



Sexual selection

Any consideration of the diversity of animal life has to take into account the power of sexual selection. Many of the most elaborate traits and behaviors of animals are associated with courtship and evolved under the influence of sexual selection: the massive antlers of the extinct Irish elk and its living relatives, the elongated tail (actually trains) of a peacock, the elaborate melodies of songbirds, the incessant chirping of many frogs and insects, and the brilliant colors of many butterflies and fish. To understand sexual selection is to understand the cause of a major component of biodiversity.

Darwin's theories

Charles Darwin's main contribution to biology did not come from convincing others that evolution took place, a fact that was not doubted by most of Darwin's contemporaries. It was, instead, his argument about the process that resulted in evolution of adaptations for survival—natural selection—that caused the most controversy. In *On the Origin of Species* (1859), Darwin explained: "if variations useful to any organic being do occur, assuredly individuals thus characterized will have the best chance of being preserved in the struggle for life; and from the strong principles of inheritance, these will tend to produce offspring similarly characterized" (p. 127).

Thus if variation in certain traits causes variation in survivorship, and if variation in those traits is caused by underlying variation in genes, then natural selection results in the evolution of these traits. Natural selection brings about adaptations for survival.

Counter to Darwin's theory of natural selection, however, are the host of traits that hinder survivorship. These traits all share some similarities. They usually are present or more elaborated in males compared to females, and if they are expressed only part of the time, it is usually during the breeding season. Darwin suggested an alternative theory to natural selection to explain the evolution of these exaggerated traits. He called it sexual selection and explained it thusly: "This form of selection depends not on a struggle for existence in relation to other organic beings or the external conditions, but on the struggle between individuals of one sex, generally the males, for the possession of the other sex" (1872, p. 69).

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acquire mates, although they often hinder male survivorship. Thus, if variation in certain traits causes variation in mating success, and if variation in those traits is caused by underlying variation in genes, then sexual selection results in the evolution of these traits. Sexual selection brings about adaptations for acquiring mates, not adaptations for survival.

Sexual selection versus natural selection

Many biologists now consider sexual selection as a form of natural selection. Both forms of selection favor traits that enhance an individual's Darwinian fitness—the number of genes an individual transmits to the next generation relative to other individuals in its population. Fitness has two major components, survival and reproduction. An individual must do both to transmit its genes into the next generation.

There can be a tradeoff between survivorship and mating success. Thus natural selection and sexual selection can exert counter selection pressures on the same traits. As mentioned above, many traits that males use in courtship seem to hinder survivorship. Developing display traits requires an expenditure of energy. When nutritional resources are low, males often divert energy from display traits and focus on survival. Also, many sexually selected traits develop under the influence of testosterone, and this hormone has detrimental effects on the immune system, which can further decrease a male's prospects for survival. Once a male has a courtship trait, such as a long tail or bright coloration, displaying it can also be energetically costly. Singing in birds, frogs, and insects, for example, can increase the metabolic rate several hundred percent. Furthermore, the primary function of a display trait is to attract the attention of females, but these traits also attract the attention of "eavesdroppers." Bright colors of male guppies attract predators as well as mates (Endler 1978). Complex calls of male túngara frogs are more attractive not only to females but also to predators and parasites such as frog-eating bats and blood-sucking flies (Tuttle and Ryan 1981).

Natural selection can constrain the degree to which sexually selected traits evolve. The longer a male bird's tail the more attractive it might be to females, but it will not evolve to the extent that the male's survivorship is so low (e.g., because it reduces the individual's ability to evade predators) that it negates the benefits the male achieves from attracting



The great frigatebird (*Fregata minor*) adult male extends his gular pouch in courtship display. © Krystyna Szulecka Photography/Alamy.

more mates. But natural selection and sexual selection need not always be in conflict. Foraging efficiently, for example, enhances survivorship and provides nutrients critical for the growth of sexual ornaments.

How sexual selection happens

Just as an individual can increase its fitness in two general ways, survivorship and reproduction, an animal can increase its ability to acquire mates in two general ways: mate competition and mate choice:

...in the one it is between the individuals of one sex, generally the male sex, in order to drive away or kill their rivals, the female remaining passive; whilst in the other, the struggle is likewise between the individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive but select more agreeable partners. (Darwin 1871, vol. 2, p. 398)

The evidence for sexual selection through male competition and female choice was clear to Darwin. Weapons of offense used in male competition abound in the animal

kingdom in the form of horns, antlers, canines, and claws. Darwin saw evidence for sexual selection by female mate choice in the beauty of animal ornaments—colors, odors, dances, and songs. Female animals, he conjectured, seem to have aesthetic senses similar to humans. Females must prefer more elaborately ornamented males, but it was not clear to him why. Sexual selection by female choice is perhaps the best studied and the most controversial aspect of sexual selection theory.

Sexual difference and sexual conflict

In 1948 A. J. Bateman conducted a simple and insightful experiment with fruit flies. He mated males and females several times. Males showed a steady increase in offspring number with number of matings, but once a female mated, additional matings had no influence on her reproductive success. These results suggested that sexual selection should favor males to increase their number of mates, but that females would not be under such selection.

Geoffrey A. Parker (1970) and Robert L. Trivers (1972) uncovered the importance of Bateman's principle in the 1970s in their theories of sexual conflict and parental investment, respectively. Their notion is that males and females invest their energy very differently as parents, especially in their respective gamete production. Males produce many small gametes, whereas females produce fewer and larger gametes. Because of these differences in gametic investment, and in order to maximize their reproductive fitness, males should tend toward promiscuity and mate with as many females as possible because they are unlikely to exhaust their abundant and comparatively "cheap" sperm supply. Conversely, females should be more circumspect in their mate choice because they produce relatively few, large, energetically expensive eggs, and should therefore choose to mate with better quality males rather than more males (i.e., they should be more picky in their choice of mates). Thus, the sexes are inherently in conflict as to how to maximize their reproductive success, and in their willingness to mate. One outcome is that all females will tend to be mated, but only a fraction of the males will ever reproduce. This introduces greater variance in mating success in males than in females. Whenever there is more variance in a trait, there is greater opportunity for selection to act as a powerful agent of evolutionary change.

The variance in mating between the sexes can be skewed further by some realities of the mating system. Females often do not mate after their eggs are fertilized, whereas males continue to do so. Thus at any point in time more males are available for mating than females. This skew in the operational sex ratio results in keen competition among males for access to females and provides females with an abundance of males from which to choose. This also promotes higher variance in mating success in males than in females, and thus sexual selection will act more strongly on male traits than on female traits. This explains why most sexually dimorphic traits are more elaborate in males than in females.

The differences between the sexes can result in sexual conflict and pit them against one another in an evolutionary "arms race." In many species, multiple matings decrease



In sea horses (*Hippocampus erectus*) the male rather than the female incubates the eggs. © Gregory G. Dimijian/Photo Researchers, Inc.

female survivorship because of the increased probability of injury or disease transmission. When a male fruit fly mates a female, he deposits toxins, along with his seminal fluid, that cause a female to delay remating. This benefits a male because it protects his paternity by killing the sperm of other males. These compounds also have the incidental consequence of increasing female mortality. Artificial selection experiments show that females can evolve resistance to these male compounds. Thus, conflict between the sexes initiates a cycle of coevolution in which males evolve more toxic sperm and females counter by evolving resistance; this is called chase-away selection (Rice 1996).

Sex reversal and mating system variation

Bateman's results with fruit flies should not be over-interpreted. Göran Arnqvist and Tina Nilsson (2000) reviewed over one hundred experimental studies of insects showing that females' reproductive success increases with multiple matings. Thus sexual selection will have the opportunity to act on females as well as males, even if it will act stronger on the latter in many cases.

Sexual selection acts strongest on females when they are competing for mates rather than choosing them. Extreme

cases of female polyandry offer incontrovertible support for the rule of sexual conflict and parental investment. In these cases, not only do females mate with multiple males, but in addition the more common roles assumed by males and females in courtship and parental care are reversed. In sea horses and pipefish, for example, the male rather than the female incubates the eggs. In these cases, the pattern elucidated by Bateman also tends to be reversed: The number of mates has a greater influence on female than on male reproductive success (Jones et al. 2000).

Competition and choice can also interact. In elephant seals, for example, a female's initial choice of a male can incite a round of male-male competition, after which the female mates with the eventual winner (Cox and Le Boeuf 1977). Thus, males and females both can compete, both actively and passively, and choose their mates, and choice and competition can interact.

Mechanism of sexual selection: male competition

There is substantial evidence of males competing for access to females. In some species, males forcefully copulate with females. In others, males defend areas where females gather for resources, or they gather females in groups and exclude other

males from these groups. In mixed male groups, dominant males often have priority access to ovulating females.

Another arena of mate competition can take place inside the female (Parker 1970). As females often mate multiply, the sperm of multiple males have the potential to interact. In some cases, the sperm mix and the outcome is similar to a lottery. The male's probability of paternity is dependent on the quantity (and quality) of sperm deposited in the female. In other cases timing is important; in the phenomenon of sperm precedence, either the first or the last male to inseminate the female fertilizes most of the eggs. Males can evolve adaptations to sperm competition. For example, a male will often guard a mate after he inseminates her to prevent her from mating with rivals. Males can also include chemicals in their seminal fluids, as do some fruit flies, to influence the female's reproductive physiology and to delay her time to remating. If a female does mate again, the males of some species will deposit mating plugs in the female's reproductive tract to block access to her eggs by the sperm of competing males.

Mechanism of sexual selection: Female choice

The most controversial aspect of Darwin's theory was that females attend to differences in male courtship traits

when they choose a mate from among conspecific males. Definitive proof became available only when researchers could manipulate male traits experimentally and demonstrate that these actually influenced a female's mating preferences and that a female's preferences were correlated with patterns of male mating success in nature.

The first such study was by Michael J. Ryan in a 1980 study of túngara frogs. Males produce a mating call consisting of a whine that can be followed by zero to seven chucks. Females prefer calls with chucks, and all males add chucks in choruses. In nature, females can swim through the chorusing males and exercise unimpeded choice of mates. They are more likely to choose larger males than smaller ones, and larger ones also tended to fertilize more of the female's eggs. Larger males produce chucks with lower frequencies because they have a larger larynx. In mate choice experiments, two calls were broadcast to females from speakers. Both had the same whine, but the chucks differed in frequency. Females were preferentially attracted to the lower-pitch chucks characteristic of larger males. Although it had been known for some time that females use calls to identify members of their own species, this experiment showed that females also evaluate differences in calls to choose larger males who, in turn, increase the female's



In Southern elephant seals (*Mirounga leonina*), a female's initial choice of a male can incite a round of male-male competition, after which the female mates with the eventual winner. Rod Planck/Photo Researchers, Inc.



The calling male Túngara frog (*Physalaemus pustulosus*) has an unusually large external vocal sac to attract a mate with his call. Kentwood D. Wells.

reproductive success by passing these traits along to her male offspring, who, in turn, will be more successful.

Many demonstrations of female mate choice have followed. Vocalizations in birds, frogs, and crickets; colors in birds, lizards, fish, and butterflies; and odors in mammals, fish, and many insects are among the many traits that have been shown to influence mate choice. The question is why?

The evolution of female preferences

Mate choice exerts sexual selection on male traits and is responsible for most of the diversity in sexually dimorphic traits that abound in nature. An important question is why selection forces favor the evolution of female preferences.

Traits can evolve under direct selection or indirect selection (Kirkpatrick and Ryan 1991). Direct selection occurs when the focal trait has an immediate effect on reproductive success. Indirect selection occurs when the focal trait does not directly influence reproductive success but is correlated with other traits that do. Female preferences can evolve under both scenarios.

Direct selection on female mating preferences is common as males often influence the number of offspring a female produces. One example is when females choose males who can fertilize more eggs. Selection will favor females who prefer the more virile males, and that preference will evolve to become fixed in the population.

Direct selection also occurs when a female's preference for more conspicuous male traits enhances her survivorship. This will occur when such preferences reduce the time and effort spent searching for a mate. Reducing the time spent searching for mates reduces both a female's energy expenditure and exposure to predation risk. Conspicuous males are easier to find than cryptically colored ones.

Females use their sensory systems—their eyes or ears or sense of smell—to choose mates. Those sensory systems, however, are used for other tasks as well. Direct selection in other contexts could influence the evolution of sensory systems. For example, in surfperch, prey detection and selection promotes the evolution of photoreceptor tuning, which is unique to each species' habitat. This, in turn, has resulted in the evolution of different visual biases for



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brightness or color. Consequently, males evolve colors that are more conspicuous to females; that is, they exploit the female's existing brightness or color-detection bias. Females prefer these males because they are easier to see, not because of any direct reproductive benefits they accrue from them (Cummings 2007). This general process has been called sensory drive selection. When males then evolve traits to exploit preexisting sensory biases of the female, it is called sensory exploitation (Endler and Basolo 1998).

Female preferences also evolve under indirect selection. One mechanism has been termed *runaway sexual selection*. Here a female's choice does not influence her immediate reproductive success, and thus there is no direct selection on her preference for particular male traits. A genetic correlation between the preference and the trait arises, however, because females with the most extreme preferences choose males with the most extravagant traits and produce offspring that carry the genes for extreme values of both. As long as some females prefer extravagant male traits, preference genes will increase in frequency because they "hitchhike" along with trait genes. As female preference genes increase in frequency over the generations, so will selection favoring exaggerated male traits. These self-reinforcing cycles of runaway selection will lead to the rapid evolution of both traits and preferences until the

elaboration of the male trait is counterbalanced by its negative impact on individual survival.

Another mode of indirect selection on female preferences is called the handicap principle, one of the several hypotheses postulating that females choose males with "good genes" for survivorship. First proposed by Amotz Zahavi (1975), this hypothesis is based on the fact that the elaborate male traits often preferred by females (long tails, bright plumage, etc.) can reduce male survivorship. Zahavi suggested that only males with extraordinary survival abilities could afford to possess such traits. If a genetic component to variation in male survivorship exists, then when choosing a male with more elaborate traits, females are passing down to their offspring genes that contribute to survival along with genes that express a preference for certain male traits. As with runaway sexual selection, genes for mating preference increase in future generations not because selection acts on them directly, but because they hitchhike along with genes that increase individual survivorship.

There are several hypotheses concerning how female mating preferences evolve. There can be direct selection on preferences because it increases number of offspring produced by the female, or some aspect of her preference makes her better at performing tasks unrelated to mating. Alternatively, there can be indirect selection on preferences because preference genes are correlated with other genes favored by selection. These mechanisms can also act in concert. Consider the surfperch example discussed above. Female vision evolves to detect prey and males then evolve traits that match the female's visual properties. But if it were challenging for males to produce and display colors that are attractive to females, then more vigorous males would be the more attractive mates. And if there were a genetic basis to male vigor, then females would be preferring males with good genes. This would be a case where sensory drive can lead to handicap evolution.

Summary

All components of Darwin's hypothesis of sexual selection have been verified through both observation and rigorous experimentation. Most of the elaborate and complex traits in the animal kingdom that contribute so much to the planet's biodiversity clearly evolved in response to this powerful and fascinating selection process.

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