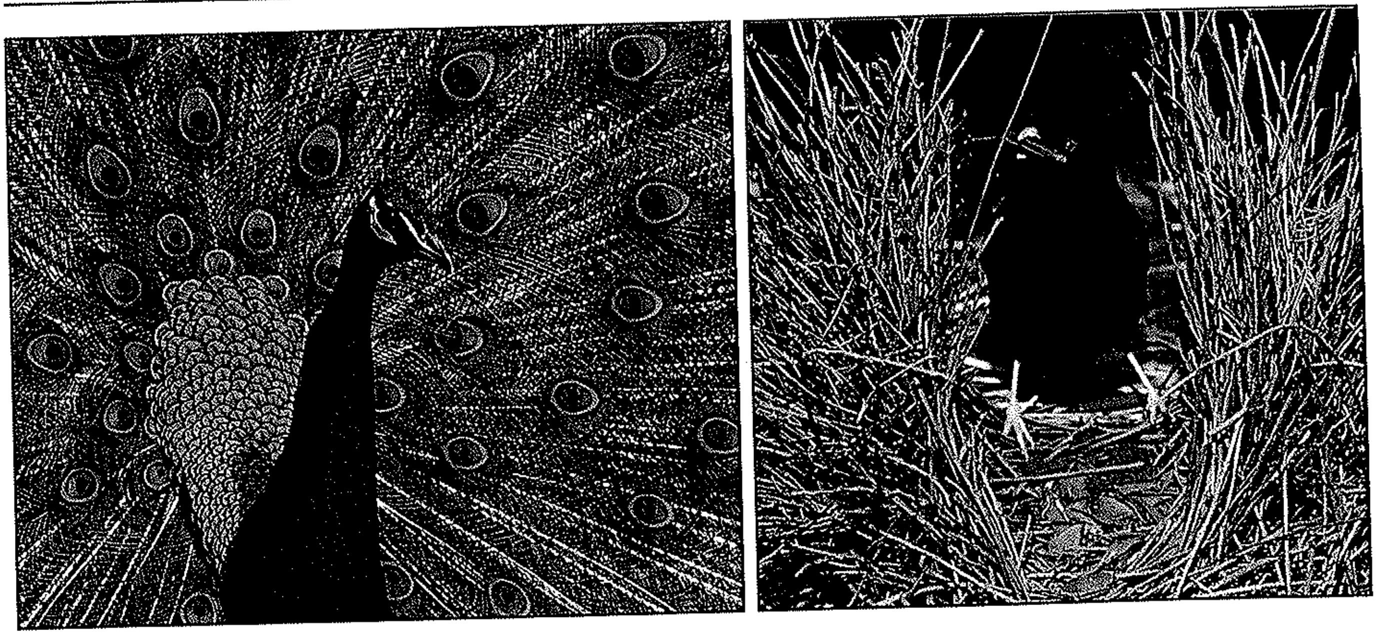


6

Evolutionary Social Theory

CHAPTER OUTLINE

- *The rudiments of evolutionary social theory*
- *Altruism toward genetic relatives and the concept of kin selection*
  - *Shared genes*
  - *Some common confusions about kin selection*
  - *Nepotism and self-interest I: The alarm calls of ground squirrels*
  - *Nepotism and self-interest II: Helpers at the nest and in the den*
- *Reciprocal altruism: Return effects in the absence of close genetic relatedness*
  - *Sharing of food by vampire bats*
- *Parent-offspring conflict*
  - *The evolutionary basis of weaning conflict*
  - *Psychological adaptations of offspring and parents*
  - *Social behavior of offspring toward near relatives*
  - *Dependence on the mating system*
  - *Conflict during pregnancy*
  - *Reproductive future of the parent*
- *Sexual Selection*
- *The role of parental investment in sexual selection*
  - *Minimal parental investment by males is frequently associated with polygynous mating systems*
  - *Large parental investment by males is often associated with monogamous mating systems*
  - *Species displaying reversed sex roles have polyandrous mating systems*
  - *Some further behavioral consequences*
- *Manipulating the sex ratio*
  - *Opossums manipulate the numbers of sons and daughters*
  - *Red deer also manipulate the sex ratio*
  - *Female dominance enhances the reproductive success of daughters*
- *Synopsis*
- *Questions for thought and discussion*
- *Suggestions for further reading*

Photo: Sexual selection for female choice can take different forms. The peacock (*left*) grows his gaudy and unwieldy tail, but the satin bower bird (*right*) builds his display of grass and then decorates it with brightly colored objects that he brings to the site. How such seemingly non-utilitarian features could have evolved by natural selection was a source of controversy for many years after Darwin's death.

Some animals such as leopards and orangutans live alone and come into contact with members of their own species only at the time of mating. Other animals live together as mated pairs—or even, in the case of certain birds, wild dogs, and wolves, small families—and cooperatively feed and protect their young. Still other species—ground squirrels, elephants, many kinds of primates—live in larger groups with variable ties of genetic relatedness but with considerable social interaction among individuals. And some species—schools of fish, flocks of birds, herds of wildebeest and zebra—congregate to migrate or breed in groups that range in size from a few individuals to thousands or millions. Although the interactions between individuals in large aggregates are often inconsequential, in some species cohesion and organization are important. For example, the social insects—bees, ants, termites—are obligatorily bound together by ties of genetic relationship in colonies containing tens of thousands to millions of individuals.

The social interactions of animals are among their most interesting phenotypic features. Why is there such variety in the sizes of groups as well as in the extent to which individuals recognize, communicate, and cooperate with each other? What special evolutionary issues are raised when the capacity for communication enables animals to behave in an organized, cooperative way? Clearly such social groups are more complex and more interesting than mere aggregations of individuals that have come together because of some mutually attractive stimulus such as food but display few meaningful interactions among themselves. This is the same distinction that makes a football team more interesting to watch than the crowd of spectators that have come to see the game.

Probably because we are ourselves a highly social species, we find the social interactions of other animals among the most interesting manifestations of their behaviors. However, the study of animal behavior played a much less important role in the early development of evolutionary biology than did studies of anatomy, embryology, and paleontology. There were understandable reasons for that neglect (Chapter 11), but beginning about forty years ago the social structures of animals began to receive concerted attention from a few evolutionary biologists who provided a theoretical framework for understanding social evolution. In this chapter we will examine this relatively new and important body of evolutionary social theory, which builds on and extends Darwinian thinking. We will consider some special issues raised by the social insects in the following chapter, and in later chapters we will explore how evolutionary social theories can be used to illuminate human behavior.

THE RUDIMENTS OF EVOLUTIONARY SOCIAL THEORY

We have seen how natural selection is a process of differential replication of genes caused by the effects of genes on the relative reproductive success of the individuals (vehicles) carrying them. Individual organisms are thus the elemental "atoms" of social behavior, and

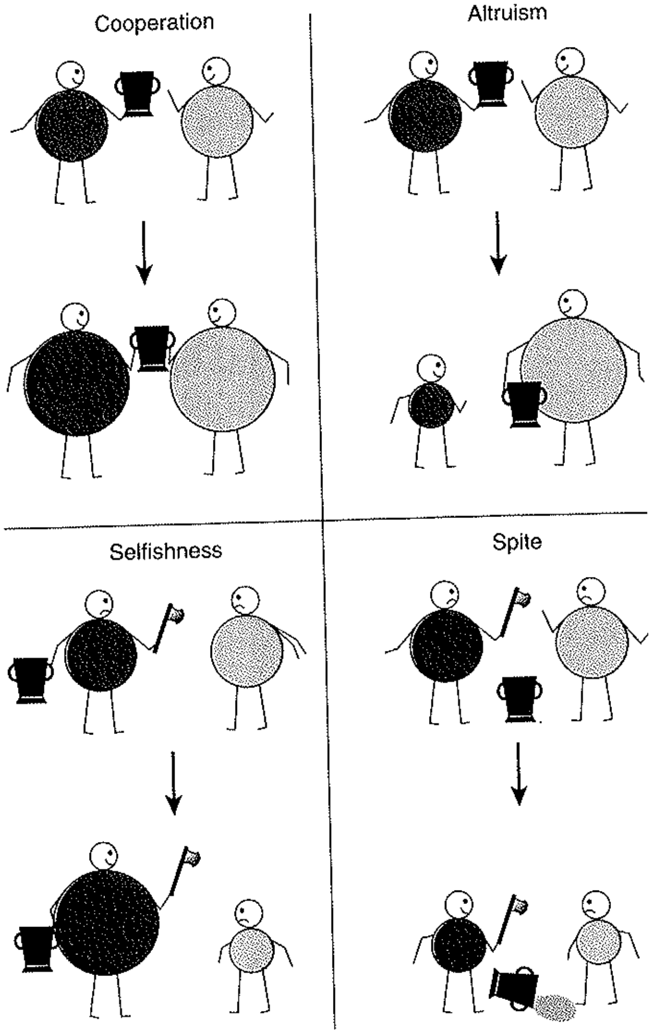


FIGURE 6.1 **When actor (*darker green*) interacts with recipient (*lighter green*) there are four classes of behavior, whose consequences are depicted by the arrows. *Cooperative* acts are beneficial to both, whereas *altruistic* acts bestow a benefit on the recipient but at a cost to the actor. *Selfish* acts retain a benefit to actor but at a cost to the recipient and *spiteful* acts are costly to both. In evolution, costs and benefits are measured in terms of *reproductive success*, which is represented in these cartoons by increases and decreases in size. As explained in the text, behavior that appears to be altruistic can be evolutionarily beneficial.**

reproductive success is the measure that should be used to assess the evolutionary consequences of behavior.

Let's consider the simplest possible social interaction: the behavior of one individual, the "actor," toward another individual, the "recipient." The reproductive success of the actor and recipient can either benefit (*B*) from the interaction or suffer costs (*C*), measured as increments and decrements in the numbers of surviving offspring. Since there are two possible effects on reproduction (*B* or *C*) for both actor and recipient, there are four categories of behavior, as shown in Figure 6.1.

If benefit accrues to both actor and recipient, the effect of the behavior is *cooperative*; if costs are incurred by both, actor's behavior can be characterized as *spiteful*. When actor's behavior benefits himself and comes at a cost to recipient, the behavior is *selfish*. Conversely, if costs are borne by actor while recipient benefits, the behavior is *altruistic*.

The words "cooperative," "spiteful," "selfish," and "altruistic" are used here to describe evolutionary outcomes and do not imply anything about the actor's conscious motives or the recipient's feelings. Actor and recipient might both be ants, zebras, or any other creature between A and Z. For the limited task of categorizing behavior and describing its reproductive consequences, it is not necessary to understand how their nervous systems process information and generate behavior. It is useful, though, to describe the several possible behavioral outcomes without creating specialized jargon.

These categories of behavior and their one-word definitions are, of course, simplifications. Social interactions of animals result from many behaviors—aggression, play, courtship, submission, food begging, food sharing, alarm calls, and cooperative hunting, to name just a few. Also, the roles of actor and recipient may be repeatedly reversed; the interactions may be "multiparty" (involving many actors and recipients); and the benefits and costs may be indirect or delayed in time. Nonetheless, these categories of behaviors and their effects describe recurring categories of interactions that have reproductive consequences in all social animals.

ALTRUISM TOWARD GENETIC RELATIVES AND THE CONCEPT OF KIN SELECTION

SHARED GENES

We expect reproductively selfish behavior to be favored by natural selection: if one lion repeatedly steals food (benefits) from another with little effort (cost), the replication of the genes underlying such behavior is likely to be enhanced. A similar argument can be made for cooperative behavior: if two lions collaborate in wresting food from a third at little cost and then share it, the genes underlying this behavior are favored. Spiteful behavior could be favored by natural selection if the cost to the actor is less than the cost to the recipient, but as spite incurs costs to both individuals, spiteful behavior is not common in animals.

Behavior that appears to be altruistic seems to present a paradox: if one hungry lion shares its small catch or helps fend off attacks of outsiders, it can be benefiting another's reproduction at a cost to its own. And yet such altruistic behavior is common in nature. How can this be?

The answer lies in inheritance: copies of one's genes reside in near relatives. As you received half of your genes from your mother, your degree of relatedness *r* to your mother is $\frac{1}{2}$. As the probability that any particular maternal gene was passed on to you is also 0.5, your mother's degree of genetic relatedness to you is also $\frac{1}{2}$. Similarly, your *r* with your offspring is $\frac{1}{2}$. You are related to full brothers and sisters through two parents. Examine Box 6.1 to see why your *r* to your siblings is $\frac{1}{2}$, the sum of $\frac{1}{4}$ through your father and $\frac{1}{4}$ through your mother.

This pattern of inheritance means that it is possible to further the replication of your alleles not only by having your own children but also by enhancing the reproduction of near relatives. Your degree of relatedness to your child is $\frac{1}{2}$, but to a niece or nephew it is only $\frac{1}{4}$. Consequently, in terms of the propagation of your alleles you can achieve the same reproductive success by rearing two nieces or nephews as by rearing one daughter or son. In general, by influencing the reproductive success of close relatives, an individual can influence the replication of identical copies of its genes that reside in close kin. This kind of natural selection—in which genes change in frequency because of an individual's influence on its relatives' reproduction—is called *kin selection*. This important idea was first developed in 1964 by the evolutionary geneticist William D. Hamilton, who showed how kin selection could account for the evolution of some instances of altruistic behavior.

The theory of kin selection predicts that whatever genes cause an actor to benefit the reproduction of relatives will increase in frequency if the benefits exceed the costs. Benefits and costs to whom, however, and how should they be reckoned? To illustrate with an extreme example, suppose an individual who is genetically disposed to behave altruistically toward relatives sacrifices his life in saving three siblings from certain death in a boating accident. Copies of those "altruist" alleles are present in each sibling by reason of common descent with a probability that is simply *r*, the degree of genetic relatedness of actor to each sibling. Each of the

Box 6.1
Calculating Degrees of Relatedness

The degree of relatedness r between any two individuals is the probability that they share copies of a gene that are identical by virtue of descent from a common ancestor. To calculate the degree of relatedness between one individual (darker green) and another (lighter green), draw arrows through the common ancestors as shown in Figure 6.2.

(A) For two siblings (sisters in this example), r is $\frac{1}{2}$. The probability that the first sister has received any one of her genes from her mother is $\frac{1}{2}$ (meiosis, Chapter 3), and the probability that same gene in her mother was passed to the sister is also $\frac{1}{2}$. These two probabilities are independent of one another, so r through their mother is $\frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$. By the same reasoning, r through their father is also $\frac{1}{4}$. Because the genetic paths through the mother and father are separate and distinct, we add their individual probabilities to get $r = \frac{1}{4} + \frac{1}{4} = \frac{1}{2}$.

(B) The degree of relatedness of a sister with her nephew (her sister's son) is calculated in the same way. The only additional step required is to extend it to the next generation by multiplying the r for the sisters ($\frac{1}{2}$) by the probability that the nephew's mother has given him one of her genes, $\frac{1}{2}$. Therefore r for the first sister with her nephew is $\frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$.

(C) Convince yourself that the degree of relatedness between first cousins is $\frac{1}{8}$.

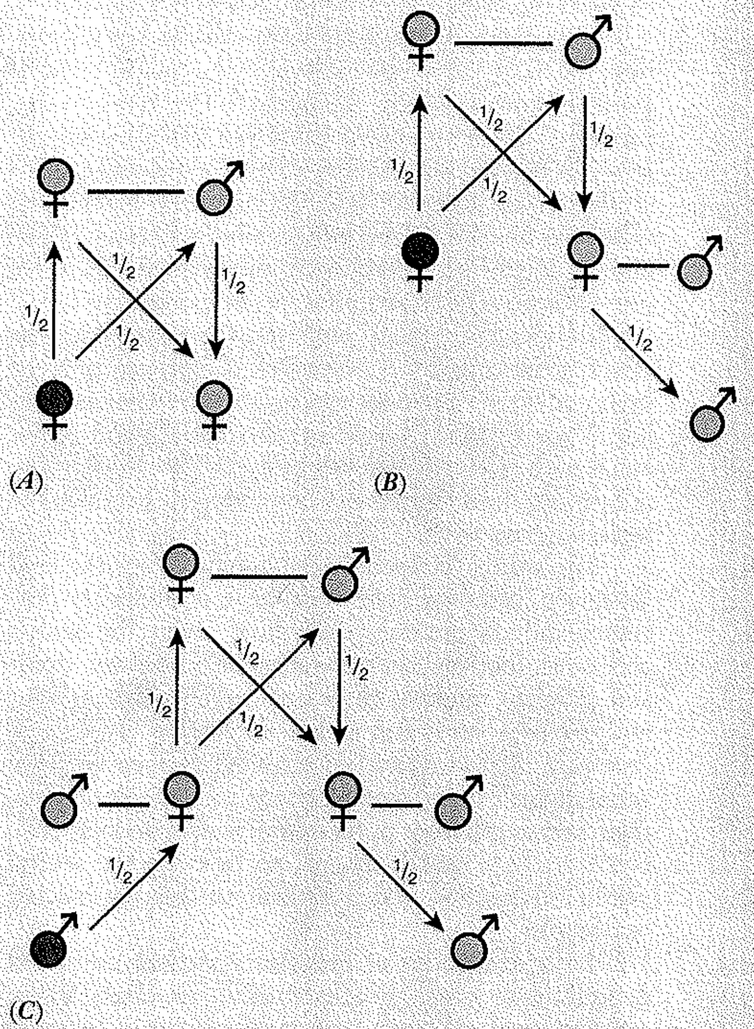


FIGURE 6.2 Tracing degrees of genetic relatedness.

actor's alleles is lost when he perishes, and so the reproductive cost, C, is 1. But as copies of those alleles are present in each sibling with probability $r = \frac{1}{2}$, the devalued benefit $B \times r = 3 \times \frac{1}{2} = 1.5$. Consequently in this example, $B \times r > C$.

Let's now state the rule more precisely. Actor's alleles that enhance the reproduction of relatives will be selected if the reproductive benefits to relatives, discounted by each relative's degree of relatedness to actor, are greater than the reproductive costs to actor. Kin selection is thus a process by which alleles change in frequency because of the behaviors they engender in an individual that in turn influence the reproduction of identical copies of those alleles in genetic relatives. The effect, however, is to promote (or detract) from the propagation of *all* of the actor's alleles in individuals with whom he shares them by common descent.

It is important to recognize that the proximate mechanisms by which genes influence behavior is through the assembly of the brain (Chapter 10). Furthermore, how the brain filters information and weighs consequences of alternative behaviors is an emergent property of neural tissue (Chapter 9) that varies among species. For kin selection to exist, brains must have the property of directing "altruistic" behavior to genetic relatives. For this property of the phenotype to have evolved means that natural selection has favored some alleles and discarded others. That is the sense in which one can speak of "altruist" alleles.

The process of kin selection has to be considered ultimately one of differential gene replication because in our example the behavior fostered by the "altruist" alleles actually prevented their vehicle (actor) from reproducing while promoting the survival of identical copies of themselves in other vehicles. This also brings us to the reason why we have put the term "altruist" within quotation marks. At the level of the phenotype, actor was altruistic in the usual sense of the word: he died so that three siblings might live. From the viewpoint of gene action and replication, however, actor's behavior was not altruistic: as a consequence of the influence of the "altruist" alleles on his behavior, more copies of those alleles survived than if he had lived and his three siblings had drowned.

SOME COMMON CONFUSIONS ABOUT KIN SELECTION

Before considering examples of kin selection at work in nature, we will discuss some of the criticisms and confusions that surround this concept. One argument is that because most organisms in a social group have the same alleles at most of their genetic loci, beneficence of an individual toward *all* members of the social group—indiscriminate beneficence—would help the same genes and therefore be favored. To see the problem with this line of reasoning, consider how indiscriminate altruism would be vulnerable to a genetic change that directs benefits *specifically* to near relatives. Imagine a population in which *all* individuals *do* carry identical copies of a gene, X, for indiscriminate beneficence—for example, a population of zebras in which lactating mothers allow each other's young to nurse at will, irrespective of genetic relatedness. Because the genes for such behavior in mother zebras promote survival of identical copies in all baby zebras, we expect those genes to persist. And they will persist until mutations or recombinations produce a new genotype that leads to a nervous system that causes the mother to allow only its own young (with $r = \frac{1}{2}$) and those of its sisters (nieces and nephews with $r = \frac{1}{4}$) to nurse. This new allele, X_1, by causing the mother to direct benefits (milk) only to close genetic relatives, would benefit its own replication more often than it would the original, alternative allele, X. However, the original allele, X, would benefit X_1 and other copies of X equally. As a result, the baby zebras carrying X_1 would get a greater share of milk than those carrying X, most likely grow faster and stronger, be less susceptible to predation, and therefore leave more descendants. Eventually X_1 would replace X in the population. In other words, the X allele for indiscriminate altruism is unstable and open to invasion by the X_1 allele for nepotism, whereas the reverse is untrue.

The process of kin selection would not stop here. Consider what would happen if another mutation, X_2, arose, which caused the mother to allow only *its* young and *not* its nieces and nephews to nurse. Again, the X_2 allele would benefit only its own continuance in the mother's young ($r = \frac{1}{2}$), but its propagation would also continue to be enhanced by the less discriminating behavior caused by X_1. So eventually X_2 would replace X_1. These two examples show that kin selection will increasingly favor beneficent behavior directed to nearest kin, and beneficence toward more distant kin will become relatively disfavored. *All that is required is a heritable mechanism for recognizing and favoring kin when directing benefits.*

A common difficulty in understanding how kin selection works is just this matter of recognizing kin. Isn't it asking a bit much of the intelligence of a zebra, or for that matter any animal other than humans, to be aware of degrees of genetic relatedness? We certainly do not expect nonhuman animals to do cost-benefit analyses. However, an animal need not understand genetic relatedness in order to favor kin, any more than a bird need understand the aerodynamics of flight in order to fly, or astronomy in order to navigate by stars, or biochemistry in order to digest its food. It is sufficient that the animal behave *as if* it understood. Humans, too, favor kin in cultures around the world (Chapter 14), but notions of genetic relatedness could not have been discussed before there was knowledge of genes.

In the case of a mother zebra, allowing only its offspring to nurse requires two behavioral mechanisms for which there is much evidence in many species: (1) the mother be programmed to learn and remember the combination of visual and olfactory cues unique to the infant to which she gave birth, and (2) only this combination of stimuli will subsequently elicit her nursing behavior. It may be useful to describe this behavior as "recognizing her own young," but this phrase does not imply that zebras have humanlike mental representations of their young or that they have the intelligence to develop the concepts of "mine" and "others." We shall return later to this problem of animal cognition (Chapter 11).

NEPOTISM AND SELF-INTEREST I: THE ALARM CALLS OF GROUND SQUIRRELS

Our so far hypothetical examples show how natural selection might shape the behavior of animals toward others of the same species. But the principles can be made much more convincing if we are able to observe these predictions at work in field studies of real animals.

Many social animals give alarm calls when they see a predator, thus alerting other members of the group. The first impression is that this is altruistic behavior: the caller seems to have helped others but jeopardized its own safety by drawing the predator's attention to itself. In fact, this assumption is implicit in calling these vocalizations "alarm calls"! There are, however, other conceivable interpretations of these calls. (*i*) Perhaps calling diverts the predator's attention to other prey. This could be possible if the alarm call caused other members of the group to run or fly quickly for cover and the predator's attention were drawn to the movement of individuals it had not seen previously. This could decrease the chance that the caller would be attacked. (*ii*) Or maybe calling discourages the predator by informing it that it has been detected and that a successful attack is unlikely. This might be effective if the animals that call were particularly fleet or evasive and could only be caught by surprise or ambush. (*iii*) Calling could possibly discourage the predator from making future attacks. That is, the risk of giving away one's position by a call might be offset by the benefit of warning other members of the group, which then denies the predator a meal and discourages it from returning to attack the same group and the caller itself. (*iv*) Calling might warn others of the group who are likely to reciprocate. The cost to the caller (increased risk of attack) could be less than the benefit to the alerted individuals (decreased risk of attack), who later reciprocate under similar circumstances. Over time the benefits of such reciprocity to each member of the group exceed the costs. We will say more about such "reciprocal altruism" shortly. (*v*) Finally, giving alarm calls could alert relatives and be favored by kin selection. The callers jeopardize their own survival but increase the probability that alerted relatives will survive, so that $B \times r > C$.

Considering the difficulties of making the required observations and measurements, it is little wonder that only a few animals have been examined in sufficient detail to distinguish among all of these hypotheses. But Paul Sherman and his coworkers have successfully studied the function of alarm calls in a population of Belding's ground squirrels (Fig. 6.3). These squirrels live in underground burrows in alpine and subalpine meadows in the far western United States and are active during the day. Females that successfully rear young retain their burrows from one year to the next, and their daughters mature and breed in their natal area. Males, however, emigrate and breed elsewhere. During their period of sexual receptivity, females mate with an average of two males, but they subsequently give birth and rear their young alone. Some males are highly polygynous (i.e., one male characteristically mates with more than one female). As a consequence, 20% of the males can account for up to 60% of the copulations, so the females of a given area are likely to be related to each other through a common father as well as by being sisters or first cousins on their maternal side.

Most of the members of a ground squirrel population at Tioga Pass Meadow in the Sierra Nevada Mountains of California were marked over a period of seven years (almost 1900 squirrels, altogether), which enabled Sherman and his associates to know their exact ages and family relationships through common female ancestors. During 3,100 hours of observation over two summers, five different species of terrestrial predators (weasels, badgers, martens, coyotes, dogs) stalked members of the population 102 separate times and killed nine animals. Upon seeing one of these terrestrial predators, a Belding's ground squirrel sits up, remains stationary, and gives a multiple-note trill. Upon hearing an alarm call, other squirrels immediately either sit up and look for the danger or run to the nearest rock and peer about.

Figure 6.3 Ground squirrel *Spermophilus beldingi* on alert (*left*) and high alert (*right*).

Observations of the squirrels and their predators make clear that calling is a nepotistic act. First, uttering an alarm call increases the risk of being killed; ground squirrels that called were chased or stalked significantly more often by all five of their predators than were squirrels that remained silent. This is because the calls are acoustically easy to locate and are uttered repeatedly—an average of twenty-seven times over six minutes. On this basis, calling therefore appears to be an altruistic act.

Second, squirrels were more likely to call when there were close relatives in the vicinity. This is why females called nearly ten times as often as males. Furthermore, females that were reproductively active or that had relatives (mother, sisters, daughters) nearby were more likely to call than other females.

This sort of discriminative nepotism requires, of course, that female ground squirrels be able to recognize their female relatives. There is other evidence that this is possible. Female ground squirrels chase out of their territories nonkin and kin of $r < 1/4$ significantly more often than they chase away relatives of $r = \frac{1}{2}$ (mothers, daughters, sisters).

The willingness of female Belding's ground squirrels to risk their own lives by warning near relatives of terrestrial predators is just the sort of behavior that is predicted from the theory of kin selection. Humans show the same kind of behavior: across all cultures concern with the fate of others in times of danger or disaster increases directly with genetic relatedness. In our own culture, the Carnegie Hero Commission has bestowed some 8,000 awards since 1904 for acts of heroism in helping others in danger, but rarely is such heroism recognized if it involved the rescue of relatives. Helping relatives is considered normal.

Interestingly, Belding's ground squirrels give another call—a single-note whistle—when hawks fly overhead, and the response of other squirrels is also different. Sherman observed fifty-eight encounters between wild hawks and ground squirrels, and he staged six hundred more with hawks that had been trained to fly directly over the colony without attacking the animals. The first caller was usually the one in greatest danger because it was close to the predator and often far from cover. Instead of remaining where it could be seen by other squirrels, the caller scurried to the nearest burrow or bush as it sounded the alarm. The other animals responded by similarly calling and running immediately to the nearest shelter, even if it was another animal's burrow. In striking contrast to the alarm trills for terrestrial predators, the tendency to whistle-alarm was not correlated with age, sex, reproductive condition, or the presence or absence of kin. And in contrast to the callers for terrestrial predators, the callers for hawks were significantly less often killed than the noncallers.

These findings leave little doubt that whereas the function of alarm calling for terrestrial predators is to alert relatives, the alarm calling for flying hawks seems to be for self-preservation. Unlike the stealthy approach of a coyote, the swoop of a hawk gives its prey little time to escape, and when the squirrels signal the presence of a hawk they do not linger on the spot. Their call in turn triggers pandemonium in the colony, with an explosion of calling, scurrying animals.

Why should ground squirrels bother to give hawk-warnings at all if not to benefit kin? For many of the animals there are likely to be relatives around, but is there an explanation that does not require either the presence of close kin or an appeal to the implausible argument of group selection? One possibility is that in the confusion of many scampering ground squirrels triggered by the first call, the hawk's attention may be distracted and the caller's chances of escape momentarily enhanced. If this explanation is correct (and it is consistent with a reason why birds are believed to flock and fish to school), the vocalization given when a hawk appears is a "manipulative call." It is a striking example of the power of natural selection that these two kinds of predators, presenting somewhat different dangers, elicit distinctly different warning calls and adaptively appropriate behaviors on the part of both caller and listener.

NEPOTISM AND SELF-INTEREST II: HELPERS AT THE NEST AND IN THE DEN

We think of "helping" as any behavior that appears to be helpful, no matter who the actors and recipients are. Behavioral biologists have come to use the term in a more restrictive way: "helping" is parent-like behavior extended to young that are not the direct offspring of the helper, exclusive of adoption (uncommon in nonhuman vertebrates), parasitism (as in cowbirds and European cuckoos, who lay their eggs in the nests of other species), and the mixing of broods by communally breeding parents (e.g., certain kinds of birds). Helping behavior is now known in over one hundred species of birds as well as jackals, African hunting dogs, and a few other mammals.

Unlike the social insects (Chapter 7), helpers among birds and mammals are fully capable of breeding on their own. So why do they spend a year, a few years, or their entire lives feeding the young of others, protecting them from predators, and defending the feeding territory from intruders? How could natural selection, acting on individuals, cause the evolution of this seemingly altruistic behavior? As in other cases of behavior that appears to be altruistic, we need additional information in order to understand these breeding systems. Under what circumstances does this behavior occur? Are the breeders measurably benefited by the helpers? What benefits accrue to the helpers? And what are the relationships between the breeders and helpers?

Helping behavior has been studied extensively in birds. With colored plastic bands placed on their legs, individual birds can be recognized over a period of years and the roles and relationships of each individual understood. Helping behavior occurs in species in which a breeding pair requires territory to supply food for themselves and the growing nestlings but available territory is limited by the presence of other breeding pairs in the surrounding area. In other words, the size of the population is close to the *carrying capacity* of the environment. Under these conditions, birds one or two years of age, although physiologically capable of producing and rearing young, may not be able to do so because they cannot establish their own territories.

These same studies answer the questions of who the helpers are and whether their assistance is valuable. Helping helps: 20–250% more young are produced when helpers are present, although the average increase in the reproductive success of the breeders (across many species) is less than a factor of two. Almost invariably the helpers are earlier offspring of the breeders or, much less commonly, they are siblings of one of the breeders. In long-term studies of the Florida scrub jay (Fig. 6.4), biologist Glen Woolfenden and his associates have shown that helpers may aid parents, grandparents, uncles, or half-brothers, but it is usually one or both parents that are helped. In this study, the average degree of genetic relatedness of 180 helpers and the offspring they helped was 0.41.

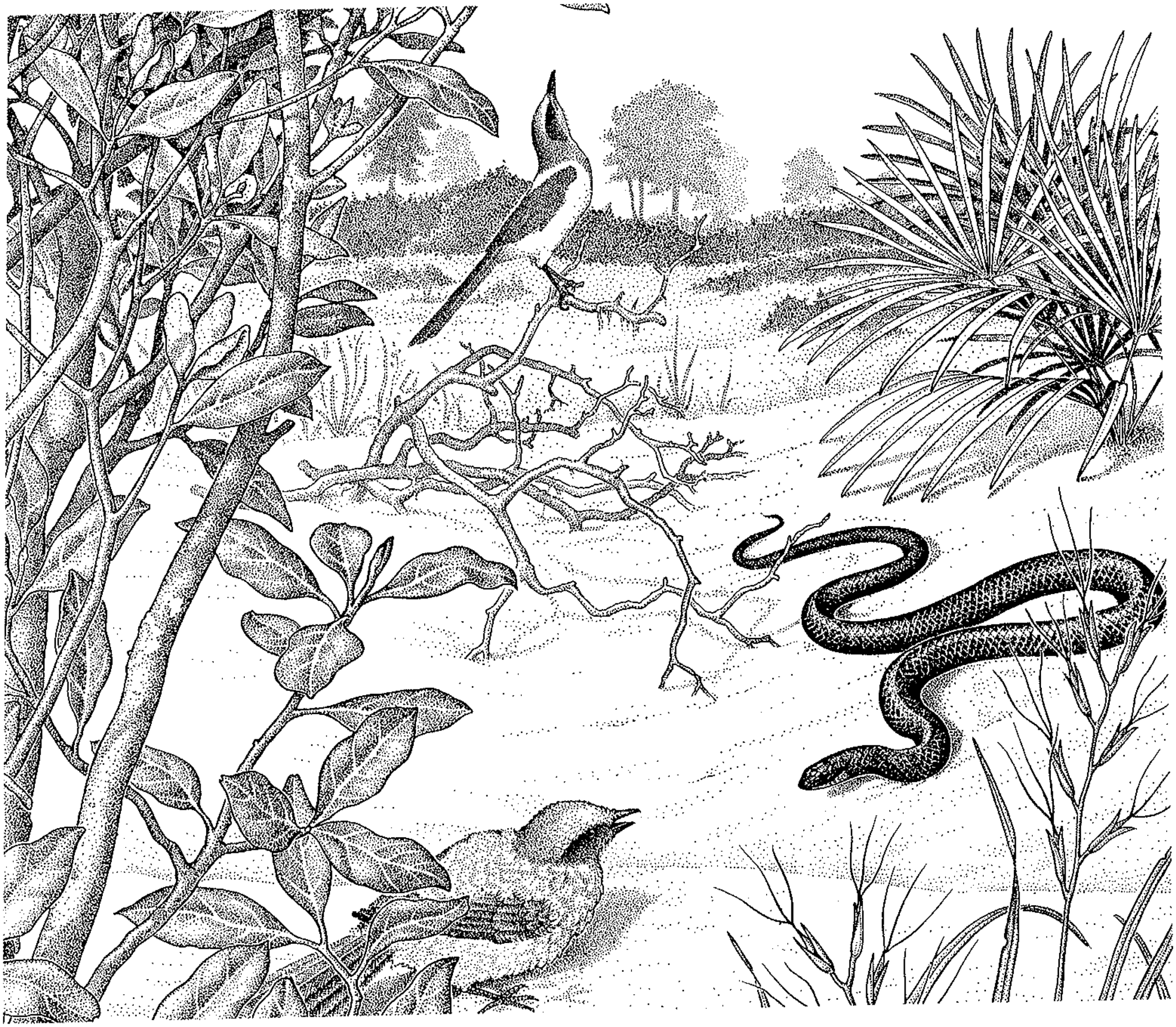
The genetic relatedness between helpers and beneficiaries is strong evidence that kin selection has played a role in the evolution of helping behavior. For full siblings, $r = 0.5$ between helper and beneficiary, the same as between a helper and its own offspring. If in a given year the chances of finding a territory and successfully reproducing with a mate is very small, a young adult can enhance its reproductive success by helping its parents. Its reproductive success will be increased as long as the number of *additional* young that its parents produce (with its help) is greater than the number of young it might have produced in its own territory with its own mate.

If we refer to the increment in the number of its siblings as a benefit (B) and the number it failed to produce with a mate as a cost (C), natural selection will

FIGURE 6.4 The scrub jay (*Aphelocoma coerulescens*) is an example of a species in which young offspring frequently delay their own reproduction and help rear siblings. This behavioral option of scrub jays is taken when there is no available territory in which the helpers can seek their own mates and rear their own offspring. From Wilson, 1975, reprinted with permission of Harvard University Press.

foster helping as long as $B > C$. Now if the helper is assisting in rearing half-siblings, his r with them is only 0.25, and the cost of foregoing his own reproduction is twice as great. Under these conditions his helping behavior must therefore have twice the impact as in the previous example in order for benefit to exceed the cost. To state the relationship in symbolic terms, benefit must be devalued by the degree of relationship the helper has with those helped ($r = 0.25$), and the cost by his degree of relationship with his own offspring ($r = 0.5$). Thus for helping to increase the reproductive success of the helper, $0.25B > 0.5C$, or $B > 2C$.

Helping behavior in these birds evolves when the reproductive prospects of young adults are restricted by the near-term opportunities for obtaining territory of their own. If their chances of breeding are close to zero, virtually any increase in the number of near relatives that is due to their help means that $B > C$. Viewed this way, we can understand why helping has evolved, although, on average, it increases the reproductive success of the breeding pair by less than a factor of two.



But in the case of the Florida scrub jay, hanging around and helping benefits the young adults in another way: they stand a better chance of acquiring a territory, either by inheriting it or, with the aid of siblings, by expanding the family territory into that of neighboring birds and then claiming a piece as their own.

Helping in birds is a behavioral alternative that makes the best of a bad situation and is only done when necessary. Successful breeding is likely to lead to greater reproductive success than helping, particularly if the helper's degree of relatedness to the beneficiaries is less than $\frac{1}{2}$, and in birds, helpers take every opportu-

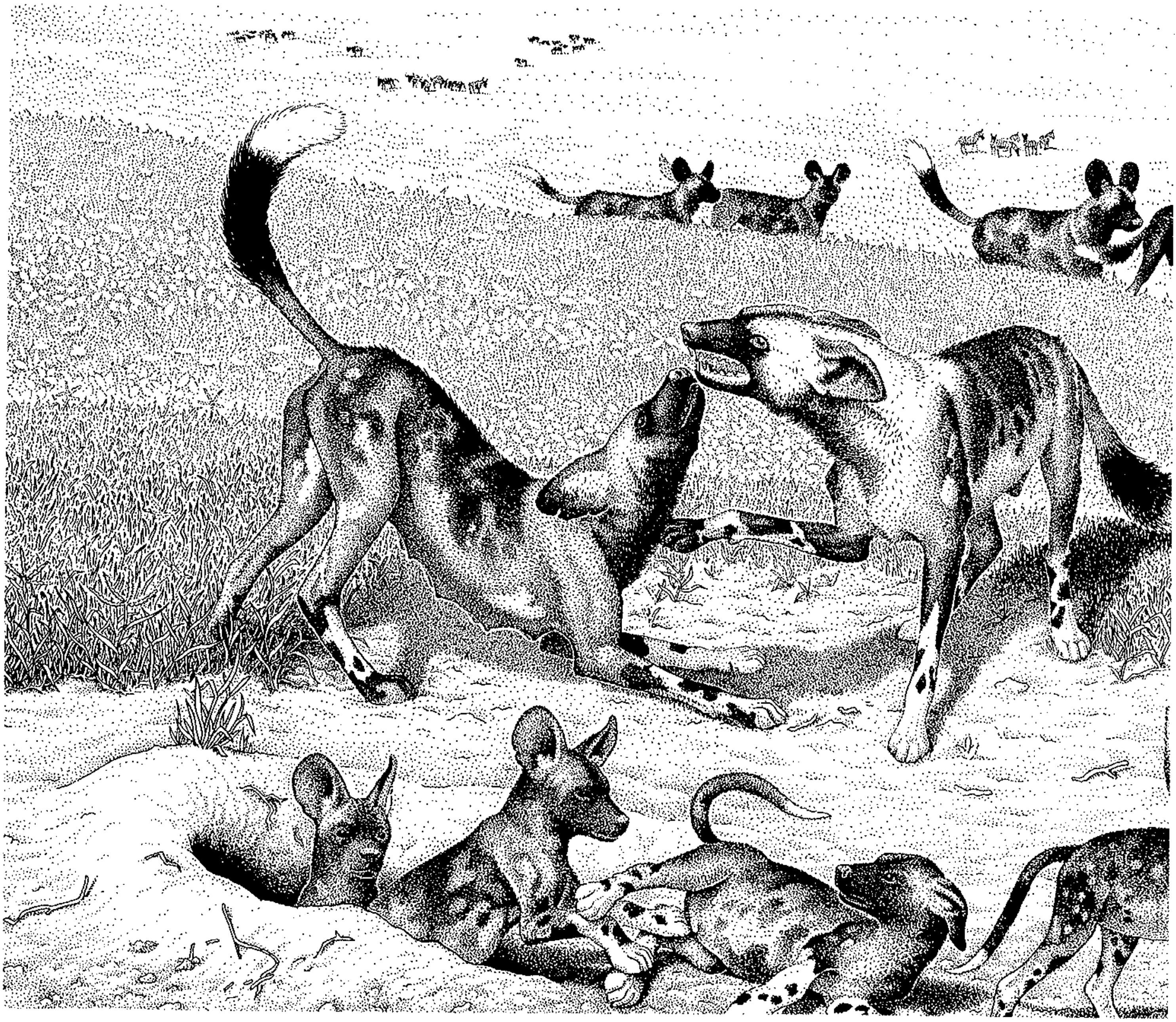
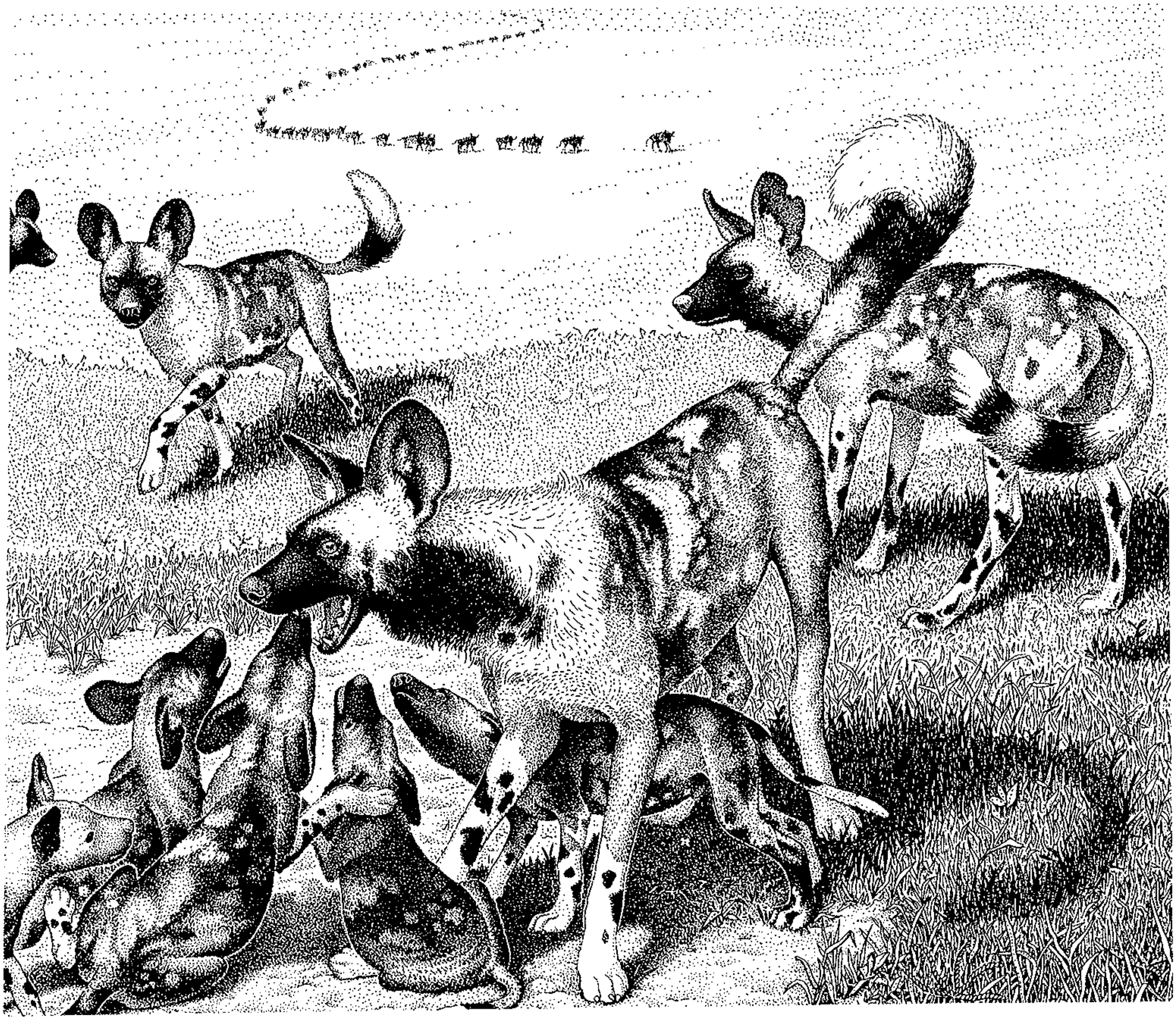


Figure 6.5 Hunting (or wild) dogs (*Lycaon picus*) are native to the savannas of Africa. They are a true, wild species and not feral animals that have escaped domestication. As the name suggests, they are proficient hunters. They are also an example of a mammal in which helpers assist in rearing younger siblings. As is also the case with jackals, the litters are large, and reproductive success of parents is significantly greater if older offspring are present to help hunt and protect the newest litter. In this picture, an adult has just returned to the den with food and is about to regurgitate to feed the eager, begging pups. From Wilson, 1975, reprinted with permission of Harvard University Press.

nity to breed on their own. Breeding status is achieved through active, aggressive defense of territory, and a breeding pair may continue to act aggressively to suppress the breeding efforts of other group members.

Among mammals helping behavior analogous to that in birds—in which individuals postpone breeding and help rear the young of their social group—is rare. Most of the known examples are found among the canids or dog family. Among the canids, wolves, jackals, and the African wild dog hunt cooperatively in packs and share what they capture with each other and the young back at the den (Fig. 6.5). The packs usually



consist of a dominant breeding pair and helpers, which are previous offspring and/or siblings. In these species the presence of one or more helpers is usually crucial to rearing offspring, and the more helpers there are, the more offspring the breeding pair are able to produce.

The fact that helpers among the canids are usually close relatives is presumptive evidence that kin selection has been important in the evolution of this behavior. Additional factors may be at work, however. Because the litters are large and hunting is cooperative, successful breeding may be more dependent on delayed reproduction and helping than in the examples of birds described above. In other words, under most circumstances helping may be virtually obligatory and an ordinary component of the life history of these mammals. One might also hypothesize that the costs to the helpers of postponed breeding are more than offset by the later enhancement of their own reproduction resulting from the experience in hunting and rearing young they gain by helping. If this were true, though, we would expect nonrelatives to be helpers more often, and we would not expect significant numbers of individuals to spend their entire lives as helpers.

RECIPROCAL ALTRUISM: RETURN EFFECTS IN THE ABSENCE OF CLOSE GENETIC RELATEDNESS

The concept of kin selection provides an explanation for how phenotypic altruism directed toward genetic relatives—nepotism—can evolve. But many societies, and particularly human societies, contain many interacting individuals who are not closely related. The evolutionary success of such societies must therefore be based on some processes in addition to kin selection. In 1971, the biologist Robert Trivers provided a key insight in solving this problem by showing how natural selection can lead to altruistic exchanges between individuals, irrespective of their degree of genetic relatedness. The process is termed *reciprocal altruism*, or sometimes simply as *return effects*. Trivers' argument is easy to understand because this sort of behavior is familiar to us in our everyday lives, and without a doubt it also played an important role in our behavioral evolution (Chapter 13).

If in a population it is common for two or more individuals to exchange altruistic acts reciprocally and repeatedly and in such a way that the summed benefits to each of them exceed the costs, in succeeding generations the genes underlying these behaviors will increase in frequency. For example, imagine that at a time of food shortage Ed gives Sam enough food to keep Sam and his family from starving, but the gift does not endanger Ed's own survival. Or Ed, upon seeing a predator, gives a warning cry that greatly increases Sam's chances of escape but only slightly increases Ed's own danger of being killed. If these hypothetical situations are later reversed—Sam helps Ed and the benefit to Ed exceeds the cost to Sam—then, over time, for both individuals, the summed benefits of these exchanges exceed the costs. Selection for this kind of behavior can operate whenever and wherever two or more individuals stand to gain more than they lose by such exchanges, even though an individual might lose more than it gains during some of the transactions (Box 6.2).

Reciprocal altruism requires several conditions. First and foremost is opportunity. Consequently, reciprocal altruism will be most likely to evolve in long-lived species in which individuals live in close proximity, providing occasions for repeated contacts. Furthermore, individuals must be able to recognize one another as individuals and be able to do things that benefit each other. A principal obstacle to the evolution of reciprocal altruism, however, is its vulnerability to cheating. Natural selection should favor participants who attempt to maximize benefits to themselves by not fully reciprocating. Following this line of reasoning, Trivers further suggested that selection should engender behavioral traits that will maximize benefits to self and minimize the costs of cheating by others. For example, individuals not only need to recognize reciprocators, they require cognitive mechanisms for (*i*) keeping track of their own credits and debits and of those individuals with whom they interact, (*ii*) for concealing their intentions to cheat, and (*iii*) for detecting cheating in others. There is thus a tendency in reciprocal exchanges for the donor to proffer aid when the benefit to the recipient exceeds the cost to self and to extend aid to individuals who have recently aided them.

As we have described reciprocal altruism, with actors Ed and Sam and with familiar cognitive requirements and psychological features, it seems to be a very human practice. Natural selection has indeed honed and embellished it in our species (Box 6.3), and we examine some of the implications in later chapters. But reciprocal altruism is not a uniquely human phenomenon. For example, vampire bats are reciprocal altruists, and their behaviors show many of the features expected of such exchanges.

SHARING OF FOOD BY VAMPIRE BATS

Vampire bats engage in reciprocal altruism by sharing food at the roost (Fig. 6.6). The stable social unit of vampire bats is a group of eight to twelve adult females with their dependent offspring that roost together during the day in hollow trees. Females, but not males, remain in their natal group. As biologist Gerald Wilkinson has shown, these associations are stable; an average of one unrelated female moves into the group every two years. The result of this pattern of birth, dispersal, recruitment, and movement between groups is

BOX 6.2
The Prisoner's Dilemma

Suppose two individuals have been arrested because they are suspected of collusion in committing a crime. If neither confesses, there will not be enough evidence to convict, and both will be released. They are kept apart, and each is told that if he implicates the other, he will not be prosecuted and will receive a modest reward. On the other hand, if he remains silent and his partner implicates him, he will receive the maximum sentence. If each implicates the other, both will be jailed, but not for the maximum time.

Here is the dilemma that each faces. If neither implicates the other, both will go free. But can either count on his partner? If my partner decides to go for the reward by implicating me and I remain silent, I will be played for a sucker! So maybe I should implicate him. But if we both do that, we will both end up in jail! What should I do? What will he do?

This problem has no solution in a single instance, but Robert Axelrod has used computer simulations to determine what strategy should be played if two individuals interact in a series of encounters where each has the possibility of either cooperating or defecting. For each encounter, there are four possible outcomes. The relative reward a player receives at each encounter is shown in the following payoff matrix (where the value for "both cooperating" is greater than the average of the two "sucker" outcomes).

	He cooperates	He defects
I cooperate	**3** (We both cooperate)	**0** (I'm a sucker)
I defect	**5** (I take him for a sucker)	**1** (We both defect)

Computer simulations show that in a long series of prisoner's dilemma interactions one strategy is superior to any other: "tit-for-tat." In other words, if two strategies are in competition, over a couple hundred encounters tit-for-tat will displace an alternative. The tit-for-tat strategy can be stated simply: Be cooperative on the first encounter, but thereafter treat the other player just as he treated you in the previous encounter. The success of tit-for-tat is enhanced if players can recognize who is playing by the same rule and interact with them preferentially and cooperatively.

In reciprocal altruism, cooperation is mutually desirable, but there is also a temptation to cheat and a severe cost to being cheated. The games of prisoner's dilemma therefore model reciprocal altruism, and the computer simulations indicate that tit-for-tat should be favored by natural selection and thus displace other strategies. Put in terms of human cognition, the computer simulations suggest that humans have not only evolved to seek cooperation, but also to retaliate when cheated, and not to hold a grudge if the other person shows a willingness to cooperate. The validity of such a general cognitive rule is not disproved if some people fail to follow it, or if most people occasionally violate it. Cognitive processes are flexible and contingent (Chapters 9 and 11).

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that the females in a roost group are related to each other by $r \leq 0.1$. This low degree of genetic relatedness, coupled with the possibility of recognizing individual bats by placing small, numbered bands on their legs, made it possible for Wilkinson to distinguish between nepotism, brought about by kin selection, and reciprocal altruism, brought about by selection for the ability to engage in reciprocal exchanges.

The feeding behavior and food requirements of the bats Wilkinson studied suggest that reciprocal altruism must be crucial to their survival. At night the bats fly out to find large mammals, use their sharp teeth to cut exposed skin, and then lap the blood. On a given night about one third of the bats less than two years of age and 7% of older animals fail to feed. Other than inexperience, no other variable was found to be correlated with failure to feed; success seems to be a matter of luck, so all individuals are likely to fail a number of times. Moreover, it does not take many failures to get the bats in trouble. If they do not feed for three nights, they starve to death! The likelihood that a given bat will fail two nights in a row is $1/3 \times 1/3 = 1/9$ for the younger bats and $0.07 \times 0.07 = 0.0049$ for the older bats. In other words, on any given night about 11% of the younger bats and 0.5% of the older bats are within a day of death by starvation. Finally, starving bats lose weight more slowly as their weight decreases, so that the longer a bat is deprived of food, the more a given amount of food increases its likelihood of survival. This means that the benefit of blood-sharing to a recipient is always greater than its cost to the donor, assuming only that the recipient has been deprived longer than the donor.

Wilkinson banded bats and observed their roosting associations and food exchanges; he also removed and returned bats to their roosts in order either to feed them or deprive them of food. He found that the sharing of ingested blood was quite specific with regard to the donors, the recipients, and their associations and

Box 6.3

Social Reasoning and Detecting Cheaters

The psychologist Peter Wason designed tests to explore whether the kind of thinking we frequently use is really the same as employed in scientific reasoning—the search for evidence that falsifies hypotheses. He devised a task that required subjects to choose information that could be used to determine whether a conditional rule—"if *P*, then *Q*"—had been violated. This rule is only violated when *P* is true and *Q* is false, so the logically correct way to check for violations of the rule is to determine whether "*P*" and "not *Q*" are found together.

As an example, suppose you are a bartender who must enforce drinking-age laws. The rule is "if a person is drinking beer, then they must be at least 21 years old" (if *P* then *Q*). Now suppose further that in order to be served, patrons must present a card that says either "drinking beer" or "drinking soda" on one side and has their age on the back. A group of four patrons places their cards on the bar, and you see "drinking beer," "drinking soda," "23," and "18." Which of the cards must you turn over in order to see if that patron is violating the rule?

If you are like most people who take this test, you chose "drinking beer" and "18." The logic is clear: one has checked for the association of "*P*" (drinking beer) and "not *Q*" (less than 21), and it doesn't matter what is on the reverse side of the other two cards.

The most interesting feature of this kind of test becomes apparent when the context is varied. Suppose the rule has the same logical form but is more abstract "if *D*, then 3." When subjects are presented with four cards showing "*D*," "*F*," "3," and "5" and asked which ones must be turned over to see if the rule is being violated, most chose just "*D*" or those marked "*D*" and "3." The correct answer is "*D*" and "5" (*P* and not *Q*). The rule says nothing about whether *F* and 3 or 5 and *D* might be associated.

These two problems are formally identical but differ in the context in which they are presented. The evolutionary psychologists Leda Cosmides and John Tooby argue that the different responses reflect evolutionary specialization of the human mind for reasoning about social interactions that involve reciprocity. More specifically, the first example involves reasoning about how to detect cheaters in social exchanges. Cosmides and Tooby have found that in a variety of other pairs of tests, subjects give different responses to purely abstract problems than they do to problems with social content.

A striking pair of similar tests carried out by the psychologists Gerd Gigerenzer and Klaus Hug supports the argument that the human mind is designed to police social exchanges. The tests had the same social context, and the conditional rule was "if an employee gets a pension, that individual must have worked for the firm at least ten years." The two tests differed, however, in the perspectives of the individuals taking the test. One group of subjects was told they were the employer, and the other was told they were the employee.

The four cards were "pension," "no pension," "worked eight years," and "worked ten years." In three separate experiments, 70–80% of the subjects playing the role of employer chose to turn over the cards saying "pension" and "worked eight years" (thus following the rule "if *P* then not *Q*"), and 1–5% chose "no pension" and "worked ten years" (applying a different rule, "if not *P* then *Q*").

Those subjects cast as employee produced the opposite pattern of responses: only 10–20% chose "pension" and "worked eight years" whereas 55–65% chose "no pension" and "worked ten years." The "employees" seem to have been unable to apply the logic of the rule, but that misses the point. What seems to constitute cheating depends on the subject's perspective. If you are the employer, an employee getting the pension without having worked ten years is cheating. On the other hand, if you are the employee, not getting the pension after ten years of service is cheating.

nutritional conditions. Bats that roosted together exchanged blood significantly more often than bats that did not; no animals that roosted together less than 60% of time fed each other. Deprived bats were fed by their roost mates soon after return to the roost, whereas well-fed bats that returned were never fed. There was preferential feeding of recipients in dire need (average of thirteen hours before starvation) by donors in average condition (average of forty hours before starvation). Finally, starved bats that received blood were significantly more likely to be donors when the predicament was reversed.

Food sharing in vampire bats is a well-documented example of reciprocal altruism in a mammal, dramatic for its occurrence in what one might think was an unlikely place. The example shows that several behaviors that seem to require human cognitive abilities are in fact displayed by animals with very different brains. Vampire bats are able to discriminate the needy from the well-fed, those likely to reciprocate from strangers, and

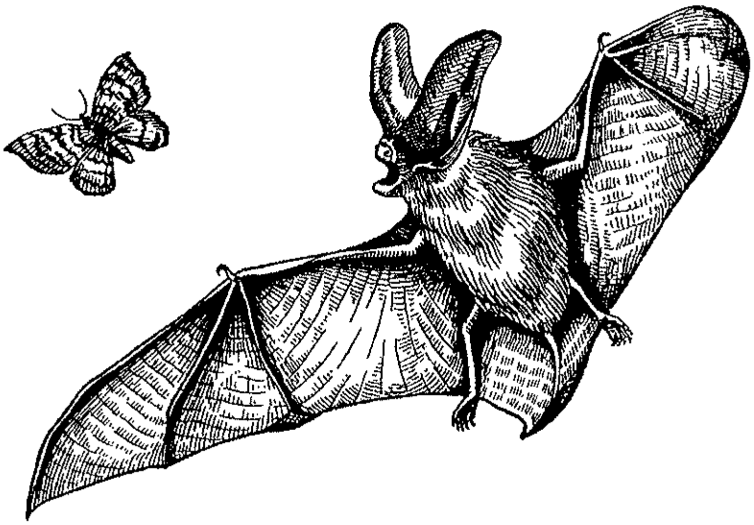

FIGURE 6.6 Bats are virtually blind and move about by echolocation—listening to the echoes of their own ultrasonic cries. This is the same principle on which sonar works. Note the enormous ears; the part of the brain dedicated to auditory input is also large. This species is not a vampire bat; it catches insects on the wing. Other species eat fruit, and still others catch fish by trolling their sharp toes through the water and gaffing minnows that have come to the surface to feed.

those who have fed them in the past. The presence of memory and the cognitive capacity to engage in complex social relations is therefore not the sole province of humans. Reciprocity in humans, its roots in our primate relatives (Chapter 13), and the role it likely played in our mental evolution requires a separate and more detailed treatment to which we will return in Chapter 14.

PARENT-OFFSPRING CONFLICT

Relationships between parents and their dependent young in the animal world are never completely harmonious, and conflict is usually most intense when the offspring are close to becoming independent. Anyone familiar with breeding domesticated animals has seen the disputes between mothers and their foals, calves, puppies, or kittens over how long they may continue to nurse. And we all know from experience that a primary source of family turmoil during adolescence is differences between actual and expected parental attention and support. Why should such behavioral conflict exist and under what kinds of circumstances should it be more or less evident?

The same Robert Trivers we met earlier in the discussion of reciprocal altruism is responsible for a seminal paper on the evolution of parent-offspring conflict, which was published in 1974. Trivers proposed that conflict in genetic interests is expected between parents and their offspring over the resources or "investment" that parents should allocate to their young. Trivers defined "parental investment" as anything a parent does that increases an offspring's likelihood of survival and reproduction at a cost to the parent's ability to invest in other offspring. For example, when a parent expends energy feeding an offspring and takes risks in protecting it from predators, the ultimate benefits of these behaviors are to the survival and eventual reproduction of that offspring, and the ultimate costs are to the parent's ability to produce and sustain other offspring, present or future.

The evolution of conflict between parents and offspring over parental investment can be understood by considering how genes for an organism's behavior affect the survival of identical copies in relatives. A parent's genes *for investing in close relatives* have an equal probability ($r = \frac{1}{2}$) of being present in each offspring, so selection should favor genes that *lead the parent to invest equally in each offspring*. An offspring's r to full siblings is also $\frac{1}{2}$, but its degree of relatedness to itself is 1. Consequently, the offspring will value benefits it receives, relative to the costs of benefits bestowed on full siblings, twice as highly as does the parent. We therefore expect parents and offspring to differ in how much parental investment the offspring should receive. Specifically, an offspring will be selected to demand more investment from a parent than the parent is selected to provide.

THE EVOLUTIONARY BASIS OF WEANING CONFLICT

The argument can be made clearer by using Trivers' example of a female mammal nursing her young. The parental investment in this case is milk, and the mother's degree of relatedness to each offspring is $\frac{1}{2}$. From the perspective of the mother's genes, benefits provided to one offspring come at a cost to other offspring, to which her degree of relatedness is the same. She will tend to stop nursing a particular offspring when the benefit B to the recipient becomes less than the cost C to other offspring (i.e., when $B/C < 1$). From the perspective of the recipient offspring's genes, however, the equation is different: he will value benefit to himself (relative to cost to siblings) twice as highly as does his mother, and he will continue to solicit food until $B/C < 0.5$.