some species are sexually dimorphic and others are not is an active area of research in evolutionary biology.

Emily DuVal

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Sexual Selection

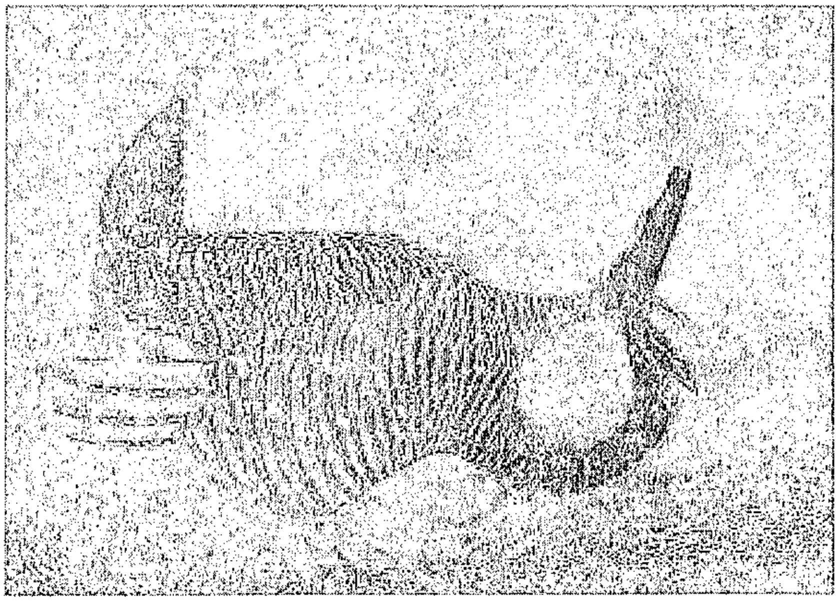
Males and females of many species exhibit significant differences in addition to the difference in reproductive organs. The distinction of gender through secondary sex characteristics is known as sexual dimorphism. This is most often expressed as a difference in size, with the males usually larger, but also involves differences such as plumage in male birds, manes on male lions, and antlers on male deer. In most cases, the male is the showier sex of the species.

What It Is and How It Works

Sexual selection is the evolutionary process that arises from competition among members of one sex (the competitive sex) for access to members of the other sex (the limiting sex). According to the theories of Charles Darwin, sexual selection should be distinguished from the process of natural selection because the traits that evolve via sexual selection often appear to have a negative effect on the survival rate of their bearers. There are two basic forms of competition for mates that affect the type of traits that evolve. One is intrasexual selection, which includes overt competition among the members of the competitive sex to gain control or monopoly over the limiting sex. This leads to selection of traits such as weapons, large body size, aggression, strength, and endurance. Intersexual selection is when the limiting sex can exercise a choice of mates, leading to elaboration of structures, displays, **vocalizations**, and odors in the competitive sex.

vocalizations sounds used for communications

Sending and receiving signals is a significant step toward mating as the type and intensity of the signal will determine whether or not a mate is obtained. One process of signal evolution that is involved in the search for a mate is called sensory exploitation. According to this model, signal receivers often have inherent, or built-in, preferences that can be exploited by a manipulative signaler to create new signals. For instance, suppose female birds searched preferentially for red seeds while foraging. Because the only time they encounter red is in seeds, it would be advantageous to evolve a general preference for red objects. A mutant male that adds red to its plumage may



This male prairie chicken displays his colors, indicating he is ready to breed.

then be able to exploit this preference for the color red as long as it can be expressed in the context of mate choice. A new signal can then evolve that had no historical link to mate choice but only to an irrelevant context such as foraging.

It is important to note that there is no new information conveyed to the females by the red males. In fact, there may be predatory risks if red males are easier to spot and thus more likely to be killed. Costs to females may be an adaptation to avoid exploitation such as better discriminating abilities or the decoupling, that is, the separation of behavioral strategies, for foraging and decisions about mating. However, females may be able to find males of the same species, termed conspecific males, more easily if the males bear a red patch. Furthermore, red males may provide additional information not provided by normal males. If the intensity of redness is a good indicator of the males' health, then a preference for red males over nonred ones could be a way for females better to identify a good mate. Whether the signal is costly or beneficial, sensory exploitation by itself is highly unstable. Instead, it is followed by **coevolution** between sender and receiver.

coevolution a situation in which two or more species evolve in response to each other

Male Attraction Signals

Females are more often the choosy sex and males the competitive, advertising sex (though in some animals the roles are reversed). Two significant models for the evolution of mate-attraction signals are the *runaway selection model* and the *good genes model*. In both of these there is a simultaneous evolution of a female preference for a particular male trait and evolution of that male trait.

Runaway selection model. This model best defines polygynous species (one in which a number of mates are taken). Initially, there must be some genetic variability associated with variability in physical characteristics of a male trait such as the brightness of a color spot. Males with the preferred trait will obtain more mates, and because the females will be those who tend to prefer that trait, the genes for the female preference will become linked with the male trait in their offspring. Females with the preference also benefit because their sons will have that trait and so will win more mates, thereby spreading the genes of the female. Under the right conditions, a runaway evolutionary process can occur with the male trait becoming larger and the female preference for it becoming stronger. This process stops when the male trait becomes so large that it imposes a cost on the male that outweighs the benefits. The traits that evolve through this model are termed arbitrary traits, because they can take any type of conspicuous form and not provide any information to the female about the male's fitness.

Although this process requires a certain set of circumstances to get under way, there are several different situations that could bring about the initial trait and the preference for it. One possibility is sensory exploitation, as discussed above. Another factor could be that the male trait is initially favored by natural selection and a female preference for this trait subsequently evolves. A third possibility is that the females evolve a preference for the trait because it helps distinguish conspecific males from those of a closely related species, thereby preventing genetic mixing between different species, a process termed interspecific hybridization.

Good genes model. This model actually proposes that costly and conspicuous male traits become the trait of choice by females because they indicate some aspect of male quality. Females will benefit from mating with these males because the offspring will have higher survivorship or viability. The male traits are called indicator traits, and the costs to males are deemed necessary costs when in pursuit of a mate. Coevolution of the male indicator trait, intrinsic male viability, and female preference for the trait is the basis for the genetic model of this process. One example of how this may work is the *classic handicap model*, in which males acquire a trait such as a heavy set of antlers, which obviously imposes a survivorship cost. Low-quality males cannot support the cost of this trait, and so it is seen as a handicap, whereas high-quality males survive and their genes dominate. However, the handicap is balanced out by the higher net fitness of males without this trait and its cost. Another theory is the *condition-dependent indicator model*, in which males vary the expression of the preferred trait, such as the speed at which the call is performed (termed call rate) so as to optimize their mating success and survival. High-quality males can afford to expend more energy on expression than can low-quality males and so trait magnitude is a good indicator of male quality. Last, in the revealing indicator model all males attempt to develop the trait to the same magnitude and pay the same cost, but the condition of the trait is lower in low-quality males. For instance, call frequency (the number of times a call is repeated) or feather condition are good examples of such traits.

Signalling for a Mate

Many aspects are taken into account when an animal signals for and chooses a mate. Anatomical traits play a role in the attraction of a potential mate. Non-weapon body structures such as color patches, elongated tails, and fins and feather plumes are termed ornaments. Many ornaments appear to be good indicators of the quality of the male. They often come into play when the male performs visual displays to attract the attention of a female. Vigorous displays are indicative of a male's high energy, and thus that male is likely to win out over the less vigorous male.

Auditory signals. In birds, insects, mammals, and fish, these are also obvious targets of female choice. In all of these groups, the females tend to prefer males with greater calling rates, sound intensity, and call duration. These features actually increase the stimulation value of the signal, so it is possible that the preference arose from the sensory bias of the female receivers and that the traits themselves are just arbitrary. These call characteristics are all energetically expensive, and it seems that females prefer the most costly calling. For example, female grey tree frogs prefer calls that have a long duration and are repeated at a slow rate over a call that is brief and at a high rate though it has the same acoustic "on" time, meaning the calls are heard for the same amount of time. Studies have shown that the long duration calls require a lot more energy than the shorter calls. Such findings suggest that display vigor is an accurate indicator of male quality. It has also been found that costly call characteristics are correlated with age, size, dominance, or parasite load. In addition, they provide females with good gene benefits such as faster growing and more viable offspring. Finally, in some species, call rate is a good index of benefits the females can expect to receive, such as large sperm or territory rich in resources.

Vocal signals. Another type of call is the **copulation** call. These are usually vocal signals and may be given by the male, female, or both sexes. In most cases it is difficult to determine the function of the signal and the intended receiver. However, copulation signals are unlikely to be incidental as they are highly structured and individually distinctive. In monogamous species, female copulation signals may be for synchronization of orgasm with the male, as there is usually no other possible intended receiver in the vicinity at that time. In socially mating species, the intended receiver could be external to the copulating pair. The female signals could be intended for other females and to increase dominance status in the group. The signals could also serve as a recruiting call for other male mates and incite competition among them so that the female can choose the dominant male as father of her offspring.

copulation the act of sexual reproduction

Male copulation signals could serve to transmit information about the male's mating success to other females. It has been found that males who make these calls are more likely to get attacked by other males, but they are also more likely to obtain more matings compared to males that 'do not call. Alternatively, the intended recipient of male copulatory signals could be other males. For example, postcopulatory male rats repeatedly **emit** vocalizations that are similar to the ultrasonic whistles signaling an alarm situation or a defensive threat. The male rats often appear lethargic and inactive at this time but will aggressively attack any other male that tries to approach the mated female. The signal then seems to be indicating mate-guarding intentions.

emit to throw or give off

The nuptial gift. This is a slightly different tactic in the search for a mate. Males of some insect and bird species will offer prey items as nuptial gifts during courtship. The females may base their decision on the size, or quality of these items, as well as the rate at which these items are provided. Females that are egg-producing would clearly benefit from receiving food as a nuptial gift. If provisioning rate is correlated with offspring feeding rate in paternal care species, the behavior is an obvious indicator with direct benefits. Another consideration is that if the cost to the male increases with gift magnitude, then it could be an indicator of heritable fitness. However, there is a risk of "false advertisement." In the marsh hawk, provision of the nuptial gifts is a good indicator of the male's nesting provisional ability. But the males sometimes use this signal deceptively in order to attract females into polygynous matings, a disadvantageous position for the female hawk.

In some species there is a sex-role reversal in terms of competing for mates. The sex-role reversal results from evolution of male parental investment, although not all paternal care species display complete reversal of courtship roles. A determining factor is the extent to which the male cares for the offspring. If the males can care for the offspring of several females simultaneously, the sex ratio is still skewed in favor of males. In those circumstances, males are still the competitive gender and will perform aggressive or persuasive courtship behaviors. However, if the males can care for the offspring of only one female, then males become a limiting resource for females. The females will then compete for males and develop aggressive behaviors, ornaments, and mate-attraction displays most often associated with the male gender. SEE ALSO REPRODUCTION, ASEXUAL AND SEXUAL; SEXUAL DIMORPHISM.

Danielle Schnur

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Sharks *See Chondricthyes.*

Shells

Every year, thousands of shells wash up on beaches around the world. Have you ever found a shell and wondered where it came from or what its function once was?

These shells come from a large phylum of animals known as mollusks which includes members such as snails, clams, oysters, scallops, squid, and octopuses. One of the prominent characteristics of most mollusks is a hard exterior shell, although some mollusks, including the squid and the sea hare, produce internal shells.

The bodies of mollusks are very soft. Their shells protect them from predators. The body of the mollusk is formed of a combined structure called