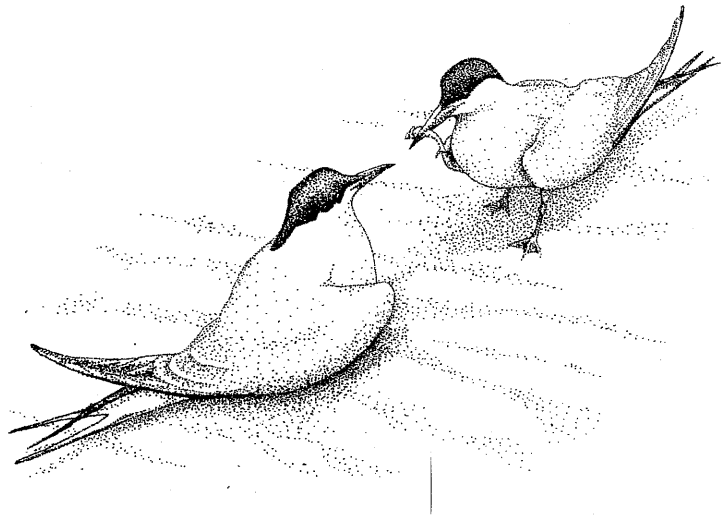
…vent cheating and can show the real motivation and ability of …eatener in a reliable way. The patterns of threat signals—like those of other …—are neither random nor arbitrary. The need for reliability links the signal …y to the message it conveys and guarantees that the cost of the signal is …able for an honest signaler but prohibitive for a cheater. In the case of a … the cost that the honest signaler is willing to undertake, and that a cheater … afford, is the risk that the signal entails. Rather than being a mere conven… …e signal itself provides the genuine information that is needed to resolve …flict. Thus there is an optimal signal for every threat—and indeed for every …lar message. The Handicap Principle not only asserts that this is so but …s why.

In Zahavi, A. and Zahavi, A. (1997). The Handicap principle (pp 25-40). NY: Oxford University Press.

CHAPTER 3

MATE SELECTION



Sexual displays often attain gigantic dimensions and take bizarre forms. The peacock's tail grows into the well-known large, colorful fan; peacocks presenting themselves to peahens spend time and energy holding their tails spread open and upright and vibrating them rapidly. Males of many other bird species grow long tail feathers for sexual displays. Relative to their size, some male pheasants and birds of paradise have tails almost as large as the peacock's, and the males of some species of songbird, such as the viduas of Africa, have tails that are proportionately even longer.

Male songbirds sing to attract mates; some of them invest most of the day in singing. Others, including many larks, sing during strenuous flight displays. Male sage grouse and male ruffs dance in special arenas for many days to compete for the favors of females. Blackcocks vocalize and display their tails as they dance, broadcasting their message by means of several modalities at once.

Sexual display is not unique to birds. Mammals, reptiles, amphibians, fish, insects—all invest in sexual displays, and in each of these groups there are species in which the investment attains striking, even fantastic dimensions. Crickets, grasshoppers, and cicadas sing for many hours to attract partners. Fireflies display with

flashes of light. Moths and many mammals emit scents. Even one-called organisms like yeast and algae emit pheromones to attract mates.

Sometimes bodily growths are means of sexual display: newts grow a finlike nuptial crest along their backs; the white pelican grows a bump of flesh between its eyes. The males of many bird species such as shrikes, terns, and gulls, as well as some insects, court their mates with nuptial gifts of food, leaves, or twigs. Male bowerbirds build complex bowers and decorate them with shells and flowers, bones, insect skeletons, and colorful fruits to attract females; some male fish and crabs build sand castles on rocks exposed to the waves, castles that have to be continually rebuilt.

The extravagant dimensions of sexual displays make them seem like crazy fashion shows. But have they run beyond reasonable evolutionary control, as is commonly assumed? Or do the dimensions of the displays and the specific forms they take serve a purpose?

THE CONFLICT INHERENT IN COURTSHIP

Williams[1] emphasized the competitive aspect of courtship: males and females have conflicting interests. Each wants the highest-quality mate it can get—the mate that can best improve its offspring's genes and, depending on the gender and species, best raise those young. Williams therefore suggested that during courtship males and females can be seen as opponents. The male, like a good salesman, does whatever he can to impress females, while the goal of the female, like that of a shrewd customer, is to check the merchandise and accept only proven quality.

Of course, females also advertise themselves to males, with the same ensuing conflict of interests.[2] Still, the possibilities open to them are different. The number of a female's offspring is limited most by her own capacity to produce eggs or undergo pregnancies, while a male's breeding success depends more on the number as well as the quality of the females he can persuade to breed with him. For the sake of convenience, and since males as a rule invest more in advertising than females, we will discuss the issue mostly in terms of males as presenters and females as choosers.

How can males prove themselves to be superior? Williams did not address that question. But in the previous chapters we have seen how reliable communication develops between enemies of different species and between rivals within a species. The same logic applies to sexual display.[3] Here too the conflict of interests—between male and female—is often resolved by communication, which depends on the evolution of reliable signals.

Signals are reliable if a cheater cannot gain by using them—if the investment in the signal is a reasonable one for a truthful suitor to make, but prohibitive or unprofitable for a cheater. The more the suitor stands to gain, and the bigger the loss to one who accepts a false suitor, the more the signaler must invest in the signal in order to reliably demonstrate his superiority.

We assume that the specific investment a signaler makes is directly linked to the message of the signal. Male rivals are only interested in the fighting ability of their adversaries; predators are concerned only with their prey's ability to escape. Individuals looking for mates, however, are interested in a wide range of qualities.

What do animals look for in a mate? That depends. Where both male and female take care of the young, the ideal mate is not just of superior genetic quality—quality that will be passed on to the offspring—but also skilled enough to provide for its family and committed to parenting the offspring effectively. In such species, the male can commit to only one female at a time—or to at most a few. A female in such a species may well have to compromise on quality in order to get a male willing to commit to her. At the other end of the spectrum are species in which males have no parental involvement whatsoever. In these species a female can concentrate on finding the most superior sperm donor she can, even if she has to share his favors with many other females. In such species a few outstanding males get most of the females, while young and low-quality males do not copulate at all.

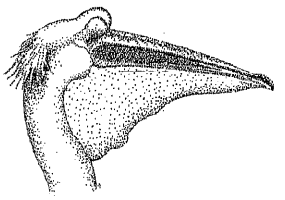
Courtship signals thus convey different messages in different species. As with all signals, we expect to find a direct relationship between the investment in sexual advertising and the specific information the courtship signal conveys to the selecting party.

COURTSHIP HANDICAPS AND THE INFORMATION THEY CONVEY

Feeding Ability

Courtship feeding—as in terns, shrikes, and great tits—reliably demonstrates both the feeder's ability to give up a good portion of the food he collects and his interest in the particular female. The female gains both the actual food provided and the knowledge that the male would be a good provider for her offspring. The more food the male brings to the female, the more reliable the message: that he is a good collector of food. Indeed, Nisbet[4] found that male terns who provide more food during courtship also feed their offspring better. Courtship feeding is a much better indicator of the male's quality as a hunter than a mere show of strength would be. The effort required to feed the female prevents pretense by

a male who can barely feed himself. It also prevents males from courting many females simultaneously.



White pelicans, both male and female, grow fleshy bumps between their eyes when they are ready to breed. The bump interferes with the pelican's ability to see the area around the tip of its bill. In order to catch prey, a pelican with a bump has to remember where it last saw its prey and project the prey's likely movements. An inexperienced or inept pelican would not be able to do so. A pelican that can fish and maintain itself in spite of the handicap of its bump is reliably demonstrating its expertise in fishing. Later, when the pelicans have to feed their brood of four or five demanding young, the bump shrinks and they are able again to hunt more efficiently.

Singing can also demonstrate the ability to provide. The time invested in singing cannot be used for foraging. A courting male who handicaps himself by singing continuously provides evidence that he needs less time to forage, either because he is very efficient or because his territory is very rich. Wilhelm and his colleagues[5] studied the effect of supplementary feeding on the singing of yellow-bellied sunbirds. They found that males who were not given insects did not sing, while those who received insects and sugar water sang often and at length. Time spent in sentinel activity, or in dancing displays, can also indicate expertise in finding food, especially when the "waste" of time comes early in the morning after a long, cold night without food.

Superterritories

O'Donald[6] has suggested that the size of an animal's territory can serve as an advertisement. Males and females of many species protect a territory and chase others away from it. Often the territory is far larger than is needed to provide food or shelter for a pair of mates and their offspring. Some suggest that these bigger territories prevent overexploitation of food resources, and thus a richer resource remains to sustain the population as a whole in the future.[7] But this argument depends on the mechanism of group selection, which, as we have seen, is questionable. When some males protect territories that are larger than they need, the population as a whole might gain from the preservation of future food resources; but the males who hold smaller territories would gain the most, since they would enjoy the resources preserved by earlier residents without squandering their own efforts protecting larger territories than they need; they would therefore be able to devote more of their energy to reproduction. Thus, over the generations, the tendency to hold a larger territory than one needs would disappear. Why, then,

should an individual spend time and energy and even fight to protect a bigger territory than it needs?

The rich build grand homes and mansions not because they need them as shelter for themselves or their children but in order to proclaim their status. The cost of building and maintaining a palatial mansion advertises the owner's wealth to his competitors and colleagues. Just so among many species of animals: a large territory proves the male's superiority and attracts a good mate. Indeed, observations show that females settle first in the larger and richer territories; very small territories may attract no females at all.

These superterritories may indeed preserve the resources available to the whole population of the species; but this is only a by-product and does not play any direct role in the evolution of the trait of establishing superterritories. A good analogy is provided by the vast hunting lands maintained by European noblemen in past centuries, while throngs of peasants starved. These territories were used for sport hunting and were strictly guarded against poachers. Such superterritories served to show off their owners' wealth, authority, and power to their peers, whom they invited to the hunt. Many of these same hunting grounds by now have become national parks, which preserve for people of our own time the animals and the natural forests of Europe—but this is hardly the reason the noblemen established and maintained their hunting estates generations ago. In just the same way, males hold large territories because by doing so they deter their rivals and attract good females. Large territories may indeed preserve the species' resources of food against overexploitation—but that is a side effect, not the superterritories' actual purpose.

Courtship Vocalization

Many animals vocalize during courtship. Lions, tigers, and deer roar; cicadas and crickets chirp; birds sing. Courtship calls can be dangerous: Ryan and his colleagues[8] showed that frog-eating bats locate frogs by the amphibians' courtship calls. Only a male frog that can successfully avoid bats despite disclosing its location to them can afford to croak much. Courtship calls can also be very demanding: Clutton-Brock and Albon[9] found that red deer are often exhausted after a roaring contest with rivals. Only a strong, well-muscled individual can roar loudly for a long time.

The details of a call, its tempo, and the number of syllables in a phrase can demonstrate the caller's quality. The song of the great tit is a series of precisely spaced syllables. Lambrechts and Dhondt[10] found a positive correlation between

the number of syllables in a phrase and the rhythmic precision of the last few syllables on the one hand, and the reproductive success of the singer on the other. The ability to maintain both the tempo and the pattern of syllables at the end of a long phrase would seem to be a good indicator of quality. As was discussed in chapter 2, the precise performance of a call demands concentration. A less able male would probably find it difficult to concentrate for long; after all, the song reveals his location, and he must keep an eye out for approaching rivals and predators. The singing conveys his confidence or lack of it, information important to a female who must decide whether to accept him as her mate.[11]

Colors

The adult males of many species of birds are far more colorful than females and young males: examples include peacocks, ducks, birds of paradise, and sunbirds. Colorful plumage attracts rivals and predators and thus serves as a reliable signal of quality: only males of high quality can risk advertising their location. Conspicuous coloration also emphasizes the exact shape, posture, and movements of its bearer. A high-quality individual "wears" bright coloring well; on a low-quality one the same coloring accentuates imperfections.[12]

Scents (Pheromones)

Scents also serve to attract mates. Studies have found that some female insects can identify a dominant male by its scent alone.[13] Many male mammals, too, use scent to attract females and deter rivals. We know a great deal about the chemistry of pheromones—chemicals that are produced by one individual in order to influence the actions of others; but very few scientists have tried to explain the adaptive significance of specific chemicals. It would be fascinating to discover what information the pheromones of each species provide about their producers.

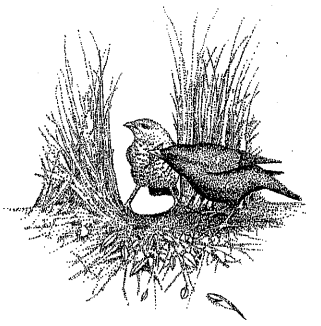
The main component of the pheromone secreted by male arcteid and danaid butterflies is a derivative of an alkaloid—a strong poison produced by plants for their own protection.[14] Arcteid larvae can metabolize the poison and thus take advantage of a food source that is not available to most other animals; the poison that they take into their system then helps protect them from predators. A male arcteid butterfly secreting this pheromone testifies that as a larva he was able to feed on the poisonous plants; the concentration of poison in the pheromone demonstrates the male's relative physiological ability to deal with the poison. Danaid butterflies secrete a similar pheromone, derived from plants that they eat as adults. Eisner and Meinwald further proposed that the pheromone could function as a chemical yardstick by which females gauge the poison load their suitors carry. The alkaloid in the pheromone may also show that the male will probably be able to

pass on a good quantity of alkaloid to the female during copulation, to protect her and their offspring against predators.

The monarch butterfly is one species in the danaid family that does not use these alkaloid derivatives in its courtship. It is a migratory species that winters every year in California, Mexico, and Florida. This species instead courts its females by means of aggressive displays. Males bounce on passing females and throw them to the ground, where they copulate.[15] The ability of the male to use force in copulation may attest to his strength and stamina, which are necessary for long migrations.

Artifacts and Constructions

A cichlid fish of Lake Malawi in Africa gathers a pile of sand and forms a depression in it for the female to lay eggs in. This nest is not used to raise young: both sand and eggs get washed away by the waves in the lake.[16] In our opinion, it is precisely the difficulty involved in gathering a pile of sand again and again in a wave-swept area that enables the male to show off his ability reliably. Crabs who live in the tidal area also build sand castles, which have to be rebuilt at every low tide.[17]



As mentioned earlier, courtship displays are especially elaborate in species where the males do not take care of offspring and are free to concentrate their efforts on attracting females all season long. The top performers get most of the females, while most males do not copulate at all. The most famous of these species include peacocks, ruffs, grouse, manakins, birds of paradise, and bowerbirds.

Male bowerbirds, a family found only in Australia and Papua, spend much of their time building bowers of twigs on the ground. These structures have no utilitarian purpose; their only function is to serve as stages on which males perform courtship displays. The bowers of each species have their own structure and characteristic decoration.[18] One species builds a platform of twigs a meter in diameter; on the platform, two parallel rows of standing twigs, each half a meter long, form a corridor in which copulation takes place. The male of another species builds a mossy wall about four inches high around a courtyard, at the center of which, as a rule, is a sapling; the bird covers a meter of the sapling's trunk with woven twigs. Still another species covers the courtyard, making a hut with only one small entrance. The builder adorns his bower with rare ornaments, such as the feathers of birds of paradise, or with fresh flowers, which must be continually replaced, showing off his ability to find decorations. In fact, the two highly decorative feathers on the head of the king-of-Saxony bird of paradise are valued both by bowerbirds and by tribesmen of Papua New Guinea.[19]

The female visits the bower several times and carefully examines both structure

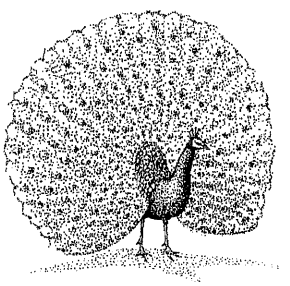
and builder before deciding whether to copulate with the hopeful candidate. The female copulates only once before egg-laying. She may well visit a bower, examine it, watch the male perform his dances, even take part in the dancing and court the male before deciding to pass him up. It seems that the decoration of the bower plays a large part in the female's choice of a father for her offspring.

The number of decorations is important to females too. They prefer males whose bowers are richly decorated. Males steal decorations from neighboring bowers. Borgia tried adding individually marked rare and sought-after ornaments to one set of bowers, then to another; he found that no matter which bowers he added the ornaments to, they always wound up in the bowers of the most successful males.[20] To be attractive to females, a male bowerbird has to spend considerable time and talent building his bower, collecting decorations, placing them, and guarding them against his neighbors, not to mention performing on the stage he has built. He thus proves that he is stronger and more energetic than his neighbors, that he can feed himself adequately and is still able to build and decorate his elaborate bower, guard it against competitors, and raid their bowers.[21]

When we visited Borgia in Australia, we saw some bowers of the great bowerbird. The platform at the entrance to the avenue included flat stones from a riverbed, bleached bones (mostly vertebrae), broken glass—most of it green—and colorful bits of foil and cardboard. Borgia observed that the arrangement of the decorations was not random. The green bits of glass were consistently placed by the northern entry, which in the southern hemisphere faces the sun. The glass glistens in the sunlight, and the male displays his violet plumes against a shiny color-coordinated backdrop.

Combinations of Signals

In most cases, several signals of different kinds are used in courtship. In birds, special feathers, bright colors, singing and calling, dancing, and gift-giving—the last three of which demand time and energy—all play their part. Each modality brings out a particular quality of the male; the female can then use several criteria to assess the male. Let's take the display of the peacock as an example. The male holds his tail upright and spread out—which demands considerable effort. From time to time he shakes his tail vigorously; this requires yet more effort and produces a remarkable rattle. The "eye" patterns on the peacock's tail, the glisten of his feathers, the crown on his head, all add up to a symphony of shape, color, pattern, movement and sound—a performance that is announced with periodic roars.



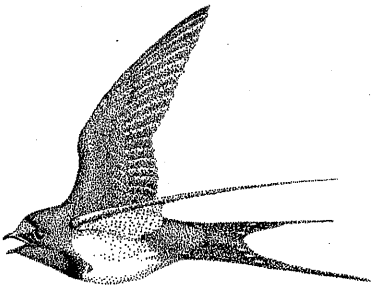
Each aspect of the display seems to convey specific, reliable information about a particular feature of the male. The long tail feathers are grown over a period of

several months, during a time of the year when food is scarce. Unhealthy birds arrest the process, so a male who displays a set of perfect tail feathers advertises that he has been in good health and has managed to find food even during molt season.

The long, heavy, brightly colored tail also attests to the owner's strength and skill, for he has succeeded in avoiding predators despite such a burden. By holding his tail upright and shaking it, the peacock proves his stamina, and his roars show he is not afraid to disclose his location to rivals and predators. The perfection of the tail's pattern testifies that the peacock's development while the tail grew was perfectly coordinated, as we shall see in chapter 8. Each of these criteria seems to be minutely scrutinized by females: Petrie and her colleagues found that taking out even five of the hundred and fifty or so feathers in a peacock's tail reduces his ability to attract females to his dancing arena.[22]

Long Tails

Moller[23] investigated the long outer tail feathers of barn swallows, small songbirds that catch their food in flight. Barn swallows have long, forked tails; the outer feathers are longer in adult males than in females or in young males. When Moller added extra pieces of tail feather to the tails of some males and shortened the tail feathers of others, he discovered that those with the longer tails, whether natural or artificially enhanced, found mates more easily than those with the shorter or shortened tails, and that they got to copulate with additional females as well (extrapair copulation). But the inadvertent cheaters—the males with artificially lengthened tails—paid a heavy price. The added length apparently impaired their ability to fly. They could not hunt large insects, and their physical condition deteriorated: they did not molt well after the breeding season, and none of them returned from their winter migration the next spring, while many of the other males did return to breed in the same area.



Smith and Montgomerie[24] repeated Moller's experiments and found that males with either naturally long or artificially lengthened tails found mates earlier and started breeding earlier than other swallows. But when they tested for paternity among the nestlings by DNA fingerprinting, they found that only half of the nestlings in the nests of the inadvertent "cheaters"—the males with enhanced tails—were in fact the offspring of those males, compared with 95 percent in the nests of males whose tails were either naturally long or artificially shortened.[25] Smith and Montgomerie suggested that the glued-on tails were too much of a burden for males who were not fit to carry them, and that such males could not prevent their females from consorting with other males.

The experiments of Moller and of Smith and Montgomerie with barn swallows, and of Evans and Thomas[26] with the scarlet-tufted malachite sunbird, show the price paid by a bird who carries a longer tail than he can handle. Thus it would seem that longer tails, like the barn swallow's, the peacock's, and those of many other birds, are reliable indicators of the agility of strong, experienced birds and are attractive to females for precisely that reason.

Movements and Dances

The display flights and dances of male birds usually involve movements that are not common in their everyday lives. Turtledoves walk when they forage, but they hop around the female they are courting. Falcons flap their wings slowly in regular flight, but the male flutters his quickly in aerial courtship displays. The tropicbird even flies backward. In many species of songbirds the male takes on the burden of singing while in flight.

In some species whose males take no part in parenting, males spend a great deal of effort for many hours a day, many days in a row, on courtship dances. The females visit the dancing arenas, called *leks,* where they watch the performances and choose fathers for their offspring; very few of the dancers are chosen. A small number of outstanding males get most of the females, while young and low-quality males do not get a chance to copulate.

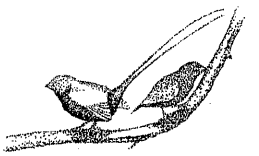
It can be difficult for human observers to identify the criteria by which the females select their mates—after all, humans often do not know enough to appreciate the difficulties involved in the particular dance. Gibson and his colleagues[27] showed that in sage grouse the best indicator of a successful male is a certain vocalization and a certain pause within it, which accompany a particular movement in the dance. Evidently, only the most superior males can achieve this particular combination within the strenuous choreography of the dance. As in human gymnastics competitions, in which most of the moves are part of a specific repertoire and are performed within a highly circumscribed framework, this very standardization is what enables competitors to best display subtle advantages and demonstrate the ability to execute difficult combinations of movements.

LEKS: CONGREGATING FOR DISPLAY

In most species males chase their rivals as far away as they possibly can, but in most lekking species males congregate, each in his own miniterritory within the lek, in order to display. Communal leks are found among insects, fish, amphibians, birds, and mammals, but only among species whose males do not participate in parenting. Among ruffs, many species of grouse, and several species of bird of

paradise, males court and display in leks; among ruffs and sage grouse, hundreds of birds may congregate in one lek.

Lekking males do not have equal success in reproduction. Most males ultimately do not copulate at all; two or three males—who are usually in the center of the lek—may do over 90 percent of the copulating. Why, then, do the other males come together where they have little to gain? Probably because elsewhere their chances are smaller still. Petrie and her colleagues note that on days when many females visit the top male, other males may attract some females too.[28] Hoglund and his colleagues found that the more males in a lek of ruffs, the more females there are *in proportion to* males.[29] Females, after all, find it easier to choose a father for their offspring when they can compare males side by side. More than one female can afford to choose the same male; they do not mind sharing him with others because they will not have his help in raising their young anyway. Under such circumstances, it is in the interest of females to be able to compare as many males as possible, as easily as possible. Gibson and Hoglund found that young female grouse tend to prefer males selected by older, experienced females: they watch the experienced ones, then choose the same males.[30] If for these reasons females ignore small congregations of males and insist on the greater choice afforded by larger ones, males are forced to compromise with other males and congregate.



Manakins are small birds of the American tropics that display in leks.[31] Among them there are males who dance in a miniterritory within the lek in groups of two to five. Only the top male of each group, who is older than the others, copulates with the females who visit the courting arena. The others cooperate with him in the dance without immediate reward; but some of them can benefit in the long run. After his death, it seems that his top helper, who is usually at least six years old, inherits the top male's miniterritory.[32]

Female manakins seem to prefer the group performers. No wonder: the top male in a group arena demonstrates both his dancing ability and the deference that other males pay him, which makes him all the more attractive to females. The other members of the group gain as well: they can both practice their dancing and increase their chances to inherit a good miniterritory.

POLYMORPHIC SPECIES AND MALES THAT MIMIC FEMALES

In leks of ruffs, one finds both dark-collared and light-collared individuals.[33] Dark-ruffed males fight for and acquire miniterritories within the lek, while males with

light ruffs move frequently from one territory to another, sharing it with the dark-collared male who presides in each.

The light-collared ruffs display subservience toward the dominant dark-collared ones by crouching with their beaks touching the ground when they approach, but even so, females copulate with the light-colored ones willingly. In fact, sometimes females seek out the light-collared males, even though nearby in the very same arena a dark-collared male is waiting.[34] Why do the dark-collared ruffs allow the light-collared ones to stay in their arenas?

Because females fancy light- as well as dark-collared males, it may well be that arenas with light-collared ruffs present attract females better than arenas without any; the dark-collared males therefore welcome the light-collared ones and proceed to "share the wealth." But why do females seek to copulate with the subservient light-collared ruffs?

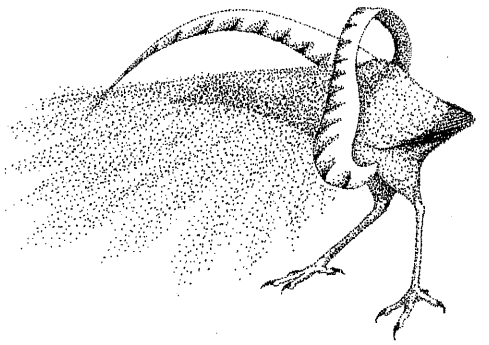
Females who copulate with both varieties (morphs) of ruff are likely doing right by their offspring. The differences between the two morphs seem to be genetic. Since both morphs have evolved, it would seem that each has its own advantages. If these advantages could be combined in the same individual male, one would assume that natural selection would have merged the two morphs long ago. We are not familiar enough with the life strategy of ruffs outside breeding season to tell what the advantages of each morph are; but similar cases among fishes and crustaceans suggest that each morph is best fitted for a specific ecological niche. Both dark-collared and light-collared ruffs thus have a good chance in life, and it is to the female's advantage to have some offspring of each morph; she hedges her bets by having some offspring that are best suited for one life strategy, and others best suited for the other.

Adult male bluegill sunfish may be either small or large. The large ones defend breeding territories and court females; the small males join them during courting, and both fertilize the eggs laid in the large male's territory.[35] The color and movements of the small male are similar to those of the female. The large territorial males do not chase the small males away as they do other large males.

The common explanation for this behavior is that the small males "cheat" both the large territorial males and the females by pretending to be females themselves, getting access to a large male's territory and fertilizing the eggs females lay unbeknownst to either the females or the big male. But human observers do not find it difficult to distinguish the small "mimetic" males from females; why should it be difficult for members of the sunfish's own species, who after all have a lot more to lose by their "mistake"?[36]

We think that in fact there is no cheating involved, that rather this is a reproduction arrangement that satisfies all parties. The two male forms face

different constraints of predation, feeding, and so on. Both survive and breed successfully. To have offspring of both morphs, which raises the odds that her offspring will survive and breed, the female's eggs must be fertilized by both morphs; therefore she may well prefer territories in which both morphs are present. Thus it is more likely that the large dominant male will attract a female if he accepts a small male as a partner. Since both females and small males display submissive behavior, each for its own reasons, it is not surprising that they use similar signals; after all, they are sending the same message. But that does not mean that the large territorial male or the female mistake the small male for another female. True, this is speculation; but the suggestion that the small male is cheating is also speculative, and a far less likely explanation in our opinion.



Similar "cheating" systems have been described in fish, reptiles, birds, and insects and are probably present in other forms of life as well. We believe that a close look at the facts in each case would reveal that each party to the system is actually straightforwardly serving its own best interests under given conditions, without deception. As we shall see in chapter 16, there are even social systems in which two species, host and parasite, cooperate in order to reproduce. In the case of some of these interactions, too, one party has been described as cheating the other; and they too are far more interesting if one looks at them as forced collaboration between two parties with conflicting interests, each of whom tries to get the best it can. The result is a compromise between the opposing interests of the parties rather than a temporary triumph by one or the other through cheating.

FISHER'S MODEL OF THE RUNAWAY PROCESS COMPARED WITH THE HANDICAP PRINCIPLE

According to our theory, "waste" in sexual display is evidence of the advertiser's quality, but very different explanations have been offered ever since the days of Charles Darwin himself. The issue first came up in Darwin's *On the Origin of Species*. Darwin suggested in 1859[37] that the features and qualities of each species are formed by the process of natural selection, in which the more efficient survived

and reproduced while others did not. This theory, though general and all-encompassing, did not explain the waste involved in the showing off that precedes sexual reproduction. Darwin could not see how an investment in showing off increases an individual's efficiency. He suggested, then, that there are two kinds of selection: natural selection, which makes an animal best suited to its environment, and sexual selection, which assists an animal in competing within its gender for the chance to reproduce.

Darwin[38] thus defined sexual selection as competition with members of the same sex. With this definition Darwin lumped together straightforward, efficient fighting between rival suitors with features that enable an individual to deter rivals of the same species and gender by means of threats, and with features that attract potential mates. Darwin did not see a problem in the evolution of bizarre signals that function in sexual advertisement—he simply turned his observations into an explanation. The simple fact that bizarre signals attract mates and deter rivals justified for him the investment animals make in these signals. He did not ask why waste attracts mates and deters rivals. Rather, he treated these effects as a given.[39]

In the early twentieth century, Fisher recognized the problem presented by animals' preference for wasteful signals. He stated, rightly, that female preference is an adaptation like any other produced by natural selection; he then asked why females prefer wasteful males.[40] The model Fisher proposed to answer this question used to be the only one available, and many still believe in it. The model can be found in almost any book on evolution.[41]

Fisher believed that the male who shows off is no better than the male who does not show off. According to that premise, the showing off itself is a drawback, and thus the show-off males are less well adapted than their fellows.[42] According to Fisher, the only advantage the ostentatious males have is the fact that females consider them attractive. Since such males pass on the show-off character to their offspring, those offspring will show off and will be attractive to females too. According to this script, males gain by investing in showing off because by showing off they attract more females. Females lose by having offspring who waste resources on showing off, but they have no other choice: only wasteful offspring will be attractive to other females, who in turn will have inherited from their mothers the tendency to be attracted to wastefulness.

Fisher's model can be seen as a catch-22, in which each individual male in the population wastes resources on showing off solely because this is the accepted method of courtship in his species. Several mathematical models support the idea that once some of the population consider a particular random feature to be attractive, then a "runaway" process may develop by which the feature spreads quickly throughout the population. In such a population, a female who went against the trend and selected a male who is more efficient and shows off less might have more efficient male offspring—but these offspring would find themselves without mates, since other females would not choose them.

Fisher assumed that the process starts when some females, who select a male

by some feature that truly correlates to his general quality, get more and better offspring than females who mate indiscriminately. But in Fisher's view, once the daughters of these females inherit the tendency to select males by this feature, then males who exaggerate the feature—irrespective of their real quality—will get more mates. From that point on, according to Fisher, females choose males not by their quality in general but rather by the exaggerated feature, which in his view no longer correlates to the male's quality. In fact, Fisher said that the exaggerated feature decreases the real quality of the males, but that the process is driven forward by the preference of the females trapped in the catch-22. In other words, females now prefer males with the exaggerated feature because other females prefer them.[43]

But there is a major problem with Fisher's model. The same wasteful characteristics that attract mates also deter rivals of the same sex, and we have to ask why. If only females reacted to a feature that did not correlate to real quality, one might conceivably explain the value of having sons who bear the same feature. But we find that not only do these exaggerated features attract females, they deter rival males too.

If the signal indeed has no connection to the real quality of the male as a rival, then a male who is not deterred by the feature will succeed better than those who are. He will produce offspring who are likewise unfazed; eventually the arbitrary feature will die out as a threatening signal in the entire population. Yet this does not happen in nature; in the real world, rivals in many cases remain intimidated by the same supposedly arbitrary features that attract females, or by features similar to them. In fact, Fisher himself noticed this weakness in his model. But as Fisher had no way of explaining how display could be correlated to prowess, he suggested that with time, rival males will stop reacting to features that amount to mere "war-paint."[44]

By Fisher's model there need not be any correlation between the male's actual prowess and the female's choice, and indeed, Fisher assumed that the wastefulness of the signal decreases the male's true prowess. Yet many findings suggest that in fact the most extravagant males are also the fittest.[45]

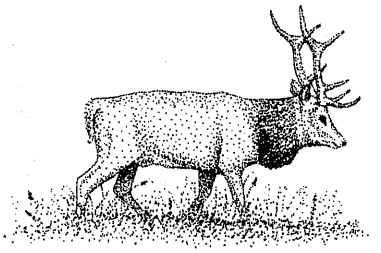
The real question is not whether Fisher's model is internally logical or whether it can be expressed in mathematical terms, but rather how one can best explain ostentatious waste in nature, including showing off toward rivals. Any explanation must show why such high-cost signals as the singing of male songbirds, the large, heavy, branched antlers of male deer, and the colorful plumage and dancing of various male birds often deter rivals at least as effectively as as they attract females. In fact, Andersson remarks that it is often difficult to tell whether a given feature is used more for the former purpose or the latter.[46] Fisher's model explains neither the evolution of features used to deter rivals, nor the logical connection between signals and their messages.

Unlike Fisher's model, the theory we offer—the Handicap Principle—does explain the relationship between the specific way in which an animal shows off and the individual's quality both in courtship, where it attracts potential mates, and in competition with rivals, whom it deters. According to our model, the cost—the "waste"—is the very element that makes the showing off reliable. The female in this model is not a silly creature attracted to extravagant males just because "every female is"; by selecting as a mate a male who can afford lavish displays, she is choosing a good father for her offspring.

UTILITARIAN SELECTION AND SIGNAL SELECTION

We believe that natural selection encompasses two different, and often opposing, processes. One kind of selection favors straightforward efficiency, and it works in all areas except signaling. This selection makes features—other than signals—more effective and less costly; we suggest calling it "utilitarian selection." The other kind of selection, by which signals evolve, results in costly features and traits that look like "waste." It is precisely this costliness, the signaler's investment in the signals, that makes signals reliable. We suggest calling this process "signal selection."

Darwin included in sexual selection—the competition for mates—both signals on the one hand and features that actually enable an animal to fight more efficiently with rivals of the same species and gender on the other hand. Our definition, by contrast, makes a clear distinction between features that can be explained by straightforward utilitarian selection and those that cannot—signals. As we see it, most of what Darwin defined as "sexual selection" is better understood to be "signal selection."[47] Signal selection differs from sexual selection in that it includes *all* signals—not just those that affect potential mates and sexual rivals, but also signals sent to all other rivals, partners, enemies, or anybody else. At the same time, signal selection excludes features that improve actual fighting ability, which are selected for straightforward efficiency.



The need for reliability explains the multitude of signals in the natural world, and the theory of signal selection thus offers new ways of looking at every species on earth, from microscopic organisms to humankind itself. How signals evolve and what their evolution implies carry us through the chapters that follow.