Chapter Seven
Social Relations

In early evening as the sun's rays shine obliquely through the clear waters over a coral reef, the activity of some of its inhabitants quickens. As if activated by some remote switch, a vast school of fish that had remained in the lagoon all day begins to move steadily toward an opening in the reef. The school is leaving the lagoon's protection and going out to the open sea for a night of feeding. Living in a school appears to have favored uniformity among its members. Approached underwater, the edge of the school looks like a giant translucent curtain stamped with the silhouettes of thousands of identical fish. Their coloration, countershaded dark above and silvery below, their similar size, highly coordinated movements, and great numbers give the fish within the school some protection from predators. Though seabirds and predaceous fish ambush the school as it makes its way, the schooling fish are so numerous and their individual movements so difficult to follow that only a small proportion of them are eaten. Gradually the school, moving like a gigantic, shape-shifting organism, passes through the channel connecting the lagoon to the open sea. The school of fish will be back by daybreak only to repeat its seaward journey next evening in a cycle of comings and goings that helps mark the rhythm of life on the reef.

Meanwhile along the reef, damselfish are distributed singly on territories. The damselfish retain exclusive possession of their territorial patches of coral rubble, living coral, and sand by patrolling the boundaries and driving off any fish attempting to intrude, especially other damselfish that would take their territory or other fish that would prey on eggs or consume food within the territory. Each day at this time, however, some territory-holding males are joined by females. For the space of time that they court and deposit eggs and sperm on the nest site prepared by the male, the territory contains two fish. Once mating is complete, however, the male is again alone on the territory, guarding the food and shelter contained within its boundaries as well as the newly deposited eggs that he fertilized minutes before.

Higher along the reef face a male bluehead wrasse mates with a member of the harem of females that live within his territory (fig. 7.1). In contrast to the male with his blue head, black bars, and green body, the female is mostly yellow with a large black spot on her dorsal fin. As the male bluehead extrudes sperm to fertilize the eggs laid by the female, small males, similar in color to the female, streak by the mating pair, discharging a cloud of sperm as they do. Some of the female's eggs will be fertilized by the large territorial bluehead male while others will be fertilized by the sperm discharged by the smaller yellow streakers. In addition to differences in color and courtship behavior, bluehead and yellow males have distinctive histories. While the yellow males began their lives as males, the bluehead male began life as a female and only transformed to a male when the local bluehead male was eaten by a predator or met some other end. At that point, because she was the largest yellow phase among the local females and males, she was in line to become the

FIGURE 7.1 *Bluehead wrasse male with yellow female of the species.*

dominant local male and so changed from the yellow to the bluehead form of the species. Within a week the former female was producing sperm and fertilizing the eggs produced by the females in the territory.

While male bluehead wrasses patrol their individual mating territories and male damselfish fight with each other at the boundaries of theirs, elsewhere on the reef groups of snapping shrimp live cooperatively in colonies that may contain over 300 individuals. Most of the individuals in the colonies are juveniles or males and each contains a single reproductive female. The female snapping shrimp, which plays a role much like the queen ant in an ant colony, breeds continuously and so is easily identified by her ripe ovaries or by the eggs she carries. Meanwhile the males of the colony, most of which will probably never mate, vigorously defend the nest site, with its "queen" shrimp and numerous juveniles against intruders. In this shrimp society most males serve the colony and its queen by protecting her offspring and the sponge where they live. While the queen reproduces profusely, the chance to reproduce is probably rare for an individual male. The colony thrives but reproduction is restricted to a few individuals in the population.

During a short swim over a coral reef you can observe great variation in social interactions among individuals belonging to the same species. Analogous variation can be found in terrestrial environments. In chapters 4, 5, and 6 of section II, we considered the relations of organisms to physical and chemical aspects of the environment, including temperature, water, energy, and nutrients. However, to an individual organism, other members of its own species are a part of the environment as significant to it as temperature, food, or the quantity and quality of available water. In chapter 7 we will consider some of the interrelations among individuals under the heading of social relations.

The study of social relations is the territory of **behavioral ecology,** which concentrates on relationships between organisms and environment that are mediated by behavior. In the case of social relations, other individuals of a species are the part of the environment of particular interest. A branch of biology

concerned with the study of social relations is **sociobiology.** Social relations, from dominance relationships and reproductive interactions to cooperative behaviors, are important since they often directly and obviously impact the reproductive contribution of individuals to future generations, a key component of Darwinian or evolutionary fitness, usually referred to simply as **fitness.** Fitness can be defined as the number of offspring, or genes, contributed by an individual to future generations, which can be substantially influenced by social relations within a population.

One of the most fundamental social interactions between individuals takes place during sexual reproduction. The timing of those interactions and their nature is strongly influenced by the reproductive system of a species. The behavioral ecologist considers several factors. Does the population engage in sexual reproduction? Are the sexes separate? How are the sexes distributed among individuals? Are there several forms of one sex or the other? Questions such as these have drawn the attention of biologists since Darwin (1862) who wrote, "We do not even in the least know the final cause of sexuality; why new beings should be produced by the union of the two sexual elements, instead of by a process of parthenogenesis [production of offspring from unfertilized eggs] . . . The whole subject is as yet hidden in darkness." As you will see, behavioral and evolutionary ecologists have learned a great deal about the evolution and ecology of reproduction in the nearly one and a half centuries since Darwin published this statement. However, much remains to be discovered.

Since mammals and birds reproduce sexually, from a human perspective sexual reproduction may appear the norm. However, asexual reproduction is common among many groups of organisms such as bacteria, protozoans, plants, and some vertebrates. However, most described species of plants and animals include male and female functions, sometimes in separate individuals or within the same individual. This brings us to a fundamental question in biology. What is female and what is male? From a biological perspective, the answer is simple. **Females** produce larger, more energetically costly gametes (eggs or ova), while **males** produce smaller, less costly gametes (sperm or pollen). Because of the greater energetic cost of producing their gametes, female reproduction is thought to be generally limited by access to the necessary resources. In contrast, male reproduction is generally limited by access to female mates. Biologists long ago proposed that this difference in investment in gametes has usually led to a fundamental dichotomy between actively courting males and highly selective females.

Despite the basic differences between males and females, distinguishing the two sexes in nature is sometimes difficult. While it is easy to distinguish between males and females in species where males and females differ substantially in external morphology, the males and females of other species appear very similar and are very difficult to distinguish using only external anatomy. Still other species are **hermaphrodites,** organisms that combine male and female function in the same individual (fig. 7.2). The most familiar

examples of hermaphrodites are plants, among which the vast majority of species produce flowers that have both male and female parts. Among animals, fish provide many interesting examples of hermaphroditism. For instance, many species of small seabasses are hermaphrodites. As pairs within these species court, one member of the pair performs male-specific courtship behaviors while the other member of the pair produces eggs. As the eggs are laid ,the first member of the pair fertilizes them. Later, the two fish may switch roles, with the second individual behaving as a male while the first assumes the female role and lays eggs.

(a)

(b)

FIGURE 7.2 *Male and female function: (a) Male and female Canada geese, a species in which males and female have very similar external anatomy, i.e., are monomorphic; (b) A "perfect" flower which includes both male (stamens) and female (pistil) parts and function.*

Many aspects of sexual function that we may take for granted represent complex biological problems that have puzzled biologists for generations. For example, what factors have favored separate sexes in some species and hermaphrodites in others. Eric Charnov, J. Maynard Smith, and James Bull (1976) addressed this question in a classic paper titled, "Why Be a Hermaphrodite?" These authors identified three conditions that should favor a hermaphroditic population over one with separate sexes: (1) low mobility, which limits the opportunities for male to male competition, which often depends on structures designed to find and compete aggressively for females, (2) low overlap in resource demands by female and male structures and functions, such as in plants, where pollen production often occurs earlier in the season than seed maturation, and (3) sharing of costs for male and female function, for instance in insect-pollinated plants where attractive flowers promote both male and female reproductive success.

Clearly, the way populations are divided between the sexes will influence social relations, which will in turn affect the fitness of individuals, particularly through influences on their reproductive rates. Here are two concepts that have emerged from studies of social relations that provide examples of the complex relationships between social interactions and fitness. These concepts form the framework of this chapter.

CONCEPTS

- Mate choice by one sex and/or competition for mates among individuals of the same sex can result in selection for particular traits in individuals, a process called sexual selection.
- The evolution of sociality is generally accompanied by cooperative feeding, defense of the social group, and restricted reproductive opportunities.

CASE HISTORIES: mate choice

Mate choice by one sex and/or competition for mates among individuals of the same sex can result in selection for particular traits in individuals, a process called sexual selection.

Darwin (1871) proposed that the social environment, particularly the mating environment, could exert significant influence on the characteristics of organisms. He was particularly intrigued by the existence of what he called "secondary sexual characteristics," the origins of which he could not explain except by the advantages they gave to individuals during competition for mates.

Darwin used the term *secondary sexual characteristics* to mean characteristics of males or females not directly involved in the process of reproduction. Some of the traits that Darwin had in mind were "gaudy colors and various ornaments . . . the power of song and other such characters." How do we explain the existence of characteristics such as the antlers of male deer, the bright peacock's tail, or the gigantic size and large nose of the male elephant seal? In order to explain the existence of such secondary sexual characteristics, Darwin proposed a process that he called **sexual selection.** Sexual selection results from differences in reproductive rates among individuals as a result of differences in their mating success.

Sexual selection is thought to be important under two circumstances. The first is where individuals of one sex compete among themselves for mates, which results in a process called **intrasexual selection.** For instance, when male mountain sheep or elephant seals fight among themselves for dominance or mating territories, the largest and strongest generally win such contests. In such situations the result is often selection for larger body size and more effective weapons such as horns or teeth. Since this selection is the result of contests within one sex, it is called intrasexual selection.

Sexual selection can also occur when members of one sex consistently choose mates from among members of the opposite sex on the basis of some particular trait. Because two sexes are involved, this form is called **intersexual selection.** Examples of traits used for mate selection include female birds choosing among potential male mates based on the brightness of their feather colors or on the quality of their songs. Darwin proposed that once individuals of one sex begin to choose mates on the basis of some anatomical or behavioral trait, sexual selection would favor elaboration of the trait. For instance, the plumage of male birds' color might become brighter over time or their songs more elaborate or both.

However, how much can sexual selection elaborate a trait before males in the population begin to suffer higher mortality due to other sources of natural selection, such as that exerted by predators? Darwin proposed that sexual selection will continue to elaborate a trait until balanced by other sources of natural selection, such as predation. Since Darwin's early work on the subject, research has revealed a great deal about how organisms choose mates and the basis of sexual selection. An excellent model for such studies is the guppy, *Poecilia reticulata.*

Mate Choice and Sexual Selection in Guppies

It would be difficult for experimental ecologists interested in mate choice and sexual selection to design a better experimental animal than the guppy (fig. 7.3). Guppies are native to the streams and rivers of Trinidad and Tobago, islands in the southeastern Caribbean, and in the rivers draining nearby parts of the South American mainland. The waters inhabited by guppies range from small clear mountain streams to murky lowland

FIGURE 7.3 *A colorful male guppy courting a female guppy: What are the influences of mate selection by female guppies and natural selection by predators?*

rivers. Along this gradient of physical conditions, guppies also encounter a broad range of biological situations. In the headwaters of streams above waterfalls, guppies live in the absence of predaceous fish or with the killifish *Rivulus hartii,* which preys mainly on juveniles and is not a very effective predator on adult guppies. In contrast, guppies in lowland rivers live with a wide variety of predaceous fish, including the pike cichlid, *Crenicichla alta,* a very effective visual predator of adult guppies.

Male guppies show a broad range of coloration both within and among populations. What factors may produce this range of variation? It turns out that female guppies, if given a choice, will mate with more brightly colored males. However, brightly colored males are attacked more frequently by visual predators. This trade-off between higher mating success by bright males but greater vulnerability to predators provides a mechanistic explanation for variation in male coloration among different habitats. The most brightly colored male guppies are found in populations exposed to few predators, while those exposed to predators, such as the pike cichlid, are much less brightly colored (Endler 1995). Thus the coloration of male guppies in local populations may be determined by a dynamic interplay between natural selection exerted by predators and by female mate choice.

While field observations are consistent with a trade-off between sexual selection due to mate choice and natural selection due to predation, the evidence would be more convincing with an experimental test. John Endler (1980) performed such a test in an exemplary study of natural selection for color pattern in guppies.

Experimental Tests

Endler performed two experiments, one in artificial ponds in a greenhouse at Princeton University (fig. 7.4) and one at field sites (fig. 7.5). For the greenhouse experiments, Endler

constructed 10 ponds designed to approximate pools in the streams of the Northern Range in Trinidad. Four of the ponds were of a size (2.4 m × 1.2 m × 40 cm) typical of the pools inhabited by a single pike cichlid in smaller streams. During the final phase of the experiment, Endler placed a single pike cichlid in each of these ponds. The six other ponds were similar in size (2.4 m × 1.2 m × 15 cm) to stream pools in the headwaters which contain approximately 6 *Rivulus.* Endler eventually placed 6 *Rivulus* in 4 of these ponds and maintained the other two ponds with no predators as controls. What did Endler create with this series of pools and predator combinations? These three groups of ponds represented three levels of predation: high predation (pike cichlid), low predation (*Rivulus*), and no predation.

However, before introducing predators, Endler established similar physical environments in the pools and stocked them with carefully chosen guppies. He lined all ponds with commercially available dyed gravel, taking care to put the same proportions of gravel colors in each of the ponds. The gravel he used in all ponds was 31.4% black, 34.2 % white, 25.7 % green, plus 2.9% each of blue, red, and yellow. Why did Endler take great care to put the same colors of gravel in the same proportions into all of his ponds? One of the most critical elements of the experiment was to standardize the background colors across all of the ponds. The influence of prey color on vulnerability to predators depends on the background against which the prey is viewed by visual predators. As a consequence, controlling background color was of critical importance to Endler's experiments.

Endler stocked the experimental pond with 200 guppies, which were descended from 18 different populations in Trinidad and Venezuela. By drawing guppies from so many populations, Endler ensured that the experimental populations would include a substantial amount of color variation. As we will see in chapter 8, genetic variation is an essential requirement for evolutionary change in populations.

Endler's second experiment was conducted in the field within the drainage network of the Aripo River (fig 7.5), where he encountered three distinctive situations within a few kilometers. Within the mainstream of the Aripo River, guppies coexisted with a wide variety of predators, including pike cichlids, which provided a "high predation" site. Upstream from the high predation site, Endler discovered a small tributary which flowed over a series of waterfalls near its junction with the mainstream. Because the waterfalls prevented most fish from swimming upstream, this tributary was entirely free of guppies but supported a population of the ineffective predator *Rivulus.* This potential "low predation" site provided an ideal situation for following the evolution of male color. The third site, which was a bit farther upstream, was a small tributary that supported guppies along with *Rivulus.* This third site gave Endler a low predation reference site for his study. Endler captured 200 guppies in the high predation environment, measured the coloration of these guppies, and then introduced them to the site lacking guppies. Six months later the introduced guppies and their offspring had spread throughout the previously guppy-free tributary. Finally 2 years or about 15
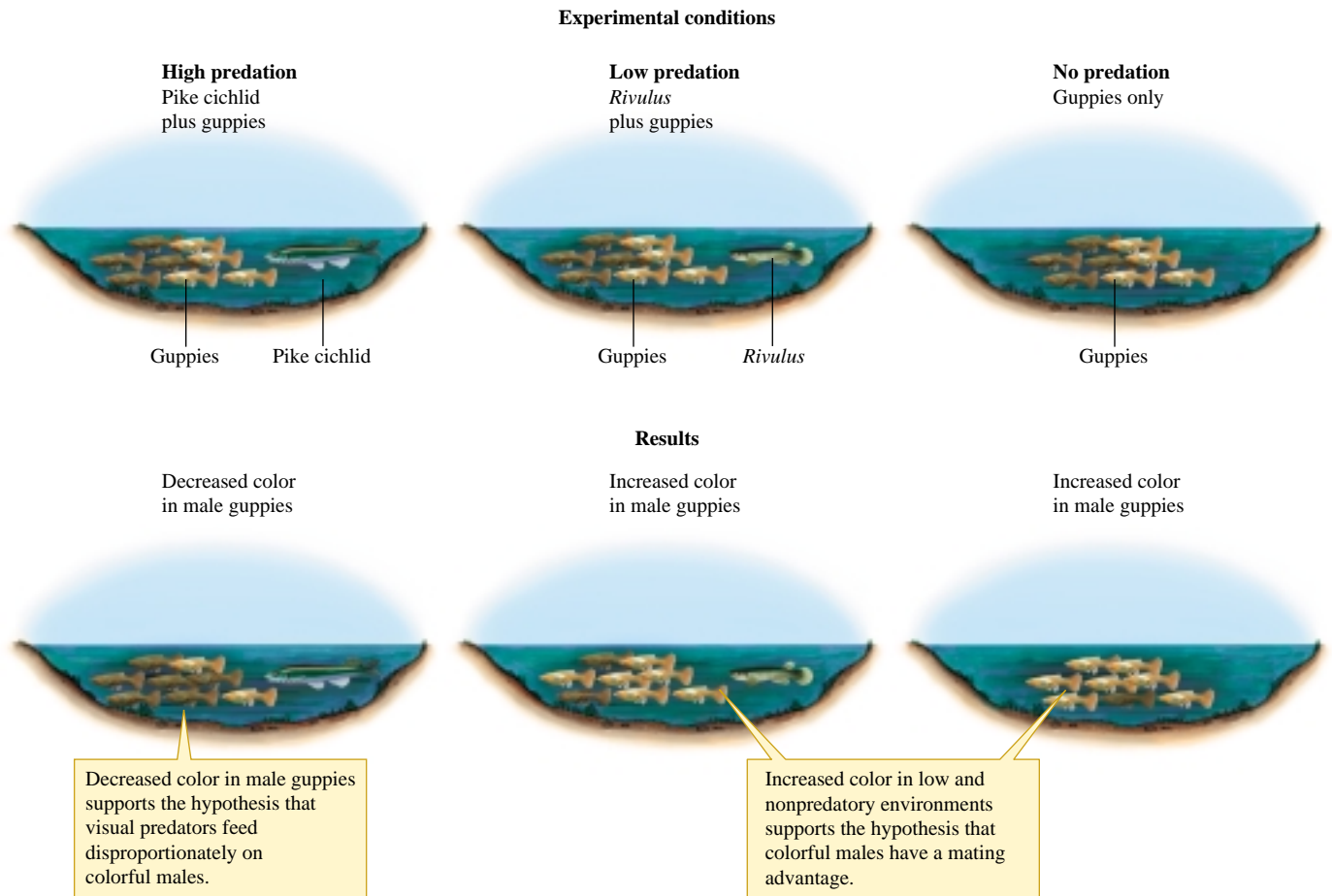
Experimental conditions

High predation
Pike cichlid
plus guppies

Low predation
Rivulus
plus guppies

No predation
Guppies only

Guppies   Pike cichlid

Guppies   *Rivulus*

Guppies

Results

Decreased color
in male guppies

Increased color
in male guppies

Increased color
in male guppies

Decreased color in male guppies
supports the hypothesis that
visual predators feed
disproportionately on
colorful males.

Increased color in low and
nonpredatory environments
supports the hypothesis that
colorful males have a mating
advantage.

FIGURE 7.4 *Summary of greenhouse experimental design and results (information from Endler 1980).*

guppy generations after the introduction, Endler returned and sampled the guppies at all three study sites.

The results of the greenhouse and field experiments supported each other. As shown in figure 7.6, the number of colored spots on male guppies increased in the greenhouse ponds with no predators and with *Rivulus* but decreased in the high predation ponds containing pike cichlids. Figure 7.7, which summarizes the results of Endler's field experiment, compares the number of spots on males in high predation and low predation stream environments with guppies transferred from the high predation environment to a low predation environment. Notice that the transplanted population converged with the males at the low predation reference site during the experiment. In other words, when freed from predation, the average number of spots on male guppies increased substantially. This result, along with the results of the greenhouse experiment, supports the hypothesis that predation reduces male showiness in guppy populations.

Research by many other researchers supports the impact of predators on male ornamentation. However, the observation that male colorfulness increased in the absence of predators or in the presence of weak predation both in the field and the laboratory invites explanation. Why did male color increase rather that just remain static? The observed changes imply that color-

ful males enjoy some selective advantage. That advantage appears to result from how female guppies choose their mates.

Mate Choice by Female Guppies

What cues do female guppies use to choose their mates? Anne Houde (1997), who summarized the findings of numerous studies, found that several male traits were associated with greater mating success. The weight of the evidence supports the conclusion that male coloration contributes significantly to male mating success. Color characteristics that have been shown to confer a male mating advantage include "brightness," number of red spots, number of blue spots, iridescent area, total pigmented area, and carotenoid or orange area. These results appear to account for the increase in male colorfulness observed by Endler in the absence of predation or in the presence of low predation pressure. That is, female preference for more colorful males gave them greater fitness in the absence of strong predation. As a consequence, male colorfulness increased in the study populations in low predation or no predation environments. Male behavior, especially their rate of making courtship displays, has also been found associated with increased male mating success.
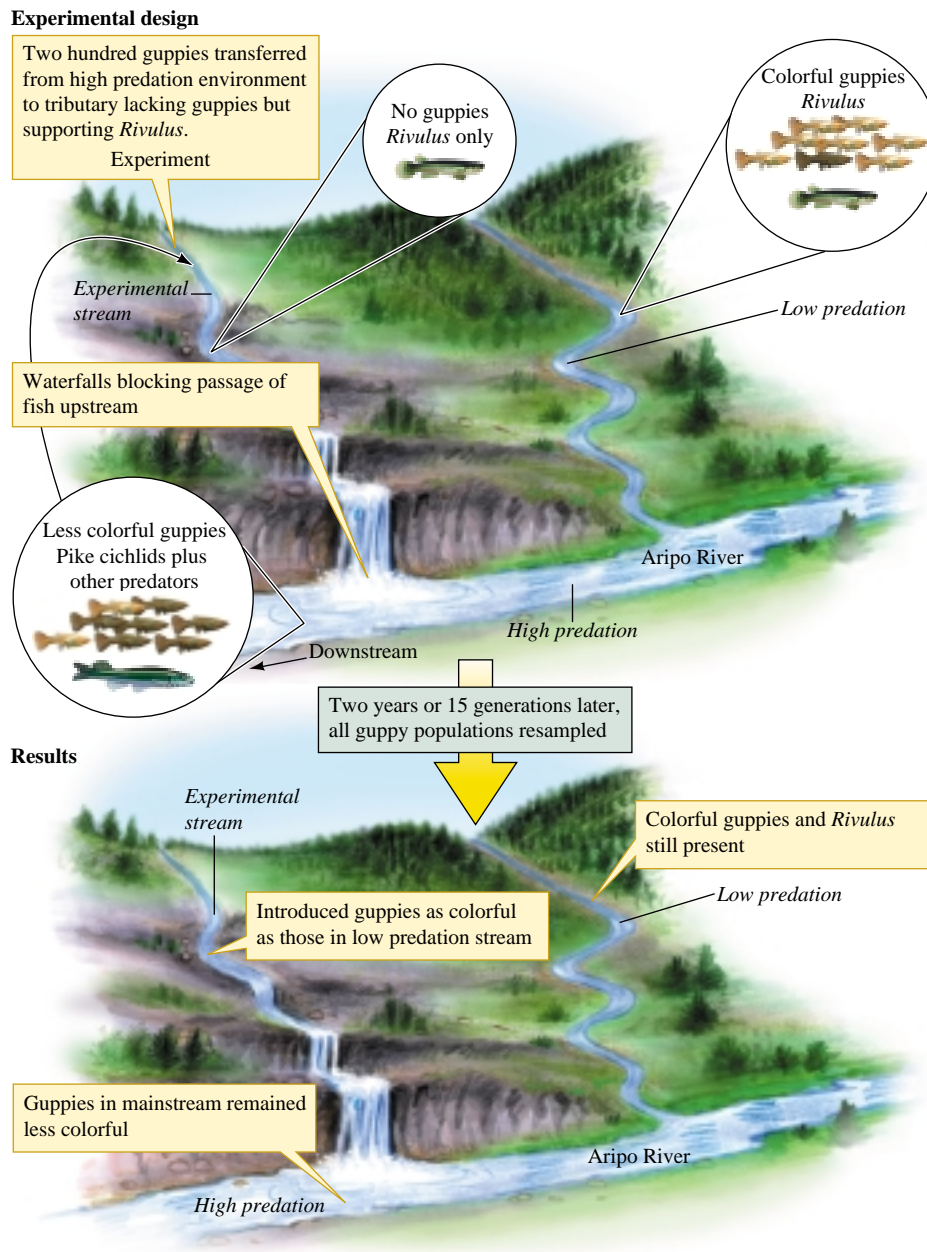
Experimental design

Two hundred guppies transferred from high predation environment to tributary lacking guppies but supporting *Rivulus*.
Experiment

No guppies
Rivulus only

Colorful guppies
Rivulus

Experimental stream

Low predation

Waterfalls blocking passage of fish upstream

Less colorful guppies
Pike cichlids plus other predators

Aripo River

High predation

Downstream

Two years or 15 generations later, all guppy populations resampled

Results

Experimental stream

Colorful guppies and *Rivulus* still present

Low predation

Introduced guppies as colorful as those in low predation stream

Guppies in mainstream remained less colorful

Aripo River

High predation

FIGURE 7.5 *Field experiment on effects of predation on male guppy coloration (information from Endler 1980).*

There have been fewer studies of how competition among males, that is intrasexual selection, may influence male mating success. Let's look at one of the few studies that does. Astrid Kodric-Brown (1993) studied whether competitive interactions among males contribute to variation in male mating success. She obtained guppies for her behavioral experiments from stock John Endler had originally collected from the Aripo and Paria Rivers in Trinidad. Males and females used in the behavioral experiments were reared separately. Males were kept in 95-liter aquaria in populations consisting of 10 males and 20 females. Meanwhile virgin females were reared in all-female groups of sisters until they were 6 months old. During this period they had no visual contact with males.

Both males and females were fed a standardized diet and maintained at the same temperatures and exposed to the same numbers of hours of dark and light.

From her stock populations, Kodric-Brown chose 59 pairs of males with contrasting colors and 59 females. To test female preference she placed a single female into the central chamber of a test tank and each member of a male pair in the side chambers flanking the central chamber. Screens covering glass partitions prevented visual contact between males and females initially. After 10 minutes of acclimation by the guppies, Kodric-Brown removed the screens. Once the screens were removed males would usually begin courtship displays and the female would inspect the males through
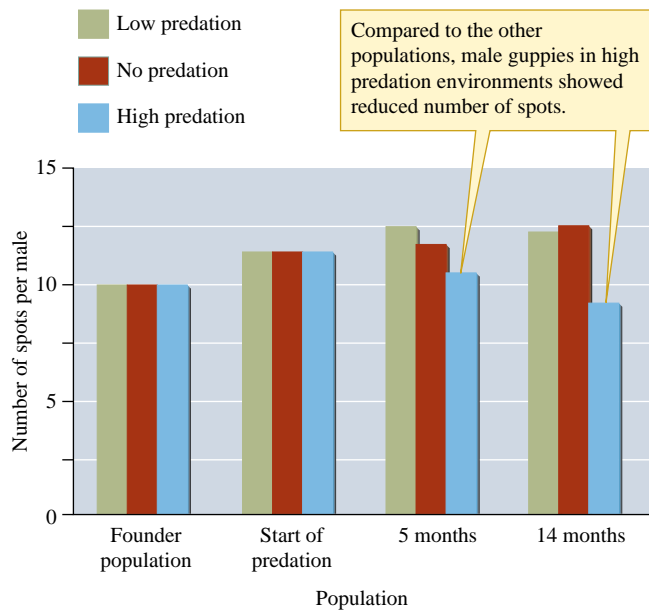
Low predation
No predation
High predation

Compared to the other populations, male guppies in high predation environments showed reduced number of spots.

FIGURE 7.6 *Results of greenhouse experiment which exposed populations of guppies to no predation, low predation (killifish) and high predation (pike cichlid) environments (data from Endler 1980).*
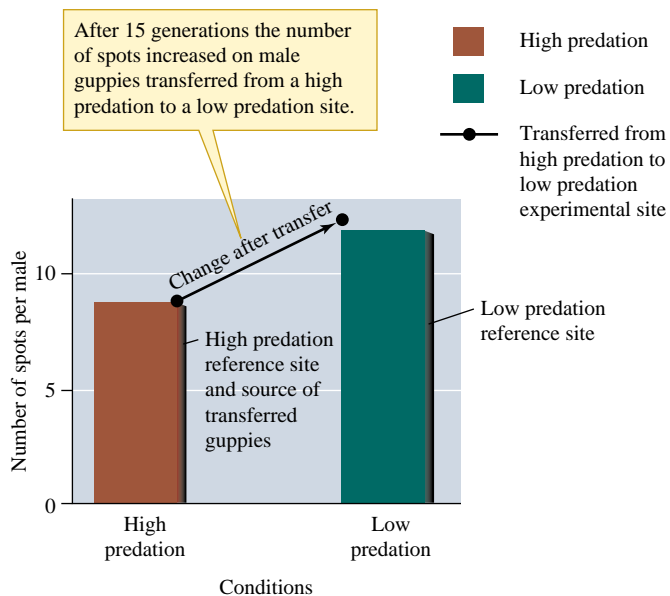

After 15 generations the number of spots increased on male guppies transferred from a high predation to a low predation site.

High predation
Low predation

Transferred from high predation to low predation experimental site

Low predation reference site

High predation reference site and source of transferred guppies

FIGURE 7.7 *Results of field experiment involving transfer of guppies from high predation site to site with killifish, a fairly ineffective predator (data from Endler 1980).*

the glass partition. Kodric-Brown recorded the behavior of males and females in the display tank for 10 minutes, recording the time and the rates at which males displayed, and the amount of time the female spent within 5 cm of the glass partition of each male. She designated the male that the female spent the most time with as the preferred or attractive male and the male with which the female spent less time as the nonpreferred or unattractive male.

After this initial 10-minute period during which females indicated their preferences, Kodric-Brown removed the glass partitions separating the guppies, allowing interactions among the males and the female. Kodric-Brown observed that males engaged in agonistic interactions, such as chasing and nipping, in over 94% of mating trials, which gave her a basis for determining which males were behaviorally dominant and which were subordinate. Kodric-Brown recorded the interactions between the two males and between the males and the female until 5 minutes after a copulation. After a mating trial the female was moved to a rearing tank where she eventually gave birth. The offspring from each female were raised separately. In order to establish paternity, male offspring were raised to maturity when they expressed their full coloration, which is inherited from their fathers.

The results of Kodric-Brown's experiments indicate that reproductive success was determined by a combination of male attractiveness and male dominance status. Female mate preference, which was determined when the guppies had visual contact only, was highly correlated with subsequent male mating success (fig. 7.8). The males that attracted females when viewed through the glass partition subsequently sired a greater percentage of broods than did unattractive males. Approximately 67% of the broods were sired by attractive males compared to 33% that were sired by unattractive males. However, it appears that male dominance status also contributes to male reproductive success. Among unattractive males that sired broods, 87.5% were dominant. The conclusion that reproductive success is determined by a combination of competition between males and female choice is reinforced by the low reproductive success by males that were neither attractive nor dominant. These males, which lacked the apparent advantages associated with either dominance or attractiveness, sired only 4% of the broods. The result indicates that reproductive opportunities are highly restricted for these males.

The characteristics associated with male mating success among guppies are often correlated. Kodric-Brown observed that attractive males tended to be dominant, court more, and have more and brighter orange and iridescent spots. These characteristics are closely associated with a male's anatomy and physiology. Let's look at a mating system where male attractiveness is dependent upon complex behaviors that in effect extend the male phenotype.

Mate Choice Among Scorpionflies

Scorpionflies (fig. 7.9) belong to the order Mecoptera, a group of insects most closely related to the caddisflies (order Trichoptera) and the moths and butterflies (order Lepidoptera). The common name "scorpionfly" is related to the way that males hold their genitalia over the back of their abdomens in a position that suggests a scorpion's sting. Despite their appearance, male scorpionflies are entirely harmless to people.
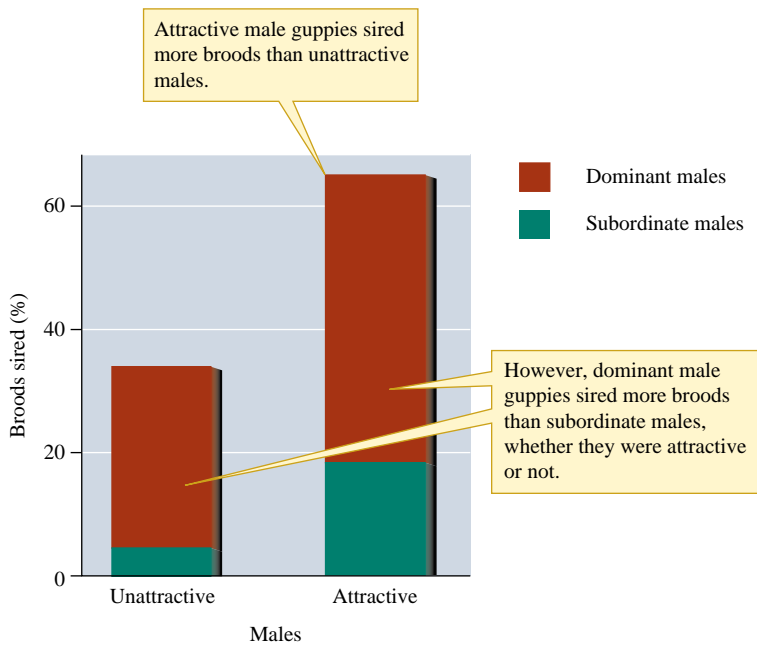
Attractive male guppies sired more broods than unattractive males.

Dominant males

Subordinate males

However, dominant male guppies sired more broods than subordinate males, whether they were attractive or not.

FIGURE 7.8 *Relative reproductive success by attractive versus unattractive and dominant versus subordinate male guppies (data from Kodric-Brown 1993).*

FIGURE 7.9 *Male scorpionfly.*

Compared to insects such as moths or beetles, there are relatively few scorpionfly species alive today. However, they have been a rich source of information on behavioral ecology, particularly on the evolution and ecology of mating systems. Randy Thornhill has been a central figure in research on mate choice and sexual selection and his studies of scorpionfly mating systems are regarded as classic studies of the evolution and ecology of mating systems (e.g., Thornhill 1981, Thornhill and Alcock 1983).

Adult scorpionflies in the genus *Panorpa* feed on dead arthropods in the shrub and herb understory of forests. Several lines of evidence suggest that the supply of dead arthropods available to scorpionflies is limited and that the intensity of competition for dead arthropods is intense, especially among males. Thornhill observed that male scorpionflies fight over dead arthropods and even steal them from spider webs, a behavior which leads to significant scorpionfly mortality. Why do scorpionflies compete so vigorously and risk death over dead arthropods? One reason they fight is that male *Panorpa* use dead arthropods to attract females. If a male finds a dead arthropod and can successfully defend it from other males, he will stand next to the arthropod and secrete a pheromone, which can attract females from several meters away. A female attracted by the pheromone will usually feed on it while the male mates with her. However, if an arthropod is not available as a nuptial offering, males will secrete a mass of saliva from their enlarged salivary glands and use that to attract females. Finally, males without gifts may attempt forced copulations.

In a series of experimental studies, Thornhill explored the details of alternative male mating strategies and the ecological conditions associated with each. In one of his most basic studies, he asked whether there is a difference in mating success among males using different mating strategies. Thornhill created an enclosed environment where he could control the availability of dead arthropods and the number of male *Panorpa* competing for them. He set up 12 replicate environments in 10-gallon terrariums. He included 6 dead crickets, 2 large, 2 medium, and 2 small, in each terrarium and added 12 male *P. latipennis* to each. Male aggression over crickets, which began soon after they were introduced, was finished after about 3 hours. At that time each of the crickets had been won by a single male, which stood near their respective prizes and secreted pheromone. The majority of the remaining 6 males secreted a mass of saliva, which they guarded, while secreting pheromones. Finally, some males had no nuptial offerings.

Once the competition among male *Panorpa* for possession of the dead crickets had been decided, Thornhill introduced 12 females and recorded mating activity once per hour for 3 hours. Across the 12 terrariums, there were 144 male *Panorpa* and 144 females. Of the males, 72 males took possession of crickets, 45 had secreted salivary masses, and 27 had no nuptial offerings. How did mating success differ among these groups of males? Figure 7.10 shows that males with a medium or large cricket as a nuptial offering had a clear advantage over those that offered females a small cricket, a salivary mass, or no nuptial offering.

What benefit do females gain by mating with males that offer larger arthropods? One of the clearest benefits is that females feeding on the arthropods offered by males do not have to forage for their own and avoid the risk of being eaten
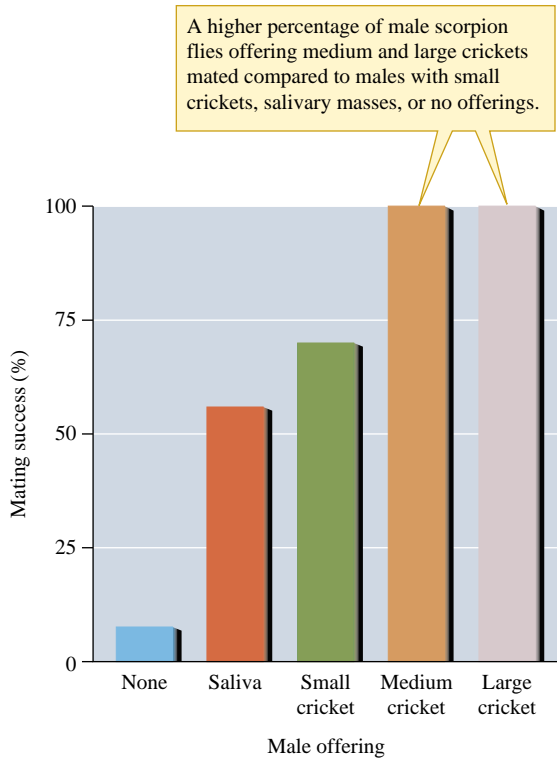
A higher percentage of male scorpion flies offering medium and large crickets mated compared to males with small crickets, salivary masses, or no offerings.

FIGURE 7.10 *Influence of alternative nuptial offerings on mating success by male scorpionflies,* Panorpa latipennis *(data from Thornhill 1981).*

competed successfully for possession of a dead arthropod are given access to one, will they take possession of it and advertise their possession by secreting pheromone. Thornhill addressed this question with a series of controlled experiments with enclosures. Again, he placed 6 crickets, all medium, in each of 12 terrariums and added 12 male *Panorpa* to each. As in previous experiments, 6 of the males took possession of the dead crickets in each aquarium, leaving 6 males without arthropods. Again, the males without arthropods secreted a salivary mass which they stood beside as they secreted pheromone. At this point, Thornhill removed all the males possessing crickets in all the terrariums. Within half an hour, almost all the remaining males moved from their salivary masses to the available crickets and secreted pheromone (fig. 7.11). It therefore appears that given the opportunity, male *Panorpa* will take possession of and guard dead arthropods.

What factors determine whether male *Panorpa* will be able to successfully claim a dead arthropod in a competitive environment? Males contesting over a dead arthropod will usually first display to each other. However, visual displays often quickly escalate to head butting and lashing at each other with the scorpion-like genital bulb with its pair of sharp claspers. The claspers of male scorpionflies are capable of tearing wings or other body parts of an opponent. As a consequence, these battles over bugs can be dangerous to both opponents. Because male body size varies widely within populations and male aggression
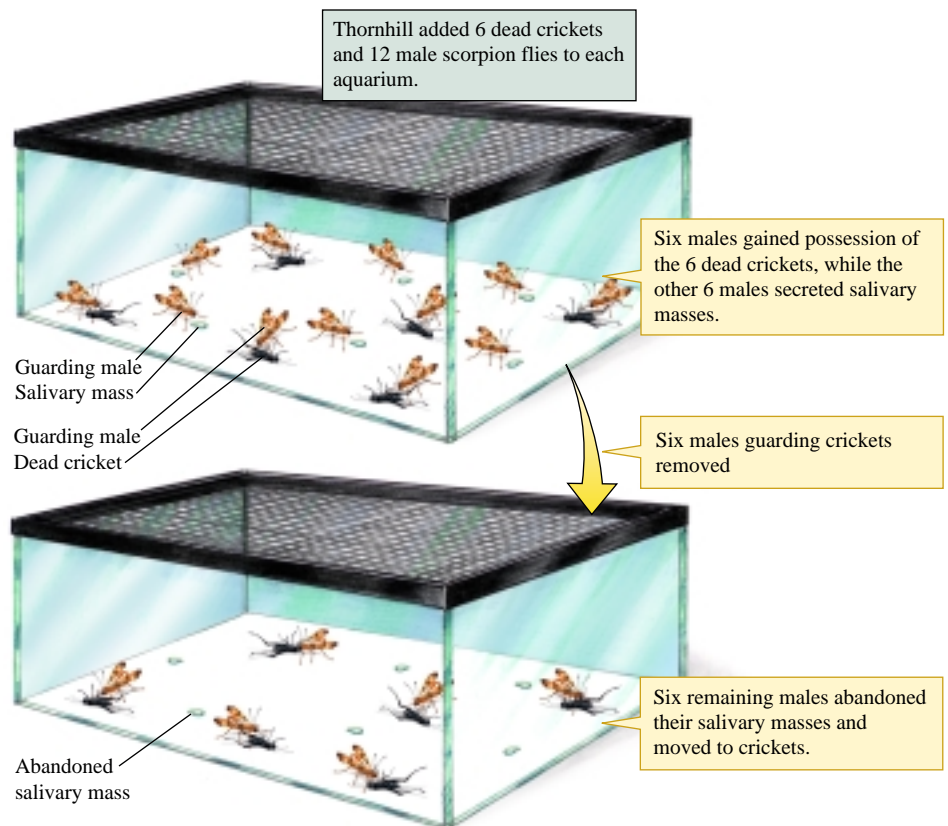
by a spider or other predator as they fly through the forest understory. In addition, feeding on these larger nuptial offerings gives females a reproductive advantage. Thornhill documented that rate of egg laying is higher among females mating with males that provide arthropod prey compared to females that mate with males offering saliva only. Meanwhile females mated to males with no offering lay very few eggs. What produces this contrast among females mated to males with different nuptial gifts? Thornhill's results likely reflect the greater nutritional benefit of arthropod prey versus saliva and the lack of a nutritional contribution by males without gifts.

Next, Thornhill asked what factors determine whether males compete successfully for arthropod offerings or resort to the alternatives of salivary masses or no nuptial gifts? One of the most basic questions that one could ask is whether males are fixed in particular behaviors. That is, if males that have not

Thornhill added 6 dead crickets and 12 male scorpion flies to each aquarium.

Six males gained possession of the 6 dead crickets, while the other 6 males secreted salivary masses.

Guarding male
Salivary mass

Guarding male
Dead cricket

Six males guarding crickets removed

Abandoned
salivary mass

Six remaining males abandoned their salivary masses and moved to crickets.

FIGURE 7.11 *Experimental test of the influence of nuptial offerings on mating success by male scorpionflies (information from Thornhill 1981).*

over dead arthropods often involves direct combat, Thornhill predicted that larger males would be most successful as competitors over arthropods.

Thornhill tested the relationship of male size on their ability to compete for and retain possession of arthropod prey in another experiment. This time he conducted his experiment in 14 larger, 3' × 3' × 3' screen enclosures set out on the forest floor of his study area. Because the enclosures had no bottom panel they just enclosed a 9-square-foot area of the herbaceous vegetation growing on the forest floor. In effect they enclosed a bit of scorpionfly habitat. Thornhill placed 4 crickets in seven of the enclosures and 2 in the other seven. He then added 10 female and 10 male scorpionflies to each of the enclosures, which were similar to natural population densities. The males in each enclosure consisted of 3 large males (55–64 mg), 4 medium males (42–53 mg), and 3 small males (33–41 mg). Because scorpionflies are nocturnal, Thornhill monitored the scorpionflies from sunset to sunrise with night vision equipment. Observations continued every night for a week during which Thornhill periodically added fresh dead crickets and replaced any female or male scorpionflies that died with new individuals to keep population densities constant.

The results of the field experiment clearly support the hypothesis that during competition for dead arthropods larger males have an advantage over small males. Figure 7.12 compares the nuptial offerings of small, medium, and large males in the enclosures with 2 crickets. While most small males either had no offerings or had a salivary mass, medium males generally offered salivary masses and occasionally competed successfully for a cricket. In contrast, large males generally
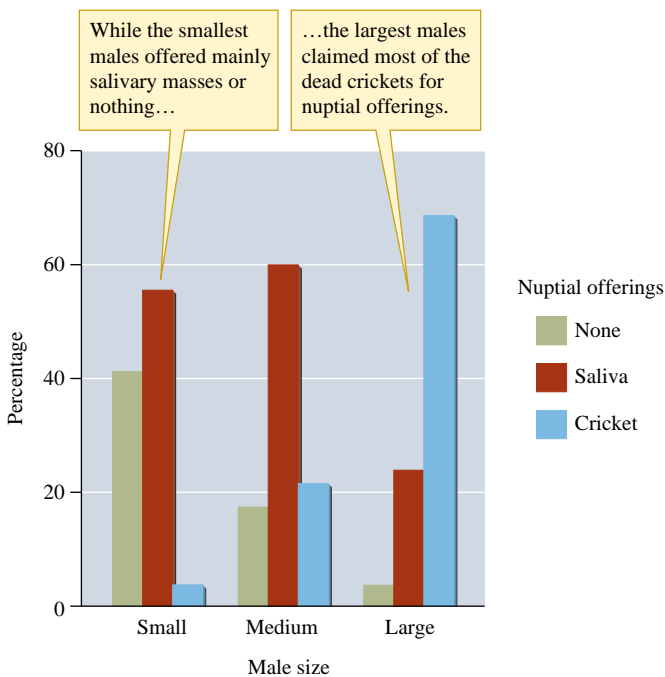

FIGURE 7.12 *Relationship between size of male scorpionflies and type of nuptial offering (data from Thornhill 1981).*
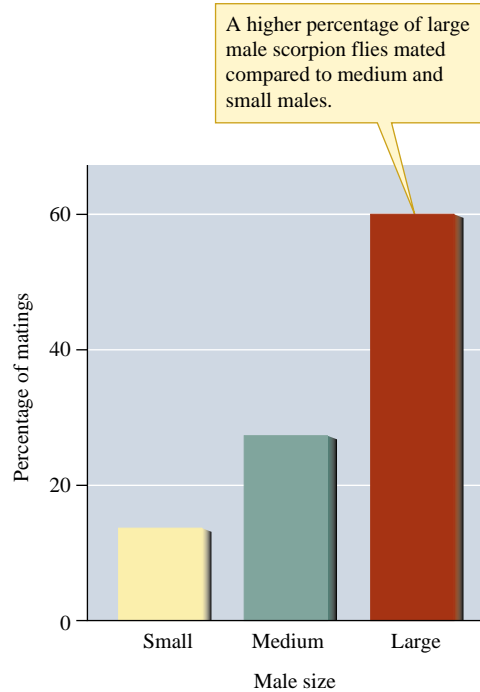

FIGURE 7.13 *Relationship between male scorpionfly size and matting success (data from Thornhill 1981).*

offered females a cricket and only occasionally offered saliva or had no nuptial offering.

Thornhill's study revealed the mechanism underlying variation among males in their ability to compete for nuptial offerings. Larger males are more likely to successfully defend the available arthropod offerings due to their advantages in aggressive encounters. Now, does this difference in offerings translate into different mating success among males? The answer is given in figure 7.13, which shows the percentage of matings observed by Thornhill in cages with 2 crickets. Large males were involved in 60% of the matings observed, compared to 27% for medium males and 13% for small males. Clearly, the ability of large males to defend higher quality nuptial offerings translates directly into higher mating success.

Let us leave animals now and consider plants. Though we know much less about the mating behavior of plants, it appears that their reproductive ecology also includes the potential for mate choice and sexual selection. One of the best studied mating systems in plants is that of the wild radish, *Raphanus sativus.*

Nonrandom Mating Among Wild Radish

Wild radish grows as an annual weed in California where it can be commonly seen along roadways and in abandoned fields (fig. 7.14). The seeds of wild radish germinate in response to the first winter rains of California's Mediterranean climate (see fig. 2.22) and the plants flower by January.

FIGURE 7.14 *A wild radish,* Raphanus sativa.

Flowering may continue to late spring or early summer, depending on the length of the wet season. During their flowering season, wild radishes are pollinated by a wide variety of insects, including honeybees, syrphid flies (see fig. 6.13b), and butterflies. Wild radish flowers have both male (**stamens**) and female (**pistils**) parts and produce both pollen and ovules. However, a wild radish plant cannot pollinate itself, a condition called **self-incompatibility.** Because they must mate with other plants, a researcher working on wild radish can more easily control matings between plants.

Diane Marshall has used the many advantages offered by wild radish, such as its rapid growth to maturity and self-incompatibility, to explore the topic of mate selection in plants. Marshall and Michael Folsom (1992) listed a number of other characteristics of wild radish that make it convenient for study. For instance, its fruits contain several seeds which allows the possibility of multiple paternity of offspring. However, the seeds are not so numerous that the researcher is overwhelmed by a vast number of seeds. In addition, each plant produces numerous flowers allowing the possibility of several kinds of matings per plant and several replications of each mating experiment on the same plant. The seeds, which

weigh about 10 mg, are also a convenient size for handling and weighing. Finally, there is sufficient genetic variation among individual radish plants to identify the male parent of each seed using electrophoresis of isozymes (see Applications and Tools in chapter 8).

The insects that pollinate wild radish generally arrive at flowers carrying pollen from several different plants, and as a consequence a wild radish plant typically has about seven mates. Under these circumstances of multiple mates, Marshall asked whether siring of offspring is a random process. In other words, do the seven mates of a typical wild radish plant have an equal probability of fertilizing the available ovules? The alternative, nonrandom mating, would suggest the potential for mate choice and sexual selection. What mechanisms might produce nonrandom mating among wild radish? Nonrandom mating could result from maternal control over the fertilization process, competition among pollen, or a combination of the two processes. If it does occur in plants, nonrandom mating establishes the conditions necessary for sexual selection in plants. However, as Marshall and Folsom (1991) pointed out, though sexual selection is well documented in animals, its occurrence among plants remains a controversial and open question.

While the existence of sexual selection in plants remains controversial, nonrandom mating is well documented. Marshall and her colleagues have repeatedly demonstrated nonrandom mating in wild radish. For instance, Marshall (1990) carried out greenhouse experiments that showed nonrandom mating among 3 maternal plants and 6 pollen donors. In this experiment Marshall mated 3 seed parents or maternal plants with 6 pollen donors, the plants that would act as sources of pollen to pollinate the flowers of the seed plants.

Marshall used the 6 pollen donors to make 63 kinds of crosses, 6 single donor crosses plus 57 mixed donor crosses, on each maternal plant. Her crosses included all possible mixtures of pollen from 1 to 6 donors. Plants were pollinated in the greenhouse by hand. All pollinations were performed on freshly opened flowers in the morning when the temperature was cool enough for researchers to work comfortably. Pollen was collected by tapping flowers lightly on the bottom of small petri dishes from an equal number of flowers of each pollen donor. Pollen was then mixed and applied to the stigmas of flowers on the maternal plant using forceps wrapped in tissue. Sufficient pollen was applied to cover each stigma. Because each cross was replicated from 2 to 20 times depending on the type of cross, the total number of pollinations performed on each plant was 300. This is a good example of the unique opportunities for experimental work offered by plants.

One of the ways that Marshall assessed the possibility of nonrandom mating was through performance of pollen donors. She estimated pollen donor performance in three ways: (1) number of seeds sired in mixed pollinations, (2) positions of seeds sired, and (3) weight of seeds sired. The results of this analysis are shown in figure 7.15. What would you expect to see in figure 7.15 if performance was equal
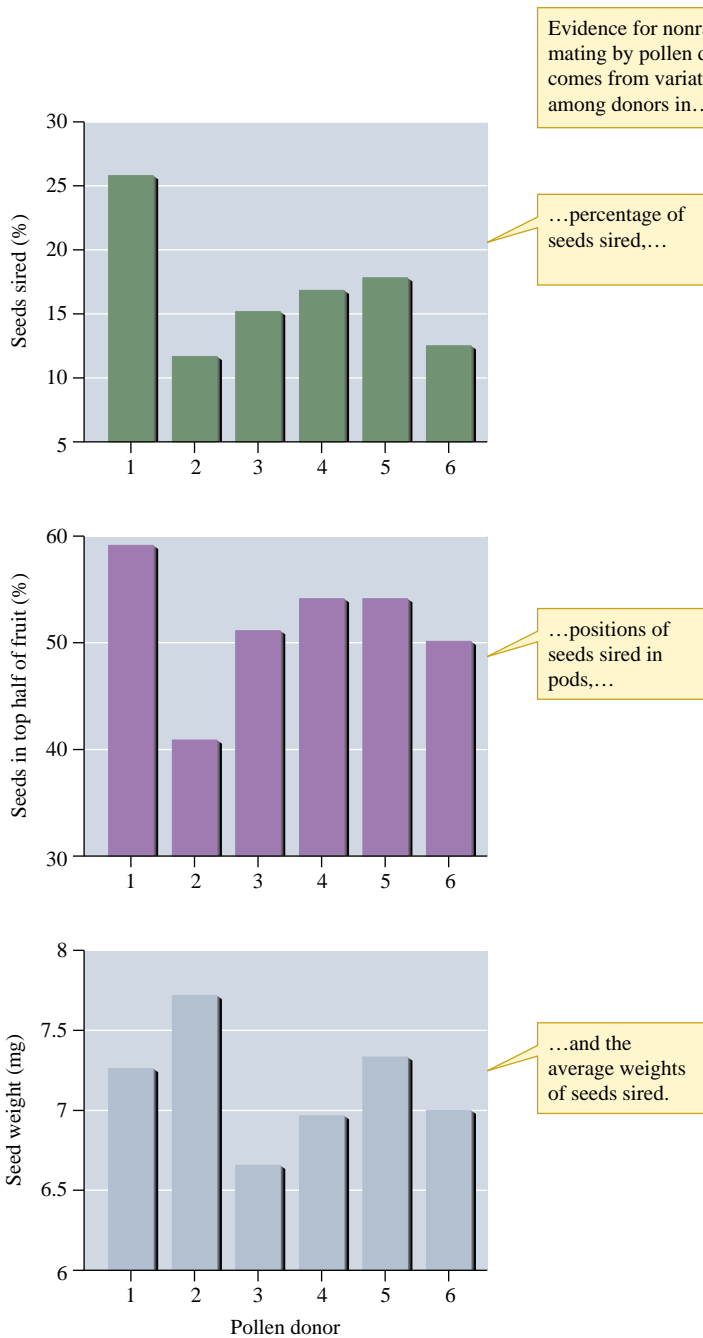
FIGURE 7.15 *Evidence for unequal mating success among wild radish pollen donors in a greenhouse environment (data from Marshall 1990).*

artifact of greenhouse conditions? Marshall and Ollar Fuller (Marshall and Fuller 1994) designed a study to address this question. Why might nonrandom mating be limited to the greenhouse environment? Marshall and Fuller point out that the harsh and variable environments to which plants are exposed in nature might mean that the condition of the maternal plant may be of overwhelming importance in determining the amount of seed produced, the weight of seeds, and so forth. Under such conditions nonrandom pollination which produces differences in seed weight in the greenhouse, might be undetectable and biologically insignificant.

Marshall and Fuller chose four maternal plants and grew their offspring in a field setting. Three other maternal lineages, (A, B, and C) were chosen to act as pollen donors. In the field, the maternal plants were covered with fine mesh nylon bags until the experimental pollinations were completed. Using the forceps and tissue method described earlier, Marshall and Fuller performed several kinds of hand-pollinations, including mixed pollinations using pollen from all three pollen donors. Once the hand pollinations were completed the nylon mesh bags were removed from the flowers.

The result of this experiment provided clear support for nonrandom mating in the field population. Figure 7.16 shows that during the mixed pollen donor pollinations, pollen donor C1 (56.5%) sired a much greater proportion of seeds compared to pollen donors A1 (24.8%) and B1 (18.7%). This finding suggests that the nonrandom matings observed in prior greenhouse pollination studies were not an artifact of greenhouse conditions.

Additional work by Marshall and her colleagues (Marshall et al. 1996) suggests that competition between pollen grains may contribute to nonrandom mating in wild radish populations. They used three maternal plants in these crosses, which they crossed with seven pollen donors (A, B, C, D, E, F, Z). The maternal plants were pollinated with pollen from single donors and from pairs of donors. The paired pollinations (A+B, C+D, etc.) were done in two ways. In one set of experiments, the pollen from the two donors was mixed as in the previous experiments described earlier. Because the two pollen types were in physical contact with each other in these "mixed" pollinations, this method of pollinating increased the opportunity for interaction between pollen types. In the second set of experiments, the pollen of the two donors used was not mixed. Each was applied to adjacent halves of the stigma, the tip of the pistil that acts as a pollen-receptive area. Since the two pollen types did not contact each other in these "adjacent" pollinations, there was a reduced chance that they would interact. Pollen response to these conditions was measured as the percentage of pollen that germinated within
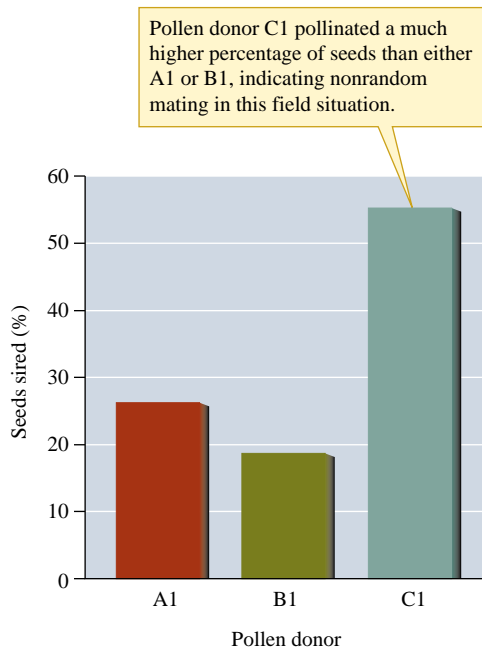
across pollen donors? If performance were equal, the heights of the bars would be approximately equal for all pollen donors. However they are not, and figure 7.15 indicates clearly that pollen donors vary widely in their performance. In other words, mating in this experiment was nonrandom.

Because Marshall conducted her 1990 study under greenhouse conditions, we might ask whether nonrandom mating also occurs under field conditions. In other words, could the nonrandom mating she documented have been an

Pollen donor C1 pollinated a much higher percentage of seeds than either A1 or B1, indicating nonrandom mating in this field situation.

FIGURE 7.16 *Variation in wild radish possen donor mating success in a field environment (data from Marshall and Fuller 1994).*

90 minutes of pollination. Reduced percentage of germination would indicate lower pollen responsiveness and the possibility of inhibition of pollen response, either through pollen to pollen interactions or through maternal tissue effects expressed through the stigma.

Some of the results of this experiment are shown in figure 7.17. The percentage of pollen that germinated after 90 minutes was essentially the same in the single donor and
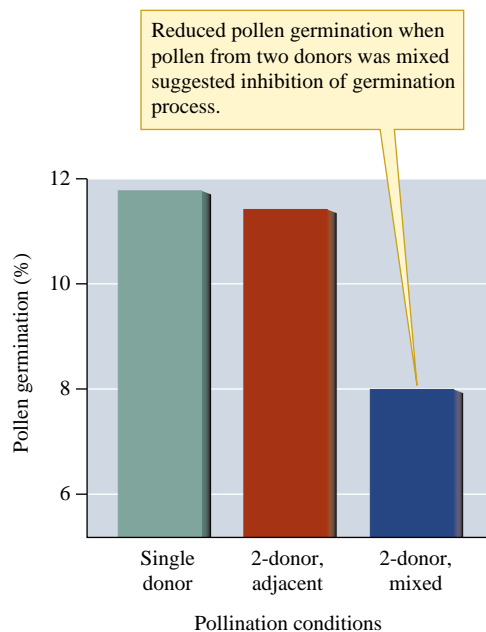

Reduced pollen germination when pollen from two donors was mixed suggested inhibition of germination process.

FIGURE 7.17 *Competition between pollen from different donors? (data from Marshall et al. 1996).*

adjacent pollinations. Meanwhile, the rate of germination when pollen from the two donors was mixed was much reduced. This reduced germination, where pollen grains of different pollen donors were in contact with each other, indicates that interactions between pollen inhibited pollen germination. These results suggest **interference competition** among pollen grains, which usually involves some form of aggressive or inhibitory interactions between individuals.

Experiments such as this one are revealing the details of plant ecology. While ecological interactions between plants are often much less obvious than those of animals, careful and ingenious experiments such as those of Marshall and her colleagues are proving that they are every bit as rich and fascinating.

In this section we have seen how organisms as different as fish, insects, and plants compete for and select mates. While competition for mates may be intense, the vast majority of mature females in most populations mate and a large proportion of males may also mate. In populations that have evolved a high degree of sociality, however, the opportunities for mating are often restricted to relatively few individuals.

CASE HISTORIES:
sociality

The evolution of sociality is generally accompanied by cooperative feeding, defense of the social group, and restricted reproductive opportunities.

Chapters 4 through 6 focused on the ecology of individual organisms, mainly on how individuals solve environmental problems. Some of the problems we considered were how animals maintain a particular range of body temperatures in the face of much greater variation in environmental temperatures or how plants sustain high rates of photosynthesis while avoiding excessive water loss. In the preceding parts of chapter 7 we've also concentrated on the ecology of individuals, examining how individuals choose mates. However, a fundamental change in relationships among individuals within a population takes place when individuals begin living in groups, such as colonies, herds, or schools and begin to cooperate with each other. Cooperation generally involves exchanges of resources between individuals or various forms of assistance, such as defense of the group against predators. Group living and cooperation signal the beginnings of **sociality.** The degree of sociality in a social species ranges from acts as simple as mutual grooming or group protection of young to highly complex, stratified societies such as those found in colonies of ants or termites. This more complex level of social behavior, which is considered to be the pinnacle of social evolution, is called **eusociality.** Eusociality is generally thought to include three major characteristics: (1) Individuals of more than one

generation living together, (2) cooperative care of young, and (3) division of individuals into sterile, or nonreproductive, and reproductive castes.

Because individuals in social species often appear to have fewer opportunities to reproduce compared to individuals in nonsocial species, the evolution of sociality has drawn a great deal of attention from behavioral ecologists. The apparent restriction of reproductive opportunities that comes with sociality appears to challenge the idea that the fitness of an individual is determined by the number of offspring it produces. How does sociality challenge this concept of fitness? The challenge emerges from the observation that in many situations, individuals in social species do not reproduce themselves, while helping others in the population to reproduce. How can we explain such behavior that on first glance appears to be self-sacrificing? It can be argued that such behavior should be quickly eliminated from populations. However, since eusocial species such as bees and ants have survived for millions of years, behavioral ecologists have assumed that in some circumstances, the benefits of sociality must outweigh the costs.

Behavioral ecologists have assumed that the key to understanding the evolution of sociality will result from careful assessment of its costs and benefits. The ultimate goal of sociobiology has been a comprehensive theory capable of explaining the evolution of the various forms of sociality, particularly its most specialized form, eusociality. However, in our quest for such a theory, where should we begin the accounting of costs and benefits? David Ligon (1999) pointed the way when he wrote, "Most, if not all, of the important issues relevant to cooperative breeding systems are . . . related to the costs and benefits of sociality." Following Ligon's suggestion, the case histories begin with cooperative breeders.

Cooperative Breeders

Species that live in groups often cooperate or help during the process of producing offspring. Help may include defending the territory or the young, preparing and maintaining a nest or den, or feeding young. Since the young which receive the care are not the offspring of the helpers, one of the most basic questions that we can ask about these breeding systems is why do helpers help? In other words, what benefits do helpers gain from their cooperation?

Sociobiologists have offered two main reasons. First, helpers may increase their own evolutionary, or genetic, fitness by improving the rates of survival and reproduction of relatives. Sociobiologists have suggested that investing resources, such as time or energy, in genetically related individuals that are not offspring (for instance, siblings, cousins, nieces, and so forth) may add to an individual's **inclusive fitness.** The concept of inclusive fitness, which was developed by William D. Hamilton (1964), proposes that an individual's inclusive, or overall, fitness is determined by its own survival and reproduction plus the survival and reproduction of individuals with whom the individual shares genes. Under some conditions

individuals can increase their inclusive fitness by helping increase the survival and reproduction of genetic relatives that are not offspring. Because this help is given to relatives, or kin, the evolutionary force favoring such helping behavior is called **kin selection.** Hamilton proposed that selection will favor diverting resources to kin under conditions where its benefit to the helper, measured as improved survival and reproduction of kin, exceeds its cost to the helper. Benefit is scaled by the genetic relatedness of individuals.

The second reason offered to explain the evolution of cooperative breeding is that helping may improve the helper's own probability of successful reproduction. Because helping gives the helper experience in raising young, helping may increase the helper's chances of successfully raising young of its own and recruiting helpers of its own. In addition, where suitable breeding habitat is limited, helpers may have a better chance of inheriting the breeding territory from the reproductive individuals they help. Again, they are improving their chances of eventually raising their own young.

What sorts of species engage in cooperative breeding? Approximately 100 species of birds are cooperative breeders. In addition, several species of mammals such as wolves, wild dogs, and African lions engage in cooperative breeding. Let's review two intensely studied species where several benefits of cooperative breeding have been demonstrated.

Green Woodhoopoes

We know a great deal about the cooperative breeding and general ecology of green woodhoopoes due to the pioneering, long-term studies of J. David Ligon and Sandra Ligon (Ligon and Ligon 1978, 1982, 1989, 1991). Adult green woodhoopoes, *Phoeniculus purpureus,* have reddish-orange bills and feet and black feathers with a metallic green and blue-purple sheen (fig. 7.18). Meanwhile, juvenile green woodhoopoes have black bill and feet, which allowed the Ligons to distinguish between mature and immature individuals in the field. Of the eight species of woodhoopoes, all of which are restricted to sub-Saharan Africa, the green woodhoopoe is the

FIGURE 7.18 *Green woodhoopoes.*

most common and widespread. Green woodhoopoes live in a wide variety of habitats at elevations from sea level to over 2,000 m. However, their most common habitat is open woodlands with trees large enough to provide cavities for nesting and roosting. For instance, the Ligon's long-term study site was located near Lake Naivasha in the central rift valley of Kenya in a woodland dominated by yellow-barked acacia.

Tree cavities keep the birds warm at night and provide some protection from predators. The habit of cavity roosting also makes green woodhoopoes ideal for field studies. To place unique color bands on green woodhoopoes in their study area, all the Ligons had to do was plug the opening to a roosting cavity after dark and then place a clear plastic bag over the opening in the morning to catch the woodhoopoes as they left the roost. Using this technique, they placed unique color bands on 386 green woodhoopoes. By closely studying the movements and interactions of banded individuals over a long period of time, the Ligons learned a great deal of the social relations of green woodhoopoes. For instance, they eventually knew the parentage of over 93% of the birds in their study area, the number and fates of offspring produced by each flock, and the identity of all breeders and nonbreeders in each flock. The results of this long-term study provide clues to the costs and benefits of cooperative breeding.

The Ligons found that green woodhoopoes live in territories that are occupied and defended by flocks of 2 to 16 individuals. Average flock size varied from approximately 4 to 6 over the course of their studies. Within a group only one pair breeds, while the remainder act as helpers. Males, which are approximately 20% larger than females, are particularly vigorous in their defense of breeding territories. The Ligons (1989) suggested that the larger body size of males is related to their intense competition with other males over territories and females. Territory defense is very important because territories appear to vary widely in quality.

One of the most obvious differences among territories is the quality of the cavities they contain. Cavity characteristics are very important because one of the major sources of mortality is predation while the birds are in their roosting or nesting cavities. The Ligons documented annual mortality rates of 30% for females and 40% for males, most of which was due to predation. Predators on nestlings include driver ants, hawks, and owls. Roosting adults are attacked at night by driver ants and large-spotted genets, small slender predators related to the mongoose. The vulnerability of nestlings and roosting adults to these predators depends on the characteristics of the cavity, especially its depth, the size of the opening, and the soundness of the wood.

Green woodhoopoes stay very close to their **natal territories,** that is the territories where they were raised. Out of 38 females that the Ligons banded as nestlings or fledglings and later observed breeding, 18 bred on their natal territory, 14 bred on an adjacent territory, and 6 only two or three territories away from their natal territory. Male dispersal is also limited. In other words, this population of green woodhoopoes shows a great deal of **philopatry.** Philopatry,

which means literally "love of place," is a term that behavioral ecologists use to describe the tendency of some organisms to remain in the same area throughout their lives.

Why do green woodhoopoes stay at home and help raise young, which are close relatives, rather than disperse to produce their own offspring? The Ligons suggested that the major factor producing this high degree of philopatry is that roost cavities on which green woodhoopoes depend in the highlands of Kenya are scarce. By staying home a young green woodhoopoe gets a warm and relatively safe place to roost at night and may eventually inherit the territory and its cavities.

Over the course of their study, the Ligons found that 91% of females and 89% of males died without leaving any descendants. However, they also documented very high reproductive success among some woodhoopoes. Variation in reproductive success within the study area seemed to have two major sources, spatial and temporal variation. Year to year variation in breeding success was largely a result of variation in rainfall and its influence on the woodhoopoes food supply. The main food that woodhoopoes give to nestlings are moth larvae that pupate in the soil and are sensitive to soil moisture. In general, rainfall during the savanna dry season kills these larvae and produces a food shortage. The result of rain during the dry season is usually reproductive failure among the woodhoopoes (fig. 7.19).

The second source of variation in reproductive success appears to be differences in territory quality. The Ligons found that territories fell into two clearly distinctive groups which they called high quality and low quality territories. Territory quality appeared to be mainly determined by the availability of roosting cavities capable of protecting the birds from predators. Figure 7.20 compares the average number of young produced per year on low quality and high quality territories. As you can see, the number of offspring produced on high quality territories is approximately twice as high as on low quality territories during both favorable and unfavorable years.
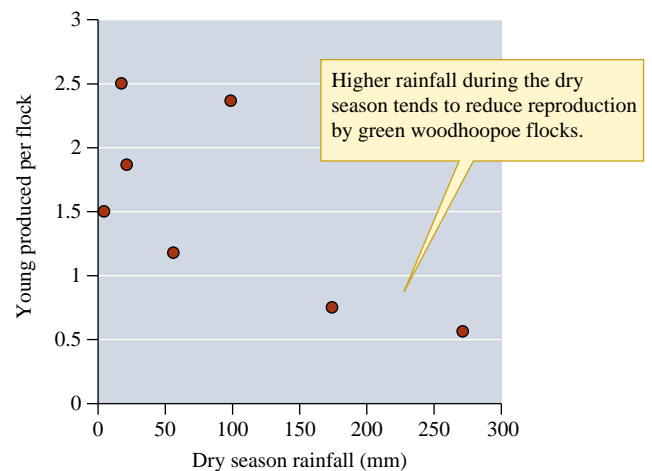

FIGURE 7.19 *Influence of rainfall on reproduction by green woodhoopoe flocks (data from Ligon and Ligon 1989).*

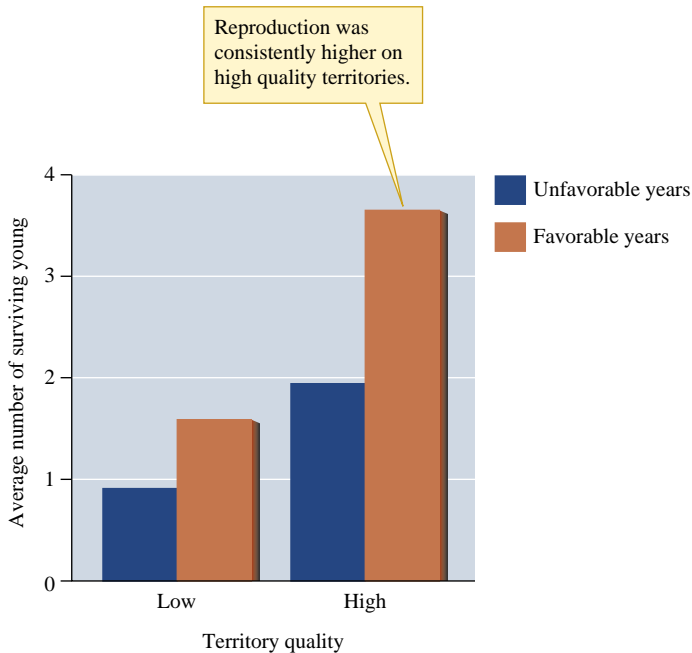Reproduction was consistently higher on high quality territories.

FIGURE 7.20 *Relationship between territory quality and reproduction by green woodhoopoe flocks (data from Ligon and Ligon 1989).*

While the birds can do nothing about the chances of rainfall during the dry season, they can and do compete for territories. Those flocks that successfully compete for the best territories, have a clear reproductive advantage. So, returning to our original question, why do green woodhoopoes stay home and help? The first reason seems to be that by helping to raise and protect close relatives, the helpers may increase their inclusive fitness. The Ligons found that the bulk of the young tended by helpers ranged from half siblings to full siblings. We should keep in mind that a full sibling, on average, would share as many genes (50%) with the helper as its own son or daughter. The second and perhaps clearest potential benefit to a helper is that since high quality territories are limited in number, the chance of inheriting the natal territory and advancing to breeding status may be greater than finding another suitable territory elsewhere.

What might we learn about the evolution of cooperative breeding from other species? Several cooperative species live in sub-Saharan Africa. For example, the African lion, a species that shares the same landscape with green woodhoopoes, also seems to be forced by a variety of environmental circumstances into a cooperative social system.

African Lions

At about the same time that the Ligons were studying cooperative breeding among green woodhoopoes, Craig Packer and Anne E. Pusey were studying cooperation among African lions in the Serengeti (Packer and Pusey 1982, 1983, 1997, Packer et al. 1991). Their studies have revealed a great deal of complexity in lion societies. Female lions live in groups of related individuals called prides (fig. 7.21). Prides of female lions generally include 3 to 6 adults but may contain as many as 18 or as few as 1. In addition to adult females, prides also include their dependent offspring and a coalition of adult males. Male coalitions may be made up of closely related individuals or of unrelated individuals.

Within lion society one can observe many forms of cooperation. Female lions nurse each other's cubs. They also cooperate when hunting large, difficult-to-kill game such as zebra and buffalo. In addition, females cooperatively defend their territory against encroaching females. However, the most critical form of cooperation among females is their group defense of the young against infanticidal males. These attacks on the young generally take place as a male coalition is displaced by another invading coalition. While a single female lion has little chance in a fight against a male lion, which are nearly 50% larger, cooperating females are often successful at repelling attacking males. Males, in turn, cooperate in defending the territory against invading males, which threaten the young they have sired, and against threats from other predators such as hyenas. The challenge for the behavioral ecologist has been to determine whether these various forms of cooperation can be reconciled with evolutionary theory.

Since the females in lion prides are always close relatives, their cooperative behavior can be readily explained within the conceptual framework of kin selection. As females cooperate in nursing or defending young against males, they contribute to the growth and survival of their own offspring or to those of close kin. Cooperative hunting and sharing the kill also contribute to the welfare of offspring and close relatives. All these contributions add to the inclusive fitness of individual females.

In contrast, because male coalitions are sometimes made up of close relatives and sometimes not, cooperation within coalitions has represented a greater challenge to evolutionary theory. However, on close consideration Packer and colleagues (Packer et al. 1991) discovered that the rules associated with the formation and behavior of coalitions are consistent with predictions of evolutionary theory. Single males have virtually no chance of claiming and defending a pride of female lions. Therefore they must form coalitions with other males. This represents a type of ecological constraint on viable choices open to males. If males form a coalition with brothers and cousins, cooperative behavior that increases the production and survival of offspring of the coalition will increase an individual male's inclusive fitness. However, theoretically, a male within a coalition with unrelated males must produce some offspring of his own or he is merely increasing the fitness of others at the expense of his own fitness.

The first question we should ask is, Do all males within a coalition have an equal opportunity to reproduce? If all males within a coalition have an equal probability of reproducing, then forming coalitions with unrelated males is easier to reconcile with evolutionary theory. However, if there is significant variation in reproductive opportunities within coalitions, then cooperating with unrelated males is more difficult

FIGURE 7.21 *African lions are highly social predators.*

to reconcile with theories predicting that individuals will attempt to maximize their inclusive fitness. It turns out that the probability of a male siring young depends on his rank within a coalition and on coalition size. As shown in figure 7.22, males in coalitions of two sire a relatively similar proportion of the young produced by the pride. In addition, these proportions are close to the proportions sired by the two top ranked males in coalitions of three and four. However, the third ranked males in coalitions of three and the third and fourth ranked in coalitions of four sire almost no young lions. Packer and his team concluded from these data that variation in reproductive success is much higher in coalitions of three and four than in coalitions of two. In other words, the chance of reproducing is less evenly distributed among males in coalitions of three and four than in coalitions of two.

What implications do the results of Packer's studies have to the formation of coalitions containing unrelated individuals? One of the implications is that an unrelated male in a coalition of three or more runs the risk of investing time and energy in helping maintain a pride without an opportunity to reproduce himself and without improving his inclusive fitness since the other coalition members are not relatives. This result suggests that males should avoid joining larger coalitions of
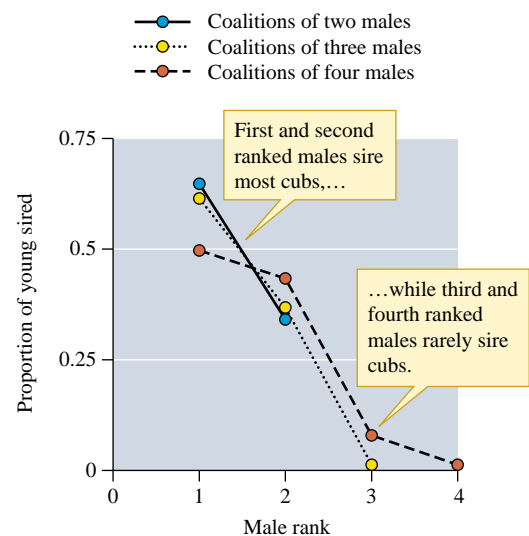

FIGURE 7.22 *Male lion rank and proportion of cubs sired in male coalitions of different sizes (data from Packer et al. 1991).*

unrelated males, and this is just what Packer and his colleagues found (fig. 7.23). Figure 7.23 shows the percentage of males with unrelated partners in coalitions of different sizes. These patterns show clearly that males that team up with unrelated individuals mostly do so in coalitions of two or three. Larger coalitions of four to nine individuals are almost entirely made up of relatives. What are the implications of these data? They suggest that males avoid joining larger coalitions unless the coalition consists of relatives. Such a strategy avoids the risk of helping without gaining in inclusive fitness.

In summary, cooperation among green woodhoopoes and African lions appears to be a response to environmental conditions that require cooperation for success. In the case of green woodhoopoes, the scarcity of high quality territories and intense competition between flocks for those territories create conditions that favor staying in the natal territory and helping raise related young and perhaps inheriting the territory at a later date. Packer and Pusey (1997) captured the situation facing African lions in a fascinating article titled, "Divided We Fall: Cooperation Among Lions." To survive, reproduce, and successfully raise offspring to maturity, African lions must work in cooperative groups. The lone lion has no chance of meeting the ecological challenges presented by living on the Serengeti in lion society with its aggressive prides and invasive and infanticidal male coalitions. However, as we have seen, within the constraints set by their environments both green woodhoopoes and African lions appear to behave in a way that contributes positively to their overall fitness.

While the complexities of African lion and green woodhoopoe societies have taken decades to uncover, they pale beside the intricacies of life among eusocial species such as bees, termites, and ants. Let's explore eusociality in some animal populations to get some insights into the evolution of these complex social systems and to introduce the comparative method, one of the most valuable tools in evolutionary ecology.
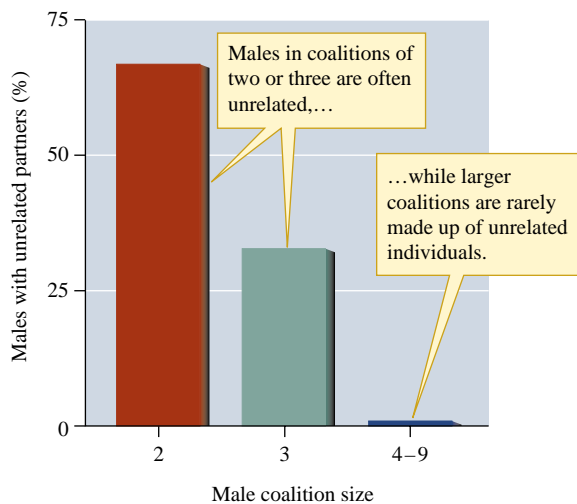

FIGURE 7.23 *Relatedness and size of male coalitions among African lions (data from Packer et al. 1991).*

APPLICATIONS AND TOOLS: the comparative method—a tool for understanding complex evolutionary histories

Behavioral ecologists are concerned with both how particular social systems work and with determining the mechanisms responsible for their evolution and maintenance. In most cases, however, the evolutionary origins of biological traits lie deep in the past and biologists cannot observe their evolution directly. So, how do scientists construct evolutionary hypotheses, test them, and eventually construct evolutionary theories? Many tools are used in such a process. We have already employed one of those tools, in a rudimentary way, without giving it a name. As we explored mate choice and sexual selection using guppies, scorpionflies, and wild radish as case histories to provide insights into the evolution of sociality, we were employing one of the most valuable tools available to evolutionary biologists. That tool is the **comparative method.**

The comparative method involves comparisons of the characteristics of different species or populations of organisms in a way that attempts to isolate a particular variable or characteristic of interest, such as sociality. Randy Thornhill (1984) suggested that in the ideal application of the comparative method, the influence of confounding, or confusing, variables on the variable of interest are randomized across the species or populations in the study. In his discussion of the comparative method, Thornhill reviewed its use to test whether or not **polygynous species,** species in which some males have several mates, show greater sexual dimorphism (males larger than females) than weakly polygynous or **monogamous species,** species in which males and females have a single mate. He pointed out that since the time of Darwin, who used the comparative method extensively, biologists have assumed that there is a connection between degree of sexual dimorphism and degree of polygyny. However, it was not until approximately a century after Darwin's work that evolutionary biologists carefully tested the idea using the comparative method. Their approach was to choose a wide variety of mammals that differed in their mating systems and degree of polygyny and then statistically test the relationship between the two variables.

When they did so, they found a significant positive relationship between the degree of sexual dimorphism and degree of polygyny among several groups of very different mammals, including hoofed mammals, primates, and seals and sea lions. It turned out that the most polygynous species in all groups showed the greatest degree of sexual dimorphism. Closely related species in these groups that differed in degree of polygyny also differed markedly in their degree of sexual dimorphism. In addition, distantly related species that have similar degree of polygyny, converged in their degree of sexual dimorphism. This convergence in dimorphism among distantly related taxa is analogous to the findings of Ligon and Ligon (1991) and Packer and Pusey (1997) that demonstrated that cooperative

breeding by both green woodhoopoes and African lions is associated with significant environmental pressures that favor remaining in a group.

Let's review a remarkable case of convergence in social organization between a eusocial insect and a eusocial mammal. The main purpose of this comparison is to see the extent to which unrelated organisms can converge in biology and to suggest that such comparisons, the foundation of the comparative method, if quantified and replicated across many species, can help disentangle the evolution of complex characteristics, including the evolution of social systems.

Eusocial Species

Probably the most thoroughly studied of eusocial species are the ants. Ants and their complex behaviors have attracted the attention of people from the earliest times and appear in the oldest writings such as the Bible and the classical writings of ancient Greece. Such written records were likely predated by older folktales. Bert Hölldobler and Edward O. Wilson (1990) pointed out that many of the earliest accounts of ants focused on ant species that make their living by harvesting seeds. These seed-harvesting species were serious agricultural pests around the Mediterranean Sea and their dependence on grains paralleled remarkably the economy of the human populations of the region.

In the intervening centuries since these earliest writings, we have learned much more about ants. Taxonomists have described nearly 9,000 species of ants, all belonging to the family Formicidae, which along with their relatives the wasps and bees, are members of the insect order Hymenoptera. Hölldobler and Wilson (1990) wrote a monumental summary of what was known about ants near the end of the twentieth century in a book titled simply *The Ants.* However, despite that book and the hundreds of studies done on ants since its publication, much is left to learn about this group of insects that Hölldobler and Wilson referred to as the "culmination of insect evolution."

One of the most socially complex groups of ants are the leafcutters (fig. 7.24). The 39 described species of leafcutter ants, which belong to two genera, are found only in the Americas, from the southern United States to Argentina. Leafcutter ants make their living by cutting and transporting leaf fragments to their nest, where the leaf material is fragmented and used as a substrate upon which to grow fungi. The fungi provide the primary food source for leafcutter ants.

Among the various species of leafcutter ants, some of the most thoroughly studied are species belonging to the genus *Atta.* *Atta* species live mainly in tropical Central and South America. However, at least two species reach as far north as Arizona and Louisiana in the United States. Leafcutter ants are important consumers in the tropical ecosystems, where they move large amounts of soil and process large quantities of leaf material in their nests. The nests of leafcutter ants can attain great size. For instance, the nests of *A. sexdens* can include over 1,000 entrance holes and nearly 2000 occupied and abandoned chambers. In one excavation of an *A. sexdens* nest (cited in Hölldobler and

FIGURE 7.24 *Leaf cutter ants carrying leaf fragments back to the nest where they will be processed to create a substrate for growing the fungi that the ants eat. Smaller ants riding on leaf fragments offer protection from aerial attack by parasitoid flies.*

Wilson 1990), researchers estimated that the ants had moved more than 22 m³ of soil, which weighed over 40,000 kg. Within this nest, the occupants had stored nearly 6,000 kg of leaves. Mature nests of *A. sexdens* contain a queen, various numbers of winged males and females which disperse to mate and found colonies elsewhere, and up to 5 to 8 million workers.

Though involving far fewer individuals, there are striking analogies between the organization of ant colonies and colonies of naked mole rats, *Heterocephalus glaber,* one of the few species of eusocial mammals (fig. 7.25). Despite their common name, naked mole rats are not completely naked and they are neither moles nor rats. Like moles, naked mole rats live underground but they are rodents not moles. However, the family of rodents to which they belong is more closely related to porcupines and chinchillas than to rats.

Naked mole rats live in underground colonies in the arid regions of Kenya, Somalia, and Ethiopia. Colonies often include 70 to 80 individuals but can sometimes contain as many as 250 individuals. The burrow system of a single colony of naked mole rats is extensive and can cover up to approximately 100,000 m², or about 20 football fields. Most of the digging required to maintain their large burrow systems is done with the naked mole rats' teeth and massive jaws. It turns out that the jaw muscles of naked mole rats make up about 25% of their entire muscle mass. This would be approximately equivalent to having muscles the size of those in your legs powering your jaws!

Both naked mole rats and leafcutter ants live in social groups in which individuals are divided among **castes** that engage in very different activities. We can define a caste as a group of physically distinctive individuals that engage in specialized behavior within the colony. E. O. Wilson (1980) studied how labor is divided among castes of ants in a laboratory colony of *A. sexdens* that he established and studied over a period of 8 years. During this period, Wilson carefully cataloged the behaviors of individual colony members. Because the colony lived in a closed series of clear plastic containers, their behavior could be

FIGURE 7.25 *Naked mole rats live in colonies of closely related individuals ruled by a single dominant female, or queen, shown here resting on top of members of her colony.*

FIGURE 7.26 *Comparison of the number of castes and number of behaviors in a colony of leafcutter ants,* Atta sexdens, *and in colonies of three other ant species (data from Wilson 1980).*

studied easily. In addition to recording behaviors, Wilson also estimated the sizes of individuals engaging in each behavior by measuring their head widths to the nearest 0.2 mm. He made his estimates visually by comparing an ant to a standard array of preserved *A. sexdens* specimens of known size.

When Wilson compared the leafcutter ant *A. sexdens* with three non-leafcutter ant species, he found that the leafcutter ants included a larger number of castes and engaged in a wider variety of behaviors (fig. 7.26). Wilson identified a total of 29 distinctive tasks performed by the leafcutter ants compared to an average of 17.7 tasks performed by the three other species. He found that the division of labor within the *A. sexdens* colony was mainly based on size. Possibly because of the large number of specialized tasks that need to be performed by leafcutter ants, they have one of the most complex social structures and one of the greatest size ranges found among the ants. Within *A. sexdens* colonies, the head width of the largest individuals (5.2 mm) is nearly nine times the head width of the smallest individuals (0.6 mm). On the basis of size, Wilson identified four castes within his leafcutter colony. However, because the tasks performed by some of the size classes change as they age, Wilson discovered three additional temporal or developmental castes for a total of seven castes within the colony, compared to an average of three castes in the non-leafcutter ant species he studied.

As a consequence of this great variation, someone watching a trail of leafcutter ants bring freshly cut leaf fragments back to their nest is treated to a rich display of size and behavioral diversity. While medium-sized ants carry the leaf fragments above their heads, the largest ants line the trail like sentries, guarding against ground attacks on the column of ants carrying leaf fragments. Very small ants ride on many of the leaf fragments, protecting the ant carrying a leaf fragment from aerial attacks by parasitic flies. Meanwhile, other size classes of leafcutters performing behaviors associated with processing leaves, tending larvae, and maintaining fungal gardens remain hidden in the nest. It was the activity of these smaller individuals that Wilson's laboratory colony was able to reveal so clearly.
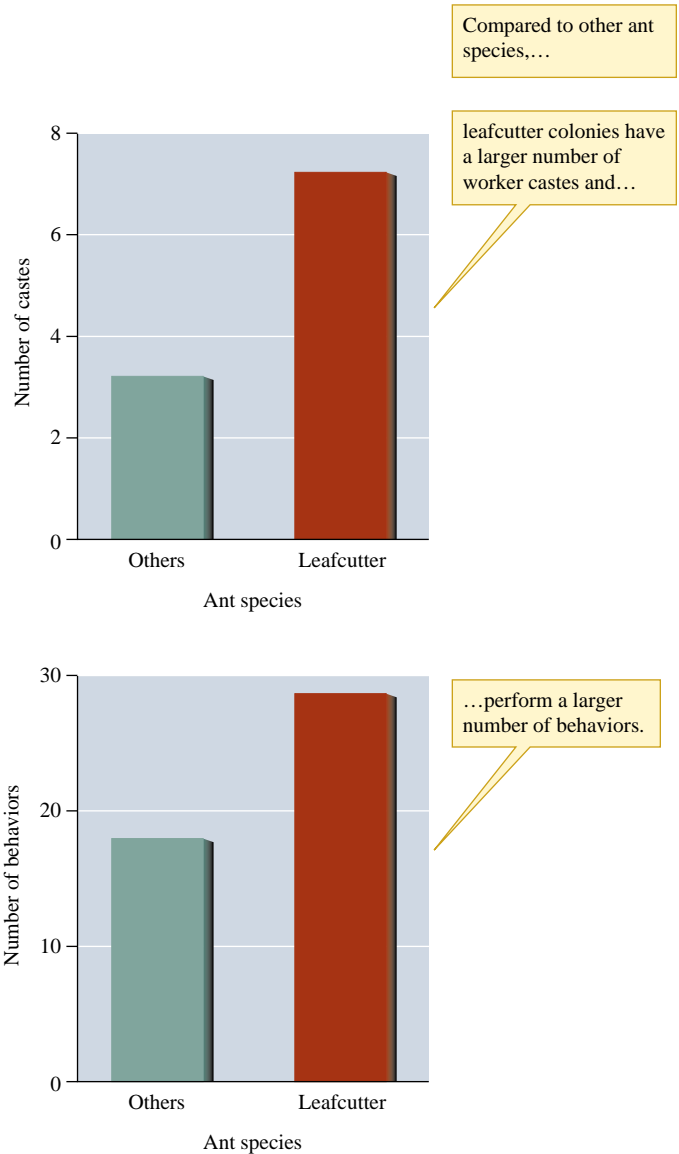
Careful study has revealed some remarkable parallels in the structures of naked mole rat and leafcutter ant societies. The social behavior of naked mole rats was first reported by Jennifer Jarvis, professor at the University of Cape Town, South Africa, in a paper in the journal *Science* (Jarvis 1981). Her published study was based on more than 6 years of observation and experimentation with colonies of naked mole rats that she had established in the laboratory. Jarvis dug up a number of colonies and relocated them to a laboratory habitat analogous to that used by Wilson in his study of leafcutter ants. She waited approximately a year after bringing the naked mole rats to the laboratory before attempting to quantify their behaviors. Once this period of acclimation was over, Jarvis spent approximately 100 hours detailing how the members of her laboratory population of naked mole rats spent their time.

The picture of naked mole rat society that emerged from Jarvis' study was immediately intriguing to behavioral ecologists. The social organization of the colony appeared more similar to an ant colony than to any other mammal population known. Jarvis' paper in *Science* stimulated dozens of studies of naked mole rats and of related species. The results provide interesting insights into the evolution of social behavior. Within a colony of naked mole rats, one female and only a few males breed. This group of reproductive individuals functions basically as a queen and her mates, while all of the rest of the colony is nonreproductive. Behavioral ecologists have found that life in a naked mole rat colony centers on the queen and her offspring, and the queen's behavior appears to maintain this focus. She is the most active member of the colony and literally pushes her way around the colony. By physically pushing individuals she appears to call them to action when there is work to be done or when the colony is threatened and needs defending. The aggressiveness of the queen also appears to maintain her dominance over other females in the colony and prevent them from coming into breeding condition. If the queen dies or is removed from the colony, one of the other females in the colony will assume the role of queen. If two or more females compete for the position of queen, they may fight to the death during the process of establishing the new social hierarchy.

In contrast to leafcutter ant colonies, where all workers are females, both males and females work in naked mole rat colonies. Jarvis found that work is divided among colony members, as in leafcutter ant colonies, according to size. However, in contrast to leafcutter ants, colonies of naked mole rats include only two worker size classes, small and large. Small workers are the most active. Small workers excavate tunnels, build the nest, which is deeper than most of the passage ways, and line the nest with plant materials for bedding. In addition, small workers also harvest food, mainly roots and tubers, and deliver it to other colony members, including the queen for feeding. Since they spend most of their time sleeping, the role

Division of labor in both leafcutter ant colonies and naked mole rat colonies is based on size.
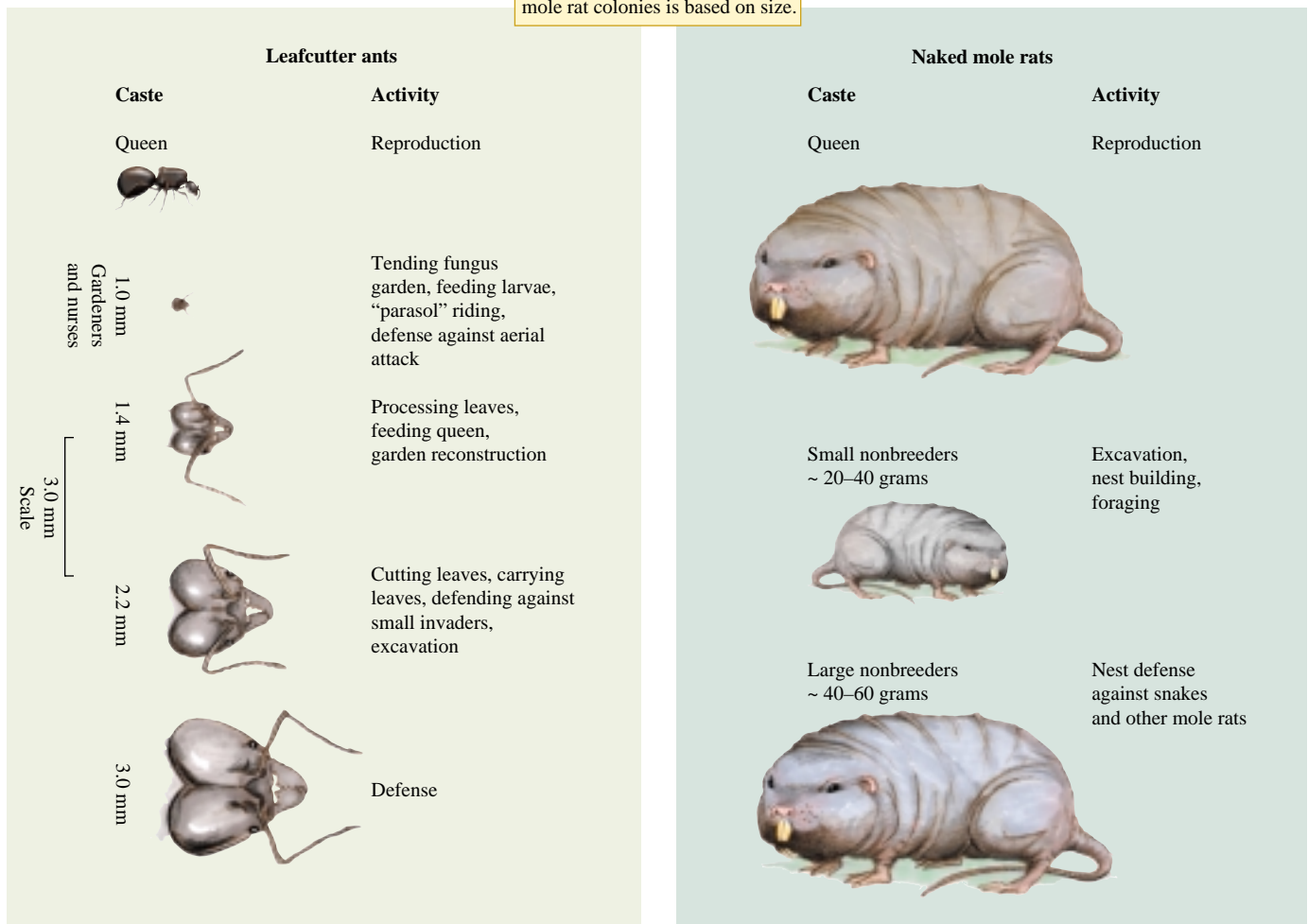
Leafcutter ants

Caste	Activity
Queen	Reproduction
Gardeners and nurses — 1.0 mm	Tending fungus garden, feeding larvae, "parasol" riding, defense against aerial attack
1.4 mm	Processing leaves, feeding queen, garden reconstruction
2.2 mm	Cutting leaves, carrying leaves, defending against small invaders, excavation
3.0 mm	Defense

3.0 mm Scale

Naked mole rats

Caste	Activity
Queen	Reproduction
Small nonbreeders ~ 20–40 grams	Excavation, nest building, foraging
Large nonbreeders ~ 40–60 grams	Nest defense against snakes and other mole rats

FIGURE 7.27 *Division of labor among castes of leafcutter ants,* Atta sexdens, *and naked mole rats,* Heterocephalus glaber. *Ant sizes are head widths of workers typically engaged in each activity (data from Wilson 1980, Jarvis 1981, and Sherman, Jarvis and Braude 1992).*

of large nonbreeders was unclear for some time. However, eventually researchers working in the field were able to observe these large nonbreeders in action. It turns out that the large workers, as in ant colonies, are a caste specializing in defense. If the tunnel system is breached by members of another colony, the large nonbreeders move out quickly from their resting places to defend the colony from the invaders, literally throwing themselves into the breach. Eventually the large nonbreeders push up enough soil to wall off the intruders. However, they may be most important in defending against snakes, the most dangerous predators of naked mole rats. When confronted with a snake, the large nonbreeders will try to kill the snake or spray it with soil until it is driven off or buried.

Evolution of Eusociality

Despite their distinctive evolutionary histories and other biological differences, the studies of Wilson and Jarvis suggest interesting parallels in the organizations of leafcutter ant and naked mole rat colonies (fig. 7.27). Similarities include division of labor within colonies based on size, with smaller workers specializing in foraging, nest maintenance, and excavation of extensive burrow systems. Meanwhile, larger workers in both species specialize in defense. In addition, reproduction in both species is limited to a single queen and her mates. These areas of convergence in social organization between such different organisms may help shed light on the forces responsible for the evolution of eusociality. Such comparisons form the basis of the comparative method.

What factors may have been important in the evolution and maintenance of naked mole rat and leafcutter ant sociality? Kin selection may play a role. Leafcutter ants along with other Hymenoptera, such a bees and wasps, have an inheritance system called **haplodiploidy.** The term haplodiploid refers to the number of chromosome sets possessed by males and females. In haplodiploid systems males develop from unfertilized eggs and are haploid, while females develop from fertilized eggs and so are diploid. One of the consequences of haplodiploidy is that worker ants within a colony can be very similar genetically. In an ant colony where there is a single queen that mated with a single male, the workers will be more related to each other than they would be to their own offspring. W. D. Hamilton (1964) was the first to point out that under these conditions the average genetic similarity among workers would be 75%, while their relationship with any offspring they might produce would be 50% (fig. 7.28).

What is the source of this high degree of relatedness? The queen mates only during her mating flight and stores the sperm she receives to fertilize all the eggs she lays to produce daughters. If she mates with a single male, since he is haploid, all her daughters will receive the same genetic information from their male parent. As a consequence, the 50% of the genetic makeup that workers receive from their male parent will be identical. In addition, workers will share an average of 25% of their genes through those that they receive from the queen, yielding an average genetic relatedness of 50% + 25% = 75%. The important point here is that the activity of workers

promotes the production of closely related individuals, their sisters, an activity that should be favored by kin selection.

Because naked mole rat colonies are relatively closed to outsiders, the individuals within each colony, like the workers within leafcutter ant colonies, are also very similar genetically. Paul Sherman, Jennifer Jarvis, and Stanton Braude (1992) reported that approximately 85% of matings within a colony of naked mole rats are between parents and offspring or between siblings. As a consequence of these matings between close relatives, the relatedness between individuals within a colony is about 81%, suggesting that kin selection may be involved in the maintenance of nonreproductive helpers in colonies of naked mole rats.

What factors other than kin selection may have contributed to the evolution of eusociality? Many factors have been implicated. While researchers working on ants and other social Hymenoptera have emphasized the potential importance of kin selection, studies of cooperative-breeding vertebrate species have emphasized ecological constraints. What sorts of ecological common constraints are faced by leafcutter ants and naked mole rats? One of the most obvious is the work associated with the creation, maintenance, and defense of extensive burrow systems. The more social organisms are studied, the less likely it has become that one or a few simple mechanisms will be adequate to explain their evolution. However, the results of studies such as those of Wilson and Jarvis should encourage continued careful comparative studies as a means for eventual understanding of the evolution of sociality. In the application of the comparative method, species such as the leafcutter ant *A. sexdens* and naked mole rats function as invaluable tools.
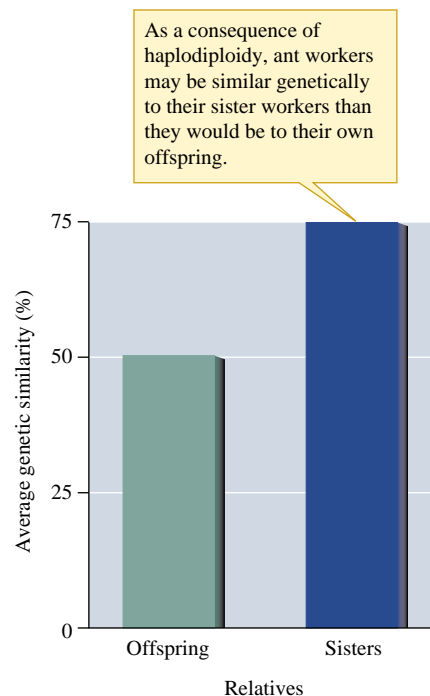

FIGURE 7.28 *Average genetic similarity between ant workers and sisters (other workers) versus their offspring if they reproduced.*

SUMMARY CONCEPTS

Social relations are important since they often directly and obviously impact the reproductive contribution of individuals to future generations, a key component of evolutionary fitness, the number of offspring, or genes, contributed by an individual to future generations. One of the most fundamental social interactions between individuals takes place during sexual reproduction.

Mate choice by one sex and/or competition for mates among individuals of the same sex can result in selection for particular traits in individuals, a process called sexual selection. Sexual selection results from differences in reproductive rates among individuals as a result of differences in their mating success. Sexual selection is thought to work either through intrasexual selection, where individuals of one sex compete with each other for mates, or intersexual selection, when members of one sex consistently choose mates from among members of the opposite sex on the basis of some particular trait.

Experimental evidence supports the hypothesis that the coloration of male guppies in local populations is determined by a dynamic interplay between natural selection exerted by predators, under which less-colorful males have higher survival, and by female mate choice, which results in higher mating success by more-colorful males. Among scorpionflies, larger males are more likely to successfully defend available arthropod offerings due to their advantages in aggressive encounters and consequently mate more frequently than smaller males without arthropod offerings. Studies of mating in the wild radish, *Raphanus sativus,* in greenhouse and field experiments indicate nonrandom mating and suggest interference competition among pollen from different pollen donors.

The evolution of sociality is generally accompanied by cooperative feeding, defense of the social group, and restricted reproductive opportunities. The degree of sociality in a social species ranges from acts as simple as mutual grooming or group protection of young to highly complex, stratified societies such as those found in colonies of ants or termites. This more complex level of social behavior, which is considered to be the pinnacle of social evolution, is called eusociality. Eusociality is generally thought to include three major characteristics: (1) individuals of more than one generation living together, (2) cooperative care of young, and (3) division of individuals into sterile, or nonreproductive, and reproductive castes.

Cooperation among green woodhoopoes and African lions appears to be a response to environmental conditions that require cooperation for success. For green woodhoopoes, the scarcity of high quality territories and intense competition between flocks for those territories create conditions that favor staying in the natal territory and helping raise related young and perhaps inheriting the territory at a later date. To survive, reproduce, and successfully raise offspring to maturity, African lions must work in cooperative groups of females, which are called prides, and of males, which are called coalitions.

One of the most valuable tools available to evolutionary biologists is the comparative method. The comparative method examines the characteristics of different species or populations of organisms in a way that attempts to isolate a particular variable or characteristic of interest, such as sociality, while randomizing the influence of confounding, or confusing, variables on the variable of interest. The comparative method has been used to study the evolution of eusociality among a wide variety of animal species including leafcutter ants and naked mole rats, both of which live in social groups in which individuals are divided among castes that engage in very different activities. Compared to other ant species, leafcutter ant colonies have a larger number of castes that engage in a wider variety of behaviors. In contrast to leafcutter ant colonies, where all workers are females, both males and females work in naked mole rat colonies. However, as in leafcutter ant colonies, work in naked mole rat colonies is divided among members according to their size. Many factors have likely contributed to the evolution of eusociality in leafcutter ants and naked mole rats, including kin selection and ecological constraints.

REVIEW QUESTIONS

1. The introduction to chapter 7 included sketches of the behavior and social systems of several fish species. Using the concepts that you have learned in the chapter, revisit those examples and predict the forms of sexual selection occurring in each species.

2. One of the basic assumptions of the material presented in chapter 7 is that the form of reproduction will exert substantial influence on social interactions within a species. How might interactions differ in populations that reproduce asexually versus ones that engage in sexual reproduction? How might having separate sexes versus hermaphrodites affect the types of social interactions within a population? How should having several forms of one sex, for example, large and small males, influence the diversity of behavioral interactions within the population?

3. Endler (1980) pointed out that though field observations are consistent with the hypothesis that predators may exert natural selection on guppy coloration, some other factors in the

environment could be affecting variation in male color patterns among guppy populations. What other factors, especially physical and chemical factors, might affect male colors and should each influence male color?

4. Endler set up two experiments, one in the greenhouse and one in the field. What were the advantages of the greenhouse experiments? What were the shortcomings of the greenhouse experiments? Endler also set up field experiments along the Aripo River. What were the advantages of the field experiments and what were their shortcomings?

5. Examine figure 7.8. While most of the male guppies that successfully mated were dominant, a substantial proportion of attractive males that sired broods were subordinate. How might we interpret this reproductive success by attractive but subordinate males? What might these results indicate about the potential influence of female choice on mating success among male guppies?

6. Using the studies of Kodric-Brown and Thornhill, compare guppy and scorpionfly mating systems. Pay particular attention to the potential roles of intersexual and intrasexual selection in each species. What are the similarities between the two species? What are some apparent differences?

7. The results of numerous studies indicate nonrandom mating among plants at least under some conditions. These results lead to questions concerning the biological mechanisms that produce these nonrandom matings. How might the maternal plant control or at least influence the paternity of her seeds? What role might competition between pollen determine in the nonrandom patterns observed?

8. The details of experimental design are critical for determining the success or failure of both field and laboratory experiments. Results often depend on some small details. For instance, why did Jennifer Jarvis wait one year after establishing her laboratory colony of naked mole rats before attempting to quantify the behavior of the laboratory population? What might have been the consequence of beginning to quantify the behavior of the colony soon after it was established?

9. Behavioral ecologists have argued that naked mole rats are eusocial. What are the major characteristics of eusociality and which of those characteristics are shared by naked mole rats?

10. Choose a problem in the ecology of social relations, formulate a hypothesis, and design a study to test your hypothesis. Take two approaches. In one approach use field and laboratory experiments to test your ideas. In the second design a study that will employ the comparative method.

SUGGESTED READINGS

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