CHAPTER 25

SEXUAL SELECTION

Any teenager will attest to the fact that courting takes considerable energy and time, whether the courtship consists of earning enough money and investing the time to have an appealing car, practicing dance steps, working to become a prominent athlete, investing in personal care products or clothing, joining specific activities or working for acceptance in specific institutions, or any other of the myriad investments designed to improve one's chances of success. Many societies follow through with this principle, maintaining elaborate and extremely athletic activities, such as folk dances, in which young people participate and for which the finest or champion participants are highly admired.

What is not often appreciated is the importance of such activities in all sexual species on earth. We can initiate this discussion by noting that animals undertake the following activities that do not obviously promote a long and healthy life: (1) They fight among themselves, most commonly males fighting over females; (2) They carry out long and arduous courtships, which not only interfere with food gathering, they can be exhausting (In some animals, such as the sea elephant, one male may collect a harem and then spend the entire summer defending the harem against other males, not even stopping to feed.); (3) In the course of courting, they expose themselves to considerable danger, by bright coloration, prominent public display (a bullfrog will attempt to position itself in the middle of a pond to sing; herons and other wading birds are aware of this and will seek it as prey), or large, complex structures—a peacock's tail—that ultimately must be considered a hindrance to its movement, camouflage, or escape; (4) many animals have extremely elaborate and exotic genitalia, so complex that sometimes the copulating partners get stuck to each other and cannot separate. The principle of elaborate courtship appears to apply even to the presumptively dumbest and least reflective of animals, such as a cockroach. Surely these creatures are not writing ballads extolling the beauty or charm of their mate, and they obviously care little beyond the sexual act, for the partners separate and go their separate ways once consummation has been achieved. Although it is not obvious, plants display similar selectivity in the identification of the appropriate pollen by the appropriate seed. Though for obvious reasons dances or other movements are not part of the courtship, the showy flowers that modern plants produce to attract insects or other pollinators are very expensive in terms of the energy needed to build them and the energy that could have been captured if the flower had been a leaf, the risk that they pose in decreasing the stability of the plant to wind, and the amount of water that they can lose.

The question, then, is why almost all sexual organisms invest such energy to attract and choose partners. Organisms such as sea urchins, starfish, and mollusks, which do not move around much, are content simply to disperse eggs and sperm into the water. There is a certain level of selectivity, as specific proteins on the surface of the sperm and egg must interact to assure that the right sperm fertilizes the right egg, but this selection is at the level of the species, not the individual. We have no evidence that sperm A finds egg A' specifically attractive or vice-versa; it simply is a matter of which sperm and egg are simultaneously available at a given location. The question therefore is this: although it might not be nearly as much fun, would there not be more profit if coupling were indifferent or random and the money were invested in college education or a house, rather than a sexy sports car or an elegant gown? For this as for all questions in evolution, the argument is that there is no mechanism for propagating within a species any modification that does not provide tangible benefit, meaning improved chance of leaving offspring to the next generation. At best, a modification of neutral impact will persist at the very low frequency at which it appeared (if it appeared in one individual of 10,000, it will remain a characteristic of one out of 10,000). If it is deleterious in any respect, it will be driven from the population[11]. Thus if we find a characteristic widely shared in a large population, we must assume that there has been selection for the trait. In other words, the first bearers of the trait were more successful in leaving young to the next generation than those who did not have it. If we find similar characteristics in many diverse groups of organisms, the strength of the argument is redoubled: the characteristic must have decided value in evolution.

By means of hypothesis, observation, experimentation, and analysis we have come to recognize several virtues defining the value of courtship. These include first, the value of sexual recombination to survival of the species; second, the importance of distinguishing between appropriate partners (partners of the same species) and inappropriate partners (similar-appearing creatures of another species); third, synchronizing the state of readiness of the partners; and fourth and extremely important, using courtship to identify and select the healthiest and most desirable partners.

VALUE OF COURTSHIP

There are many asexual creatures in this world, starting with bacteria, amoebae and other small organisms that reproduce simply by dividing—no muss, no fuss. Even some small animals such as flatworms and sea anemones do this quite regularly.

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[11] This is not strictly true. For instance, a small population of birds may be blown to an island in a storm. If this population consisted of one pregnant white pigeon from a large population of mostly grey pigeons, the island could continue as a white, not grey, population. But this is an exception, as discussed in Chapter 24. The argument here assumes that there is no isolation of a small, non-random segment of the population.

Many plants propagate by sending out runners, dropping branches to take root (Fig. 25.1), or producing seeds or plantlets without benefit of sexual recombination, and there are races of predominantly sexual organisms such as lizards in which females lay fertile eggs without troubling themselves to find a male. By and large, however, the vast majority of the living world is sexual. The sexuality may take highly ingenious forms, with several sexes for a single species (yeast), sex decided by temperature at which the egg is incubated (some reptiles) or by the environment

Figure 25.1 Plant runners. (a) A banyan tree. This relative of the popular houseplant called the Benjamin Fig native to the South Pacific but has been imported into Florida and Hawaii. The branches drop runners that, when they touch ground, develop into new trunks. One tree in Lahaina, Hawaii, has hundreds of trunks and now covers more than a city block. (b) A strawberry plant. Note that this single runner has started six new plantlets (white arrows)

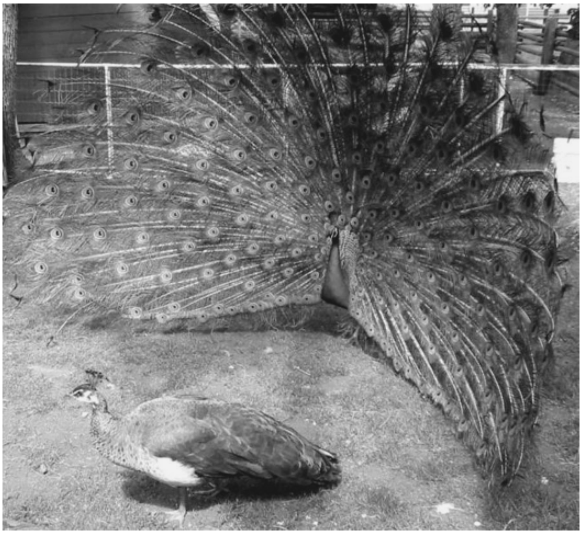
or presence of a potential partner of the opposite sex (some mollusks, worms, and fish), readily convertible sexes (some fish), species in which the sexual choices are male or hermaphrodite (combined male and female), and species in which the male is reduced to small, parasitic bump on the female (some fish, insects, and other animals). There are organisms (ferns) in which the sexual phase, the equivalent of us, is a tiny, microscopic structure, while an asexual phase, which if it existed in mammals might be roughly equivalent to our eggs and sperm forming entire organisms on their own, is a large, dramatic plant, even reaching the size of trees. There are others (aphids) that spend the entire summer reproducing asexually, female begetting female in a series of immaculate conceptions—no time wasted or risk taken in courtship. To be anthropomorphic about it, she invests no money or time in makeup, lipstick, or fancy dresses, does not go to dances, nightclubs, or bars, and there are no males performing dangerous stunts to show off or getting into fights over her. This might not be so much fun but, in terms of efficiency, the energy invested will produce far more young. But, even in the case of the aphid, when fall comes she produces a winged generation of both males and females, and these undertake the usual forms of courtship and mating to produce overwintering eggs. So, the question remains, why do the vast majority of animals and plants undertake sexual reproduction, with all its attendant hazards and costs? Nevertheless, to common and justifiable impression, the world is sexual: "Male and female, created He them." We do not question the role of sex for all life: two-year olds will insist that you do not mis-classify them—"I'm a boy, not a girl!"—and three- and four-year olds will want to know, when encountering any animal, if it is a boy or a girl animal. Why should the world be so constructed?

What we can do is to look at what sexual reproduction achieves that is different from asexual reproduction, generate a hypothesis as to the benefit of this difference, and, hopefully, design an experiment to test the hypothesis. The assumption that was common in earlier textbooks was that the mixing of genes produced healthier children and greater variety. The argument that sexual recombination produced healthier children derived from the phenomenon of heterosis, the observation that hybrid progeny (children) were often stronger and healthier than their purebred parents. This difference probably derives from the fact that purebreds often have two copies rather than one of mildly defective genes, and thus minor defects, while in their children the defective genes are covered or compensated by good copies (from the other parent) of the genes. However, in nature most organisms are not purebred, and it appears that the heterosis effect is an artifact of human tendency to create purebreds for human purposes. Thus the issue is more an inbred weakness of the purebred rather than an increase in health of the hybrid. We therefore need better arguments.

The argument of variety is rather theoretical: It is based on the assumption that, while species are frequently well adapted to their environments, eventually the environment will change in some manner, and that some of the variant forms produced by sexual reproduction will prove better adapted, more "fit," than their parents. While this is possible, it does not explain the retention of sexuality in organisms such as horseshoe crabs (pages 37 and 163), living in relatively constant environments, which have consequently evolved very little throughout evolutionary history.

A new hypothesis was based on keen observations of the characteristics of the winners and losers of sexual selection, which led to experiments to test the validity of interpretations of choice, and finally to experiments to test the effectiveness of the choice. The hypothesis was that sexual selection chose the healthiest specimens. Recognizing that sexual characteristics require high metabolic or other demands, researchers tested two related sub-hypotheses: that females chose the showiest or most spectacular males, and that these males were the healthiest or most likely to successfully father and, if necessary, raise a brood. (This argument is presented on the assumption that males display or otherwise court females, and that females make their choice among competing males. This is often but not always the case; there are instances in which females court males, or in which the courtship is mutual.)

The first sub-hypothesis was easy to test. While there were many attempts to test the hypothesis, perhaps the easiest to picture is the spectacular display of a peacock's tail (Fig. 25.2). There is no doubt that this is a sexual display: the male proudly opens his tail feathers and struts in front of the female, posturing so as to show his tail to best advantage. The female observes these preening displays of several males and ultimately moves to and accepts the overtures of the lucky male. Researchers counted the numbers of feathers and spots on the tails of the competing males and found that the females almost invariably selected the male with the most eyespots on his tail. They then plucked a few feathers from the tail of the successful male, whereupon he immediately dropped in popularity with the young ladies. This observation has been amply confirmed among many species: females select the male with the most symmetrical tail feathers or with the brightest or showiest color; where males compete in battle or other physical struggle, they select the strongest, the winner, or the male that does the most elaborate dance. Some spiders, insects, and ospreys bring their dates "nuptial offerings"—food or other indication of what good providers they will be. The females select the suitor with the best gift. Where it is possible to interfere with the native physical characteristics of the males, dulling the colors of a champion, or improving the colors of low-ranking males, or similar adjustments, predictably alter the ranking of the male. There is not much thought or nuance in these decisions. The females identify one characteristic, called a releaser, and respond to it, ignoring any other parameter. For some animals this response can experimentally be led to the ridiculous. In stickleback fish, for instance, the belly of the male turns red during courtship. Males will drive each other away, and females will come to red-bellied males. However, males will attack, and females will come to, disks with the lower half painted red, and if one paints the belly of a female red, this hapless creature will be harassed by males and approached by females. Observation of giraffes, and of the neck bones (and therefore neck musculature) of brontosaurus, suggest that seeking of food was not the advantage achieved by their long necks. Rather, male giraffes spar during courtship by pushing each other back with their heads and necks. The long neck is more likely to be an appurtenance of sexual display, courtship, or rivalry. Similarly, since it appears that the long-necked



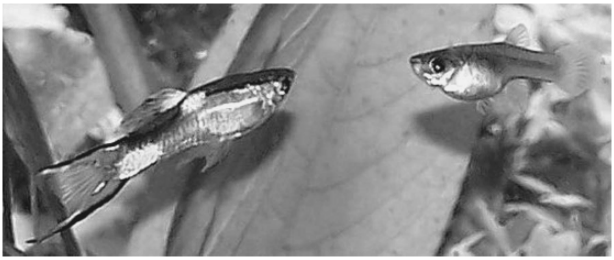


Figure 25.2 Elaborate sexual displays. Upper: A male peacock displays before a not-very-interested peahen. Lower: The male guppy (left) is brightly colored and has elaborate fins, whereas the female is uncolored and with normal-shaped fins, Credits: Peacock - Taken by Darkros and released to the public domain. (Wikipedia), Guppy - Date 2005-10-11 Author Silvana Gericke (http://people.freenet.de/silvanagericke/startsaqua.htm) (Wikipedia)

dinosaurs did not normally carry their heads erect, it is possible that they reared to full height only to show off, presumably the males toward the females.

If females always prefer the most spectacular males, what is the value of this choice? This question led to further examination of the hypothesis. Certainly in tests of physical strength, the more powerful male will be able to defend the best nesting site or more successfully drive off predators, but even color or agility in dancing tells something important. Sickly animals are not very peppy, they are a bit ragged, and their colors are not very good—sallow is the term we use for an unhealthy complexion. Researchers investigated bright and dull male birds and fish and quickly realized that the duller, less energetic males bore the heaviest load of parasites such as fleas and ticks. Bright, metabolically expensive, risky, or arduous activities were indicators of good health and freedom from disease, by the following logic: “I have so much energy available that I can squander it on this elaborate display that will not improve, and may even risk, my life.” For the females, this is a very attractive pick-up line. Even for humans this type of logic plays some role, as manifested in strenuous folk dances, sometimes requiring great agility and speed, as well as the ability to perform with swords, fire, or other dangerous implements. Also, it is striking how often human concepts of ugliness correlate with the symptoms of common or previously common diseases.

THE VALUE OF SEX

Thus the observational and experimental evidence supports the hypothesis that selection of mate is selection of the best provider, whether this is represented as the ability to secure and defend the preferred nesting site or the least burdened by parasitic or other chronic disease. But what about the fact of sexuality itself? Would it not be easier simply to avoid all the fuss and muss of courtship, and simply produce young without a mate? It is possible, as seen in many animals, to skip all the expense and time involved in courtship and get straight to reproduction. Picture a world in which there were no teenage boys, and teenage girls at, say, the age of 18, simply became pregnant by themselves with female clones of themselves. It might not be much fun, but consider how much less effort it would be: no expensive cars, clothes, makeup, hairdos; no time invested in trying to meet an attractive partner, initiate a conversation, coyly ask for a date; no expense or time wasted on dates; no bravado or risky stunts to impress someone; no anxiety or hours spent on fretting about marriage, or planning and conducting a marriage; no need to arrange privacy for coupling—the list can go on and on. Sexual reproduction is a big investment. Again, using the evolutionary argument, such energy is not invested unless there is a big (biological) reward.

Here, unlike the earlier argument about heterosis raised above, there is a logical hypothesis that can be tested. Taking a cue from the experimenters who recognized the influence of parasitism, the idea developed from the 1970’s that parasitism was itself the basis for sexuality. The logic of the hypothesis is the predicament in which predator and prey find themselves. This predicament may be described as follows: if the predator gets too efficient, it will capture all its prey and ultimately starve to death. If the prey become too good at escaping the predator, they will quickly overbreed and strip the land of all food, finally starving to death. Thus neither can become too good at what they do. This problem, called the Red Queen Hypothesis, is discussed more fully on page 366 and, in the case of the lynx and the snowshoe hare, on page 364 in Chapter 27. For sexuality, let us consider what genetic recombination can do for guppies, a small tropical fish from Central and South America. They live in small ponds, which often contain fish parasites. Suppose that the parasite becomes very good at what it does, and attacks all the guppies in the pond. They all become very sick or die, the parasite has no more hosts, and everyone loses. However, parasites are often very specific in their choice of hosts. One defense that the fish has is that there is perhaps a variation that, for one reason or another, is not very appealing to the parasite. This variant guppy will survive and flourish, while its more susceptible brothers and sisters suffer from the parasite. Ultimately, the pond will be filled with the resistant fish. However, the parasite is now in trouble, unless, of course, it too can generate varieties of parasites. One variety may be able to attack the flourishing variety of guppy. Thus, eventually, the parasite comes back (evolves) to infest this type of guppy. The guppy species' primary defense is to generate a variety resistant to this new variety of parasite, and the round goes on.

Clones or purebred lines cannot easily generate many varieties, but heterozygous populations can by sexual intermixture of genes. Thus, the logic says, sexuality provides the range of variation necessary to maintain these host-parasite interactions. This suggests an experiment: if we release guppies into ponds teeming with parasites or free of parasites, will we see a greater range of variation in the pond with the parasites? The experiment was done in Trinidad, where volcanic springs have recently in geological history produced ponds that have not yet been reached by either guppy or parasite. The results were as predicted. Fish thrived in ponds with parasites only when they maintained a large genetic variety, subject at any time to considerable mixing. (It was not possible to assess the genetic variability of the parasite; this was assumed.) Thus the argument is as follows: for the *population*, if the population maintains variety, it has the capability of resisting invasions of new parasites. Although the selection at the minute-to-minute level works on the individual, on the larger scale it is the selection for the highly variable population that can adapt to numerous, rapidly changing, onslaughts of parasites, as opposed to the genetically pure, non-variant population, that counts. Perhaps the genetically pure population can do extremely well in some circumstances, but it is vulnerable to massive destruction. This is a big problem for our agriculture, in which we have sought specific high-yield strains and raise them in monoculture. An epidemic disease can wipe out the entire crop. If there were many varieties of, for instance, wheat or corn, the population as a whole would resist much better, but then its yield might even in good years be much less than the monoculture. We try to get the best of both worlds, by holding in reserve varieties of seeds that are resistant to various diseases, but it is difficult. As a final note and a consideration for our understanding of experimental science, it took us a very long time to recognize this very important and ultimately obvious advantage of sexual reproduction precisely because, in the laboratory setting, we strive to maintain the healthiest cultures of animals and therefore attempt to eliminate from our cultures parasitic and other diseases.

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STUDY QUESTIONS

1. For your own life, try to estimate what percent of your budget and your time are invested in activities reasonably considered to be courtship.
2. In the springtime, observe the courtship of any animals that you can readily see, such as pigeons or other birds, or aquarium fish. (Domestic animals are less easy to study, since they are usually selected to breed without much fuss or to-do.) To what extent do the courting partners do things that simply define who they are? To what extent do the partners undertake activities that appear to be displays of strength, endurance, or health?
3. Can you observe courtship patterns or display of traits that you can reasonably interpret to be hazardous to the displayer?
4. Can you identify behaviors teenage boys use to impress girls that might otherwise be considered hazardous?
5. Although farmers tend to raise at any one time a specific purebred variety of wheat, the U. S. Department of Agriculture maintains in reserve many varieties, each of which is resistant to a different type of disease or climatic condition. Is this equivalent to allowing free sexual recombination of the wheat? Is it more or less efficient?