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

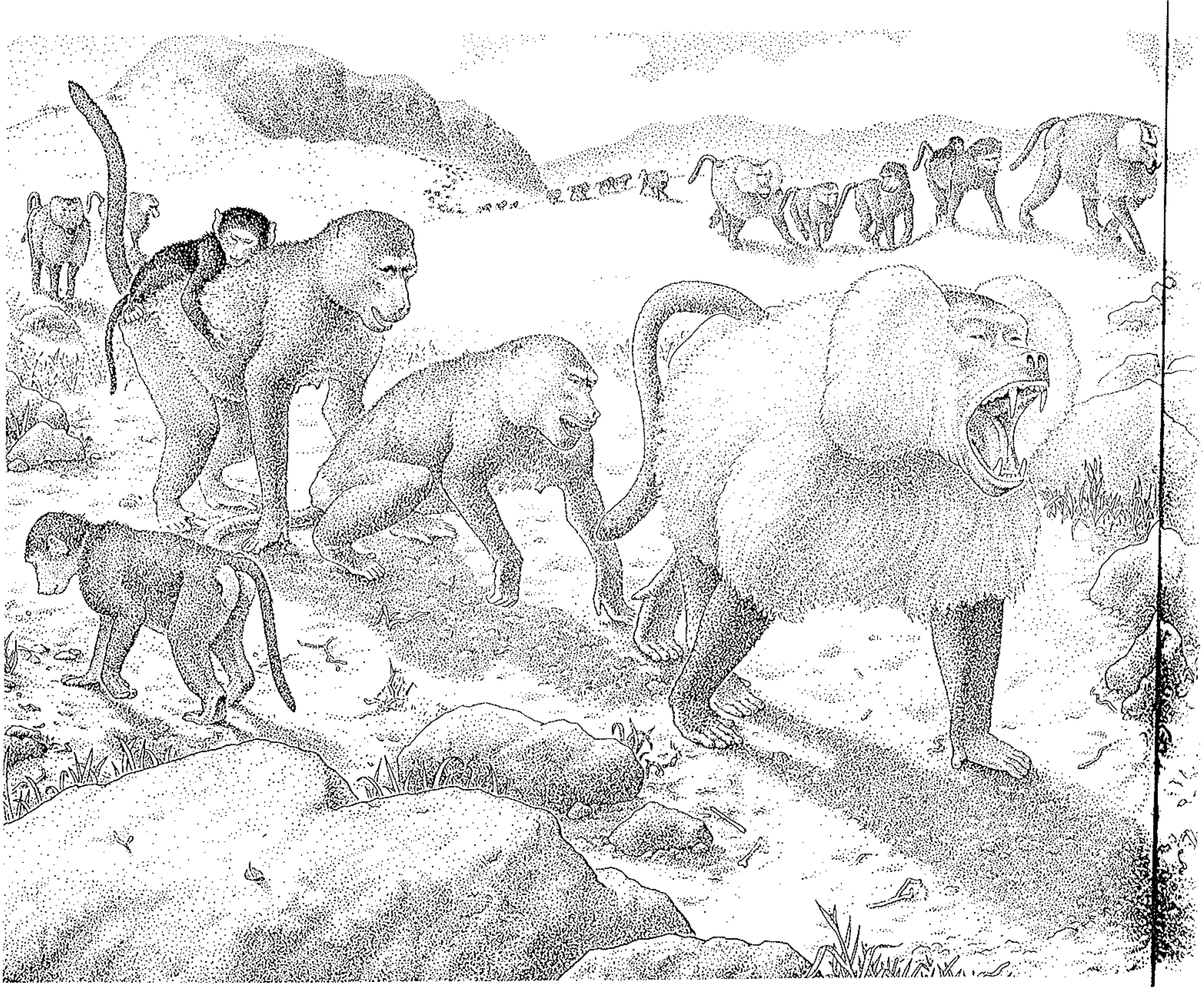
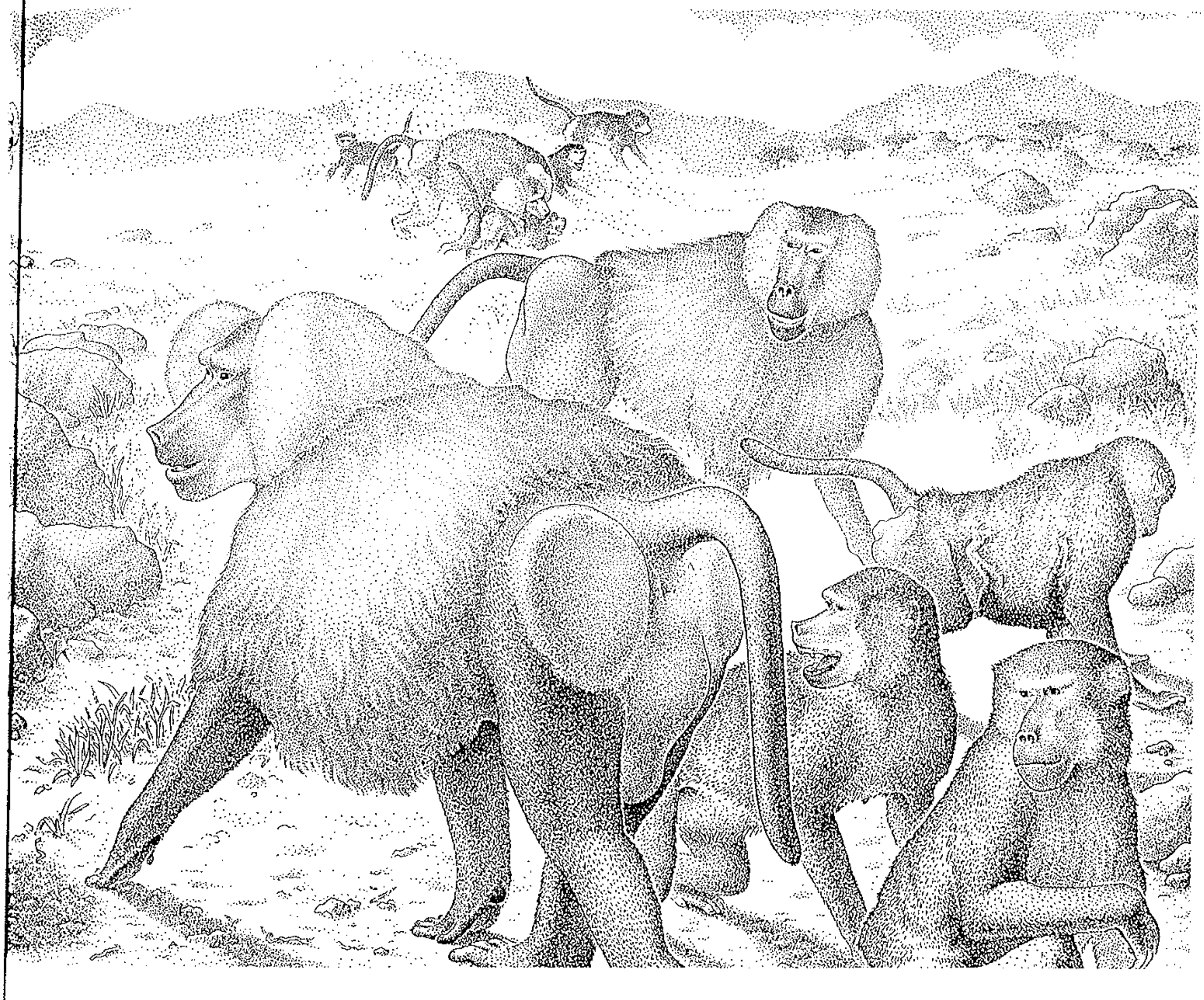


FIGURE 6.10 The Hamadryas baboon (*Papio hamadryas*) is an example of a mammal in which there has been considerable sexual selection. The animals feed during the day in groups consisting of one male and several females and their young. Here the large male, with its heavy mane and large canine teeth is 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-

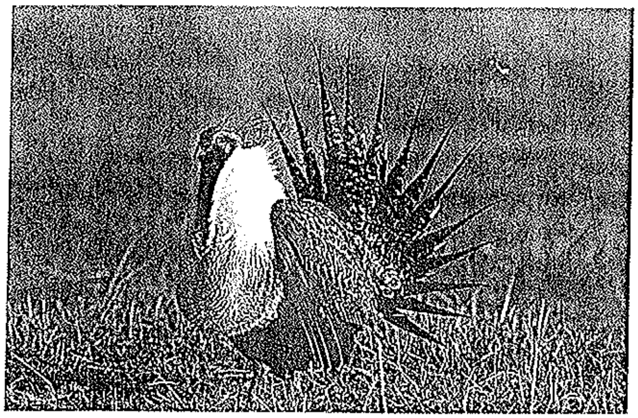


FIGURE 6.11 Male sage grouse (*Centrocercus urophasianus*) displaying before females by spreading its tail and rapidly inflating and deflating air sacks in its neck. The neck sacks are not only visually prominent, they amplify the bird's vocalizations. The sage grouse is an example of a species where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

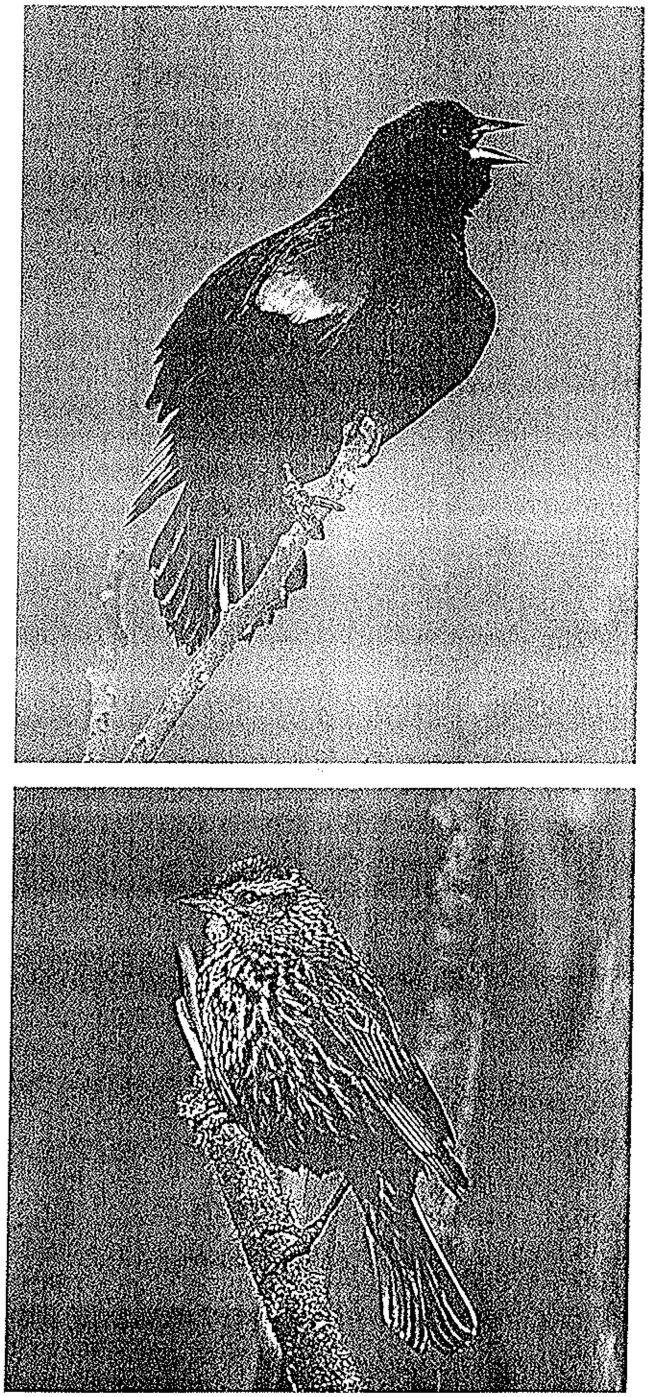


FIGURE 6.12 Male red-winged blackbirds are glossy black with bright red and yellow epaulettes. They sing and display (*above*) to defend their territories and attract females. The females (*below*) are brown with streaked undersides, thus camouflaged.

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.

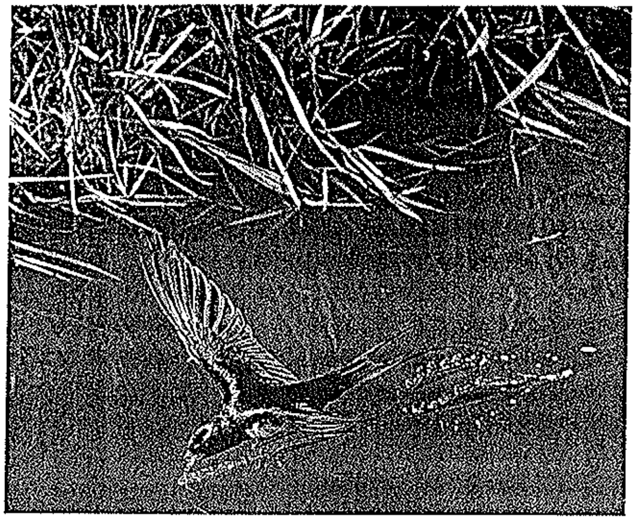


FIGURE 6.13 The long tail feathers of barn swallows are important in mate choice. Experiments have shown that changing the symmetry of the tail by altering the length of one feather can compromise the attractiveness of birds to prospective mates.

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