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# EVOLUTIONARY ANALYSIS

FOURTH EDITION

Scott Freeman

*University of Washington*

Jon C. Herron

*University of Washington*



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# 3

## Darwinian Natural Selection

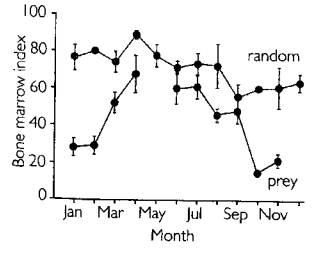
It is quite conceivable," Darwin wrote in his introduction to *On the Origin of Species* (1859, p. 3) "that a naturalist, reflecting on the mutual affinities of organic beings, on their embryological relations, their geographical distribution, geological succession, and other such facts, might come to the conclusion that each species had not been independently created, but had descended... from other species."

This assertion concerns the pattern of life's history. A growing body of evidence, amassed by Darwin and the early evolutionists who were his intellectual forebears, indicated that both fossilized and living organisms were derived with modification from either a single common ancestor or a few. The evidence was indirect and the interpretation startling, but Darwin's argument was so compelling that scientific debate over descent with modification virtually ended by the mid-1870s. Evolution was, and is, an established fact.

"Nevertheless," he continued, "such a conclusion, even if well founded, would be unsatisfactory, until it could be shown how the innumerable species inhabiting this world have been modified. . . ."

Darwin knew as well as anyone that the mere recognition of a pattern does not amount to a complete scientific theory. If we are to claim any understanding of life's history, we must explain not only what happened, but how. What is the mechanism that produces the pattern we call evolution? Chapter 2 focused on the evidence for descent with modification; this chapter introduces the process, natural selection, that Darwin asserted produces the pattern.

Survival of the fittest. The photo shows a pack of African wild dogs bringing down an impala. Data gathered by Alistair Pole and colleagues (2003) show that wild dogs prey on the skinniest, weakest impala. The graph shows, for different times of year, the mean amount of stored fat in the bone marrow of impala taken by wild dogs versus a random sample of impala.



To increase the frequency of desirable traits in their stocks, plant and animal breeders employ artificial selection.

### 3.1 Artificial Selection: Domestic Animals and Plants

To understand the mechanism of evolution in nature, Darwin studied the mechanism of evolution under domestication. That is, he studied the method plant and animal breeders use to modify their crops and livestock. Darwin's favorite domestic organism was the pigeon. Darwin became a pigeon breeder himself to learn the experts' techniques. To refine a particular breed of pigeon so that, for example, the birds' tail feathers fan more spectacularly, or their body feathers curl more elegantly, breeders employ artificial selection. They scrutinize their flocks and select the individuals with the most desirable traits. These birds the breeders mate with each other to produce the next generation. If the desirable traits are passed from parents to offspring, then the next generation, consisting of the progeny of only the selected birds, will show the desirable traits in a higher proportion than existed in last year's flock.

Our favorite domestic organism is the tomato. The domestic tomato, *Solanum lycopersicum*, occurs around the world, both in cultivation and as a weedy escapee. It is closely related to, and can interbreed with, several species of wild tomatoes, all found in western South America (Spooner et al. 2005). The domestic tomato was first cultivated by Native Americans before Europeans arrived in the New World (Tanksley 2004). It traveled back to Europe with the early explorers and spread around the globe from there (Albala 2002).

The power of artificial selection is evident in Figure 3.1. All species of wild tomato have small fruit like the currant tomato on the left, typically less than a centimeter across and weighing just a few grams (Frary et al. 2000). The ancestor of the domestic tomato probably had similarly tiny fruit. Modern varieties of domestic tomato, like the Red Giant on the right, have fruit 15 cm or more across that can weigh more than a kilogram. Descent with modification, indeed.

**Figure 3.1 Wild and domestic tomatoes** Wild tomatoes have tiny fruit, like that of the currant tomato on the left. Domestic tomatoes are descended from tiny-fruited ancestors, but as a result of artificial selection have large fruit, like that of the Red Giant on the right. From Frary et al. (2000).

Wild tomato  
(*Solanum pimpinellifolium*)

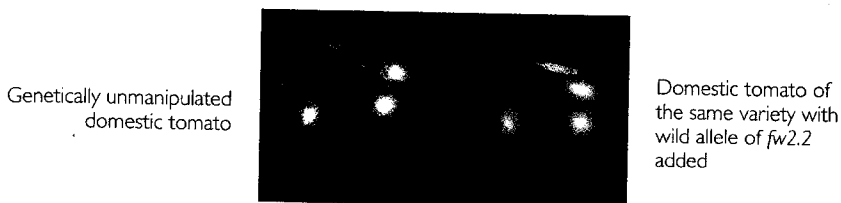


Domestic tomato  
(*Solanum lycopersicum*)

Research by molecular biologists allows us to understand at least part of what happened during the domestication of tomatoes at the level of individual genes. Tomatoes carry, on chromosome 2, a gene called *fw2.2* (Tanksley 2004). The gene encodes a protein made during early fruit development (Frary et al. 2000). The protein's job is to repress cell division; the more of the protein a plant makes, the smaller its fruit (Liu et al. 2003). Changes in the nucleotide sequence in the *fw2.2* promoter—the gene's on-off switch—alter the timing of production and the total amount of protein made (Cong et al. 2002; Nesbitt and Tanksley 2002).

Every wild tomato ever tested has carried alleles of *fw2.2* associated with high production of the repressor protein and small fruit (Tanksley 2004). Every cultivated tomato has carried alleles associated with low production of the protein and large fruit. Anne Frary and colleagues (2000), working in the laboratory of Steven Tanksley, used genetic engineering to place copies of a small-fruit allele

into domestic tomatoes. The fruit on the left in Figure 3.2 is from an unmanipulated plant; the fruit on the right is from a sibling of the unmanipulated plant that has been genetically modified to carry the wild, small-fruit allele of *fw2.2*. The fruits differ in size by about 30%.

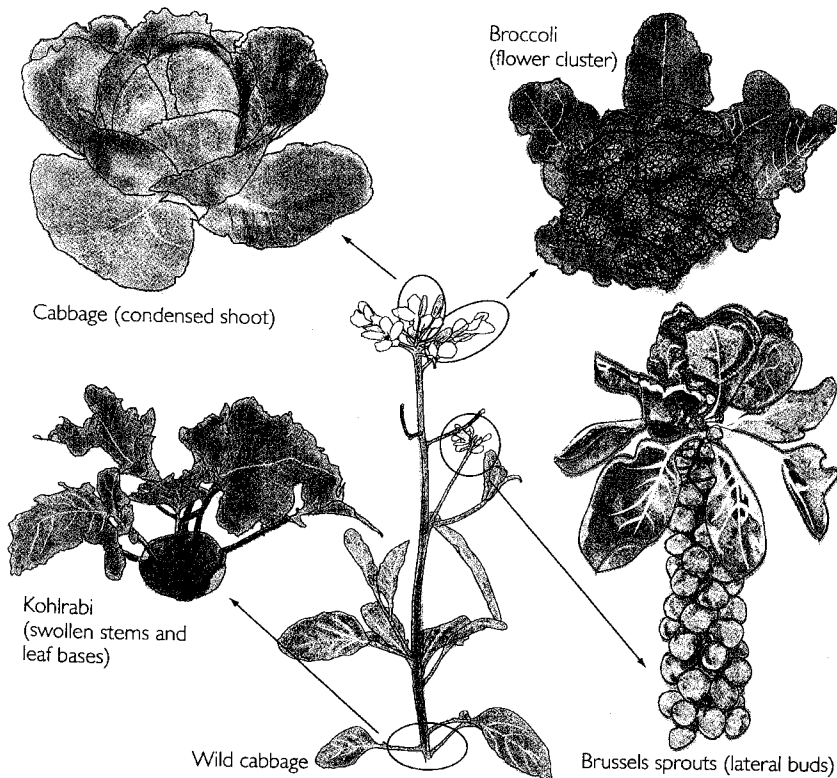


**Figure 3.2** A genetically determined difference in fruit size

These tomatoes are from sibling plants. The one on the left carries only domestic alleles of the *fw2.2* gene. The one on the right carries, in addition, copies of the wild allele. The *fw2.2* gene encodes a protein that represses fruit growth. From Frary et al. (2000).

Tanksley envisions a scenario in which early tomato farmers noticed variation in fruit size among their plants (Nesbitt and Tanksley 2002; Tanksley 2004). Some of this variation was due to the plants' possession of different alleles of the *fw2.2* gene. Large fruit alleles might have been present as rare variants prior to domestication, or they might have arisen as new mutations in cultivated populations. Because the farmers preferred larger tomatoes, year after year they planted their fields with seeds from the largest fruit of the previous crop. By this discipline the farmers eventually eliminated small-fruited alleles from their stocks.

Farmers practicing artificial selection can change more than size. The domesticated vegetables shown in Figure 3.3—broccoli, brussels sprouts, cauliflower, kale, and kohlrabi—are strikingly different in architecture. Yet all can readily interbreed, and are classified by botanists as varieties of wild cabbage, *Brassica oleracea*, from which they are derived.



**Figure 3.3** Wild and domestic varieties of *Brassica oleracea*

Cauliflower (*Brassica oleracea botrytis*), broccoli (*Brassica oleracea italica*), brussels sprouts (*Brassica oleracea gemmifera*), kale (*Brassica oleracea acephala*), and kohlrabi (*Brassica oleracea gongylodes*) are all derived from wild cabbage (*Brassica oleracea oleracea*). After Niklaus (1997).

### 3.2 Evolution by Natural Selection

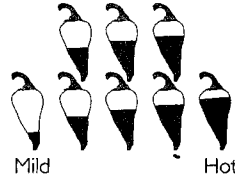
Darwin realized that a process much like artificial selection happens in nature. His Theory of Evolution by Natural Selection holds that descent with modification is the logical outcome of four postulates, which he laid out in his introduction to *On the Origin of Species by Means of Natural Selection*. Darwin (1859, p. 459) considered the rest of the book one long argument in their support. Darwin's postulates, claims about the nature of populations, are as follows:

*Darwin and Wallace realized that a process similar to artificial selection happens automatically in nature.*

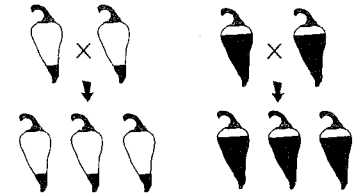
1. Individuals within populations are variable.
2. The variations among individuals are, at least in part, passed from parents to offspring.
3. In every generation, some individuals are more successful at surviving and reproducing than others.
4. The survival and reproduction of individuals are not random; instead they are tied to the variation among individuals. The individuals with the most favorable variations, those who are better at surviving and reproducing, are naturally selected.

If these four postulates are true, then the composition of the population changes from one generation to the next. Figure 3.4 shows how Darwin's theory might play out in a population of chilies eaten by packrats.

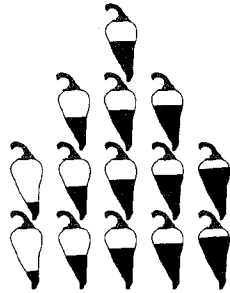
(1) There is variation among individuals.



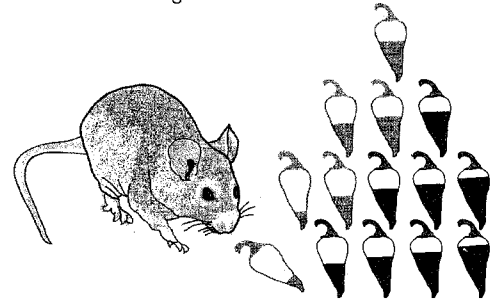
(2) The variation is inherited.



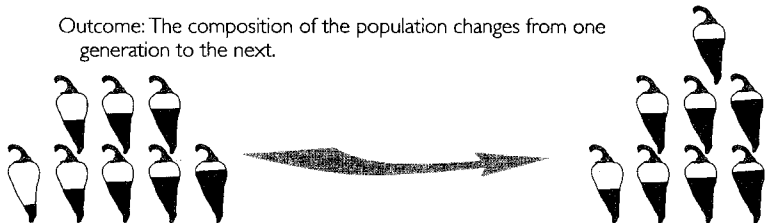
(3) More individuals are born than will survive to reproduce.



(4) Some variants survive and reproduce at higher rates than others.



Outcome: The composition of the population changes from one generation to the next.



**Figure 3.4 Darwin's Theory of Evolution by Natural Selection** Darwin's theory consists of four claims about populations of organisms and a logical outcome that follows, as a matter of simple mathematics, if the four postulates are true. These cartoons show how the theory might work in a population of chili plants whose fruits are attacked by packrats. If the chilies vary in the spiciness of their fruit, and if packrats prefer milder chilies, and if the hot survivors pass their spiciness to their offspring, then the population will show a higher proportion of hot-fruited chilies each generation. Inspired by Tewksbury and Nabhan (2001).

The logic is straightforward: If there are differences among the individuals in a population that can be passed on to offspring, and if there is differential success among those individuals in surviving and/or reproducing, then some traits will be passed on more frequently than others. As a result, the characteristics of the population will change slightly with each succeeding generation. This is Darwinian evolution: gradual change in populations over time.

*Natural selection is a process that produces descent with modification, or evolution.*

Note that while the logic is straightforward it contains a subtlety that can cause confusion. To understand how natural selection works, we have to think statistically. The selection itself—the surviving and reproducing—happens to individuals, but what changes is populations. Recall the HIV virions discussed in Chapter 1. Because of differences in the amino acid sequences of the reverse transcriptase active site, individual virions within the same host varied in their ability to synthesize DNA in the presence of AZT. Virions with mutant forms of reverse transcriptase that were less likely to bind AZT reproduced more successfully. When they reproduced, they passed their reverse transcriptase mutations to their offspring. In the next generation, then, a higher percentage of virions carried the modified form of reverse transcriptase than in the generation before. This change in the population is evolution by natural selection.

Darwin referred to the individuals who are better at surviving and reproducing, and whose offspring make up a greater percentage of the population in the next generation, as more fit. In so doing he gave the everyday English words *fit* and *fitness* a new meaning. **Darwinian fitness** is the ability of an individual to survive and reproduce in its environment.

An important aspect of fitness is its relative nature. Fitness refers to how well an individual survives and how many offspring it produces compared to other individuals of its species. Biologists use the word **adaptation** to refer to a trait or characteristic of an organism, like a modified form of reverse transcriptase, that increases its fitness relative to individuals without the trait.

*An adaptation is a characteristic that increases the fitness of an individual compared to individuals without the trait.*

Darwin's mechanism of evolution was, incidentally, discovered independently by a colleague of Darwin's named Alfred Russel Wallace. Though trained in England, Wallace had been making his living in Malaysia by selling natural history specimens to private collectors. While recuperating from a bout with malaria in 1858, he wrote a manuscript explaining natural selection and sent it to Darwin. Darwin, who had written his first draft on the subject in 1842 but never published it, immediately realized that he and Wallace had formulated the same theory. Brief papers by Darwin and by Wallace were read together before the Linnean Society of London, and Darwin then rushed *On the Origin of Species* into publication (17 years after he had written the first draft). Today, Darwin's name is more prominently associated with the Theory of Evolution by Natural Selection for two reasons: He had clearly thought of it before Wallace, and his book provided a full exposition of the idea, along with massive documentation.

One of the most attractive aspects of the Darwin–Wallace theory is that each of the four postulates and their logical consequence can be verified independently. That is, the theory is testable. There are neither hidden assumptions nor anything that has to be accepted uncritically. In the next two sections, we examine each of the four assertions, and Darwin's predicted result, by reviewing two studies: a recent experiment on snapdragons and an ongoing study of finches in the Galápagos Islands off the coast of Ecuador. These studies show that the Theory of Evolution by Natural Selection be tested rigorously, by direct observation.

*The Theory of Evolution by Natural Selection is testable.*

### 3.3 The Evolution of Flower Color in an Experimental Snapdragon Population

Kristina Niovi Jones and Jennifer Reithel (2001) wanted to know whether natural selection by bumblebees could influence the evolution of a floral trait controlled by alleles of a single gene. To find out, they established an experimental population of 48 snapdragons in which they made sure that Darwin's postulates 1 and 2 were true. Then they monitored the plants and their offspring to see whether postulates 3 and 4, and the predicted outcome, were true as well.

#### Postulate 1: There Is Variation among Individuals

The snapdragons in Jones and Reithel's population varied in flower color. Three-quarters of the plants had flowers that were almost pure white, with just two spots of yellow on the lower lip. The rest had flowers that were yellow all over.

#### Postulate 2: Some of the Variation Is Heritable

The variation in color among Jones and Reithel's plants was due to differences in the plants' genotypes for a single gene. The gene has two alleles, which we will call  $S$  and  $s$ . Individuals with either genotype  $SS$  or  $Ss$  have white flowers with just two spots of yellow. Individuals with genotype  $ss$  are yellow all over. Among the 48 plants in the experimental population, 12 were  $SS$ , 24 were  $Ss$ , and 12 were  $ss$ . Figure 3.5a shows the variation in phenotype among Jones and Reithel's snapdragons, and the variation in genotype responsible for it.

#### Testing Postulate 3: Do Individuals Vary in Their Success at Surviving or Reproducing?

Although Jones and Reithel ran their experiment in a meadow in Colorado, they kept their snapdragons in pots and made sure all of the plants survived.

The researchers did not intervene, however, to help the snapdragons reproduce. Instead, they let free-living bumblebees pollinate the plants. To gauge the plants' success at reproducing by exporting pollen, Jones and Reithel tracked the number of times bees visited each flower. To gauge the plants' success at reproducing by making seeds, the researchers counted the seeds produced from each fruit. Consistent with Darwin's third postulate, the plants showed considerable variation in reproductive success, both as pollen donors and as seed mothers.

#### Testing Postulate 4: Is Reproduction Nonrandom?

Jones and Reithel expected that one color would attract more bees than the other, but they did not know which color it would be. The yellow spots on otherwise white snapdragons are thought to serve as nectar guides, helping bumblebees find the reward the flower offers. All-yellow flowers lack nectar guides and so might be less attractive to bees, or they might be more visible against the background vegetation and thus *more* attractive. Jones and Reithel found that white flowers attracted twice as many bee visits as yellow flowers (Figure 3.5b, left).

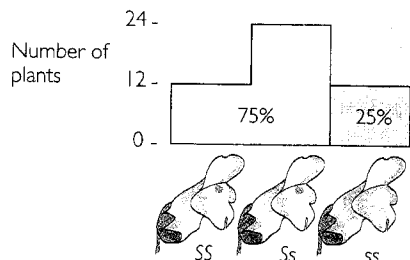
Reproductive success through seed production was less strongly associated with color than was success through pollen donation. Nonetheless, the white plants were somewhat more robust than the yellow plants and so produced, on average, slightly more seeds per fruit (Figure 3.5b, right).

*When researchers set up a plant population in which postulates 1 and 2 were true, they found that postulate 3 was true as well . . .*

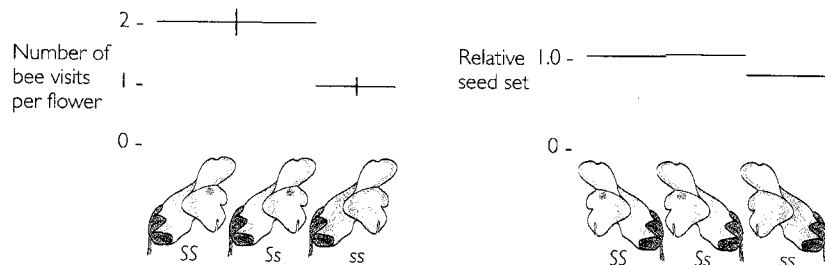
*. . . as were postulate 4 . . .*



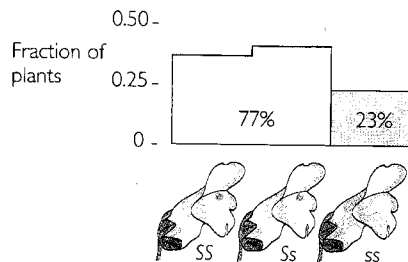
(a) Composition of parental population



(b) Differences in reproductive success through male function (left) and female function (right)



(c) Composition of offspring population



**Figure 3.5 Darwin's Theory of Evolution by Natural Selection demonstrated in an experimental population of snapdragons** (a) The plants in the parental population vary in flower color. This variation in phenotype is due to variation in genotype. The graph shows the number of plants in the population with each of the three possible genotypes. (b) The white plants are more successful at reproducing. They are visited by bumblebees twice as often (left), and make more seeds (right). (c) Because plants with white flowers are more successful at passing on their genes, they occupy a larger fraction of the population in the next generation. Prepared from data in Jones and Reithel 2001. [In (b) left, the vertical bars show the size of the standard error; they indicate the accuracy of the researchers' estimate of the mean number of bee visits. In (b) right, the values for relative seed set were calculated as the fraction of seeds actually produced by plants with a particular genotype divided by the fraction of seeds expected based on the frequencies of the genotypes.]

Consistent with Darwin's fourth postulate, reproductive success was not random. Through both pollen donation and seed production, white plants had higher reproductive success than yellow plants.

### Testing Darwin's Prediction: Did the Population Evolve?

The bumblebees that volunteered to participate in Jones and Reithel's experiment played the same role that Darwin did in breeding pigeons: They selected particular individuals and granted them high reproductive success. Since white plants had higher reproductive success than yellow, and since flower color is determined by genes, the next generation of snapdragons should have had a higher proportion of white flowers.

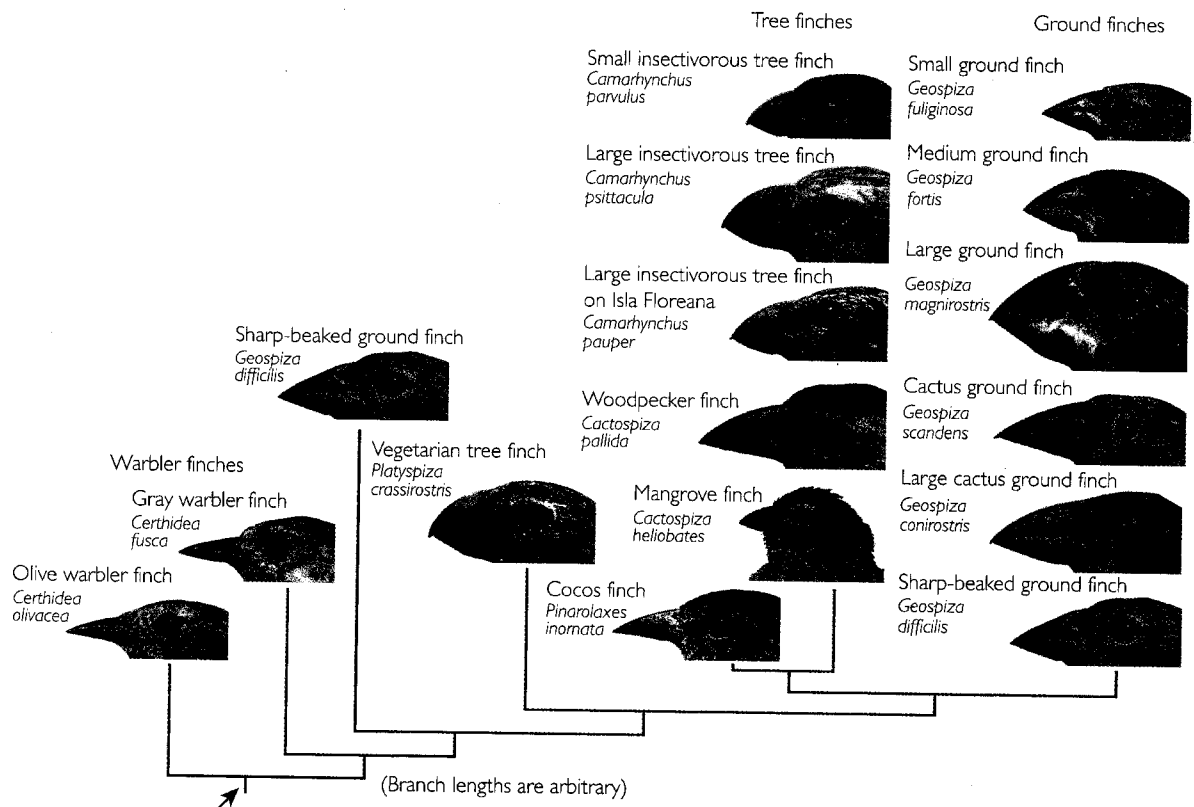
Indeed, the next generation did have a higher proportion of white flowers (Figure 3.5c). Among the plants in the starting population, 75% had white flowers; among their offspring, 77% had white flowers. The snapdragon population evolved as predicted. An increase of two percentage points in the proportion of white flowers might not seem like much. But modest changes can accumulate over many generations. With Jones and Reithel's population evolving at this rate, it would not take many years for white flowers to all but take over.

*... and Darwin's prediction that the population would evolve as a result.*

Jones and Reithel's experiment shows that Darwin's theory works, at least in experimental populations when researchers have made certain that Darwin's first two postulates hold. But does the theory work in completely natural populations, in which researchers have manipulated nothing? To find out, we turn to research on Darwin's finches in the Galápagos Islands.

### 3.4 The Evolution of Beak Shape in Galápagos Finches

Peter Grant and Rosemary Grant and their colleagues have been studying finches in the Galápagos Archipelago since 1973 (see P. R. Grant 1999; B. R. Grant and P. R. Grant 1989, 2003; P. R. Grant and B. R. Grant 2002a, 2002b, 2005, 2006; B. R. Grant 2003). Collectively called Darwin's finches, the birds are derived from a small flock of grassquits that invaded the archipelago from Central or South America some 2.3 million years ago (Sato et al. 2001). The descendants of this flock today comprise 13 species that live in the Galápagos, plus a 14th that lives on Cocos Island. Close examination of the evolutionary tree in Figure 3.6 reveals that all of these species are closely related. The deepest split on the tree separates two lineages of warbler finches that still recognize each other as potential mates and are thus classified (despite each having its own name) as belonging



**Figure 3.6 Diversity in Darwin's finches** These finches are all descended from a common ancestral population (red arrow) that traveled from Central or South America to the Galápagos Archipelago. The evolutionary tree, estimated from similarities and differences in DNA sequences by Kenneth Petren and colleagues (2005), shows the sometimes complex relationships among the major groups. The photos, from Petren et al. (1999) and Grant and Grant (1997), show the extensive variation among species in beak size and shape.

to a single species. The next deepest split separates two lineages of sharp-beaked ground finches that are likewise considered a single species. Consistent with their close kinship, all species of Darwin's finches are similar in size and coloration. They range from 4 to 6 inches in length and from brown to black in color. They do, however, show remarkable variation the size and shape of their beaks.

The beak is the primary tool used by birds in feeding, and the enormous range of beak morphologies among the Galápagos finches reflects the diversity of foods they eat. The warbler finches (*Certhidea olivacea* and *Certhidea fusca*) feed on insects, spiders, and nectar; woodpecker and mangrove finches (*C. pallida* and *C. heliobates*) use twigs or cactus spines as tools to pry insect larvae or termites from dead wood; several ground finches in the genus *Geospiza* pluck ticks from iguanas and tortoises in addition to eating seeds; the vegetarian finch (*Platyspiza crassirostris*) eats leaves and fruit.

For a test of the Theory of Evolution by Natural Selection, we focus on data Grant and Grant and colleagues have gathered on the medium ground finch, *Geospiza fortis*, on Isla Daphne Major (Figure 3.7).

Daphne Major's size and location make it a superb natural laboratory. Like all of the islands in the Galápagos, it is the top of a volcano (Figure 3.8). The island is tiny. It rises from the sea to a maximum elevation of just 120 meters. It has one



Figure 3.7 The medium ground finch, *Geospiza fortis* (top) An adult male; (bottom) an adult female.

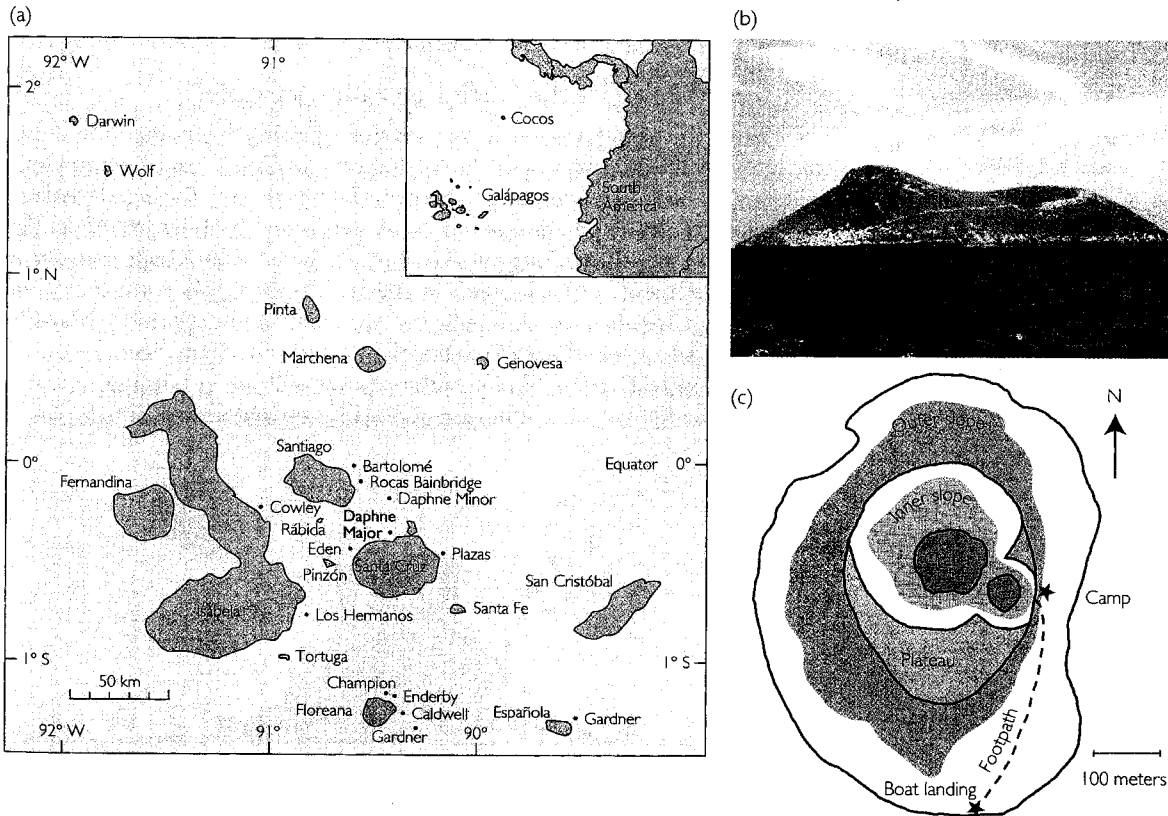


Figure 3.8 The Galápagos Archipelago and Isla Daphne Major (a) Cocos Island and the Galapagos Archipelago, home of Darwin's finches. Isla Daphne Major is a tiny speck between Santa Cruz and Santiago. (b) Isla Daphne Major, seen from a boat approaching the island. Visible as a faint white line running upward from left to right is the footpath that runs from the boat landing (at the waterline) to the campsite (on the rim of the crater). (c) A map of Daphne Major. Note the island's tiny size. Rerendered from Boag and Grant (1984a).

main crater, with a small secondary crater adjacent to it. There is only one spot on the island that is both flat enough and large enough to pitch a camp. It takes just 20 minutes to walk from the campsite all the way around the main crater's rim and back to camp. The climate is seasonal even though the location is equatorial. A warmer, wetter season from January through May alternates with a cooler, drier season from June through December. The vegetation consists of dry forest and scrub, with several species of cactus.

The medium ground finches on Daphne Major make an ideal study population. Few finches migrate onto or off of the island, and the population is small enough to be studied exhaustively. In an average year, there are about 1,200 individual finches on the island. By 1977, Grant and Grant's team had captured and marked more than half of them; since 1980, virtually 100% of the population has been marked. Medium ground finches live up to 16 years (Grant and Grant 2000). Their generation time is 4.5 years (Grant and Grant 2002).

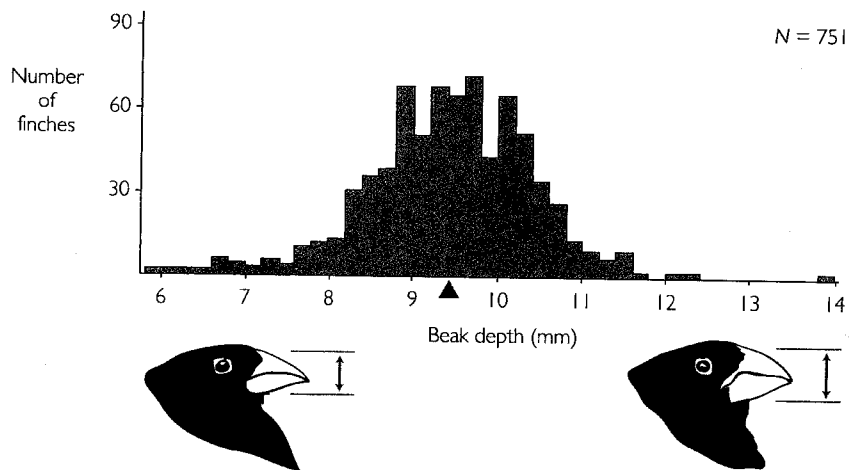
Medium ground finches are primarily seed eaters. The birds crack seeds by grasping them at the base of the bill and then applying force. Grant and Grant and their colleagues have shown that both within and across finch species, beak size is correlated with the size of seeds harvested. In general, birds with bigger beaks eat larger seeds, and birds with smaller beaks eat smaller seeds. This is because birds with different beak sizes are able to handle different sizes of seeds more efficiently (Bowman 1961; Grant et al. 1976; Abbott et al. 1977; Grant 1981b).

### Testing Postulate 1: Is the Finch Population Variable?

The researchers mark every finch they catch by placing on its legs one numbered aluminum band and three colored plastic bands. This allows them to identify individual birds in the field. The scientists also weigh each finch and measure its wing length, tail length, beak width, beak depth, and beak length. All of the traits they have investigated are variable. For example, when Grant and Grant plotted measurements of beak depth in the Isla Daphne Major population of medium ground finches, the data indicated that beak depth varies considerably (Figure 3.9). All of the finch characteristics Grant and Grant have measured clearly conform to Darwin's first postulate. As we will see in Chapter 4, variation among the individuals within populations is virtually universal.

*Some Geospiza fortis have beaks that are only half as deep as other individuals.*

**Figure 3.9** Variation in beak depth in medium ground finches  
This histogram shows the distribution of beak depth in medium ground finches on Daphne Major in 1976. A few birds have shallow beaks; a few birds have deep beaks; most birds have medium beaks. (*N* stands for sample size; the blue arrow along the x-axis indicates the mean, or average.) Rerendered from Boag and Grant (1984b).



### Testing Postulate 2: Is Some of the Variation among Individuals Heritable?

Within the Daphne Major population, individual finches could vary in beak depth because the environments they have experienced are different or because their genotypes are different, or both. There are several ways that environmental variation could cause the variation in beak depth documented in Figure 3.9. Variation in the amount of food that individual birds happened to have received as chicks can lead to variation in beak depth among adults. Injuries or abrasion against hard seeds or rocks can also affect beak size and shape.

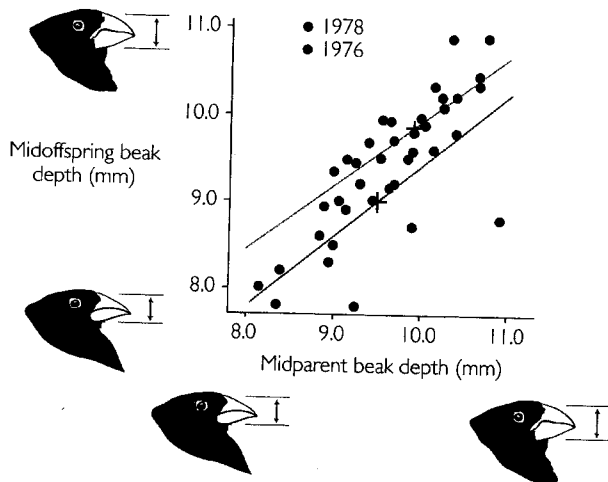
To determine whether at least part of the variation among finch beaks is genetically based, and thus passed from parents to offspring, Peter Boag, a colleague of Peter Grant and Rosemary Grant, estimated the **heritability** of beak depth.

The heritability of a trait is defined as the proportion of the variation observed in a population that is due to variation in genes. Because it is a proportion, heritability varies between 0 and 1. We will develop the theory behind how heritability is estimated more fully in Chapter 9. For now, we point out that if the differences among individuals are due to differences in the alleles they have inherited, then offspring will resemble their parents.

Boag compared the average beak depth of families of *G. fortis* young after they had attained adult size to the average beak depth of their mother and father. Boag's data reveal a strong correspondence between relatives. As the plot in Figure 3.10 shows, parents with shallow beaks tend to have chicks with shallow beaks, and parents with deep beaks tend to have chicks with deep beaks. This is evidence that a large proportion of the observed variation in beak depth is genetically based and can be passed to offspring (Boag and Grant 1978; Boag 1983).

Boag himself would be the first to say that caution is warranted in interpreting his data. Environments shared by family members, maternal effects, conspecific nest parasitism, and misidentified paternity can cause graphs like the one in Figure 3.10 to exaggerate, or to underplay, the heritability of traits (see Box 3.1). However, Lukas Keller and colleagues (2001) have used modern genetic analyses to eliminate most of these confounding factors (Box 3.1). It is clear that Darwin's second postulate is true for the medium ground finches on Daphne Major: A substantial fraction of the variation in beak size is due to variation in genotype.

*In finches, the beak depths of parents and offspring are similar. This observation suggests that some alleles tend to produce shallow beaks, while other alleles tend to produce deeper beaks.*



**Figure 3.10 Heritability of beak depth in *Geospiza fortis***  
This graph shows the relationship between the beak depth of parents and their offspring. Midparent value is the average of the maternal and paternal measurements; midoffspring value is the average of the offspring measurements. The lines in the graph are statistical best-fit lines. The green line and circles are from 1978 data, and the blue line and circles are from 1976 data. Both years show a strong relationship between the beak depth of parents and their offspring. Renrendered from Boag (1983).

### Box 3.1 Issues that complicate how heritabilities are estimated

Heritabilities are estimated by measuring the similarity of traits among closely related individuals. The idea is that genes run in families. If the variation in phenotype among individuals is due in part to variation in genotype, then relatives will tend to resemble one another. But a number of confounding issues can complicate this approach. We will consider four such issues here: misidentified paternity, conspecific nest parasitism, shared environments, and maternal effects.

**Misidentified paternity** In many species of birds, even socially monogamous birds like medium ground finches, females sometimes have extrapair sex. This means that a chick's social father is not always its biological father. If researchers simply assume that the social father at a nest is the biological father of all the chicks, they may underestimate the heritability. Although it is expensive and time consuming, misidentified paternity can be avoided by using genetic paternity tests.

**Conspecific nest parasitism** In some species of birds, females sneak into each other's nests and lay extra eggs. This means that even the social mother at a nest might not be the biological parent of all the chicks. Again, researchers may underestimate the heritability. As with misidentified paternity, this problem can be avoided by using genetic tests.

**Shared environments** Relatives share their environment as well as their genes, and any correlation that is due to their shared environment inflates the estimate of heritability. For example, it is well known that birds tend to grow larger when they have abundant food as chicks. But the most food-rich breeding territories are often claimed and defended by the largest adults in the population. Young from these territories will tend to become the largest adults in the next generation. As a result, a researcher might measure a strong relationship between parent and offspring beak and body size, and claim a high heritability for these traits, when in reality there is none. In this case, the real relationship is between the environments that parents and their young each experienced as chicks.

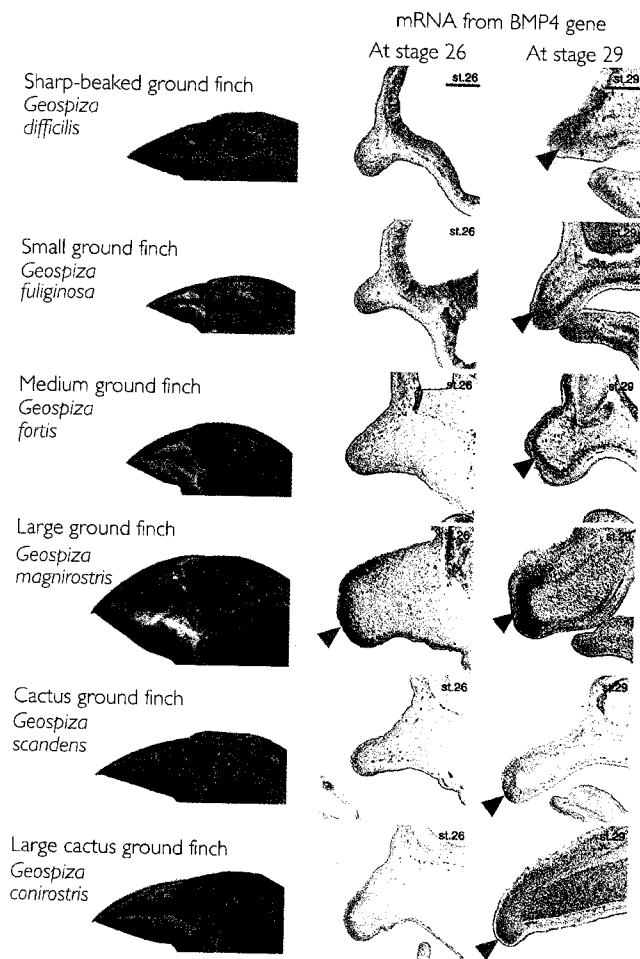
In many species, this problem can be circumvented by performing what are called cross-fostering, common garden, or reciprocal-transplant experiments. In birds, these experiments involve taking

eggs out of their original nest and placing them in the nests of randomly assigned foster parents. Measurements in the young, taken when they are fully grown, are then compared with the data from their biological parents. This experimental treatment removes any bias in the analysis created by the fact that parents and offspring share environments.

**Maternal effects** Even cross-fostering experiments cannot remove environmental effects that are due to differences in the nutrient stores or hormonal contents of eggs. These are called maternal effects. They can be largely avoided by estimating heritabilities from the resemblance between offspring and their fathers only.

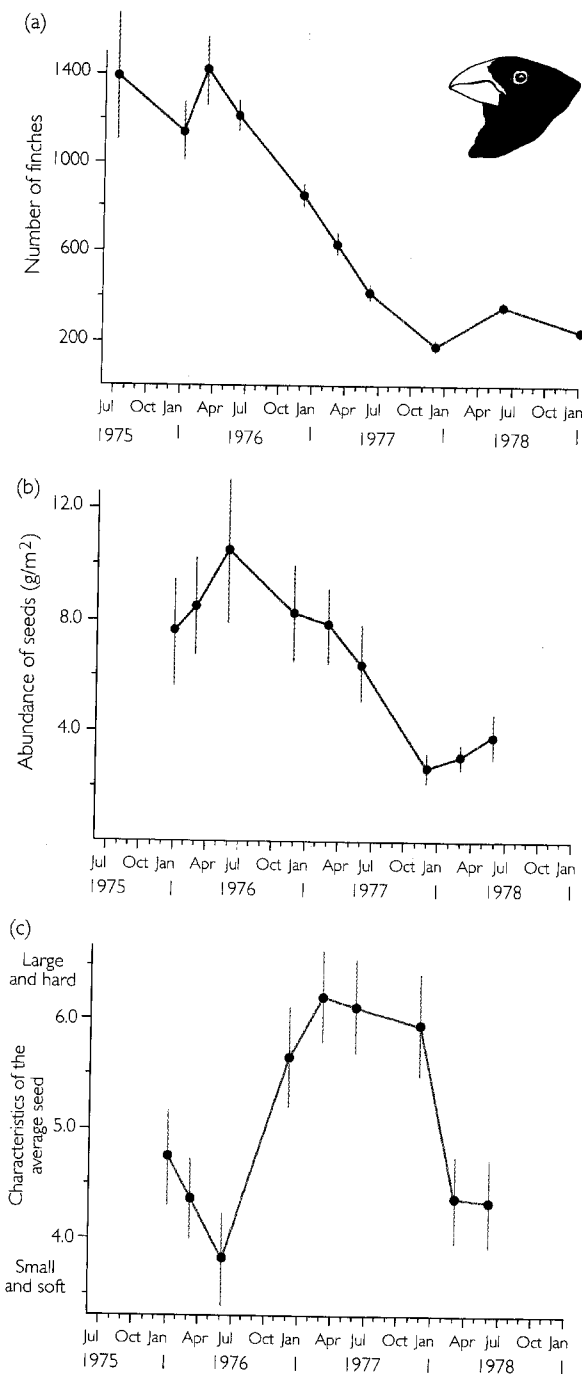
Lukas Keller and colleagues (2001) have made the most painstaking estimates to date of the heritability of morphological traits in Daphne Major's medium ground finches. The researchers performed genetic analyses to confirm the parentage of all the chicks in their sample. They found no evidence of conspecific nest parasitism, but they did find that 20% of the chicks had been fathered by extrapair males. Excluding these chicks from their data set, Keller and colleagues estimated that the heritability of beak depth is 0.65 (with a standard error of 0.15). In other words, about 65% of the variation among finches in beak depth appears to be due to differences in genes. This estimate is unconfounded by extrapair paternity, conspecific nest parasitism, and maternal effects. It might, however, contain some error due to shared environments.

It has not been possible for the Galápagos researchers to perform a cross-fostering experiment on Darwin's finches. Because the Galápagos are a national park, experiments that manipulate individuals beyond catching and marking are forbidden. But the finches themselves have conducted a sort of cross-fostering experiment: As we mentioned above, about 20% of the chicks have been raised by males who are not their biological fathers. If some of the resemblance between parents and offspring is due to shared environments, then these chicks should resemble their social fathers. Using data on the social fathers and their foster offspring, Keller and colleagues calculated the "heritability" of beak depth. It was less than 0.2 and was not statistically distinguishable from zero. This suggests that shared environments have little influence on the resemblance among relatives' beaks.



**Figure 3.11 Bone morphogenic protein 4 and beak development in Darwin's ground finches** The first column illustrates the differences in beak size and shape among the six species of ground finches. The second and third columns show cross sections of the upper beak bud in embryos of each species at two stages of development. The cross sections have been treated with a probe that stains mRNA made from the gene for bone morphogenic protein 4, or BMP4. The stained mRNA appears as dark areas indicated by arrowheads. Adult finch photos from Petren et al. (1999); embryos from Abzhanov et al. (2004).

We do not know the identity of the specific genes responsible for variation in beak size in medium ground finches. However, Arhat Abzhanov and colleagues (2004), working in the laboratory of Clifford Tabin, discovered a tantalizing clue. These researchers focussed on growth factors known to be active during embryonic development. Among them was bone morphogenic protein 4, or BMP4, a signalling molecule that helps sculpt the shape of bird beaks (Wu et al. 2004). For all six species of ground finches, Abzhanov and colleagues treated embryos of different ages with a probe that stains messenger RNA made by the gene that encodes BMP4. As the photos in Figure 3.11 show, ground finch species with larger beaks make BMP4 mRNA (and presumably BMP4) earlier and in larger quantities than species with smaller beaks. The large ground finch, *Geospiza magnirostris*, for example, has by far the biggest beak; it is also the only species that begins making BMP4 mRNA at stage 26 of development. Abzhanov and colleagues suggest that the different species of ground finches harbor alternate versions of one or more of the genes that determine when, where, and how strongly the BMP4 gene is activated. A reasonable hypothesis would be that a similar genetic mechanism is responsible for some of the variation among individuals in the medium ground finch population on Daphne Major.



**Figure 3.12** Decline of ground finch population and available seeds during the 1977 drought (a) This graph shows the number of ground finches found on Daphne Major before, during, and after the drought. The vertical lines through each data point represent a quantity called the standard error, which indicates the amount of variation in census estimates. The lines in this graph are simply drawn from point to point to make the trend easier to see. (b) This graph shows the abundance of seeds on Daphne Major before, during, and after the drought. (c) This graph shows the characteristics of the average seed available as food to medium ground finches before, during, and after the drought. The hardness index plotted on the y-axis is a special measure created by Boag and Grant (1981).

### Testing Postulate 3: Do Individuals Vary in Their Success at Surviving or Reproducing?

Because Grant and Grant and their colleagues have been monitoring the finches on Daphne Major every year since 1973, two members of the research team, Peter Boag and Laurene Ratcliffe, were on the island in 1977 to witness a terrible drought (Boag and Grant 1981; Grant 1999). Instead of the normal 130 mm of rainfall during the wet season, the island got only 24 mm. The plants made few flowers and few seeds. The medium ground finches did not even try to breed. Over the course of 20 months, 84% of the *Geospiza fortis* on Daphne Major disappeared (Figure 3.12a). The researchers inferred that most died of starvation. The decline in population size was simultaneous with a decline in the availability of the seeds the birds depend on for food (Figure 3.12b); 38 emaciated birds were actually found dead, and none of the missing birds reappeared the following year. It is clear that only a fraction of the population survived to reproduce. This sort of mortality is not unusual. For example, Rosemary Grant has shown that 89% of *Geospiza conirostris* individuals die before they breed (Grant 1985). Trevor Price and coworkers (1984) determined that an additional 19% and 25% of the *G. fortis* on Daphne Major died during subsequent drought events in 1980 and 1982, respectively.

In fact, in every natural population studied, more offspring are produced each generation than survive to breed. If a population is not increasing in size, then each parent will, in the course of its lifetime, leave an average of one offspring that survives to breed. But the reproductive capacity (or biotic potential) of organisms is astonishing. Darwin (1859) picked the elephant to illustrate this point, because it was the slowest breeder then known among animals. He calculated that if all the descendants of a single pair survived and reproduced, then after just 750 years there would be 19 million of them. The numbers are even more startling for rapid breeders. Dodson (1960) calculated that if all the descendants of a pair of starfish survived and reproduced, then after just 16 years they would exceed  $10^{79}$ , the estimated number of electrons in the visible universe.



Similarly, data show that in most populations some of the individuals that survive to breed are more successful at mating and producing offspring than others. Just as variation in survival does, variation in reproductive success represents selection. Darwin's third postulate is universally true.

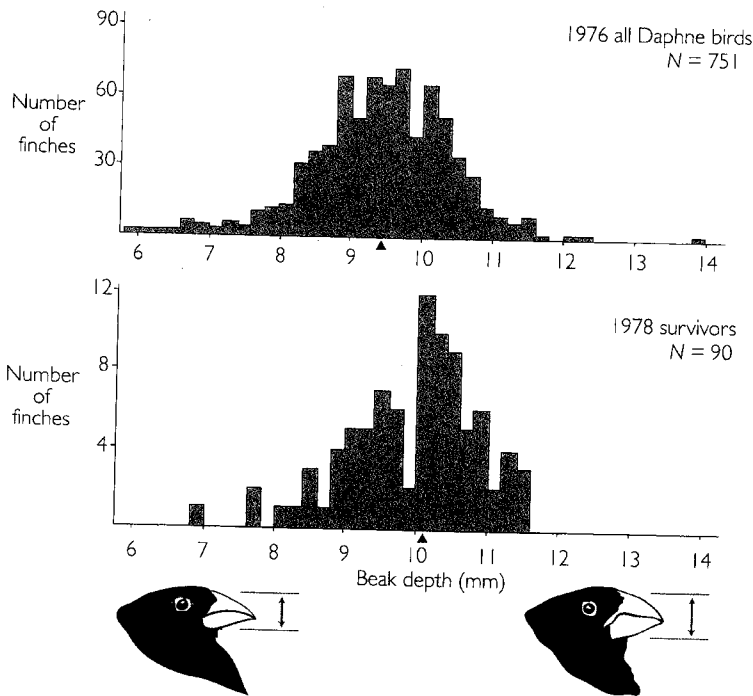
### Testing Postulate 4: Are Survival and Reproduction Nonrandom?

Darwin's fourth claim was that the individuals who survive and go on to reproduce, or who reproduce the most, are those with certain, favorable variations. Did a nonrandom, or selected, subset of the medium ground finch population survive the 1977 drought? The answer is yes.

As the drought wore on, not only the number, but also the types of seeds available changed dramatically (Figure 3.12c). The finches on Daphne Major eat seeds from a variety of plants. The seeds range from small and soft to large and hard. The small, soft seeds, easy to crack, are the birds' favorites. During the drought, as at other times, the finches ate the small, soft seeds first. Once most of the small, soft seeds were gone, the large, hard fruits of an annual plant called *Tribulus cistoides* became a key food item. Only large birds with deep, narrow beaks can crack and eat *Tribulus* fruits successfully. The rest of the finches were left to turn over rocks and scratch the soil in search of the few remaining smaller seeds.

The top graph in Figure 3.13 is from Figure 3.9 on page 82. It shows the beak sizes of a large and random sample of the birds living on Daphne Major the year before the drought. The bottom graph in Figure 3.13 shows the beak sizes of a random sample of 90 birds who survived the drought. The average survivor had a deeper beak than the average nonsurvivor. Because deep beaks and large body sizes are positively correlated, and because large birds tend to win fights over food, the average survivor had a larger body size too.

*During the drought, finches with larger, deeper beaks had an advantage in feeding, and thus in surviving.*



**Figure 3.13** Beak depth before and after natural selection. These histograms show the distribution of beak depth in medium ground finches on Daphne Major, before and after the drought of 1977. The blue triangles indicate the population means. Rerendered from Boag and Grant (1984b).

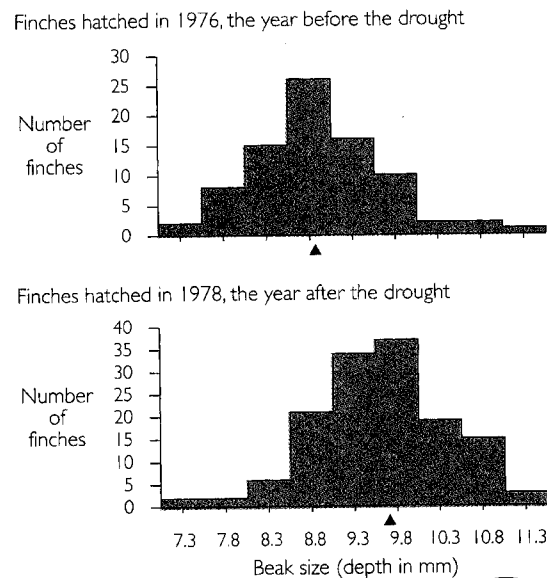
The 1977 selection event, as dramatic as it was, was not an isolated occurrence. In 1980 and 1982 there were similar droughts, and selection again favored individuals with large body size and deep beaks (Price et al. 1984). Then, in 1983, an influx of warm surface water off the South American coast, called an El Niño event, created a wet season with 1,359 mm of rain on Daphne Major. This dramatic environmental change (almost 57 times as much rain as in 1977) led to a superabundance of small, soft seeds and, subsequently, to strong selection for smaller body size (Gibbs and Grant 1987). After wet years, small birds with shallow beaks survive better and reproduce more because they harvest small seeds much more efficiently than large birds with deep beaks. Larger birds were favored in drought conditions, but smaller birds were favored in wet years. Natural selection—as we pointed out in our analysis of HIV evolution in Chapter 1—is dynamic.

### Testing Darwin's Prediction: Did the Population Evolve?

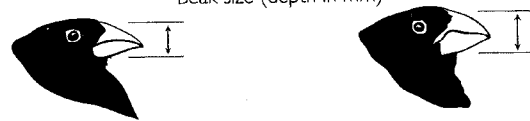
All four of Darwin's postulates are true for the medium ground finch population on Daphne Major. Darwin's theory therefore predicts a change in the composition of the population from one generation to the next. When the deep-beaked birds who survived the drought of 1977 bred to produce a new generation, they should have passed their genes for deep beaks to their offspring. Figure 3.14 confirms that they did. The chicks hatched in 1978, the year after the drought, had deeper beaks, on average, than the birds hatched in 1976, the year before the drought. The population evolved.

Peter Grant and Rosemary Grant and their colleagues have continued to monitor the Daphne Major finch population since the 1970s. As a result of unpredictable changes in the climate and bird community, and consequent changes in the Daphne Major plant community, the researchers have seen selection events

*As a result of the drought,  
the finch population evolved.  
Selection occurs within  
generations; evolution occurs  
between generations.*



**Figure 3.14** Beak depth in the finches hatched the year before the drought versus the year after the drought. The red triangles represent population means. Redrawn from Grant and Grant (2003).



in which deep-beaked birds were more likely to survive and selection events in which shallow-beaked birds were more likely to survive.

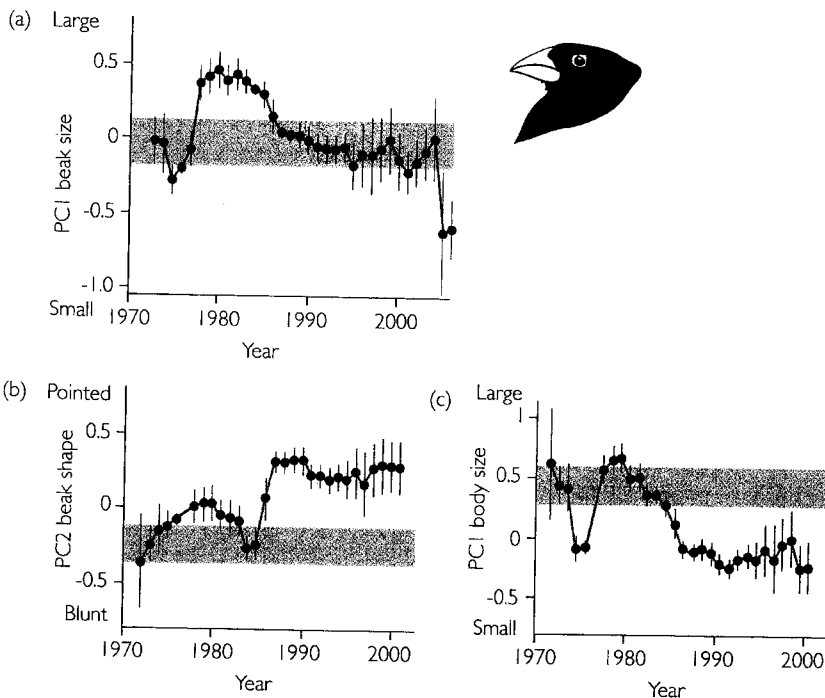
Figure 3.15 shows the pattern of change in the population averages for three traits across three decades. Each of the three traits is a statistical composite of measurable traits, like beak depth. For example, "PC1 beak size" (Figure 3.15a) combines beak depth, beak length, and beak width. The evolutionary changes that occurred as a result of 1977 drought are highlighted in red.

Figure 3.15a shows, first, what we have already seen: During the drought of 1977 the finch population evolved a significantly larger average beak size. In addition, the figure shows that the population remained at this large mean beak size until the mid-1980s, then evolved back to the mean beak size it started with. There the population stayed for many years, until another drought struck.

The drought of 2003 and 2004 was as bad as the drought of 1977 (Grant and Grant 2006). Once again the medium ground finches ran short of food and many perished. This time, however, the medium ground finches faced an additional challenge: competition from a substantial population of large ground finches (*Geospiza magnirostris*) that had become established on the island. The large ground finches dominated access to, and consumed, the *Tribulus* fruits on which the large-beaked medium ground finches had survived in 1977. As a result, the medium ground finches with large beaks died at higher rates than the ones with small beaks did, and the population evolved toward smaller beak size.

In its mean beak shape and mean body size the medium ground finch population also showed substantial evolution [Figure 3.15b and (c)]. The average bird in 2001 had a significantly sharper beak, and was significantly smaller than the average bird in the mid-1970s (Grant and Grant 2002).

Grant and Grant's long-term study demonstrates that Darwin's mechanism of evolution can be documented in natural populations. When all four of Darwin's



**Figure 3.15** Thirty years of evolution in the medium ground finch population on Isla Daphne Major. These graphs track the average adult values for beak size, beak shape, and body size among the *Geospiza fortis* on Daphne Major from the early 1970s into the 2000s. The vertical whiskers represent the 95% confidence interval for the estimated mean. If there had been no evolution, the confidence intervals for all dots would have overlapped the tan band—the 95% confidence interval for 1973, the first year with complete data. The changes that occurred during the drought of 1977 are indicated in red. In (a) the change that occurred during the drought of 2004 is indicated in orange. The population showed significant evolution in all three traits. (a) Rerendered from Grant and Grant (2006). (b) and (c) Rerendered from Grant and Grant (2002).

postulates are true in a population, the population evolves. The study also shows that small evolutionary changes over short time spans can accumulate into larger changes over longer time spans.

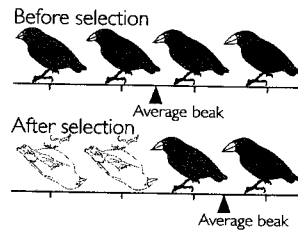
### 3.5 The Nature of Natural Selection

Although the Theory of Evolution by Natural Selection can be stated concisely, tested rigorously in natural populations, and validated, it can be difficult to understand thoroughly. One reason is that under Darwin's theory descent with modification is essentially a statistical process: a change in the trait distributions of populations. Statistical thinking does not come naturally to most people, and there are a number of widely shared ideas about natural selection that are incorrect. Our goal in this section is to cover some key points about how selection does and does not operate.

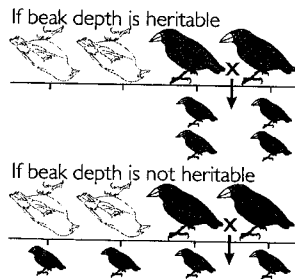
#### Natural Selection Acts on Individuals, but Its Consequences Occur in Populations

When HIV strains were selected by exposure to AZT, or finch populations were selected by changes in seed availability, none of the selected individuals (virions or finches) changed in any way. They simply lived through the selection event while others died or reproduced more than competing virions or birds. What changed after the selection process was the characteristics of the populations of virions and finches, not the affected individuals themselves. Specifically, a higher frequency of HIV virions in the population were able to replicate in the presence of AZT, and a higher proportion of finches had deep beaks.

To state this point another way, the effort of cracking *Tribulus* seeds did not make finch beaks become deeper and their bodies larger, and the effort of transcribing RNA in the presence of AZT did not change the amino acid composition of the reverse transcriptase active site. Instead, the average beak depth and body size in the finch population increased because more smaller finches died than larger ones (Figure 3.16), and the average active site sequence in reverse transcriptase changed because certain mutants did a better job of making new virions.



**Figure 3.16** Natural selection happens to individuals, but what changes is populations. During the drought on Daphne Major individuals did not change their beak depths; they simply lived or died. What changed was the average beak depth, a characteristic of the population.



**Figure 3.17** Populations evolve only if traits are heritable. If variation is due to differences in genotype, then the survivors of selection pass their successful phenotypes to their offspring.

#### Natural Selection Acts on Phenotypes, but Evolution Consists of Changes in Allele Frequencies

Finches with large bodies and deep beaks would have survived at higher rates during the drought even if all of the variation in the population had been environmental in origin (that is, if heritabilities had been zero). But no evolution would have occurred. Selection would have altered the frequencies of the phenotypes in the population, but in the next generation the phenotype distribution might have gone back to what it was before selection occurred (Figure 3.17).

Only when the survivors of selection pass their successful phenotypes to their offspring, via genotypes that help determine phenotypes, does natural selection cause populations to change from one generation to the next. On Daphne Major, the variation in finch phenotypes that selection acted on had a genetic basis. As a result, the new phenotypic distribution seen among the survivors persisted into the next generation.



# 11

## Sexual Selection

Male collared lizards (*Crotaphytus collaris*, above) wear brighter colors than females (below). They also attract more attention from predators. Jerry Husak and colleagues (2006) left painted clay models of males and females in the Wichita Mountains of Oklahoma and checked them over several days for bite marks left by mammals, snakes, and birds. Of 20 models of each sex, predators attacked 14 males and 0 females.

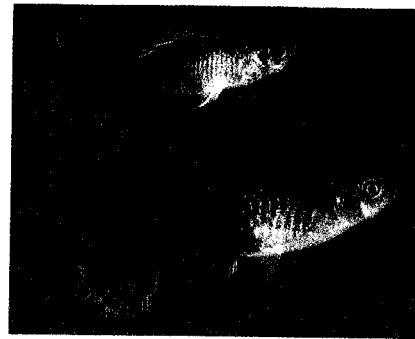


**M**ales and females often differ strikingly in size, appearance, and behavior. In marine iguanas, for example, males weigh twice as much as females. Males become intensely territorial during the breeding season, while females remain gregarious throughout the year. In long-tailed widowbirds, the adults of the two sexes have plumage so distinct that it would be easy to mistake them for different species. Males are jet black, carry tail feathers several times the length of their own bodies, and have red and yellow shoulder patches. Females are colored a cryptic brown, with short tail feathers and no shoulder patches. In gray tree frogs, males have dark throats and sing. Females have white throats and are silent. In stalk-eyed flies, both sexes wear their eyes on the ends of long thin stalks, but males have longer eyestalks than females. In some species of pipefish, females have blue stripes and skin folds on their bellies. Males lack these ornaments. The photos of males and females in Figure 11.1 provide additional examples.

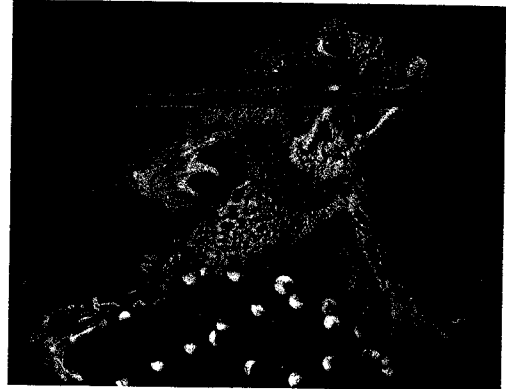
In humans, too, females and males are conspicuously different. Our differences exceed the obvious and essential ones in genitalia and reproductive organs. They are found in the appearance of our faces, the sound of our voices, the distribution of our body fat and body hair, and our size. The size difference between women and men is documented in Figure 11.2.



(a) Red deer



(b) Guppies



(c) Golden toads

**Figure 11.1** The differences between males and females (the sexual dimorphism) in red deer (*Cervus elaphus*), guppies (*Poecilia reticulata*), and golden toads (*Bufo perigrinus*). In (a), the male is on the left; in (b) and (c), the male is on the top.

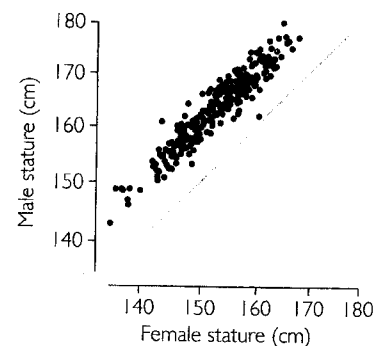
*A difference between the sexes is called a sexual dimorphism.*

A difference between the males and females of a species is called a **sexual dimorphism**. In this chapter, we ask why sexual dimorphism occurs in such a great variety of organisms. It is a question Charles Darwin (1871) wrote half a book about, and it has captivated evolutionary biologists ever since.

## 11.1 Sexual Dimorphism and Sex

In previous chapters, we have explained the traits of organisms with the theory of evolution by natural selection. In Chapter 3, for example, we saw how natural selection shapes the beaks of medium ground finches on Daphne Major. When the finches face a drought and small soft seeds are rare, big beaks confer an advantage. Big beaks help finches survive by enabling them to open large, hard seeds and

**Figure 11.2 Women and men differ in height** For each of more than 200 human societies, the average height of the men is plotted against the average height of the women. The diagonal line shows where the points would fall if men and women were of equal height. People vary widely in height from society to society: In the shortest society, the average man is about 143 cm tall (about 4 feet, 8 inches) and the average woman about 135 cm (~4'5"); in the tallest society, the average man is about 180 cm tall (~5'11"), and the average woman about 165 cm (~5'5"). But in every society the average man is taller than the average woman, usually by about 10%. From Rogers and Mukherjee (1992).



thus get more to eat. When the big-beaked survivors reproduce, they pass genes for big beaks to their offspring. In a similar way, natural selection can explain a great variety of other traits, from the bars on fly wings (see Figure 10.7, page 369) to the hiding places chosen by garter snakes (see Figure 10.11, page 375). But differences between the sexes of a species, like those shown in Figure 11.1, are often not among them.

To see why, try to imagine how we might use evolution by natural selection to explain the tail streamers in male long-tailed widowbirds (Figure 11.3). Two problems arise. First, if long tail feathers can improve the survival or fecundity of a widowbird, then why do only males have them? Second, how could enormously long tail feathers improve the survival, or the fecundity, of widowbirds in the first place? As with bright colors in collared lizards, long tail feathers probably make male widow birds easier for predators to find and catch. Furthermore, long tail feather requires considerable energy to grow, maintain, and drag around (see Pryke and Anderson 2005; Walther and Clayton 2005). Energy spent on feathers is energy that cannot be spent on making offspring. It appears that the theory of evolution by natural selection can explain neither why male and female widow birds are different nor why the birds' most striking trait, long tail feathers, exists at all.

As Darwin himself was the first to recognize, sex provides a solution to the puzzle of sexual dimorphism. To see why, consider life without sex. For organisms that reproduce without sex (see Chapter 8), getting genes into the next generation is straightforward, if not always easy. The two big challenges are surviving long enough to reproduce, then reproducing. Sex adds a third major challenge: finding a member of the opposite sex and persuading him or her to cooperate.

Charles Darwin realized that individuals vary not only in their success at surviving and reproducing, but also in their success at persuading members of the opposite sex to mate. About birds, for example, Darwin wrote,

“Inasmuch as the act of courtship appears to be with many birds a prolonged and tedious affair, so it occasionally happens that certain males and females do not succeed during the proper season, in exciting each other's love, and consequently do not pair” (1871, page 107).

In its evolutionary consequences, failing to mate is the same as dying young. The victim makes no genetic contribution to future generations. Darwin had already applied the label natural selection to differential reproductive success due to variation among individuals in survival and reproduction. Differential reproductive success due to variation among individuals in success at getting mates he called **sexual selection**. We can develop a theory of evolution by sexual selection that is logically equivalent to the theory of evolution by natural selection: If there is heritable variation in a trait that affects the ability to obtain mates, then variants conducive to success will become more common over time.

### Asymmetries in Sexual Reproduction

If sexual selection is to explain differences between the sexes, it will have to act on the sexes differently. Angus John Bateman (1948) argued that it can. The logic he developed to support his claim was later refined by Robert Trivers (1972). It hinges on a simple observation: In many animals, eggs (or pregnancies) are more expensive than ejaculates.

In more general terms, mothers typically make a larger parental investment in each offspring than fathers. By **parental investment** we mean energy and time

*Sexual dimorphism is often a puzzle, because natural selection cannot always explain it.*

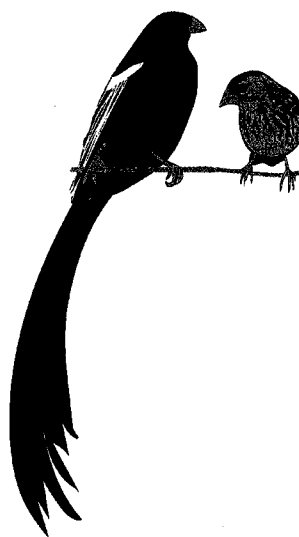


Figure 11.3 The sexual dimorphism in long-tailed widowbirds (*Euplectes progne*) The male is black with long tail feathers and red and yellow shoulder patches; the female is brown and cryptic.

### Asymmetric Limits on Reproductive Success in Newts and Pipefish

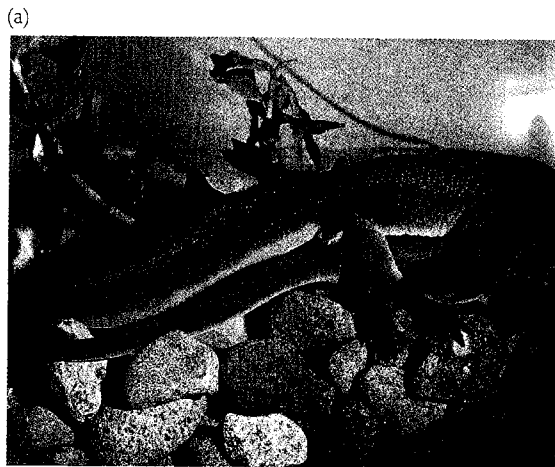
Adam Jones and colleagues (2002) quantified the relative strength of sexual selection on male and female rough-skinned newts (*Taricha granulosa*). Male rough-skinned newts gather in ponds in early winter to wait for females. Females saunter in during January and February, easily attract amorous males (Figure 11.5a), and finish mating shortly after arriving. As a result, at any given time more males than females are prowling the pond. After mating, females lay 300 or more eggs, one at a time, over several weeks or months. Neither parent cares for the young. The cost of eggs and sperm thus accounts for the entirety of parental investment. The investment per offspring is larger for females than for males.

Jones and colleagues captured all the newts from a single pond when the newts had finished mating and the females were laying eggs. The biologists housed the females in individual containers, induced them to lay the rest of their eggs by injecting them with hormones, and reared the eggs to hatching. The researchers used genetic tests to identify each hatchling's father. This gave Jones and colleagues sufficient information to determine the number of mates, and the number of offspring, for all the adults in their sample.

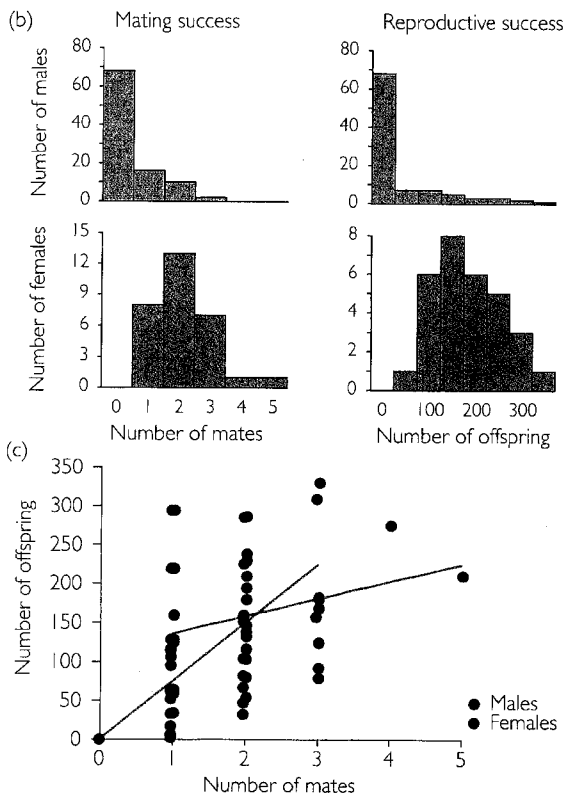
The majority of the males, it turned out, failed to mate (Figure 11.5b, upper left). Of those that succeeded, most mated just once or twice. In sharp contrast, all of the females mated at least once, and most mated two or three times (Figure 11.5b, lower left).

Not surprisingly, the males showed a pronounced variation in number of offspring (Figure 11.5b, upper right). Those who failed to mate, of course, fathered no offspring, while the lucky few fathered as many as 300 or more. All of the females had offspring, most between 100 and 300 of them (Figure 11.5b, lower right).

Of greatest interest is the extent to which access to mates determined reproductive success. Figure 11.5c plots number of offspring versus number of mates for both sexes, along with best-fit lines showing the average effect of a change in mating success on reproductive success (Arnold and Duvall 1994). Look first at the data for females (red dots and line). It appears that mating with more than one male may have carried some benefit. The slope of the best-fit line, however, is not statistically distinguishable from zero. For males, however, the association between number of mates and number of offspring was strong and highly significant (blue dots and line). For males, more mates meant more offspring.

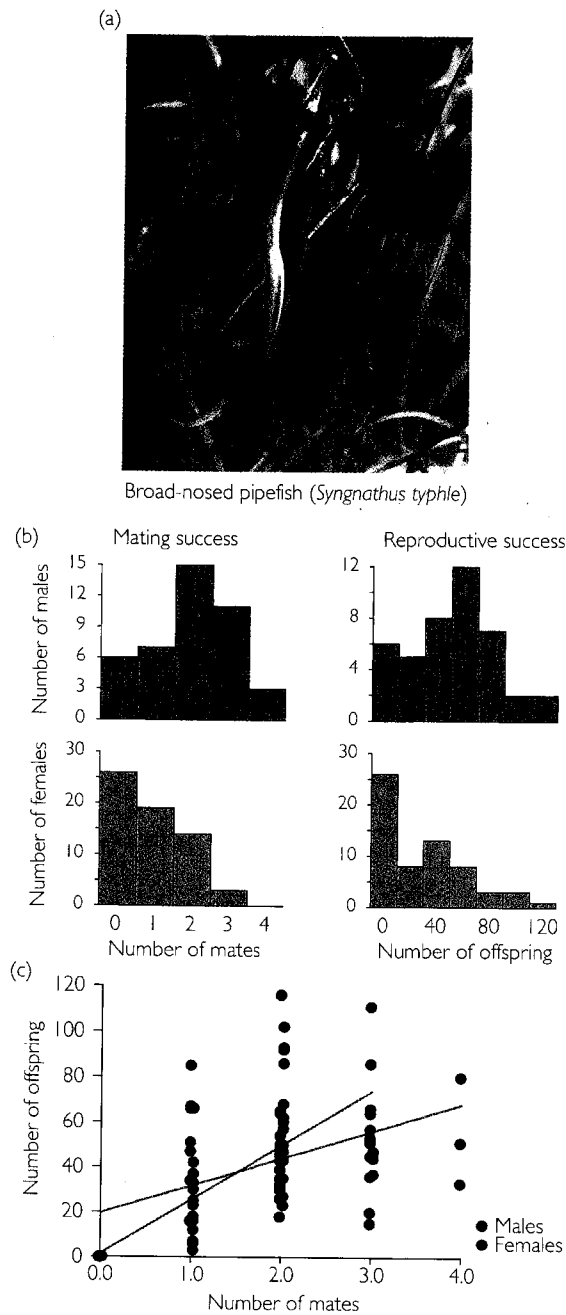


Rough-skinned newt (*Taricha granulosa*)



**Figure 11.5** Asymmetries in sexual reproduction in rough-skinned newts (a) A mating pair: The male is above, the female below. (b) The distributions of number of mates and number of offspring for male (blue) and female (red) newts in a natural population. (c) Reproductive success versus number of mates for male (blue) and female (red) rough-skinned newts in a natural population. The slope of the best-fit line, or Bateman gradient, is steeper for males than for females ( $P < 0.001$ ). Plotted from data provided by Adam G. Jones, Georgia Institute of Technology.





**Figure 11.6** Asymmetries in sexual reproduction in broad-nosed pipefish (a) A mating pair: The male is on the left, the female on the right. (b) Reproductive success versus number of mates for male (blue) and female (red) broad-nosed pipefish in a laboratory experiment. (c) Reproductive success versus number of mates for male (blue) and female (red) broad-nosed pipefish in a laboratory experiment. The slope of the best-fit line is steeper for females than for males ( $P = 0.004$ ). Graphs plotted from data provided by Adam G. Jones, Georgia Institute of Technology.

This result is consistent with Bateman's prediction. In rough-skinned newts, sexual selection is a more potent force in the evolution of males than in the evolution of females. This means that heritable traits that are associated, in males, with failure to mate will tend to disappear, while heritable traits associated with mating success will tend to become common. Male rough-skinned newts develop crests on their tails during the breeding season, and Jones and colleagues found that males who found mates displayed significantly taller crests than males that failed. We can infer that tail crests evolved as a result of sexual selection.

The pattern we have seen in rough-skinned newts is common. For males more than females in many species, fitness is determined by access to mates. But the pattern is by no means universal. This we can see from data on sexual selection in broad-nosed pipefish.

Broad-nosed pipefish (*Syngnathus typhle*) live in eelgrass beds (Figure 11.6a). In pipefish families, as in their kin, the seahorses, the father provides all the parental care. The male has a brood pouch into which the female lays her eggs. The male carries the eggs, protects them, and provides them with oxygen and nutrients until they hatch (Figure 11.7). Adam Jones and colleagues (2000; see also Jones et al. 2005) caught pipefish off the coast of Sweden before the breeding season began and let them mate in barrels in the lab. The data in Figure 11.6 come from two experiments. In the first, each barrel contained four males and four females. In the second, each barrel contained two males and six females. The second experiment probably mimics natural conditions more closely than the first. It takes a female less time to produce a clutch of eggs than it takes a male to rear them to hatching (Berglund et al. 1989). As a result, at any given time there are more females with eggs to lay than males with space to accept them.

Jones and colleagues used genetic tests to determine each offspring's mother. As in the newt study, this enabled the biologists to determine the number of mates and the number of offspring for each adult.

The results for pipefish are similar to those for newts, except that the roles of the sexes are reversed. In pipefish, more females than males failed to mate (Figure 11.6b, upper and lower left). Consequently, the reproductive success of females was more skewed than the reproductive success of males, with a sharper distinction between the winners and the losers (Figure 11.6b, upper and lower right). Most importantly, it was in females that reproductive success depended most strongly on mating success (Figure 11.6c). In broad-

nosed pipefish, sexual selection is a more potent force in the evolution of females than it is in the evolution of males. Heritable traits that are associated, in females, with failure to mate will tend to disappear, while heritable traits associated with mating success will become more common. We need to keep this result in mind as we consider the behavioral consequences of asymmetrical limits on fitness.

### Behavioral Consequences of Asymmetric Limits on Fitness

An asymmetry in the factors that limit reproductive success for females versus males allows us to predict differences in the mating behavior of the two sexes. Consider the pattern seen in Jones et al.'s rough-skinned newts. For males reproductive success is limited by access to mates, and at any given time there are more males than females in the pond looking for love. Under such circumstances, we can predict that males will compete amongst themselves for opportunities to fertilize eggs. For females, in contrast, reproductive success is limited by capacity to make eggs, mating involves the commitment of a large investment, and there is an excess of willing partners. We can expect that females will be selective about which partners they accept and which they reject.

More generally, when sexual selection is strong for one sex and weak for the other we can predict that:

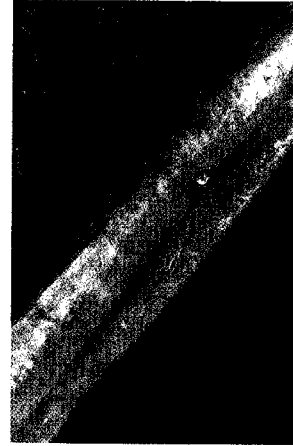
- **Members of the sex subject to strong sexual selection will be competitive.**
- **Members of the sex subject to weak sexual selection will be choosy.**

These predictions have been confirmed in a great variety of animal species. We will look at some examples shortly.

In making these general predictions, we have used inclusive language for a reason. It is easy to get carried away with generalities, as Bateman and many who followed appear, in hindsight, to have done (see Knight 2002). Bateman thought that greater sexual selection on males than on females is inherent in maleness and femaleness as such. He and others therefore assumed that the optimal strategy for males, in virtually any species, would be to mate with as many females as possible, and that the optimal strategy for females would be to choose one male and mate with him only. These assumptions have often turned out to be wrong. We will see, later in the chapter, that males often have good reasons to stick with one mate and that females often have good reasons to be promiscuous.

Furthermore, as Jones et al.'s pipefish study shows, greater sexual selection on males than on females is not inherent in the identity of the sexes themselves. When access to mates is limiting for females instead of males, we predict that females will compete with each other over access to males and that males will be choosy.

Competition for mates in one sex and choosiness in the other can play out in two ways. First, members of the competitive sex may fight amongst themselves, head-to-head, claw-to-claw, or antler-to-antler. Sometimes they fight over direct control of mates, sometimes they fight over control of a resource vital to mates, and sometimes they just fight. The members of the other sex then mate with the winners. This form of sexual selection is called **intrasexual selection**, because the key event that determines reproductive success (the fighting) involves interactions among the members of a single sex. Second, instead of fighting the members of the competitive sex may advertise



**Figure 11.7** A pregnant male pipefish, *Syngnathus typhle*, gives birth. This hatchling is emerging from his father's brood pouch, where it developed under its father's care after its mother deposited her eggs there.

*Theory predicts that when one sex is subject to sexual selection and the other is not, the members of the sex experiencing selection will compete over mates and the members of the other sex will be choosy.*

for mates by singing, dancing, or showing off bright colors. The members of the other sex then choose the individual with the best display. This form of sexual selection is called **intersexual selection**, because the key event that determines reproductive success (the choosing) involves an interaction between members of the two sexes.

In the next two sections, we will look at examples of intrasexual and intersexual selection on males. We then will look at sexual selection on females.

## 11.2 Sexual Selection on Males: Competition

Sexual selection by male–male competition often occurs when individual males can monopolize access to females. Males may monopolize females through direct control of the females themselves or through control of some resource important to females, such as feeding territory or nest sites. Male–male competition can also occur for no apparent reason beyond simply impressing females. In this section, we consider examples of research into three forms of male–male competition: outright combat, sperm competition, and infanticide.

### Combat

Outright combat is the most obvious form of male–male competition for mates. Intrasexual selection involving male–male combat over access to mates can favor morphological traits including large body size, weaponry, and armor. Male–male combat also selects for tactical cleverness.

Our example of male–male combat comes from the marine iguanas (*Amblyrhynchus cristatus*) of the Galápagos Islands (Figure 11.8). Marine iguanas have a lifestyle unique among the lizards. They make their living grazing on algae in the intertidal zone. Between bouts of grazing, they bask on rocks at the water's edge. Basking warms the iguanas, which aids digestion and prepares them for their next foray into the cold water. Marine iguanas grow to different sizes on different islands, but, as we mentioned earlier, on any given island the males get larger than the females (Figure 11.9a).

*Male–male competition can take the form of combat over access to females.*



**Figure 11.8** A Galápagos marine iguana. These unusual lizards make their living foraging on algae in the intertidal zone.

therefore adaptive for male flowers to train bees to avoid other male flowers, so long as they do not also train the bees to avoid female flowers. If this scenario is correct, forcible attachment of the pollinarium to the bee and sexually dimorphic flowers make sense together, and both are due to competition for mates—that is, to sexual selection.

## 11.6 Sexual Dimorphism in Body Size in Humans

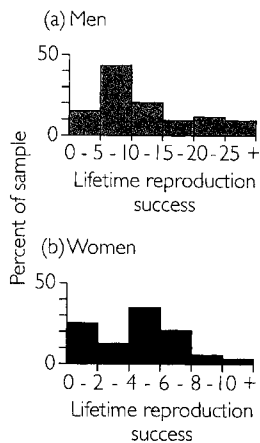
One of the examples of sexual dimorphism that we cited at the beginning of this chapter was body size in humans (Figure 11.2, page 402). We now ask whether the sexual dimorphism in human size is the result of sexual selection. It is a difficult question to answer because sexual selection concerns mating behavior. The evolutionary significance of human behavior is hard to study for at least two reasons:

- Human behavior is driven by a complex combination of culture and biology. Studies based on the behavior of people in any one culture provide no means of disentangling these two influences. Cross-cultural studies can identify universal traits or broad patterns of behavior, either of which may warrant biological explanations. Cultural diversity is rapidly declining, however, and some biologists feel that it is no longer possible to do a genuine cross-cultural study.
- Ethical and practical considerations prohibit most of the kinds of experiments we might conduct on individuals of other species. This means that most studies of human behavior are observational. Observational studies can identify correlations between variables, but they offer little evidence of cause and effect.

Human behavior is inherently fascinating, however, and we therefore proceed, with caution, to briefly consider the question of sexual selection and body size in humans.

The most basic knowledge of human reproductive biology indicates that the opportunity for sexual selection is greater in men than in women. Data from a single culture will suffice to illustrate this point. Research by Monique Borgerhoff Mulder (1988) on the Kipsigis people of southwestern Kenya revealed that the men with highest reproductive success had upwards of 25 children, while the most prolific women rarely had more than 10 (Figure 11.38). In Kipsigis culture, it appears that the reproductive success of men was limited by mating opportunities to a greater extent than was the reproductive success of women. But is there any evidence that reproductive competition, either via male–male interactions or female choice, selects for larger body size in men?

The most obvious kind of sexual selection to look at is male–male competition, because it drives the evolution of large male size in a great variety of other species. Men do, on occasion, compete among themselves over access to mates, but so do women. Do men compete more intensely? On the reasoning that homicide is an unambiguous indication of conflict, and that virtually all homicides are reported to the police, Martin Daly and Margo Wilson (1988) assembled data on rates of same-sex homicide from a variety of modern and traditional cultures. In all of these cultures, men kill men at much higher rates than women kill women. In the culture with the most balanced rates of male–male versus female–female killings, men committed 85% of the same-sex homicides. In several cultures, men committed all of the same-sex homicides.



**Figure 11.38** Variation in lifetime reproductive success among Kipsigis men and women

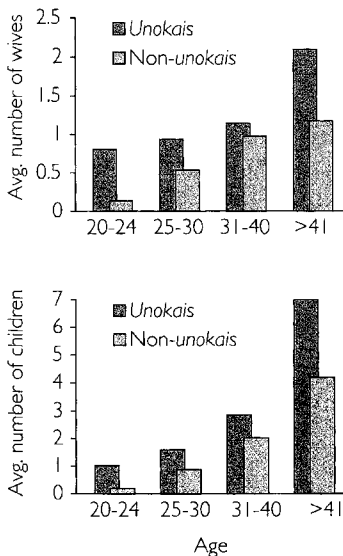
(a) For the men, the height of each bar represents the percentage of men who had 0 to 5 children, 6 to 10 children, and so on. (b) For the women, the height of each bar represents the percentage of women who had 0 to 2 children, 3 or 4 children, 5 or 6 children, and so on. Some of the men had more than 25 children; few of the women had more than 10. From Borgerhoff Mulder (1988).

Data from the United States and Canada show that the majority of perpetrators, and victims, of male–male homicides are in their late teens, twenties, and early thirties. On these and other grounds, Daly and Wilson interpret much male–male homicide as a manifestation of sexually selected competition among men.

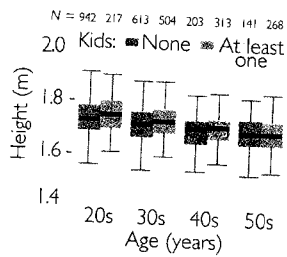
If Daly and Wilson’s interpretation is correct, then men who are more successful in male–male combat should have higher mating success and higher fitness, at least in pre-modern cultures without formal police and criminal justice systems. Napoleon Chagnon (1988) reported data on the Yanomamö that confirm this prediction, at least for one culture. The Yanomamö are a pre-modern people that live in the Amazon rain forest in Venezuela and Brazil. They take pride in their ferocity. Roughly 40% of the adult men in Chagnon’s sample had participated in a homicide, and roughly 25% of the mortality among adult men was due to homicide. The Yanomamö refer to men who have killed as *unokais*. Chagnon’s data show that *unokais* have significantly more wives, and significantly more children, than non-*unokais* (Figure 11.39).

The Yanomamö fight with clubs, arrows, spears, machetes, and axes. It would be reasonable to predict that *unokais* are larger than non-*unokais*. Chagnon (1988) reports, however, that “Personal, long-term familiarity with all the adult males in this study does not encourage me to conclude at this point that they could easily be sorted into two distinct groups on the basis of obvious biometric characters, nor have detailed anthropometric studies of large numbers of Yanomamö males suggested this as a very likely possibility.” Data on the relationship between male–male competition, body size, and mating success in other cultures are scarce.

B. Pawlowski and colleagues (2000) investigated the hypothesis that the sexual dimorphism in human body size is a result of female choice. The researchers gathered data from the medical records of 3,201 Polish men. They used statistical techniques to remove the effects of a variety of confounding variables, including residence in cities versus rural areas, age, and education. Pawlowski and



**Figure 11.39 Mating and reproductive success of unokais (killers) versus non-unokais among Yanomamö men** These graphs show the average number of wives (top) and children (bottom) for adult men of various ages. Taken together, the data show that *unokais* are more successful than non-*unokais* ( $P < 0.00001$ ). Plotted from data in Chagnon (1988).



**Figure 11.40 Men with children are taller, on average, than childless men.** The heavy horizontal bars show, for a sample of Polish men, the average height of individuals in each age class, by whether or not they have children. The colored boxes show  $\pm 1$  standard deviation around the mean; the whiskers show the range about the mean that includes 95% of the men.  $N$  is the number of men in each category. Though small, the differences between men with versus without children are statistically significant for men in their twenties ( $P = 0.005$ ), thirties ( $P = 0.001$ ), and forties ( $P = 0.002$ ). The difference is not significant for men in their fifties ( $P = 0.863$ ). From Pawlowski et al. (2000).

*It is unclear whether sexual selection helps maintain the sexual dimorphism in body size in humans. Males compete for mates, but larger males do not necessarily win. Females are choosy, and limited data suggest a slight preference for taller men.*

colleagues then compared bachelors to married men. The married men were taller by a slight but statistically significant margin. In addition, men with one or more children were significantly taller than childless men (Figure 11.40). The exception to this pattern was the group of men in their fifties, within which there was no difference in height between fathers versus childless men. Pawlowski and colleagues note that the men in their fifties reached marrying age shortly after World War II, when the ratio of women to men in Poland was unusually high. The researchers speculate that the men in their fifties had experienced less intense sexual selection, through female choice, than is the norm.

Additional evidence suggesting that female choice favors tall men comes from a study by Ulrich Mueller and Allan Mazur (2001). Mueller and Mazur surveyed members of the class of 1950 from the United States Military Academy at West Point. Among these career officers, unlike in many other more diverse populations, height was not associated with social status or socioeconomic success. Height was, however, associated with reproductive success. The tallest men had, over their lifetimes, more wives, and younger second wives, than other men. As a result, the tallest men had more children.

Daniel Nettle (2002) examined the relationship between height and reproductive success in women. Analyzing data from a large national health survey in Britain, Nettle found a weak but significant effect. Unlike in men, selection on women is stabilizing. Women of slightly less than average height had more children than either shorter or taller women. The cause appears to be that women of moderate height were healthier, on average, than extremely short or extremely tall women. That is, the higher fitness of slightly shorter-than-average women is due to natural selection.

On the data we have reviewed, then, there is some evidence that sexual selection, primarily through female choice, is responsible for the fact that men are taller than women. It is best, however, to consider the evolutionary significance of sexual size dimorphism in humans unresolved. The studies we have reviewed are observational, and the associations they documented are small. As a result, the evidence they provide about causation is only suggestive. It is possible that we humans simply inherited our sexual size dimorphism from our ancestors, who were more sexually dimorphic in size than we are (McHenry 1992). What is really needed to settle the issue is data from a larger number of cultures on the relationship between body size, number of mates, survival, and reproductive success for both women and men. Preferably, the data would come from hunter-gatherer cultures, whose members live the lifestyle ancestral for our species. The most technically challenging factor to measure accurately is the reproductive success of men. Modern techniques for genetic analysis have made it feasible, in principle, to collect such data (Figure 11.32, page 431). However, the research remains to be done.

## Summary

Sexual dimorphism, a difference in form or behavior between females and males, is common. The difference often involves traits, like the enormous tail feathers of the peacock, that appear to be opposed by natural selection. To explain these puzzling traits, Dar-

win invoked sexual selection. Sexual selection is differential reproductive success resulting from variation in mating success.

Mating success is often a more important determinant of fitness for one sex than for the other. Often,

# 12

## Kin Selection and Social Behavior

**S**ocial interactions create the possibility for conflict and cooperation. Consider two American crows (*Corvus brachyrhynchos*) patrolling the edge of their adjacent nesting territories. If one moves across the established boundary, its action may trigger aggressive calls, a flight chase, or even physical combat. But if a hawk flies by, the two antagonists will cooperate in chasing the predator away. Later in the day, these same individuals may spend considerable time and effort feeding the young birds in the nests in their respective territories, even though the nestlings are the crows' siblings or half-siblings and not their own offspring.

When and why do these individuals cooperate with each other, and why do they help their parents raise their siblings instead of leaving home to rear their own offspring? What conditions lead to conflicts with each other and with their parents, and how are these conflicts resolved? These are the types of questions addressed in this chapter.

In fitness terms, an interaction between individuals has four possible outcomes (Table 12.1). Cooperation (or **mutualism**) is the term for actions that result in fitness gains for both participants. **Altruism** represents cases in which the individual instigating the action pays a fitness cost and the individual on the receiving end benefits. In other words, altruism entails a sacrifice on behalf of another.

Genetically related female banded mongooses live and breed in groups, and care for each other's young (Gilchrist 2004; Gilchrist et al. 2004; Hodge 2005).

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**Table 12.1** Types of social interactions

The “actor” in any social interaction affects the recipient of the action as well as itself. The costs and benefits of interactions are measured in units of surviving offspring (fitness).

	Actor benefits	Actor is harmed
Recipient benefits	Cooperative Selfish	Altruistic Spiteful
Recipient is harmed		

**Selfishness** is the opposite: The actor gains and the recipient loses. **Spite** is the term for behavior that results in fitness losses for both participants.

Understanding the evolution of these four interactions is simplified because spite, if it exists in nature, is rare (Keller et al. 1994; for discussion of possible examples see Hurst 1991, Foster et al. 2000, Foster et al. 2001, Gardner and West 2004, Johnstone and Bshary 2003). The rarity of spite is readily explained: An allele that results in fitness losses for both actor and recipient would quickly be eliminated by natural selection. Intuition might suggest that a spiteful actor could come out ahead if the cost he imposes on a competitor is greater than cost he suffers himself. Consider, however, the fitness of a third party who avoids involvement in spiteful acts and pays neither the cost of doling them out nor the cost of receiving them.

Altruism would seem equally difficult to explain because the actor suffers a fitness loss. Altruistic behavior appears to be common, however. Examples range from the crows that help at their parents’ nests to a human who dives into a river and saves a drowning child. This is the first question we need to address: Why does altruism exist in nature?

## 12.1 Kin Selection and the Evolution of Altruism

Altruism is a central paradox of Darwinism. It would seem impossible for natural selection to favor an allele that results in behavior benefiting other individuals at the expense of the individual bearing the allele. For Darwin (1859: 236), the apparent existence of altruism presented a “special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory.” Fortunately he was able to hint at a resolution to the paradox: Selection could favor traits that result in decreased personal fitness if they increase the survival and reproductive success of close relatives. Over a hundred years passed, however, before this result was formalized and widely applied.

### Inclusive Fitness

In 1964, William Hamilton developed a genetic model showing that an allele that favors altruistic behavior could spread under certain conditions (Hamilton 1964a). The key parameter in Hamilton’s formulation is the **coefficient of relatedness,  $r$** . This is the probability that the homologous alleles in two individuals are **identical by descent** (Box 12.1). The parameter is closely related to  $F$ , the coefficient of inbreeding, which we introduced in Chapter 6.  $F$  is the probability that homologous alleles in the same individual are identical by descent.

*Explaining altruistic behavior is a challenge for the Theory of Evolution by Natural Selection.*



### Box 12.1 Calculating coefficients of relatedness

Calculating  $r$ , the coefficient of relatedness, requires a pedigree that includes the actor (the individual dispensing the behavior) and the recipient (the individual receiving the behavior). Starting with the actor, all paths of descent are traced through the pedigree to the recipient. For example, half-siblings share one parent and have two genealogical connections, as indicated in Figure 12.1a. Parents contribute half their genes to each offspring, so the probability that genes are identical by descent (ibd) in each step in the path is  $1/2$ . Put another way, the probability that a particular allele was transmitted from parent to actor is  $1/2$ . The probability that the same allele was transmitted from parent to recipient is  $1/2$ . The probability that this same allele was transmitted to both the actor and the recipient (meaning that the alleles in actor and recipient are ibd) is the product of these two independent probabilities, or  $1/4$ .

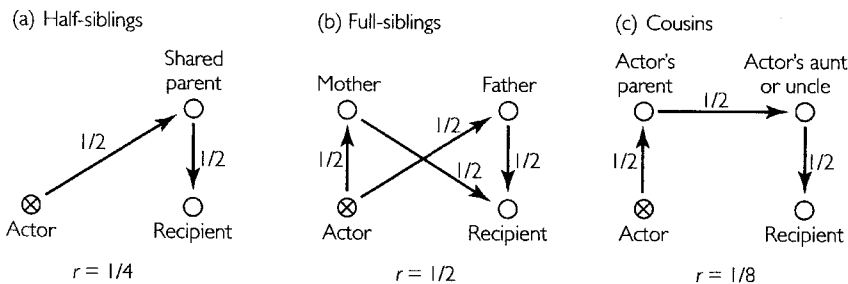
Full siblings, on the other hand, share genes inherited from both parents. To calculate  $r$  when actor and recipient are full-siblings, we have to add the probabilities that genes are ibd through each path in the pedigree. In this case, we add the probability that genes are ibd through the mother to the probability that they are ibd through the father (see Figure 12.1b). This is  $\frac{1}{4} + \frac{1}{4} = \frac{1}{2}$ .

Using this protocol results in the following coefficients:

- First cousins,  $\frac{1}{8}$  (Figure 12.1c)
- Parent to offspring,  $\frac{1}{2}$
- Grandparent to grandchild,  $\frac{1}{4}$
- Aunt or uncle to niece or nephew,  $\frac{1}{4}$

The analyses we have just performed work for autosomal loci in sexual organisms and assume that no inbreeding has occurred. If the population is inbred, then coefficients will be higher. But when studying populations in the field, investigators usually have no data on inbreeding and have to assume that individuals are completely outbred. On this basis, coefficients of relationship that are reported in the literature should be considered minimum estimates. Another uncertainty in calculating values of  $r$  comes in assigning paternity in pedigrees. As we indicated in Chapter 10, extra-pair copulations are common in many species. If paternity is assigned on the basis of male-female pairing relationships and extra-pair copulations go undetected, estimates of  $r$  may be inflated.

When constructing genealogies is impractical, coefficients of relatedness can be estimated directly from genetic data (Queller and Goodnight 1989). Microsatellites and other marker loci are proving to be extremely useful for calculating  $r$  in a wide variety of social insects (e.g., Peters et al. 1999).



**Figure 12.1** Computing relatedness with pedigrees The arrows describe paths by which genes can be identical by descent. The text explains how these paths are used to calculate  $r$ , the coefficient of relatedness.

Given  $r$ , the coefficient of relatedness between the actor and the recipient, **Hamilton's rule** states that an allele for altruistic behavior will spread if

$$Br - C > 0$$

where  $B$  is the benefit to the recipient and  $C$  is the cost to the actor. Both  $B$  and  $C$  are measured in units of surviving offspring. This simple law means that

*Inclusive fitness consists of direct fitness due to personal reproduction and indirect fitness due to additional reproduction by relatives. Behavior that results in indirect fitness gains is favored by kin selection.*

altruism is more likely to spread when the benefits to the recipient are great, the cost to the actor is low, and the participants are closely related.

To generalize this result, Hamilton offered the concept of **inclusive fitness**. He pointed out that an individual's fitness can be partitioned into two components. **Direct fitness** results from personal reproduction. **Indirect fitness** results from additional reproduction by relatives that is made possible by an individual's actions. Indirect fitness accrues when relatives achieve reproductive success above and beyond what they would have achieved on their own—that is, without aid. Natural selection favoring the spread of alleles that increase the indirect component of fitness is called **kin selection**. As we will see, most instances of altruism in nature are the result of kin selection.

Robert Trivers (1985:47) called Hamilton's rule and the concept of inclusive fitness "the most important advance in evolutionary theory since the work of Charles Darwin and Gregor Mendel." To see why, we will apply the theory by venturing to the Sierra Nevada of California and observing a social mammal: Belding's ground squirrel (*Spermophilus beldingi*).

### Alarm Calling in Belding's Ground Squirrels and Prairie Dogs

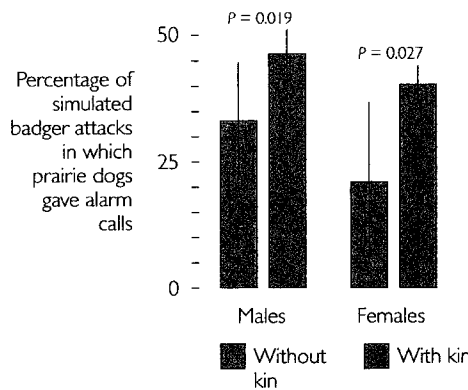
Explaining alarm calling in birds and mammals is a classical application of inclusive fitness theory. When flocks or herds are stalked by a predator, prey that notice the intruder sometimes give loud, high-pitched calls. These warnings alert nearby individuals and allow them to flee or dive for cover. They may also expose the calling individual to danger.

The first question to ask is whether alarm calls are genuinely altruistic. Research by Paul Sherman (1985) on Belding's ground squirrels shows why. Belding's ground squirrels give two kinds of alarms: they trill in response to predatory mammals and whistle in response to flying hawks. During 14 years of observation, Sherman and his assistants witnessed 30 natural predator attacks in which ground

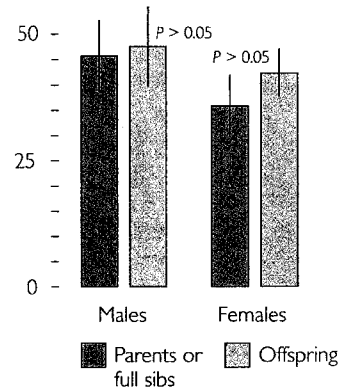
(a) A black-tailed prairie dog giving an alarm call



(b) Prairie dogs without kin in home coterie versus prairie dogs with kin in home coterie



(c) Prairie dogs with parents or full siblings (but no offspring) in home coterie versus prairie dogs with offspring in home coterie



**Figure 12.2 Black-tailed prairie dogs give more alarm calls when kin are nearby** (a) This black-tailed prairie dog is giving an alarm call. (b) This bar chart reports the rates of alarm calling by prairie dogs who have vs. do not have kin living with them. Both sexes call more often when kin are near. (c) This chart reports the rates of alarm calling by males and females living with non-offspring kin vs. offspring. Both sexes call nearly as often when non-offspring kin are near as when offspring are near. Redrawn from Hoogland (1995).

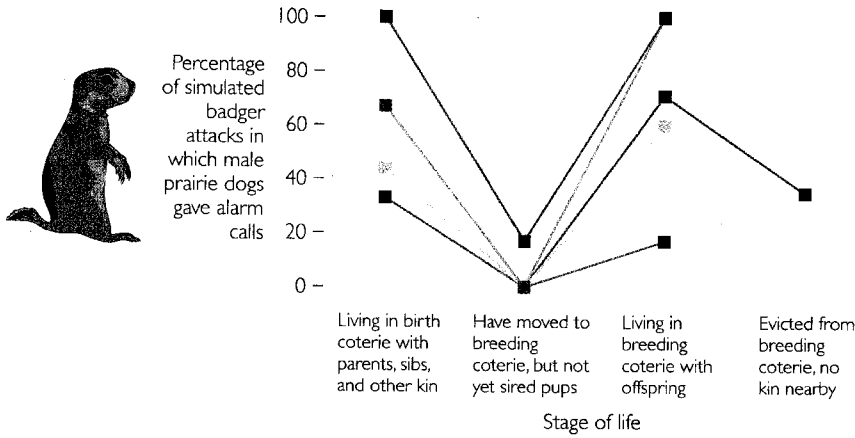


Figure 12.3 Male black-tailed prairie dogs change their alarm calling behavior when their living situation changes. This graph plots the rate of alarm calling by five individual males at different stages of life. The males increased or decreased their rate of calling according to whether kin were nearby. Redrawn from Hoogland (1995).

squirrels were captured and killed. It turns out that when squirrels spot an attacking hawk and whistle, the whistling squirrel is captured only 2% of the time while nonwhistling squirrels are captured 28% of the time. The squirrel raising the alarm reduces its own chances of dying, perhaps by informing the hawk that the caller has seen it and at the same time sowing panic and confusion among the other squirrels. When squirrels spot an attacking mammal and trill, however, the trilling squirrel is killed 8% of the time while non-trilling squirrels are killed only 4% of the time. The squirrel raising the alarm increases its own peril to the benefit of other squirrels nearby. Whistles are selfish, but trills are altruistic.

John Hoogland (1983, 1994, 1995) studied alarm calls given by black-tailed prairie dogs (Figure 12.2a). Prairie dogs live family groups called coterie; each coterie occupies a territory within a prairie dog town. Females typically remain in their birth coterie for life, whereas males usually disperse when sexually mature. Despite logging over 50,000 person-hours watching individually marked prairie dogs in a town in South Dakota, Hoogland and his assistants were unable to document for certain whether prairie dog alarms are selfish or altruistic. Hoogland suspected that they are altruistic, however, and sought to determine whether the prairie dogs' calling behavior was consistent with the hypothesis that it evolved as a result of kin selection. Hoogland simulated predator attacks by having an assistant pull a stuffed badger through a prairie dog town on a sled, and watched to see who gave alarm calls and who just dove for cover.

Both male and female prairie dogs are more likely to give alarm calls if their coterie includes genetic kin (Figure 12.2b). These calls are not simply a form of parental care, as individuals give calls nearly as often when the kin they live with are parents and siblings as when they are offspring (Figure 12.2c). Hoogland was even able to follow individual males across different stages of life, and saw them modify their rate of calling with changes in their proximity to kin (Figure 12.3).

The data show that apparently altruistic alarm-calling behavior is not dispensed randomly. It is nepotistic. Self-sacrifice is directed at close relatives and should result in indirect fitness gains.

*Individuals are more likely to give alarm calls when close relatives are nearby.*

### White-Fronted Bee-Eaters

Another classical system for studying kin selection in vertebrates is helping behavior in birds (see Brown 1987; Stacey and Koenig 1990). In species from