slovenians, Hungarians, Polish, Lapps, French-south, Kitdin Saami, Komi Permiak, Italians-north, Greeks, Russians, Roma/Sinti, Italians-south, Sicilians, Turks

B

Milk drinkers
Others

Frequency of lactose persistence allele (*L/CT*P*) in population

Bedouin, Other, Sinai Desert, Other, Beja groups, Baggara, Dinka, Tutsi, Hutu, Tuareg, Fulani/Fuelbe, Yoruba, Bantu grous

Jordan, Egypt, Sudan, Uganda/Rwanda, Niger, Nigeria/Senegal, South Africa

Figure 8.14 A: Human populations differ in lactose tolerance, due in part to the presence of a mutant allele of the lactase gene (*LCT*) that causes lactase to persist from infancy through to adulthood. European populations differ widely in the relative frequency of this lactase persistence allele (shown ranked in decreasing order of allele frequency, illustrating the North/South and West/East clines). B: Comparison of allele frequencies in different Arab and African cultural groups, showing milk-drinking pastoralists and non-milk-drinkers from neighboring communities. The lactase persistence allele (*LCT*P*) occurs in higher frequencies in groups with a cultural tendency to drink milk. (Modified from Swallow 2003.)

ring the rapid growth of bacteria that feed on the sugar. The waste released by the bacteria causes indigestion and gas. In about 30 percent of people, however, cells in the gut continue to produce lactase into adulthood. These people can consume milk and other dairy products without any discomfort because they can break down the lactose, leaving less of the sugar for the gas-generating bacteria to feed on. The difference between lactose-tolerant and lactose-intolerant people is largely due to alleles of the lactase gene, *LCT* (Swallow 2003).

To understand how 30 percent of people ended up with alleles for lactose tolerance, we must take a look at the history of cattle. Starting about 10,000 years ago, humans began to domesticate cattle in northwest Europe, East Africa, and certain other regions, leading to a dramatic change in their diet. Now energy-rich milk and milk-based foods were available well into adulthood.

The geography of lactose tolerance matches the geography of domestication fairly well. **Figure 8.14A** shows how an *LCT* allele for lactose tolerance (called *LCT*P*) is most common today in northwest Europe—where cattle were domesticated in Europe—and rarest in southeast Europe, the farthest point from that origin. Scientists have also compared the frequency of the allele in traditional milk-drinking soci-

Adaptive mutation arises   Positive selection
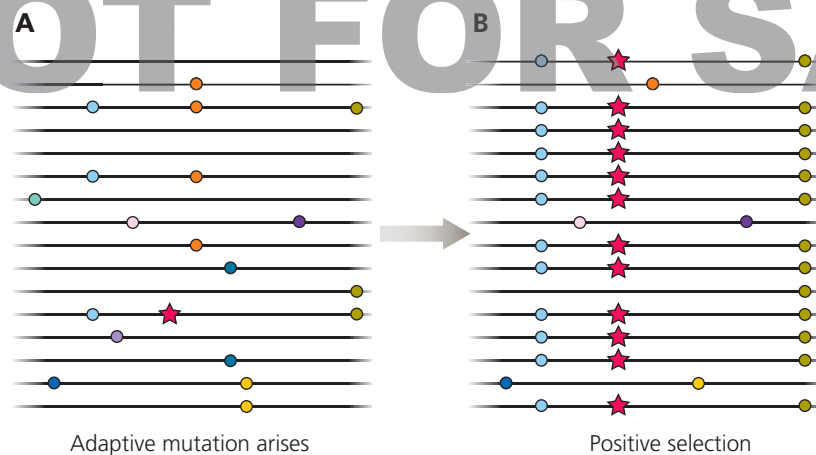
Figure 8.15 Scientists can detect the signature of natural selection in an allele by comparing its neighboring alleles in different individuals. In the absence of natural selection, recombination will separate neighboring alleles over the course of many generations. But strong natural selection favoring one allele will spread its entire neighborhood to high frequencies in a population. A: Each line represents a segment of DNA of one individual in the population. Circles represent nucleotide bases unique to that individual. A new mutation (red star) arises in one individual and raises its fitness. B: The same population, a number of generations later. Individuals who inherited a segment of DNA with the new mutation had higher fitness. The mutation increased in frequency, carrying along its neighboring DNA. As a result, this particular recombinant will be unusually abundant in the population.
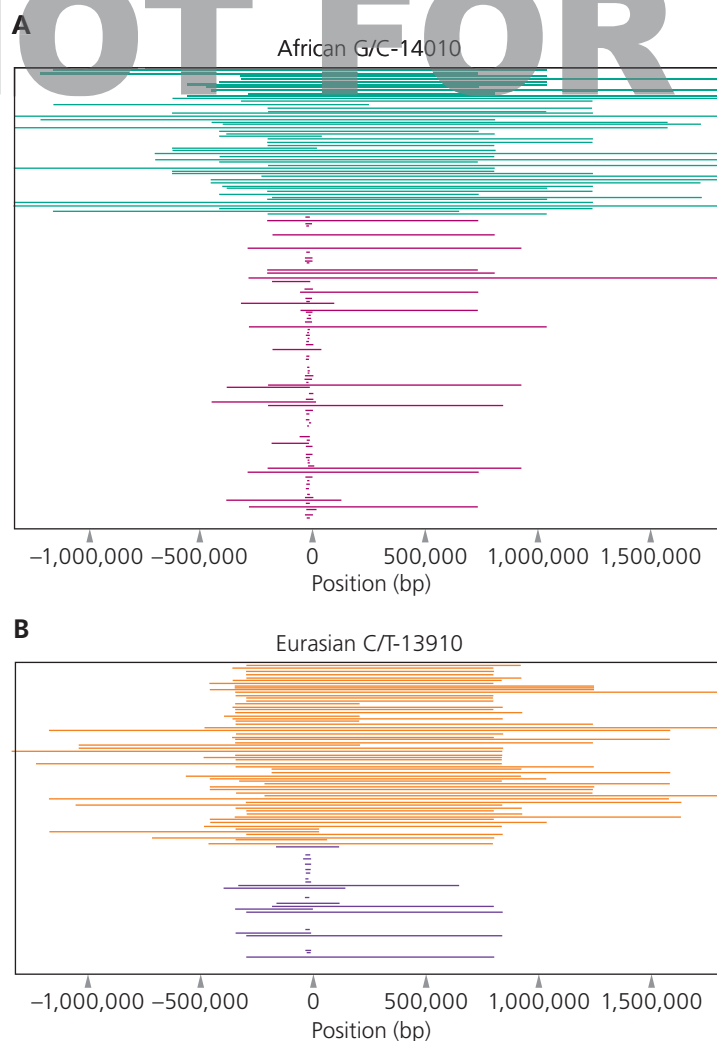
eties and non-milk-drinking ones in the same countries (**Figure 8.14B**). *LCT*P* is generally much more common in the milk drinkers (Swallow 2003). If *LCT*P* had spread thanks merely to genetic drift, we would not expect such a strong association between the presence of both cattle herding and the allele. Instead, this pattern points strongly to natural selection.

Scientists have found another line of evidence in favor of natural selection (versus random genetic drift) by comparing the DNA of individuals in milk-drinking societies. Every time parents produce new gametes, their chromosomes swap chunks of DNA through recombination (Chapter 5). If a new allele arises through a mutation, it's passed down from one generation to the next with some surrounding DNA—a process known as hitchhiking. Over time, as chromosomes are cut and swapped again and again, an allele remains in close physical proximity to fewer and fewer of its original neighbors. The physical proximity of the alleles at different loci is known as **genetic linkage**. The closer a neighboring region of DNA is to the mutation, the longer it is likely to remain linked to that particular mutation. But eventually, even closely linked alleles will become increasingly separated through recombination.

Genetic linkage: The physical proximity of alleles at different loci. Genetic loci that are physically close to one another on the same chromosome are less likely to be separated by recombination during meiosis, and are thus said to be genetically linked.

Selective sweep: Strong selection can "sweep" a favorable allele to fixation within a population so fast that there is little opportunity for recombination. In the absence of recombination, large stretches of DNA flanking the favorable allele will also reach high frequency.

Natural selection can counter this dispersion, by causing a **selective sweep**. An allele experiencing strong natural selection spreads quickly through a population, faster than recombination can separate it from the nearby regions of the genome. As a result, strongly selected alleles frequently will be found in a population surrounded by the same set of alleles at neighboring locations (**Figure 8.15**). Researchers have looked for this signal of natural selection around the *LCT* gene in two milk-drinking populations: East Africans and Europeans. The results are shown in **Figure 8.16**. Strong natural selection has preserved large segments of homologous DNA around *LCT*. Significantly, however, a different allele was favored by natural selection in each population. In other words, a mutation arose independently in each population that conferred lactose tolerance and then spread rapidly in both continents (Tishkoff et al. 2007).

We can combine this evidence to come up with a hypothesis for the origin of lactose tolerance. Originally, humans had an *LCT* allele that stopped producing lactase after nursing. Sometimes mutations gave rise to *LCT* alleles conferring lactose tolerance in adults, but they did not raise fitness because feeding on milk as adults was rare. In cattle-herding cultures, however, milk was plentiful, and the ability to digest

A

African G/C-14010

−1,000,000 −500,000 0 500,000 1,000,000 1,500,000
Position (bp)

B

Eurasian C/T-13910

−1,000,000 −500,000 0 500,000 1,000,000 1,500,000
Position (bp)

Figure 8.16 A: Sarah Tishkoff of the University of Pennsylvania and her colleagues examined genetic linkage in Africans to detect natural selection around *LCT*. They compared 123 people from Kenya and Tanzania with an allele for lactose tolerance and one for intolerance. The people with the lactose tolerance allele (green lines) share much larger segments of homologous DNA around the gene, represented by the length of lines, than those with the alternative lactose intolerant allele (red lines).

B: Working with 101 people of European and Asian descent, Joel Hirschhorn of Harvard and his colleagues also found that an allele for lactose persistence was surrounded by large swaths of homologous DNA (orange lines). Note that the mutations for these two alleles are located in different parts of the same gene. They are lined up in this graph simply to show the different sizes of the hitchhiking regions. (Adapted from Tishkoff et al. 2007.)
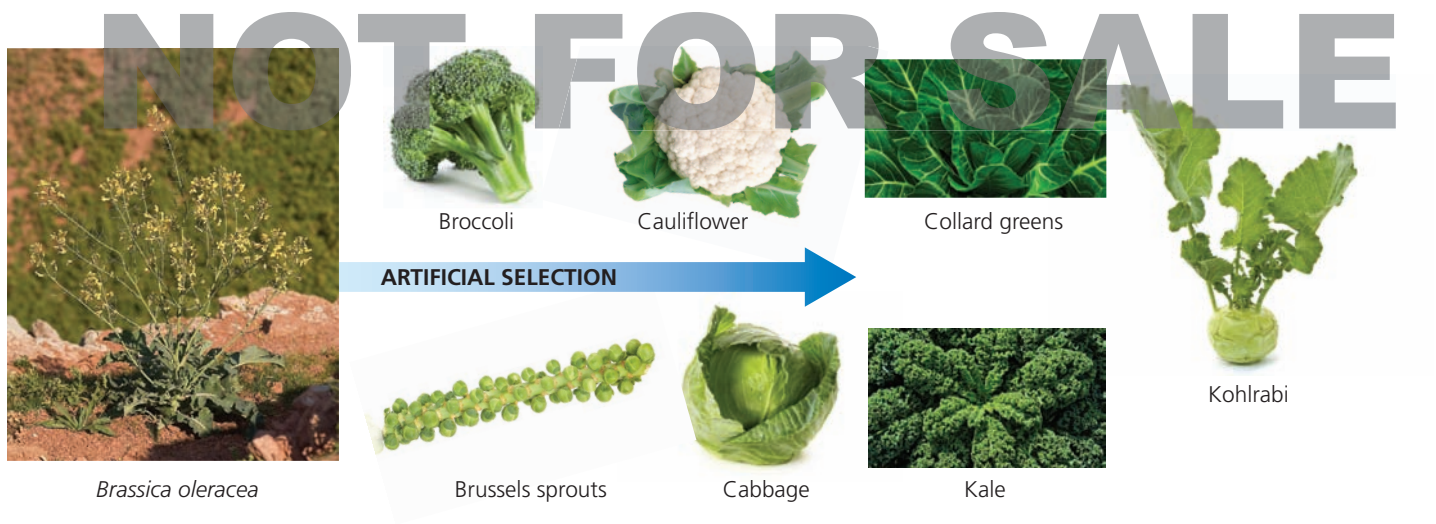
milk brought huge benefits. People who could get protein and other nutrients from milk were more likely to survive and to pass on their mutant copy of *LCT* to their offspring.

8.7 Humans as Agents of Selection

The agents of selection we've encountered so far in this chapter include predators, parasites, and new kinds of food. But we humans are powerful agents of selection as well. Human-driven selection had its first huge impact on the world about 10,000 years ago, when we domesticated plants and animals (Doebley 2006).

The early stages of domestication may have started inadvertently. Wild wheat plants, for example, grow seeds that break away through a process called shattering. In the wild, a mutation that causes wheat to fail to shatter is deleterious because the seeds remain trapped on their parent plants and germinate less often. People began to gather wheat plants, preferring the ones that failed to shatter because the seeds were still attached. They may have planted some of the seeds near their settlements. As a result, they inadvertently began to select for reduced shattering. Thousands of years later, people began to raise the plants on large-scale farms and to consciously select certain plants to breed (Diamond 2002, Doebley 2006).

Regardless of whether these early episodes of artificial selection were incidental or deliberate, the impacts were dramatic. Wheat plants have many traits not found

Broccoli   Cauliflower   Collard greens

ARTIFICIAL SELECTION

Kohlrabi

*Brassica oleracea*   Brussels sprouts   Cabbage   Kale

Figure 8.17 Artificial selection on wild cabbage (*Brassica oleracea*) resulted in the evolution of diverse plant forms, including broccoli, cauliflower, brussels sprouts, cabbage, collard greens, kale, and kohlrabi.

in their wild relatives. Their seeds ripen simultaneously, grow in tight bunches at the end of branches, and don't shatter—all traits making them easier to harvest (Zeder et al. 2006). Domestic animals underwent a similar transformation. Humans selected behavioral traits in their livestock, such as increased tolerance to penning, increased sexual precocity, and reduced wariness and aggression (Clutton-Brock 1999). Sometimes the same wild species was subsequently selected in many different directions. Wild cabbage (*Brassica oleracea*) was selected for its leaves (cabbage, kale), stems (kohlrabi), flower shoots (broccoli, cauliflower), and buds (brussels sprouts).

Figure 8.18 Domesticated crops and their closest wild relatives are separated by dramatic differences in morphology. Top left: Teosinte (left), from which maize was developed, grows multiple stalks and long branches. Maize, by contrast, grows only a single stalk. The ears on teosinte and maize plants (insets) are also different. Kernels grow naked on the surface of maize, while teosinte grains are enclosed in a triangular casing. Top right: Wild rice (left) shatters easily. Cultivated rice (right) resists shattering. Bottom left: A massive cultivated tomato and the small fruit of its wild progenitor. Bottom right: A wild sunflower plant (left) has many small heads borne on multiple slender stalks, whereas a cultivated sunflower plant (right) has a single large head borne on a thick stalk. (Adapted from Doebley, Gaut, and Smith 2006.)
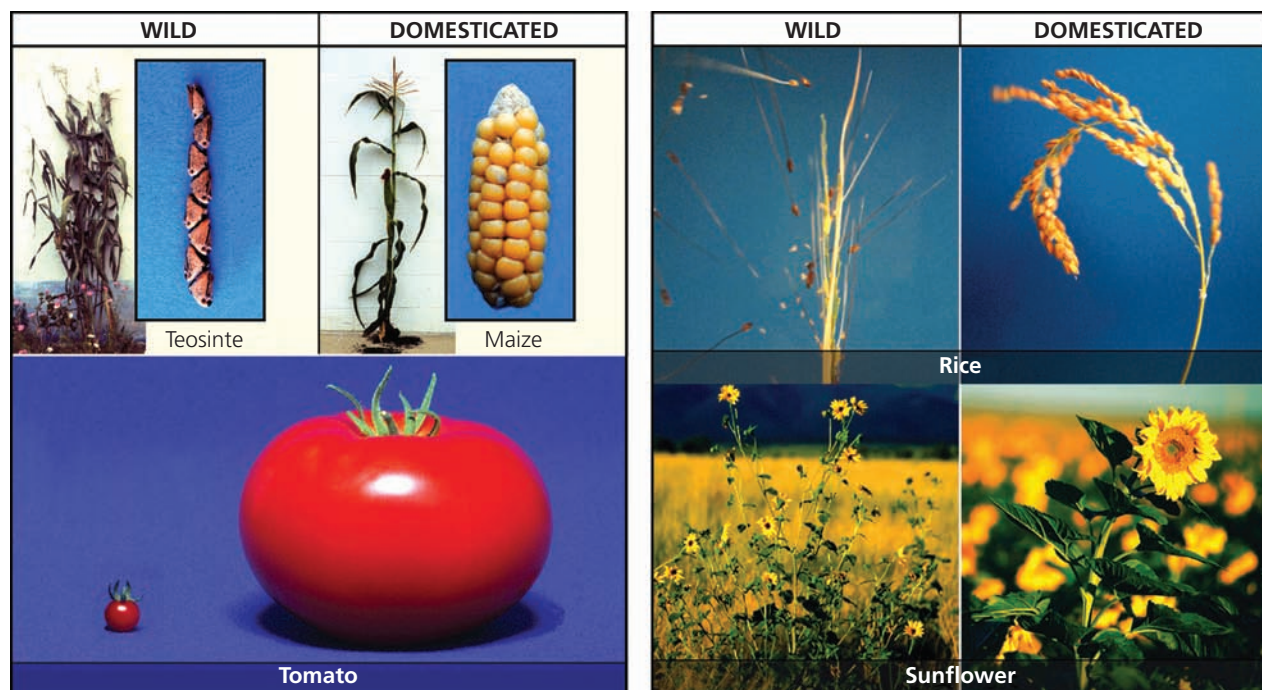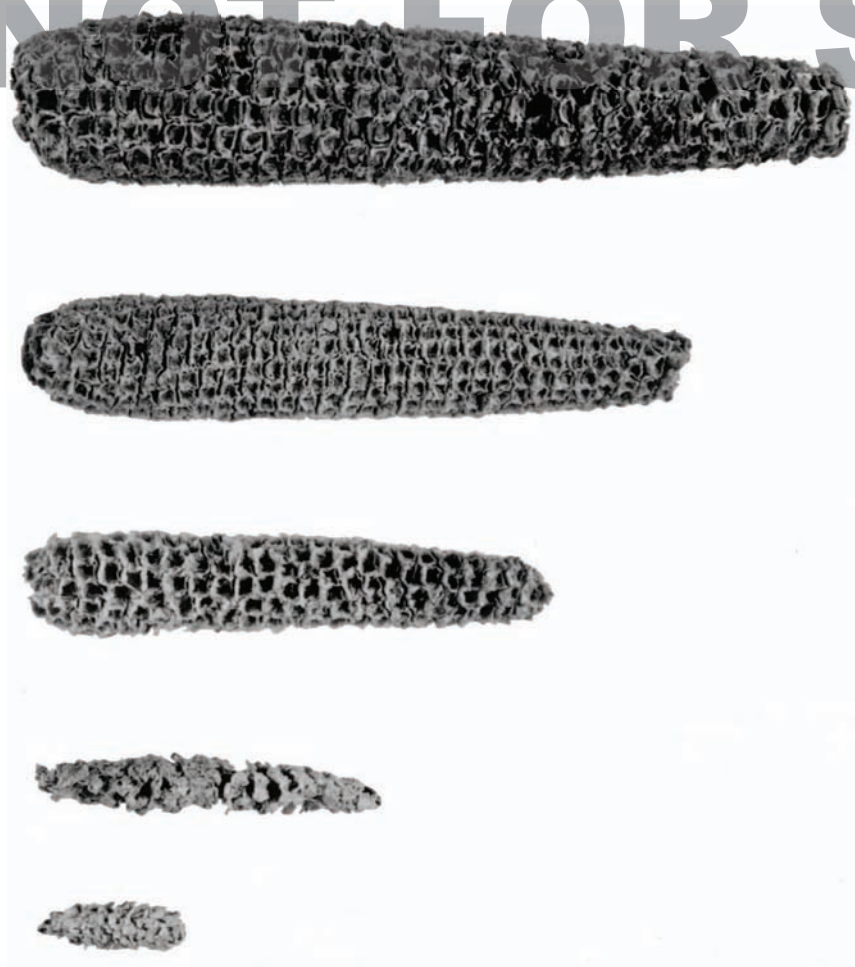
Figure 8.19 Archaeologists have uncovered discarded maize cobs from sequential periods of occupation of Tehuacán, Mexico—the oldest cob is at the bottom in this figure. These specimens document the gradual evolutionary increase of kernel number and cob size.

In recent years, scientists have been able to use genetic tools to reconstruct the evolutionary steps that some crops took from their wild ancestors (Bruford, Bradley, and Luikart 2003; Zeder et al. 2006). One of the best characterized of these events is the evolution of maize. Approximately nine thousand years ago, farmers in the Balsas River Valley of southern Mexico began selectively planting and harvesting individuals of a streamside plant called teosinte. Teosinte was taller and broader leaved than most grasses, and people collected their seed heads for food. All modern maize appears to have descended from this original domestication event (Doebley 2004).

After domesticating teosinte, farmers continued to select for advantageous traits for thousands of years. Archeologists have documented the evolutionary response of maize to artificial selection by unearthing ancient cobs (**Figure 8.19**). By 5500 years ago, cobs had already increased in the number of rows of kernels and in kernel size. Analysis of allelic diversity in these early cobs suggests that by 4400 years ago, early maize had lost almost 30 percent of the allelic diversity originally present in wild teosinte populations. Such loss of variation is indicative of strong selection and a genetic bottleneck (Chapter 6), as would be expected if selective harvesting entailed breeding only a small subset of the wild population (Jaenicke-Després et al. 2003).

John Doebley of the University of Wisconsin and his colleagues identified mutations of major effect to three genes that contribute to the evolved morphology of maize. One of them (*teosinte branched 1*) carries a maize variant that represses the growth of lateral meristems. It helps give rise to fewer branches on maize compared

Figure 8.20 Centuries of artificial selection have influenced the size, shape, and behavior of domesticated dogs. Recent genetic studies are identifying some of the genes that appear to have contributed to diversity in dog morphology. A: Sutter et al. (2007) showed that an allele of the *IGF1* gene contributes to small body size. B: Akey et al. (2010) found that *HAS2* is associated with skin wrinkling. C: Shearin and Ostrander (2010) identified alleles of three genes that affect coat properties: *RSPO2* is associated with wiry hair and moustaches, *FGF5* alleles cause long or short fur, and *KRT71* alleles lead to curly or straight hair.

to teosinte. A second gene, *prolamin box binding factor,* is involved in the production of seed storage proteins in the kernels. A third gene, *sugary 1,* encodes an enzyme that alters the properties of starch in the kernels in ways that affect the textural properties of tortillas (Jaenicke-Després et al. 2003).

A similarly impressive history of human-caused evolution occurred with the domestication of dogs. Genetic studies pinpoint the origin of domestic dogs to East Asia at least 15,000 years ago, when people began to tame small subsets of the ancestral population of gray wolves. Early domestication appears to have involved primarily selection for behavior. Dogs, unlike wolves, can understand humans surprisingly well. They can, for example, recognize that a pointed finger indicates something they should pay attention to.

A more recent phase of domestication occurred in the past few centuries as people began selecting for a variety of morphological and physiological traits associated with hunting or recreational tasks. Today, there are more than four hundred recognized breeds, and dogs exhibit more phenotypic variation than any other species (Vilà et al. 1997; Cruz, Vilà, and Webster 2008). As in the case of maize, researchers are beginning to identify the genetic changes responsible for these remarkable evolutionary transformations in form (**Figure 8.20**).

As dog breeders selected for certain alleles, many deleterious mutations got swept along for the ride. Under natural circumstances, these mutations would likely have reduced individual performance and fitness. As a result, purebred dogs today are faced with an inordinate frequency of genetic maladies (Cruz et al. 2008).

Chemical Warfare

When humans domesticated crops, they created a new food supply not only for themselves, but also for huge hordes of insects. The very traits that farmers favored in plants—a failure to shatter, large seeds, and a tightly synchronized life history—made their crops an ideal source of nutrition for many species of pests. These insects already had an impressive capacity for rapid growth and reproduction, and once we provided them with a banquet of crops, their numbers exploded. Swarms of pests besieged the fields, laying waste to entire farms. The battle between humans and insects was on.

Farmers searched for ways to fight off pests. Some of their attempts seem laughable today. Roman farmers believed that rubbing trees with green lizard gall could repel caterpillars, and that nailing a toad to a barn door could scare weevils away from

stored grain. But early farmers also stumbled across chemicals that were effective at warding off insects. For example, 4500 years ago in the ancient empire of Sumer, farmers put sulfur on their crops. Early Europeans learned to extract chemicals from plants, and by the nineteenth century, farmers had a fairly extensive arsenal of pesticides for killing insects.

Around 1870, a tiny Chinese insect turned up in farm fields around the city of San Jose, California. The creature would inject a syringe-like mouthpart into a plant and suck up the juices. The San Jose scale, as the insect came to be known, spread quickly through the United States and Canada, leaving ravaged orchards in its path. Farmers found that a mixture of lime and sulfur was most effective against the scale. After a few weeks of spraying, the San Jose scale would disappear. By 1900, however, the lime-sulfur cure was failing. Here and there, the San Jose scale returned to its former abundance.

An entomologist named A. L. Melander found some San Jose scales living happily under a thick crust of dried lime-sulfur spray. Melander embarked on a widespread experiment, testing out sulfur-lime on orchards across Washington State (Melander 1914). He found that in some orchards, the pesticide wiped out the insects completely. In other orchards, as many as 13 percent of the scales survived. But those surviving scales could be killed off with kerosene.

Melander wondered why some populations of scales were becoming able to resist pesticides. Could the lime-sulfur spray trigger a change in their biology, the way manual labor triggers the growth of calluses on our hands? Melander doubted it. After all, 10 generations of scales lived and died between sprayings. The resistance must be hereditary, he reasoned. He sometimes would find families of scales still alive amidst a crowd of dead insects.

This was a radical idea at the time. Biologists had only recently rediscovered Mendel's laws of heredity (page 140). They talked about genes being passed down from one generation to the next, yet they didn't know what genes were made of yet. But they did recognize that genes could spontaneously change—mutate—and in so doing alter traits permanently.

In the short term, Melander suggested that farmers switch to fuel oil to fight scales, but he warned that they would eventually become resistant to fuel oil as well. In fact, the best way to keep the scales from becoming entirely resistant to pesticides was, paradoxically, to do a bad job of applying those herbicides. By allowing some susceptible scales to survive, farmers would keep the susceptible genes in the scale population.

Unfortunately, Melander's prophetic words appear to have fallen on deaf ears. Today, 12 percent of all the ice-free land on Earth is farmed, and farmers apply pesticides and herbicides across this vast expanse of cropland. When farmers apply a new chemical pesticide to a field, they kill a large proportion of its vulnerable population of pests. This die-off produces strong selection on the insect. Individual insects with mutations for biochemical mechanisms enabling them to survive, to somehow detoxify the chemical poison, do very well. They live, while most of their competitors do not. There is more food for these survivors to eat, boosting their survival and fecundity. As they propagate themselves, they populate subsequent generations of the pest population with offspring who are also resistant to the pesticide, and alleles conferring resistance spread. The large size of insect populations can produce substantial genetic variation. When the intense selection of pesticides is applied to the insects, resistance can evolve rapidly.

It takes only a few years, in fact, for resistance to a new pesticide to emerge. As of 1990, there were over five hundred species of pest insect known to be resistant to at least one pesticide (**Figure 8.22**). Farmers often have to apply more of a pesticide to control resistant pests; today, farmers in the United States spend $12 billion on pesticides (Palumbi 2001a). Many species are now resistant to so many pesticides that they are impossible to control, and up to a third of farm production is lost to pest damage (Palumbi 2001b). The evolution of resistance also poses a risk to public health because the high concentrations of pesticides can contaminate groundwater and streams.

Figure 8.21 When farmers spray their fields with either pesticides or herbicides, these chemicals act as agents of selection on the affected populations.
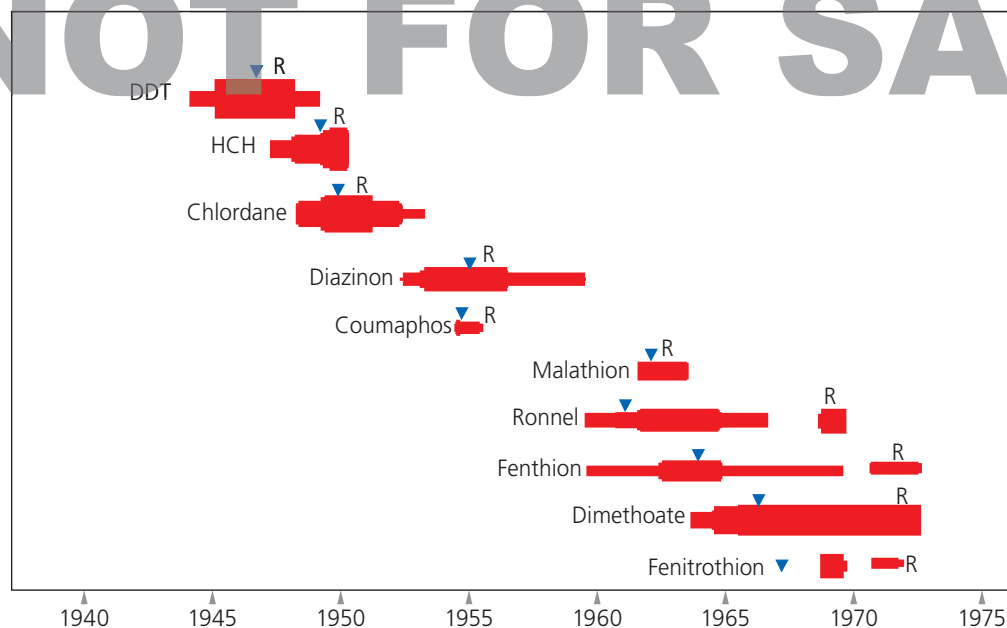
Figure 8.22 Evolution of resistance to insecticides by houseflies on Danish farms. The width of each bar reflects the extent of use, the inverted triangle symbol the date of the first confirmed case of resistance of a given insecticide, and the letter *R* the date when most populations were resistant. (Redrawn from Wood and Bishop 1981.)

Insects are not the only organisms that can make life difficult for farmers. Weeds can invade farm fields and outcompete crop plants for space. On large farms, pulling weeds out of the ground is simply not practical. So farmers fight weeds by spraying their fields with chemicals known as herbicides, which can kill plants. Once the weeds are dead, the farmers can plant their crops. Yet time and again, weeds have evolved resistance to herbicides, just as insects have evolved resistance to pesticides (Heap 1997, Powles and Yu 2010; **Table 8.1**).

One of the latest failures of herbicides involves the chemical glyphosate, which the company Monsanto sells under the brand name Roundup. Glyphosate kills weeds by blocking the construction of amino acids that are essential for the survival of plants. It attacks an enzyme called EPSPS that only plants use, with the result that it's harmless to people, insects, and other animals. And unlike other herbicides that wind up in groundwater, glyphosate stays where it's sprayed, degrading within weeks (Powles and Yu 2010).

In 1986, Monsanto scientists improved the performance of glyphosate on weeds by engineering crop plants to be resistant to glyphosate. They did so by inserting genes from bacteria that could produce amino acids even after a plant was sprayed with herbicides. In the 1990s Monsanto began to sell glyphosate-resistant corn, cotton, sugar beets, and many other crops. The crops proved hugely popular. Instead of applying a lot of different herbicides, farmers found they could hit their fields with a modest amount of glyphosate alone, which wiped out weeds without harming their crops. Studies indicate that farmers who used these transgenic crops used fewer herbicides than those who grew regular plants—77 percent less in Mexico, for example—while getting a significantly higher yield from their fields.

For a while, it seemed as if glyphosate would avoid Melander's iron rule. Monsanto scientists ran tests that showed no evidence of resistance. But after glyphosate-resistant crops had a few years to grow, farmers began to notice horseweed and morning glory encroaching once more into their fields. Some farmers had to cut down fields of cotton rather than harvest them, because of infestations of a weed called Palmer amaranth. Other farmers had to abandon glyphosate and turn back to older, more toxic herbicides.

A century ago, Melander could study the evolution of resistance only by observing which insects lived and died. Today, scientists can pop the lid off the genetic toolbox that insects and weeds use to resist chemicals. What's striking is how many

TABLE 8.1 Evolution of Resistance to Herbicides

Herbicide	Year deployed	Resistance observed
2,4–D	1945	1954
Dalapon	1953	1962
Atrazine	1958	1968
Picloram	1963	1988
Trifluralin	1963	1988
Triallate	1964	1987
Dicloflop	1980	1987

Table 8.1 It took as little as seven years for scientists to observe evolution of resistance in plants in response to herbicides. This kind of rapid evolution has also been observed with antibiotics and pathogens (Chapter 18). (Modified from Palumbi 2008.)

different ways weeds have found to overcome glyphosate. Scientists had thought that glyphosate was invincible in part because the enzyme it attacks, EPSPS, is similar in all plants. That uniformity suggests that plants can't tolerate mutations to it. But it turns out that one mutation, which has independently turned up in many populations of ryegrass and goosegrass, changes a single amino acid in EPSPS. The plant can still survive with this altered enzyme. And glyphosate has a hard time attacking the altered form of EPSPS thanks to its different shape.

An entirely different strategy evolved in Palmer amaranth to overcome glyphosate: one based on overwhelming the herbicide with sheer numbers. The plants make the ordinary, vulnerable form of EPSPS; but through gene duplication, they have acquired many extra copies of the *EPSPS* gene—up to 160 extra copies in some populations. All those extra genes make extra copies of the enzyme. While the glyphosate may knock out some of the EPSPS in the Palmer amaranth, it cannot knock out all of them. The plants make so much more enzyme that they can go on growing.

Even in the twenty-first century, natural selection can still defeat the most sophisticated genetic engineering. But the easy evolution of resistance does not mean that the plight of farmers is hopeless. The case of a pesticide known as Bt demonstrates how effectively farmers can manage evolution, if they understand how it works.

Bt actually refers to crystalline protein toxins produced by a family of genes (*Cry* genes) in a bacteria called *Bacillus thuringiensis.* The bacteria produce the toxic crystals when they sporulate; and, when ingested by susceptible insects, the toxins bind to receptors in the insects' gut and make them sick. For decades farmers have sprayed Bt on crops. Among its attractions is its short life. It rapidly breaks down in sunlight, and so it does not create dangerous groundwater pollution. More recently, scientists developed genetically modified crops that carried the *Bt* gene. When farmers plant these crops, the plants make their own pesticide.

Figure 8.23 Ryegrass (A), goosegrass (B), and Palmer amaranth (C) evolved mechanisms to overcome the glyphosate in Roundup. In ryegrass and goosegrass, an altered form of the EPSPS enzyme evolved. Palmer amaranth, on the other hand, produces more of the original form of EPSPS.

When Bt was applied to cotton and to other crops, Bruce Tabashnik of the University of Arizona and other researchers warned that insects might evolve a resistance to the toxin (Tabashnik et al. 2008). In a field planted with Bt-treated crops, insects that could resist Bt were able to flourish. But the scientists pointed out that farmers could slow the rise of resistance by creating Bt-free "refuges" on their farms.

Tabashnik and his colleagues based this prediction on the fact that resistance mutations come at a cost. As we saw with sticklebacks, insects have a finite supply of resources that they can invest in physiological processes. If an insect is genetically programmed to put extra resources into resisting a pesticide, it has fewer resources to invest in other activities, such as growth and reproduction. In a field without Bt, a Bt-resistant insect is therefore at a disadvantage compared to susceptible insects. In a field with Bt, the cost of Bt resistance is outweighed by its benefits, and the resistant insects take over.

If farmers planted nothing but Bt-producing crops, they could drive the rapid evolution of Bt-resistant insects and make their genetically modified crops useless. Tabashnik and his colleagues suggested that farmers plant a few of their fields with ordinary crops instead. In these refuges, Bt-resistant insects would be outcompeted by other insects that didn't invest so much in detoxifying Bt. The insects from the Bt-producing fields and the refuges would interbreed, and their offspring would inherit some genes for Bt susceptibility.

Several years after Bt crops were introduced, Bt-resistant insects began to appear in significant numbers. In 2008, Tabashnik and his colleagues surveyed the rise of resistance. In states with large areas of refuge, resistance evolved much more slowly than in states with small areas of refuge. The farmers had carried out a giant experiment in evolution, and it had turned out as the evolutionary biologists had predicted. Today, farmers using Bt corn are required by law to set aside 20 percent of their crop area as a Bt-free refuge, and farmers planting Bt cotton must set aside 50 percent of their crop area as refuge (Cullen, Proost, and Volenberg 2008).

Altered Environments and Invasive Species

Along with domestication and chemical resistance, humans have also influenced selection on many other kinds of species. By building cities, for example, we have favored animals and plants that can survive in urban environments instead of the rural ones that existed beforehand. In southern France, scientists have documented this urban selection acting on a small flowering plant called *Crepis sancta* (Cheptou et al. 2008). Populations of the flower grew in the countryside, while others grew in Marseille, colonizing the patches of ground around trees planted along the streets. The scientists examined the plants that grew in a part of the city that had been paved in the early 1990s.

C. sancta can make two different kinds of seeds—one that can drift off in the wind, and another that simply drops to the ground. The scientists hypothesized that in Marseilles, wind-carried seeds would be a burden to plants because they would be likely to land on the pavement instead of the ground. Dropped seeds would have a better chance of surviving because they'd fall onto the patch of ground where the parent plants grew.

To test their hypothesis, the scientists raised *C. sancta* from Marseilles in a greenhouse alongside *C. sancta* from the countryside. Under the same conditions, the scientists found that the city plants were making 4.5 percent more nondispersing seeds than the ones in the countryside.

The scientists estimated that about 25 percent of the variation in the ratio of the two types of seeds is controlled by genetic differences. With these levels of heritability and selection, it should have taken about 12 generations to produce the observed change of 4.5 percent in the seed ratio. As predicted, about 12 generations of plants have lived in Marseilles since the sidewalks were built. Without intending it, humans

created a new environment for these plants, which are now adapting to it. As more time passes, the city plants may continue to make more dropping seeds and fewer windborne ones.

We humans not only change the habitats of many species, we can also move species to new habitats. In some cases, we move them intentionally. Potatoes, for example, were domesticated thousands of years ago in Peru and then introduced into Europe in the sixteenth century. In other cases, the introductions to new habitats occur by accident. Ships take up ballast water when they begin their voyages and then dump it when they arrive at their destination. In that ballast water may be a vast number of exotic animals, plankton, and bacteria.

Figure 8.24 Cane toads (*Bufo marinus)* were introduced to eastern Australia (A) in the 1930s and have expanded steadily and rapidly since that time (B). Toads are rapidly evolving to smaller body sizes in these new habitats (C). Native snakes (D) are killed by toxins in skin glands of cane toads, and these predators also are evolving rapidly in response to this introduced species. (Redrawn from Phillips and Shine 2005.)
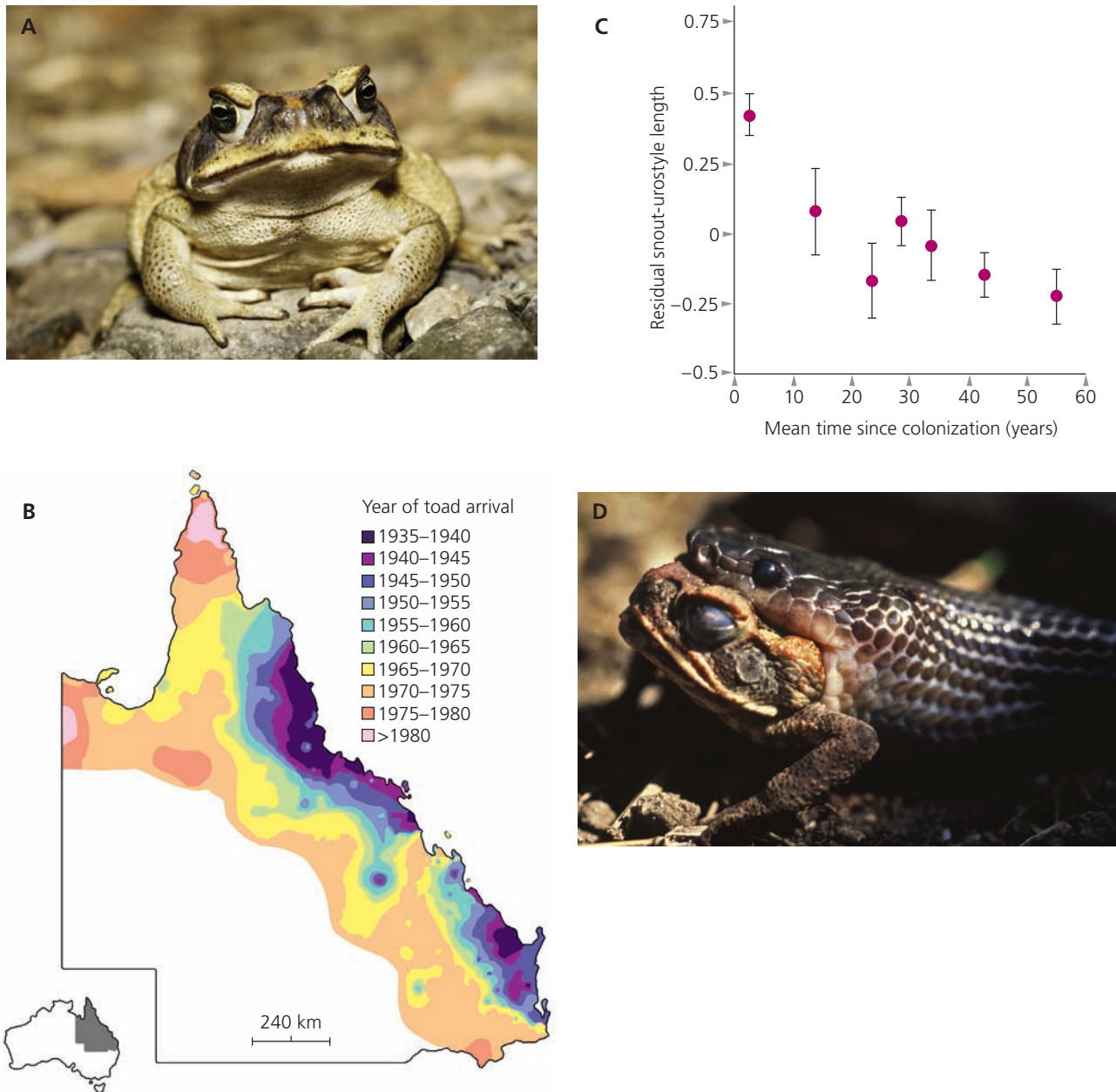
Most relocated species die off. Others, however, are able to persist, and in some cases to spread. Invasive species often undergo strong directional selection for adaptations to their new habitat. Both the invader species and the native species in their path may rapidly evolve. For example, cane toads (*Bufo marinus*) were introduced to Australia in the 1930s to control insect pests in sugarcane fields. The introduction was a disaster (Phillips and Shine 2005). Instead of controlling farm pests, the frogs fed on harmless animals—even small mammals. Native predators that attacked the new prey got an awful surprise. Cane toads exude a milky poison from large glands behind their eyes, and it is toxic to many animals including humans and dogs.

Ben Phillips and Richard Shine, two biologists at the University of Sydney in Australia, have shown that toad lineages responded to altered patterns of selection in this new environment by rapidly evolving smaller body sizes and smaller gland sizes (Phillips and Shine 2005). Relatively long legs also evolved. With these longer legs, the cane toads moved faster, and they expanded their range in Australia at a faster rate (Phillips et al. 2006).

The cane toads are also strong agents of selection on their predators—native Australian snakes, overall, have become larger since cane toads were introduced. The scientists propose that larger body size raises the fitness of the snakes because it lowers the concentration of toxin they ingest when they attack a cane toad. Bigger snakes are thus more likely to survive a given dose of toxins. Phillips and Shine also found evidence that smaller gape widths evolved in the snakes. Snakes with smaller gape widths cannot swallow the biggest toads—which are also the most toxic and thus most likely to kill the snakes (Phillips and Shine 2004).

Hunting and Fishing as Agents of Selection

To feed ourselves, we humans not only farm much of the world's arable land, we also hunt wild animals on land and catch fish at sea. As the world's human population has grown, and as technology has grown more sophisticated, our harvest has increased dramatically. As we'll see in Chapter 14, hunting and fishing are endangering a number of species. But they're also exerting selection on many populations. That's because this harvesting of wild animals is not random. Individuals with certain traits are more likely to be killed than others.

Hunting and fishing have an evolutionary effect that's the opposite of domestication. Farmers select individual plants to breed because they have desirable traits. But
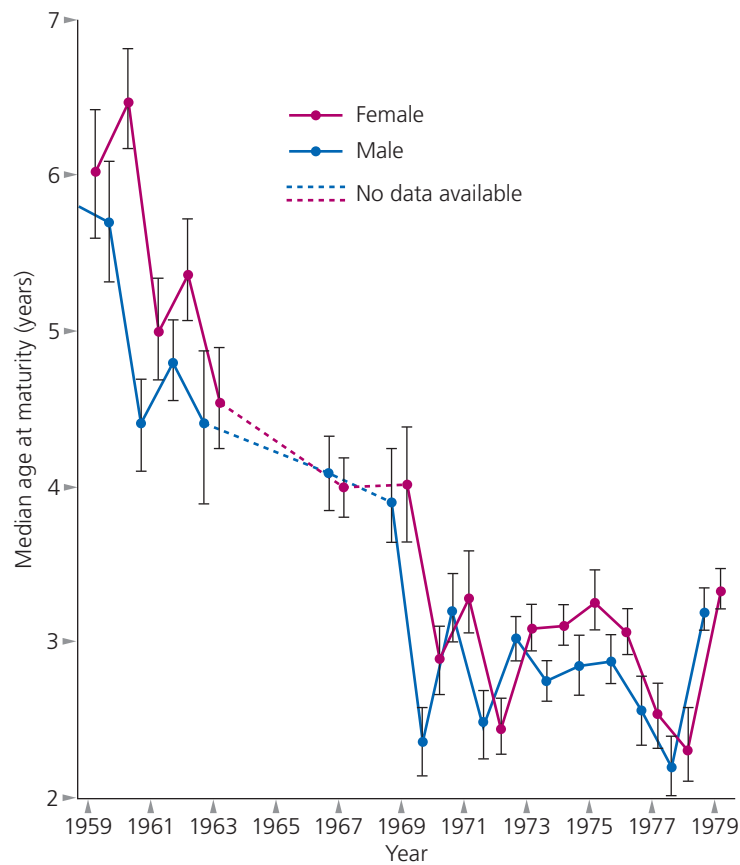
Figure 8.25 A: Bighorn sheep (*Ovis canadensis*) have experienced selection from hunters who prefer large males with long horns. B: Over the past 30 years, this "unnatural" selection has resulted in the evolution of shorter male horns. (Adapted from Coltman et al. 2003.)

A
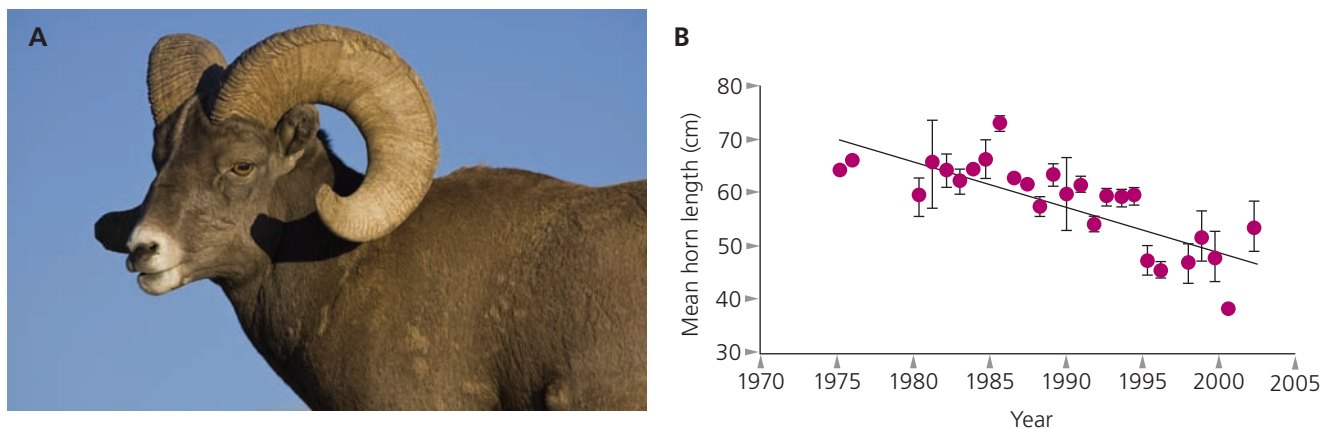
B

Figure 8.26 Atlantic cod (A) have experienced decades of selection for smaller body size as a result of selective harvest by fisheries. This has led to the evolution of a life-history trait, the age of maturity, so that fish today reach sexual maturity at significantly smaller sizes than fish 50 years ago (B). (Redrawn from Beacham 1983.)

TABLE 8.2 Traits That Experience Selection Due to Human Hunting and Fishing

Trait	Selective action	Response(s)	Remedy
Age and size at sexual maturation	Increased mortality	Sexual maturation at earlier age and size, reduced fertility	Reduce harvest mortality or modify selectivity of harvest.
Body size or morphology, sexual dimorphism	Selective harvest of larger or more distinctive individuals	Reduced growth rate, attenuated phenotypes	Reduce selective harvest of large or distinctive individuals.
Sexually selected weapons (horns, tusks, antlers, etc.)	Trophy hunting	Reduced weapon size or body size	Implement hunting regulations that restrict harvest based on size or morphology of weapons under sexual selection.
Timing of reproduction	Selective harvest of seasonally early or late reproducers	Altered distribution of reproduction (truncated or altered seasonality)	Harvest throughout reproductive season.
Behavior	Harvest of more active, aggressive or bolder (more vulnerable to predation) individuals	Reduced boldness in foraging or courtship behavior, potentially reduced productivity	Implement harvest methods less likely to impose selection on activity or aggressive behavior.
Dispersal/migration	Harvest of individuals with more predictable migration patterns	Altered migration routes	Interrupt harvest with key time and area closures tied to primary migration routes.

Table 8.2 In harvested populations, some specific traits are likely to be affected. Unlike natural selection, however, this type of directional selection can be managed and controlled. (From Allendorf and Hard 2009.)

when animals are heavily hunted, it's the undesirable individuals that can survive and pass on their traits to the next generation (Allendorf and Hard 2009; **Table 8.2**).

Trophy hunters of big game almost universally prefer to kill the largest, most ornamented males of deer, elk, moose, and bighorn sheep. David Coltman of the University of Sheffield has analyzed records of big game animals and discovered evidence of selection. The preference of hunters has led to the rapid evolution of smaller horn and body sizes (Coltman et al. 2003).

This recent evolution may be altering how these big game animals choose mates. As we'll see in Chapter 11, male bighorn sheep and other game species use their horns to compete with other males and attract females. The size of their horns is also linked to high quality in males most preferred by females. So hunters are killing off the very individuals that would normally have the highest breeding success.

Fish are experiencing strong selection from hunting as well. In some salmon populations, 90 percent are caught by fisherman (Hard et al. 2008). But these catches are not random samples of fish populations. Fishermen tend to catch more large fish than small ones. The result of this practice has been strong "unnatural" selection for salmon with smaller body sizes (Allendorf and Hard 2009). In salmon, as in many other heavily fished species, the fecundity of individuals increases exponentially with body size (Marteinsdottir and Begg 2002). The small fish favored by this new pattern of unnatural selection have dramatically reduced reproductive potential, potentially fueling the utter collapse of these harvested populations.

Key Concepts

The speed of evolution is a product of the amount of available genetic variation and the strength of selection. Weed and pest populations can be highly variable, and herbicides and pesticides can impose extremely strong selection. The result: rapid evolution of resistance.

An understanding of evolutionary biology can lead to novel management practices, which slow the evolution of resistance in pest populations.

To sum up . . .

- Episodes of natural selection may be associated with particular seasons or events (such as droughts or floods). This means that selection need not be visible or measurable all the time.

- Natural selection can at times be strong and lead to rapid evolution that is observable in wild populations. Even infrequent episodes of strong selection can have important effects on the evolution of populations.

- The strength and the direction of natural selection can change over time.

- Selection may be similarly heterogeneous over space, so that individuals in different parts of a species' range encounter very different patterns of selection. When adjacent populations (or parts of a population) experience divergent (opposing) forces of selection, the extent to which they will evolve in different directions will depend on the magnitude of the difference in selection and the amount of genetic exchange between the populations.

- During their lifetime, organisms experience many different sources and types of selection. Often these "agents" of selection act in opposing directions, and this can generate a net balance. When this balance occurs, their combined effects result in stabilizing selection for intermediate trait values.

- Although recombination is an important driver of genetic variation within a population, genetic linkage is the tendency for loci that are physically close to one another on the same chromosome to stay together during meiosis.

- Selection can be such a powerful force that alleles can be swept to fixation in a population, carrying genetically linked alleles along with them.

- Humans have dramatically altered their environments, and this has resulted in novel types of selection on many organisms.

- Domestication, application of pesticides or herbicides, translocation of species, and hunting and fishing all have led to rapid and recent evolution of affected populations.

- In some cases, an understanding of the principles of evolution can lead to new strategies for mitigating unintended consequences of human activity.

NOT FOR SALE

1. Which is NOT one of the three conditions that must be met for evolution by natural selection to take place?
   a. Variation in phenotypic traits must exist in the population.
   b. Differences in phenotype influence the probability of survival or reproduction.
   c. One extreme of the phenotype leads to greater survival.
   d. Differences in phenotypic traits must be at least partially heritable.
   e. All of the above are necessary for evolution by natural selection.

2. How did Sacha Vignieri and Hopi Hoekstra test whether coat color affected oldfield mouse fitness?
   a. They used dark and light models of oldfield mice to determine predation rates in forest and beach habitats.
   b. They trapped oldfield mice in both forest and beach habitats and counted whether there were more dark mice in forest habitats or in beach habitats.
   c. They followed oldfield mice with dark coats in beach habitats to determine whether they reproduced or not.
   d. They conducted late-night surveys in both forest and beach habitats to determine whether they could see mice with dark or light coats better in either habitat.

3. If gene flow were eliminated between northern and southern portions of the scarlet kingsnake's range, what do you predict would happen to the frequency of alleles that produce a coral-snake-like pattern as a result of natural selection?
   a. The frequency of the alleles would increase in the northern part of the range.
   b. The frequency of the alleles would decrease in the northern part of the range.
   c. The frequency of the alleles would increase in the southern part of the range.
   d. The frequency of the alleles would decrease in the southern part of the range.

4. The text describes the galls of flies as examples of extended phenotypes. What are extended phenotypes?
   a. Phenotypes that are shared by multiple generations.
   b. Behaviors that influence the survival of offspring.
   c. Morphological features that affect reproductive output.
   d. Structures constructed by organisms that can influence their performance or success.
   e. All of the above are extended phenotypes.

5. How do selective sweeps on an allele affect flanking stretches of DNA?
   a. Flanking regions are the same in many individuals in the population.
   b. Flanking regions are eliminated.
   c. Higher levels of recombination occur.
   d. Selective sweeps do not affect flanking regions.

6. Which of the following is NOT a potential agent of selection?
   a. Human fishing.
   b. Genetic drift.
   c. A flood.
   d. A predator.
   e. All of the above are potential agents of selection.

7. What is the best course of action for a farmer who wants to slow the evolution of resistance of a pest population feeding on his crops?
   a. Allowing some nonresistant pests to survive.
   b. Decreasing the amount of pesticide, but increasing the concentration.
   c. Planting genetically modified crops that make their own pesticide.
   d. Nailing a toad to the barn door.

8. The text describes a flower called *Crepis sancta* that grows in the city of Marseille. What is a likely reason for city populations of this plant to produce more nondispersing seeds than plants in the countryside?
   a. Plants in the countryside have access to more nutrients.
   b. Seeds from plants in the countryside have to travel farther to find suitable habitat.
   c. City plants are more affected by pollution.
   d. City plants with genes that make seeds drop are more likely to reproduce successfully.
   e. City plants don't produce more nondispersing seeds.

9. Which of these statements about selection is FALSE?
   a. During their lifetime, plants may experience many different sources of selection.
   b. Insects often experience different types of selection as larvae than they do as adults.
   c. Birds can experience different directions of selection in different years.
   d. Selection in mammals always operates more strongly on survival than on reproduction.

10. What is the most likely reason that lactose tolerance alleles selectively swept through certain human populations?
    a. Lactose intolerance reduced reproduction.
    b. Lactose tolerance had a large effect on survival.
    c. Drinking lots of milk caused a greater mutation rate.
    d. It was random which populations experienced the selective sweep.
    e. None of these reasons explains the selective sweep.

Short Answer Questions

1. What things did Peter and Rosemary Grant's team need to measure or record in order to demonstrate the effect of natural selection on the beak size of finches in the Galápagos?

2. What are the differences and similarities between directional and stabilizing selection?

3. For evolution by natural selection to occur, why is it important for the coat color of oldfield mice to be variable and at least partly heritable? What would happen if the variation or heritability were reduced?

4. What general kinds of data have been used to understand the evolution of sticklebacks? What does each kind of evidence tell researchers about their evolution?

5. Is domesticated corn (maize) better adapted to its environment than teosinte, the wild plant it evolved from? Why or why not?

6. Why is the evolution of resistance so rapid? How do farmers and scientists attempt to slow the evolution of resistance in pest populations?

7. What were the steps involved for snakes to evolve a smaller gape width in Australia after the introduction of cane toads?

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