anticipation of the fetus's demands, so that the fetus cannot remove more than it needs and more than is in the mother's genetic interest.

The fetus, operating from its advantageous placental beachhead, employs countermeasures. During the third trimester of pregnancy, the mother's blood level of insulin (the hormone that promotes removal of glucose from her blood) increases in concentration and at the same time becomes much less effective in removing glucose, especially after meals. This leads to higher glucose levels in her blood, and in extreme cases to gestational diabetes. There is good evidence that two hormones released by the fetus into the mother's blood, placental lactogen and placental growth hormone, interfere with the mechanism by which the mother's insulin lowers her blood glucose. The placental secretion of these hormones cannot be regulated by the mother, and despite their high concentrations neither is essential for a successful outcome of pregnancy. It appears that these hormonal interactions between the fetus and its mother are designed for interactions other than efficient and cooperative communication. As David Haig puts it: "If a message can be conveyed in a whisper [low concentrations of hormones], why shout? Raised voices are frequently a sign of conflict."

REPRODUCTIVE FUTURE OF THE PARENT

In many animals for which the supply of food varies during the rearing of young, the parents produce more offspring than are likely to survive to adulthood if food should become scarce. Under such conditions, some of the eggs or young may be abandoned or cannibalized by the parents and/or the siblings. Examples are found among hawks and owls, whose young grow rapidly in early spring. At this time of year, a late winter storm can make food difficult to find. There may be three young in the nest, one of which is smaller because it hatched last and because its larger siblings frequently monopolize the food as it is brought to the nest by the parents. If one of the young is cannibalized by parents or siblings, it is always the smallest.

We can readily see why and how natural selection has favored this behavior. Conditional infanticide, exercised when food is scarce and the entire brood is threatened, can rescue reproductive success for the current season. From the genetic perspective of the parents, benefits exceed costs ($B > C$) if the sacrifice of one offspring substantially increases the chances that at least some of the young will survive. The argument is equally clear from the genetic perspective of the larger of the nestlings: kin selection will favor siblicide when $B > \frac{1}{2} C$. But even from the perspective of the victim, kin selection should support the behavior if $B > 2C$.

Observations thus demonstrate that parents can assess the reproductive prospects of their offspring and redirect their parental investment so as to maximize the number of grand-offspring they leave, even if it requires reducing the number of young in the immediate future. Once again we must caution you about the simple language we are using. Do not read the word "assess" as implying conscious calculation of probabilities. We simply do not have many common English words that characterize the effects of behaviors without also suggesting human mental processes (Chapter 11).

As an organism ages, its potential for reproduction declines. In time it will not have enough resources or live long enough or be physiologically capable of producing another offspring. (In women this line is crossed at the time of menopause.) If at this juncture the organism has dependent young in its care, selection should favor parents who invest their remaining energies and resources in those last offspring. Such a pattern of behavior has been found: older animals generally feed, protect, and accede to the demands of their offspring more than do younger parents, and parent-offspring conflict is correspondingly less. This pattern of indulging the last child or a grandchild is familiar to humans as "doting."

SEXUAL SELECTION

Males and females are defined on the basis of primary universal differences related to the production of different kinds of gametes: males produce small motile gametes called *sperm*, whereas females produce larger, less-mobile gametes called *eggs*. Eggs are many times larger than sperm because they contain virtually all the cytoplasm that will be present in the zygote as well as nutrients that sustain growth during the early development of the embryo. Eggs can be enormous, particularly in birds. The need to make large gametes containing sufficient reserves to launch development was a by-product of the evolution of multicellular life. To be multicellular is to be larger, and how are gametes to find each other over a distance, particularly if they are big cells? The evolutionary solution was for

FIGURE 6.9 Bull elk following cow. The males of elk, deer, and many other hoofed mammals have large antlers or horns that are the product of sexual selection.

one sex to supply the cytoplasmic reserves in relatively large immobile eggs while the other sex delivered its DNA to the door in small packages (sperm, pollen), frequently motile, and invariably produced in large numbers. This is the quintessential example of disruptive selection, introduced in Chapter 4.

In addition to this primary distinction, males and females also differ in a external genetalia and *secondary sexual characters*. The former are directly related to the transfer and reception of sperm and the nurture of young—for example, the penis of male mammals and the vagina and mammary glands of female mammals. Charles Darwin called attention to an additional array of secondary sexual characters not directly connected with the act of reproduction but used in gaining matings with members of the opposite sex. In his introduction to

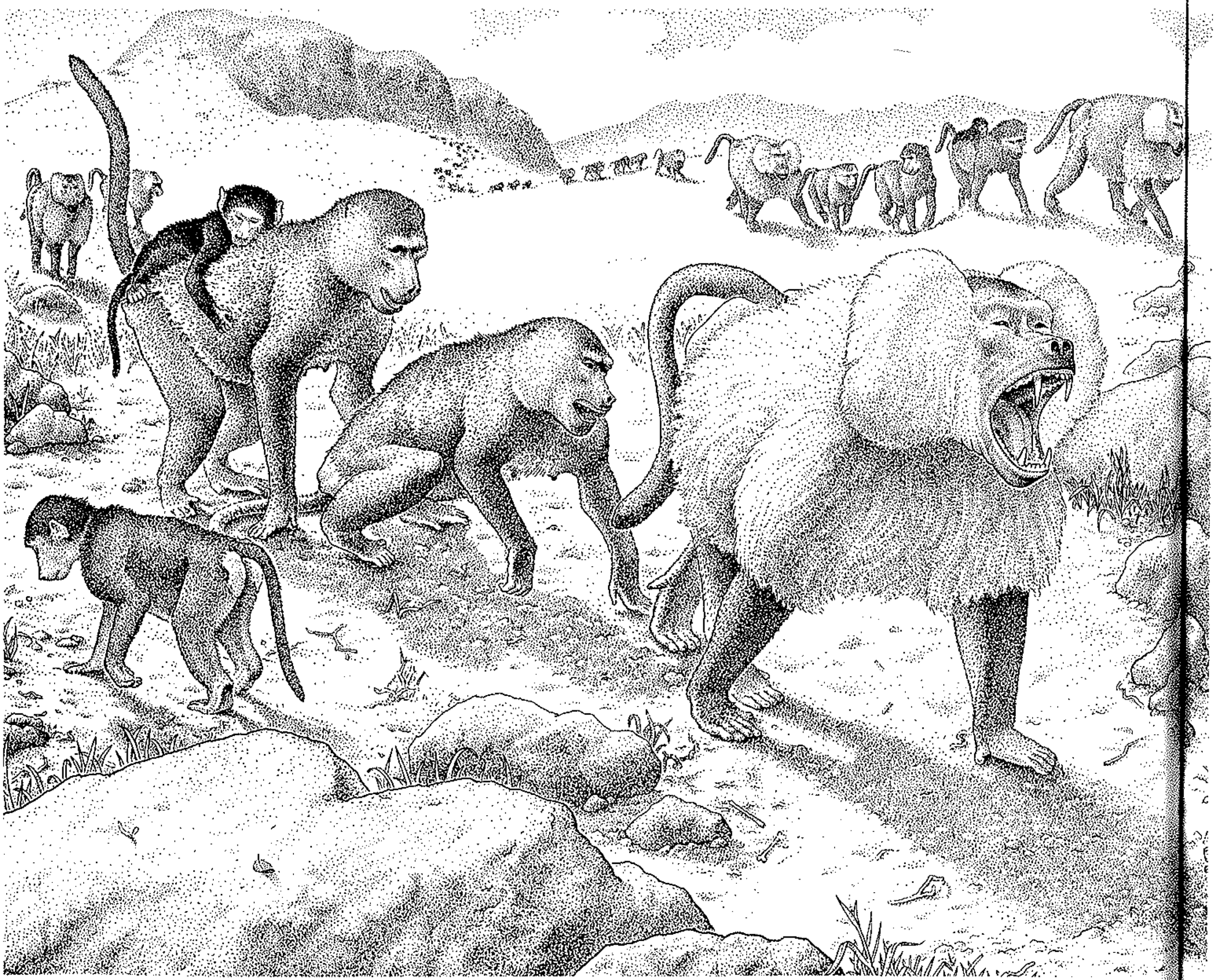
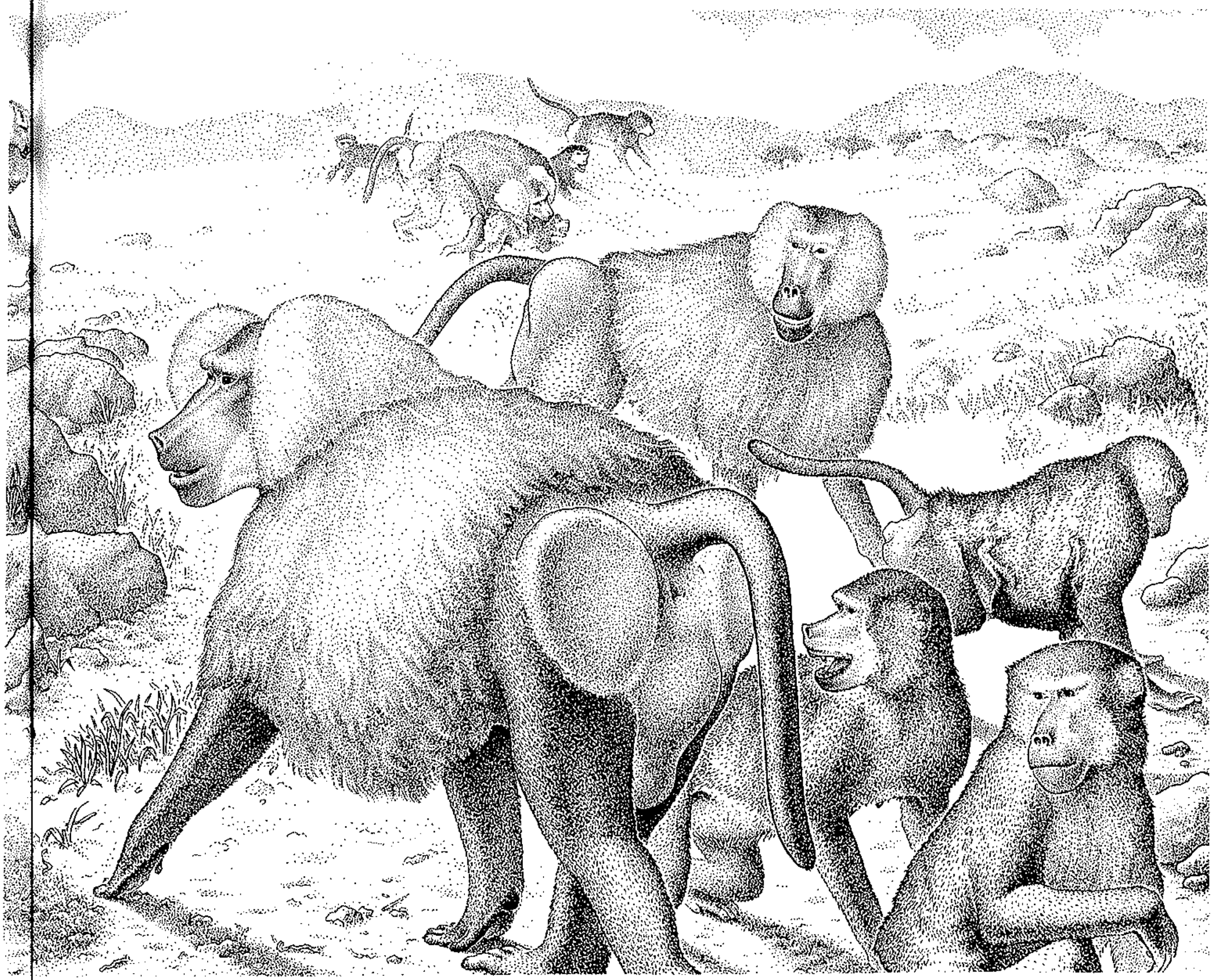


FIGURE 6.10 The Hamadryas baboon (*Papio hamadryas*) is an example of a mammal in which there has been considerable sexual selection. The animals feed during the day in groups consisting of one male and several females and their young. Here the large male, with its heavy mane and large canine teeth is threatening another male in order to keep him from the females. Two of the several females in his group are standing behind him, one with an infant, still with its juvenile black coat, clinging to her back. At night the single-male, multi-female family groups congregate in trees or on rocky ledges for protection from predators like leopards. Such a large troop is seen in the background as it disperses for the day to feed. From Wilson, 1975, reprinted with permission of Harvard University Press.

this topic in the 1880 edition of *The Descent of Man and Selection in Relation to Sex* Darwin gave some familiar examples: ". . . the weapons of offence and the means of defense of the males for fighting with and driving away their rivals—their courage and pugnacity—their various ornaments—their contrivances for producing vocal or instrumental music—and their glands for emitting odours . . . ." Darwin is referring here to such features as the antlers of male deer and the large canine teeth of male baboons, the bright plumage and characteristic songs of many species of male birds, and the habit of many male mammals of marking their territory with scent glands. When, as in these examples, males and females appear different because of either size or such elaborate secondary characters, they are said to display *sexual dimorphism* (Greek for two forms) (Figs. 6.9–6.12).



Although it is true that males are frequently larger and more combative and possess bigger weapons (antlers, spurs, horns, tusks, canine teeth) or are more colorful and vocal than females, there are many species in which males and females are indistinguishable in behavior and appearance. Furthermore, there are some species in which the usual sexual dimorphism is reversed: the females are larger and more colorful, vocal, and combative than males. What sense can we make of this diversity?

Because these secondary sexual characters are used most conspicuously when males and females either mate or form pair bonds, Darwin suggested that a variant of natural selection, which he termed *sexual selection*, had caused their evolution. Darwin's idea was that although two individuals might differ little in their ability to obtain food and escape predators, they might differ greatly in the ways they acquire mates. One way that differences in mating success arise is by competition among individuals of the same sex (typically males) for access to the other sex. Sexual selection then enhances those characteristics that make individuals successful competitors; for example, the presence of large antlers and great stamina in male deer and elk (Fig. 6.9) and the large size and long canines of male hamadryas baboons (Fig. 6.10). In another form of sexual selection, individuals of one sex (typically females) chose their mates on the basis of characters displayed by the opposite sex. In this variant, selection elaborates those traits that are used in displays. The most familiar example is probably the spectacular ornamental plumage of male birds such as peacocks, pheasants, and birds of paradise that are displayed to females during courtship (Fig. 6.11). Traits like the peacock's tail seem to have no function other than in courtship displays.

As just described, these two forms of sexual selection represent polar extremes. Thus some traits might be favored both because they are advantageous in com-

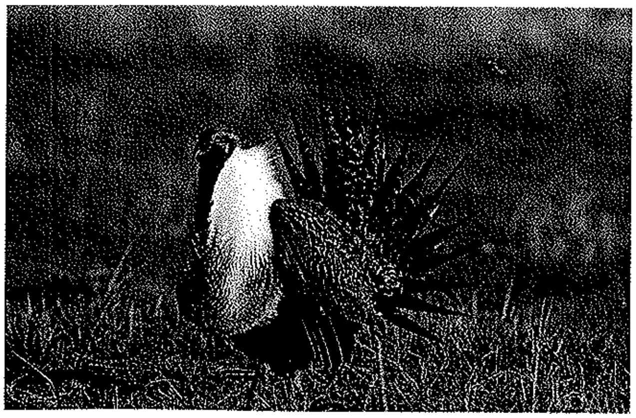


FIGURE 6.11 Male sage grouse (*Centrocercus urophasianus*) displaying before females by spreading its tail and rapidly inflating and deflating air sacks in its neck. The neck sacks are not only visually prominent, they amplify the bird's vocalizations. The sage grouse is an example of a species where males congregate at sites called *leks* and compete with each other through elaborate displays for the attention of the females.

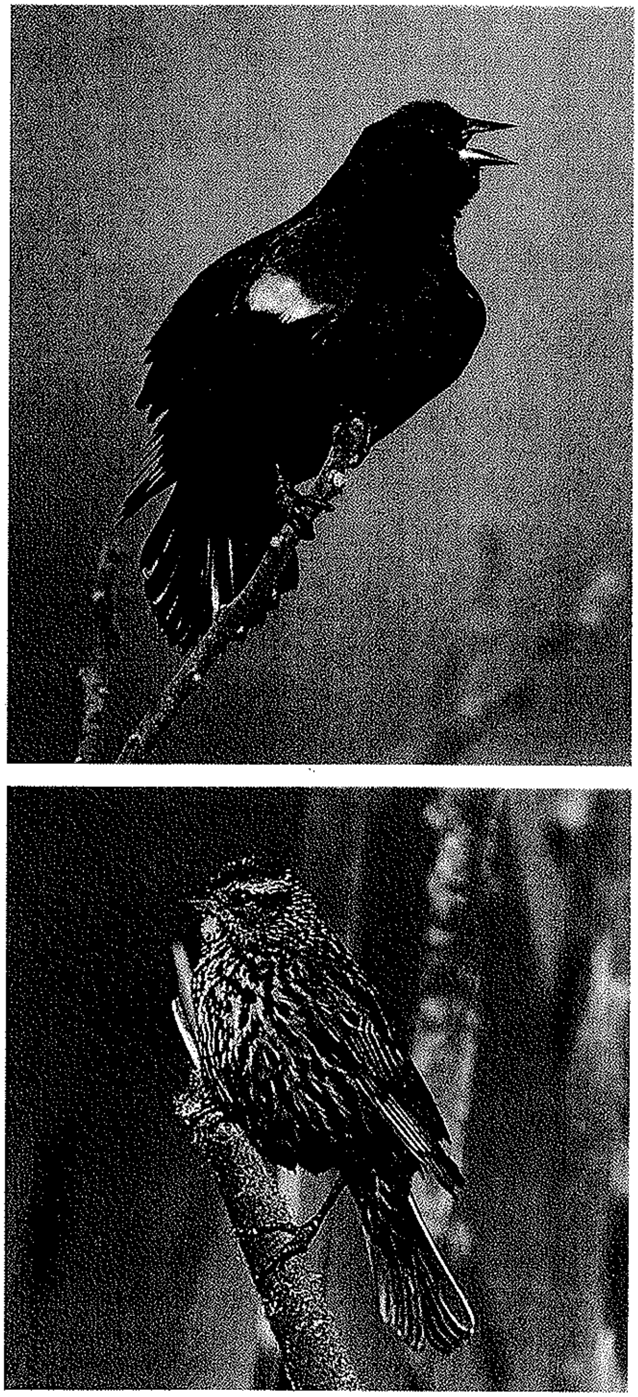


FIGURE 6.12 Male red-winged blackbirds are glossy black with bright red and yellow epaulettes. They sing and display (*above*) to defend their territories and attract females. The females (*below*) are brown with streaked undersides, thus camouflaged.

petition among males and also because they serve (indirectly) the genetic interests of the females. For example, large antlers and body size are advantageous to male deer in competition with other males, but in addition, females gain by mating with the winning males because if size of antlers and strength of body are heritable traits, their sons will more likely be successful competitors. Furthermore, as Trivers has suggested, daughters too can benefit. Large bodies and hefty antlers indicate males with superior abilities in procuring food and sequestering the calcium required for growing new antlers every year, two traits that are crucial to a daughter's ability to provide milk for *her* rapidly growing fawns.

There can be an even more direct interaction between male competition and female choice. Male red-winged blackbirds stake out a nesting territory and advertise their presence by singing and with visual displays of their red "epaulets" (Fig. 6.12). They thereby attract females, who in turn chose males that are in possession of the best territories, i.e., those that provide the best cover for nesting sites. At the same time, however, males are competing with other males for possession of the territory and will attempt to drive off rivals that intrude. The capacity to hold prime territory, like the ability to grow big antlers, is likely to reflect a more general genetic makeup that makes such males desirable mates.

The advantages of larger body size and better weaponry in competition are apparent, but it is not obvious why a female should prefer one male over another because it has tail feathers that almost require a valet to carry them about. The male peacock's tail is in fact a handicap outside the mating game, for it makes it more difficult for him to take flight when a fox or a tiger approaches. Why, then, did the peacock's tail evolve?

Darwin's explanation was simply that females are inherently the choosy sex and just prefer ornamented males. He reasoned that because at the microscopic level motile sperm seek out and fertilize the immobile egg, at the macroscopic level it must be males who seek matings wherever they can find them while females do the choosing. This argument is thin. First, there is no reason why adult mating behavior should reflect the behavior of gametes. Second, in many animals the male and female are equally choosy, and in some the females are colorful and combative and court choosy males (see below). Third, and more important, a preference for ornamentation seems to imply an aesthetic choice—a sort of "good taste" for displays that are multicolored, complexly patterned, and symmetrical. It is clear why a female deer might favor a large male with big antlers, but an appeal to aesthetics does not explain how preference for male ornaments could improve a female's reproductive success. Is there not a deeper explanation?

In 1915, the statistician and evolutionary theorist R.A. Fisher provided a possible explanation for how "good taste" for male ornaments could be favored by natural selection. He argued that if a particular male with an unusual variation of song, or color, or pattern of tail feathers happens—for whatever capricious reason—to gain the mating attention of females somewhat more often than other males, it is to the advantage of all females to prefer this "new fashion" because their sons will be more attractive to females as mates during the next generation. As a result, more daughters with their mother's preference for the new trait will be produced, and a runaway selection ensues in which further attractive elaborations reinforce the advantage of female preference for the trait. Selection for male ornamentation and female taste thus proceed hand-in-hand, and, depending upon the evolutionary path initially taken, may produce a complex, colorful, and symmetrical feather display or a song with extravagant or musical qualities.

More recently, however, evolutionists have been attempting to identify utilitarian connections between male ornaments and their reproductive advantage to females. One possibility is that the quality of an animal's display reflects the general quality of its genetic endowment; that is, it is an indication of whether the male has "good genes." This is actually an extension of the idea that large antlers of deer or the capacity of red-winged blackbirds to defend territory signify the presence of "good genes." One way in which such a connection could be established is the "handicap hypothesis" suggested by the biologist Amotz Zahavi. The more conspicuous and encumbering the peacock's plumage—the more of a handicap it presents—the better must be the bird's general genetic endowment that underlies his ability to create and support such an impediment and avoid the increased risk of predation it entails. Theoretical models suggest that such a mechanism could work, but measuring the summed lifetime benefits and costs of a secondary sexual character in different individuals is very difficult.

Another related explanation, offered by William Hamilton and Marlene Zuk, is that parasites have acted as a selective force in establishing a connection between male display and female choice. Parasites, and infectious organisms in general, are a particularly insidious and persistent threat because they are present everywhere, and their short generation times and genetic variability enable them to produce new variants to which their host is not immune. This threat requires constant genetic reshuffling by the hosts in order to mount new defenses against new parasites (Chapter 8), and males may be using more costly (by inviting predation) songs and displays to advertise that their health is not impaired by parasites. Thus females would be selected to mate with such males because their offspring would be more resistant to parasites.

FIGURE 6.13 The long tail feathers of barn swallows are important in mate choice. Experiments have shown that changing the symmetry of the tail by altering the length of one feather can compromise the attractiveness of birds to prospective mates.

Recently symmetry has been suggested as another possible link between male ornamentation, "good genes," and female choice. In most mobile animals the right side of the body is a mirror image of the left, and this symmetry is important in accurately gathering information from paired sensory organs and precisely coordinating movement of paired limbs. The development of complex, macroscopic, paired structures of the same size, shape, and distance from the midline of the body requires tuning of cell migrations, differentiation, and the activation of genes during development (Chapter 10). Moreover, high body symmetry has been found to be associated with higher metabolic efficiency, better immunity to infections, and lowered parasite loads. There is thus evidence for linkage between body symmetry and "good genes." Furthermore, there is increasing evidence from studies of insects, birds and mammals (including humans) that females prefer to mate with males with the most symmetrical features. For example, clipping one of the long tail feathers of a barn swallow (Fig. 6.13) reduces its attractiveness as a mate.

THE ROLE OF PARENTAL INVESTMENT IN SEXUAL SELECTION

The major deficiency in the theory of sexual selection, beginning with Darwin and extending to the middle of this century, was that it did not account for why, in most mating systems, males compete with each other for access to females and females are the choosier sex. Why isn't the reverse found more often?

The first step in answering this question was provided in 1948 in a study of sex differences in mating behavior and reproductive success in the fruit fly *Drosophila melanogaster*. The geneticist A.J. Bateman observed individuals with different genetic markers while the flies were feeding, mating, and laying eggs in closed bottles containing fly food. The pattern that he observed for the fruit fly is typical of many other animals in which the only investment males make in offspring is to contribute sperm during mating. First, male flies attempt to mate with as many females as they can, and females chose the males with which they will mate. Second, there is much greater variation in the reproductive success of males than among females. In Bateman's study the most successful male had three times as many offspring as the most successful female, and whereas only 4% of females had no offspring, 21% of the males fathered none. Finally, whereas the number of offspring a male fly fathered increased in direct proportion to the number of females with which he mated, females gained nothing by mating more than once; in fact, most of them mated only once. This reflects the fact that female *Drosophila* possess sperm storage organs, which enable them to sequester sperm from a single copulation and dispense it over many days.

Why is it in this animal, as in most other sexually reproducing species, that males mate relatively indiscriminately whereas females are more selective? Bateman argued that these differences evolved because of the differences in the metabolic costs of offspring to males and females: one sperm can fertilize an egg, but an egg is likely to be thousands to many millions of times more costly to produce than a sperm. The reproductive success of a male is therefore not limited by the number of sperm it can produce but by the number of females with which it can mate. Under these circumstances natural selection should thus favor males who produce large numbers of sperm and attempt to mate with as many females as possible, irrespective of the quality of the eggs any particular female produces. Conversely, because of the high metabolic cost of eggs, the reproductive success of a female is limited by her ability to find food and convert it into egg yolk. Given the high cost of eggs and the eager, indiscriminate, mating efforts of males, selection should favor females who find food well and choose from among competing males those individuals whose appearance and behavior suggest high quality.

In 1972 Robert Trivers extended Bateman's ideas into a more general conception of how sexual selection is regulated by the relative contributions of each sex to the production of offspring. Earlier we defined *parental investment* as any parental effort that promotes the survival of an offspring at the cost of producing another offspring. Parental investment starts with the making of eggs and sperm but includes all aspects of parental care. Male and female differences in the amount of parental investment are at the center of Trivers' thesis.

MINIMAL PARENTAL INVESTMENT BY MALES IS FREQUENTLY ASSOCIATED WITH POLYGYNOUS MATING SYSTEMS

For each egg that is fertilized, there has to be a sperm. Consequently (for most species, in which the sex ratio is close to 1:1 at birth) the *average* number of offspring produced by females and males is the same. But if the parental investment made by one sex (usually females) is substantially greater than that made by the other, then females become a limiting reproductive resource. In other words, the reproductive success of females is then limited by their capacity for parental investment (providing nutrients for eggs, fetuses, and nurslings), whereas the reproductive success of males is limited only by the number of opportunities they have to find and mate with females. Under these conditions, individuals of the sex that makes the smaller parental investment (typically males) compete with each other for matings. As a result, sexual selection is more intense among males, and its intensity is proportional to the disparity between the sexes in relative parental investment. Moreover, in long-lived species most females that survive to an age where they are capable of reproducing will manage to reproduce. But in the competition among males, only a minority will manage most of the copulations. Therefore, although the average reproductive success of males and females must be equal, there will be greater variation among males.

Finally, in species in which the parental investment of males is much smaller than in females, the mating system is *polygynous* (Gr., many females) in which one male mates with several to many females. This is another manifestation of the greater variation in male reproductive success; because of strong sexual selection among males, a few winners among the competitors are able to control the reproduction of a disproportionate number of females.

As we discussed earlier, greater female parental investment very likely started in the earliest multicellular animals with the divergent evolution of expensive eggs and inexpensive sperm. Once these separate evolutionary paths were taken, individual females would always have more to lose than males by discontinuing investment, so selection for parental investment after fertilization was likely to impact more on them than on males. Additionally, eggs and embryos can be more safely provisioned and nourished by remaining within the body that produced them. With the evolution of mammals, such a self-reinforcing process of increasing female investment has led to large disparities between the sexes in parental investment. A minuscule investment of sperm accomplished by a male in a few moments initiates a costly and risky investment by a female that may take years, from the implantation of the embryo in the uterus, through development, birth, nursing, weaning, and adolescent dependence. In most mammals the mating system is polygynous, male reproductive success is more variable than that of females, and the degree of sexual dimorphism is greater than in any other class of vertebrates (most fish, amphibia, reptiles and birds). Figure 6.14 shows an example of a species with little male parental investment, a polygynous mating system, and considerable sexual selection for male size.

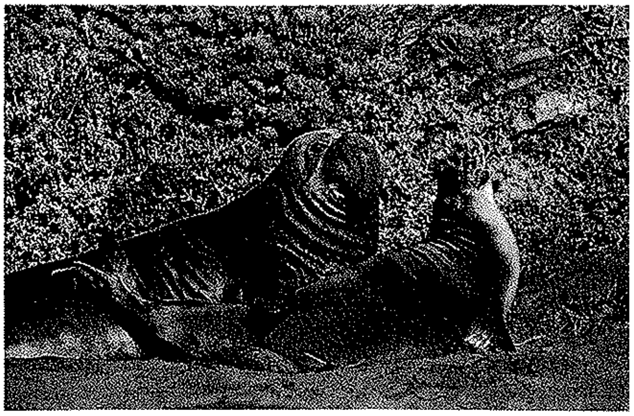


FIGURE 6.14 Elephant seals in the northern hemisphere were driven nearly to extinction by human hunting, but they now breed successfully in a colony on the coast of California where they have been studied extensively by biologists at the University of California at Santa Cruz. In late winter the animals congregate on the shore in large colonies for breeding. The males weigh about 6000 pounds (3 tons!) and are about three times larger than the females. They engage in vicious fights among themselves, and the winners do most of the mating. In one study 4% of the males accounted for 85% of the copulations.

In Chapter 13 we will return to the different breeding systems employed by primates, and in Chapter 14 we will consider the extent to which humans are or are not typical mammals.

LARGE PARENTAL INVESTMENT BY MALES IS OFTEN ASSOCIATED WITH MONOGAMOUS MATING SYSTEMS

Birds occupy a number of points on the continuum of relative parental investment and thus illustrate the consequences for sexual selection and mating systems. In more than 90% of avian species the two sexes contribute approximately equally to the production of young. We might suppose that the large investment of female birds in egg yolk—compared to the tiny male investment in sperm—would make birds polygynous like most mammals. For many species, however, developmental and ecological factors outweigh the relative parental contributions to the fertilized egg (Fig. 6.4). For most of the small familiar songbirds of field and forest, the young hatch in a naked helpless state. Successfully rearing a brood requires that both parents forage for food, and that males make a substantial contribution to feeding the young and protecting them from predators. Additionally, the food of most small terrestrial birds usually consists of small items—insects, seeds, and berries—that are evenly distributed in the environment and can be efficiently exploited and defended by a mated pair. To all appearances, the mating system appears to be monogamous.

But appearances are deceiving. Careful observations of mating behaviors combined with molecular techniques for assigning genetic paternity reveal that in close to 60% of "socially monogamous" species of birds, one or both members are likely to seek extra-pair matings. Among the species in which this behavior occurs, 3–30% of the young are fathered by one or more extra-pair males. In some species the proportion reaches 40–60%.

In most bird species, the females control the success of copulation and sperm transfer, and the evidence suggests that females seek extra-pair fertilizations in order to improve the genetic quality of their offspring. They do not have difficulty in finding willing males, because extra-pair copulations cost males little. For one bird that has been studied in detail, the great reed warbler of northern Europe, females seek extra-pair matings with males that have larger song repertoires than the males with which they are paired. This is a successful tactic, because the offspring sired by these opportunistic males have better survival rates after fledging than young fathered by the resident male.

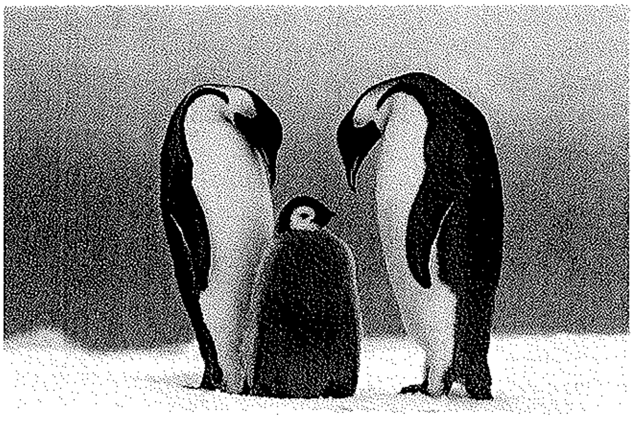


FIGURE 6.15 The extreme southern latitudes pose a severe environmental challenge for ground-nesting penguins. Both the male and female are required to raise a pair of chicks—a single chick in the case of the winter-breeding Emperor penguin; consequently the birds have strong pair bonds, much male parental investment, a monogamous breeding system, and males and females appear identical (i.e., no sexual dimorphism).

Although in most small birds the two sexes are similar in size, in many of these species the males sing and display, and there has been sexual selection on males for bright plumage. Female choice in such species is usually more important than in animals with intensely polygynous mating systems. Figure 6.15 shows an extreme example of a species with essentially equal parental investment by the two sexes, little difference in sexual selection, and a monogamous mating system.

In some species of birds, nests are built on the ground, the young hatch from the egg covered with downy feathers, and in temperate latitudes the hatchlings are able to feed themselves immediately. Male parental investment is consequently less. In grouse, sexual selection acting on males has produced ornamentation and noisy displays. These birds have an unusual mating system in which the males gather at display sites called leks, strut about, and winners are chosen by the females (Fig. 6.11).

SPECIES DISPLAYING REVERSED SEX ROLES HAVE POLYANDROUS MATING SYSTEMS

Nature provides a dramatic corroboration of the hypothesis that differences between the sexes in parental investment regulate sexual selection. The confirmation is seen in species in which the usual pattern of parental investment is reversed, and males make a greater parental investment than females. The attention of naturalists has long been drawn to such species of birds, particularly phalaropes, shorebirds that nest in the far north. The females are larger and more colorful than males, arrive earlier in the breeding area than males, and fight with each other to gain and retain males as mates. Moreover, females do not provide any parental care after they lay their eggs. The male broods the eggs and young and protects them from predators.

Ecological factors seem to have caused this reversal of the usual roles of males and females. These shorebirds nest on open ground in northern latitudes where the breeding season is short and the eggs are especially susceptible to predation. The young are able to feed themselves immediately after hatching, so only one parent is needed after the eggs are laid. After laying her eggs the female usually departs and attempts to mate and leave another batch of eggs with a new male. In other words, the mating system is *polyandrous* (Gr., more than one male). On average, successful females mate with more different males than males do with females.

Reversal of parental investment and sex roles is also found among some species of fish and frogs, and here too the males' provision of safe places for eggs to develop is a major factor limiting reproduction. In the tropical poison arrow frog, females are larger, more colorful, and more active in courtship than the male, who broods fertilized eggs in his mouth and takes the hatched tadpoles to water. In the sea horse (a fish), the female is active in courtship, and the male takes the fertilized eggs into his ventral brood pouch, kangaroo style, for safe keeping and growth.

To summarize, the reasoning of Bateman and Trivers is confirmed in species exhibiting male-female role reversal. It therefore seems to provide an encompassing understanding for how and why relative parental investment regulates sexual selection, which in turn leads to sex differences in size, morphology, and behavior.

SOME FURTHER BEHAVIORAL CONSEQUENCES

Because females (typically) make the larger parental investment, they have more to lose reproductively should a mating not lead to reproductive success. In species where successful rearing of young requires the continued participation of the male, it is in the interests of the female to mate with males who are likely to provide that additional parental investment. This is the reason for the evolution of courtship periods in which males demonstrate that they have more than "good genes" to offer. An obvious example is the male's possession of territory as a source of food for the young, as described earlier for red-winged blackbirds and reed warblers. Courtship provides an extended opportunity for the exercise of female choice and is an example of an evolutionary outcome that has been driven primarily by the genetic interests of females.

Males, with smaller parental investment than females, can benefit reproductively if they are able to fertilize the eggs of more than one mate, particularly if another male is left to tend the additional set of young. But in species where males make a substantial parental investment, their opportunities for extra-pair matings become more limited. The male who leaves his territory unguarded while in search of reproductive opportunities elsewhere runs the risk of loosing his resource base to another male. He also runs the risk of having his mate inseminated by another male, whose offspring he will then rear. This outcome—known as cuckoldry—is a genetic disaster because his investment is all cost and no benefit. Cuckoldry is a particularly acute problem in species where fertilization is internal and where males must observe their mates constantly to be certain they have not been inseminated by other males. Thus male swallows follow their mates on feeding flights until the female lays her eggs, and male mammals frequently seek copulations with their mates after periods of separation. The human emotion associated with such mate guarding is sexual jealousy, a topic to which we will return in Chapter 14.

MANIPULATING THE SEX RATIO

Why are there approximately equal numbers of males and females at the start of each generation? In 1930, the mathematician Ronald Fisher provided the answer to this question in evolutionary terms. Each fertilization requires the participation of a male and female, so the *average* reproductive success of males will be the same as the average reproductive success of females. This is as true in polygynous species as in monogamous ones so long as sons require the same average parental investment as daughters.

What would happen in a population in which ten times as many sons were produced as daughters? In the following generation, each daughter would have ten times the number of offspring as the sons. Natural selection would then favor individuals that produced more daughters than sons, and this would continue until the sex ratio approached 1:1. In other words, natural selection is expected to favor the sex ratio that gives parents the same return in grand-offspring per unit investment in each sex. In humans, pre-reproductive mortality of males is significantly greater than among females (a consequence of sexual selection), and the human sex ratio at conception and birth is significantly biased toward males.

In 1973 Robert Trivers and Dan Willard extended Fisher's reasoning by proposing that selection should favor parents that produce greater numbers of the sex that under certain conditions are likely to have more offspring than the other. They argued that in highly polygynous mammals, for example, larger males achieve disproportionately more matings than smaller ones, and adult size is closely correlated with birth size. Sons born large—because their mother is well nourished and healthy—are better able to compete for food, with the result that their initial size advantage is actually magnified. Males born smaller and weaker—because when food is scarce their mother is in below-average condition—are likely to remain so and achieve disproportionately fewer matings. The impact of scarce food is less severe on the reproductive prospects of daughters, however. Because the greater parental investment of females makes them a limiting reproductive resource for males, most females who survive to adulthood will manage to breed. Consequently, an adult female of less than average size and vigor is likely to outreproduce a comparably small male.

Trivers and Willard therefore reasoned that when polygynous mammals are able to produce sons that are larger and healthier than the population average, they should favor sons; conversely, if their offspring are likely to be smaller and less healthy than average, daughters are a safer bet.

OPOSSUMS MANIPULATE THE NUMBERS OF SONS AND DAUGHTERS

The Trivers-Willard hypothesis was considered improbable by many, including biologists Steven Austad and Mel Sunquist. So they decided to test the idea by manipulating the food supply in a population of opossums and observing what effect this had on the sex ratio of offspring. Opossums are familiar as the only North American marsupial mammal (Chapter 2). The young are born very immature and are nourished in the mother's pouch, as in kangaroos. Female opossums establish feeding territories, mate with a male, and rear their young alone. During the day a female sleeps in an underground den. The mating system is polygynous: males defend large mating territories that overlap the territories of many females, and they range widely to chase away other males. The larger a male, the more successful he is at dominating other males and mating with females. Body size does not affect a female's ability to mate or produce young, except when she is undernourished.

Austad and Sunquist trapped and radio-collared forty virgin female opossums in order to be able to find their dens and monitor their movements. Twenty females were provisioned with extra food—sardines left at the entrance to their dens—and twenty females were not given extra food. Both sets of females produced the same number of young, but those of the food-supplemented mothers were 50% larger. Along with an increase in size there was a 16% increase in survival of daughters and a nearly 30% increase in the survival of sons.

Most dramatic was the difference in the sex ratio of offspring of the two groups of mothers. Mothers whose food was not supplemented produced equal numbers of sons and daughters, but mothers with the extra rations of sardines produced 40% more sons. This finding led Austad and Sunquist to reexamine data they had gathered over several years on the offspring of aged females (two or more years old), which develop cataracts, lose weight, wean fewer young, and are generally in poorer condition than during their first year. Unlike the younger, well-nourished animals, these females produced 80% more daughters than sons. These experiments confirmed both sides of the Trivers-Willard prediction—the female opossum can bias the sex ratio toward sons or daughters, depending on which sex is likely to achieve greater reproductive success and thus propagate more of the mother's genes.

RED DEER ALSO MANIPULATE THE SEX RATIO

Another test of the Trivers-Willard hypothesis was provided by a long-term study by Timothy Clutton-Brock and his co-workers on reproduction in a herd of red deer on the isle of Rhum off the coast of Scotland. Socially dominant females are in better physical condition than subordinate females because they are able to gain preferential access to good browse. As a result, dominant females have sons who grow up to be dominant, and subordinate females have sons who grow up to be subordinate. Clutton-Brock and his associates found that dominant mothers produced more sons than daughters, and they had more grandchildren by their sons than by their daughters. Precisely the reverse was found for subordinate mothers. These deer had more daughters than sons, and the daughters experienced greater reproductive success than the sons.

FEMALE DOMINANCE CAN ENHANCE THE REPRODUCTIVE SUCCESS OF DAUGHTERS

One of the many unforeseen discoveries of this research on the sex ratio is the finding that a female's rank in a dominance hierarchy can be more important to her daughter's reproductive success than to the reproductive success of her son. This has been found in two kinds of Old World monkeys: baboons and macaques. In these species daughters remain in their natal group and "inherit" the social rank of their mothers while males emigrate and are unaffected by their mother's rank. In the populations of bonnet macaques studied by the primatologist Joan Silk, dominant females and their allies gain preferential access to food and water and so severely harass the daughters of subordinate females that few of them live. Dominant bonnet macaque females give birth to more daughters than sons, and subordinate females do the reverse. Furthermore, in this social system subordinate females care for their daughters after birth much less than they do sons.

The evidence is now widespread and extensive that Trivers and Willard were right in suggesting that animals might respond to ecological and social conditions by adjusting the sex ratio of their offspring so as to maximize the number of grandchildren. Could this apply to humans, an animal in which the reproductive prospects of offspring can be greatly affected by the social rank and resources of parents? We will return to this question in Chapter 14.

SYNOPSIS

In this chapter we presented a framework for explaining the evolution of social systems. Behavioral interactions between individuals influence the reproductive success of one or both parties; accordingly they can be characterized as selfish, cooperative, spiteful, or altruistic. Behavior that is seemingly altruistic is very common among many species of animals, but it raises a question for evolutionary theory: If individuals who sacrifice their reproductive success for others leave fewer offspring than those who behave selfishly, how can altruistic behavior be supported by natural selection?

There are two ways. First, copies of one's genes are present in near relatives, so it is possible to enhance one's reproductive success through benefits extended to close kin. This is the basis for nepotistic behavior. It has its most elaborate expression in social insects, as we will describe in the next chapter. The changes in gene frequency that result from the effects individuals have on the reproductive success of relatives is *kin selection.*

Second, many social systems include individuals who are not closely related but who interact on a regular basis, and behavioral mechanisms have evolved to facilitate the reproductive success of individuals living in social groups. These behaviors involve reciprocal interactions in which benefits extended are followed by benefits returned. This *reciprocal altruism* is found in long-lived species with sufficient cognitive capacity to recognize individuals and remember and assess the results of previous interactions. We will examine its expression in nonhuman primates in Chapter 13 and in humans in Chapter 14.

The genetic uniqueness of individuals of sexually reproducing species is not only the basis of self-interest, it leads to conflicts of self-interest where one might least expect to find them. Forms of parent-offspring conflict provide examples, some of which can be identified during the gestation of mammals.

Many species are characterized by noticeable differences between the sexes in size, coloration, and behavior. Such sexual dimorphism was described by Darwin, who pointed out that it tended to be greater in species in which males (usually males) compete among themselves for access to females. Darwin coined the term *sexual selection* to designate a kind of natural selection that works on males and females of the same species in quite different ways because the two sexes have different strategies for acquiring mates.

Understanding of sexual selection was extended in the 1970s by Robert Trivers, who pointed out that the controlling factor is the degree of *parental investment* that each sex makes in offspring. Parental investment means anything that a parent does to benefit an offspring that comes at a cost to investing in other offspring, thus possibly compromising the lifetime reproductive success of the parent.

Parental investment is great in female mammals and quite modest in males (although humans are something of an exception to this generalization). The consequent limited lifetime reproductive capacity of females makes them a limiting resource for which males then compete, and the mating system is typically *polygynous.* In many species of birds, the need to feed helpless young requires both parents, and with a greater relative parental investment by the male the mating system is *monogamous* (or nearly so). A powerful demonstration of the validity of these ideas is provided in nature by species in which the degree of parental investment by males and females is reversed, as is sexual selection, and the mating system is *polyandrous.*

In polygynous mating systems, the relative reproductive prospects of male and female offspring can differ, depending on ecological conditions or the dominance status of the mother. There are several examples known where female mammals alter the sex ratio of their offspring so as to maximize the number of grandoffspring.

QUESTIONS FOR THOUGHT AND DISCUSSION

1. Occasionally identical twin sisters marry identical twin brothers. What is the degree of relationship between the offspring of the two couples? What is their nominal relationship: cousins, siblings, or what?
2. In order to attract females as mates, male bowerbirds build elaborate displays of shiny and colored objects they have collected, including things discarded by humans. How might this behavior have arisen through natural selection? What would you predict about the degree of sexual dimorphism in plumage coloration in these birds?
3. Is there fundamental conflict or meaningful convergence between the biological concept of sexual selection and the tenets of feminism? Explain. (You may want to revisit this question after reading Chapter 14.)

4. A critic of the theory of kin selection said that it could not explain the evolution of nepotistic behavior in animals because animals know nothing of fractions (by which r, the degree of genetic relatedness is expressed), and it could not apply to humans because fractions are a recent invention in some cultures but are unknown to most. Comment on this criticism.
5. In our society many people adopt and raise children to whom they are not genetically related. Is this evidence against the operation of kin selection during our evolution? Explain.
6. Evolutionary social theory predicts conflict between individuals in inverse relation to their degree of genetic relatedness. Compare the degree of conflict predicted between parents and offspring for a monogamous versus a polyandrous mating system. Consider the behavior of siblings toward each other, the father's and mother's view of how the siblings should behave toward each other, the father's and mother's views of how much each of them should invest in the offspring, and the offsprings' view of how much each of the parents should invest in them.

SUGGESTIONS FOR FURTHER READING

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