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FEATURE

## Sexual Selection

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In an article titled "The Myth of Sexual Selection" (*California Wild*, Summer 2005), Joan Roughgarden, a Stanford University ecologist, maintained that Charles Darwin had got his theory explaining some of the differences between males and females all wrong. But it is Roughgarden, not Darwin, who is in error.

In her opening paragraph, Roughgarden purported to describe one of Darwin's fundamental mistakes. She told us that Darwin thought that differences between the sexes result from a kind of natural eugenics. In support of that claim, she presented a quotation from Darwin's book *The Descent of Man, and Selection in Relation to Sex*:

*He [Darwin] theorized that these male/female characteristics result from females choosing mates who are "vigorous and well-armed . . . just as man can improve the breed of his game-cocks by the selection of those birds which are victorious in the cock-pit."*

In fact, this is a bogus quotation. Roughgarden evidently contrived it by joining two phrases that appear on different pages and on different topics in the second edition of *The Descent of Man*. The words "vigorous and well-armed," lying to the left of Roughgarden's ellipsis periods, are followed by the words "and in other respects more attractive." They are from a passage that explains how the sexual characteristics in question can evolve even in monogamous species. The rest of the material quoted comes from a passage three pages earlier, and discusses the perpetuation of traits that enable some males to defeat other males in contests for mating opportunities. The original sentence in its entirety reads: "Just as man can improve the breed of his game-cocks by the selection of those birds which are victorious in the cock-pit, so it appears that the strongest and most vigorous males, or those provided with the best weapons, have prevailed under nature and led to the improvement of the natural breed or species."

Roughgarden's use of a fake quotation in the very first paragraph was appropriate, because the whole article was grossly misleading, both with respect to what it said and what it failed to say. Because Roughgarden's article misrepresented Darwin's views and confused them with those of other authors, I shall review some of the things that Darwin actually did say and some of the concepts he actually put forth. On that basis I will then explain why Roughgarden's claim that Darwin's theory is a myth is out of line with well-established scientific facts.



**Elephant seals are an extreme case of sexual selection at work. Males can weigh more than twice as much as females- the better to fight other males for the right to mate with females.**

PHOTOGRAPH BY  
GERALD AND BUFF  
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Darwin's book *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* was published in 1859. It provided compelling evidence that organic evolution has indeed taken place, presented natural selection as a mechanism that can cause evolution to occur, and made Darwin famous as the founder of modern evolutionary biology.

When students in middle school and high school science courses are taught about evolution, they typically learn about natural selection, including the roles of mutation, variation, and the struggle for existence. They may not realize, however, that Darwin also elucidated two other evolutionary mechanisms: artificial selection and sexual selection. Each of these modes of selection played its own role in Darwin's thinking about evolution.

Natural selection, artificial selection, and sexual selection are all variations on a common theme, and all work in the same basic way. They involve some members of a population being particularly successful in producing offspring. In the long run, as each generation is succeeded by another, the characteristics of these more successful individuals become more frequent within the population. What distinguishes each mode of selection from the others is the agent that does the selecting.

In artificial selection, the selective agent is a human—a breeder—who picks an individual out of a population of domesticated animals or plants, then uses that individual for breeding purposes. The human thus ensures that the selected individual will enjoy greater reproductive success than others. This process of artificial selection, commonly called selective breeding, has given rise to highly modified varieties of cattle, chickens, pigeons, dogs, tomatoes, apples, grasses (such as wheat, maize, and barley) and countless other domesticated animals and plants. Artificial selection was fundamental to Darwin's thinking about evolution because it showed that selection has in fact transformed real populations of organisms and even enabled a single ancestral population to give rise to multiple descendant populations that differ from each other and from the ancestral stock.

In natural selection, there is no human selective agent. The environment does the selecting. The members of a population compete to extract resources from their environment and to convert those resources into offspring. Some individuals are more successful at doing that than others, and contribute more offspring to the next generation. As a result, their characteristics become more common. Natural selection was crucial in Darwin's thinking because it provided a plausible explanation for adaptation, abolishing any need for explanations that invoked the supernatural.

In sexual selection, the selective agent that influences each individual's reproductive success is another member of the population—either a potential mate or a sexual rival. If the individual gains a mating opportunity by appealing to a potential partner or by defeating a sexual rival, the individual's reproductive success is enhanced; if the individual fails to attract a potential mate or is vanquished by a rival, the individual's reproductive success is diminished.

The existence of not one, but three, modes of selection, provided Darwin with a broader theory than natural selection alone. They generated different predictions, and, taken together, strengthened his case for selection as a mechanism. Sexual selection was particularly important, because it showed how purely reproductive competition could produce features that are not adaptations that further survival or somehow benefit the species.

Conceptually, sexual selection is more similar to artificial selection than

to natural selection. Sexual selection occurs in several forms, two of which are particularly relevant to the present discussion: female choice and male combat.

In female choice, females are courted by males, and the females choose as mates the males that they find most attractive. Darwin suggested that the females possess an aesthetic taste, akin to our own but less refined, and that this aesthetic sense governs the choices that the females make.

To the extent that female choice is acknowledged in introductory biology textbooks, it typically is described as the mechanism that accounts for the evolution of gaudy coloration and exaggerated plumage in certain bird species. If hens are attracted to, and mate preferentially with, cocks that exhibit bright colors and elaborate tails, then the males that possess these features will be more successful in acquiring opportunities to sire offspring. Conversely, males that lack these features will fare poorly in the mating game. Over generations of such selection by the females, the males will have increasingly bright colors and elaborate tails. Furthermore, continued selection by the process can go to an extreme—witness the peacock. (Darwin compared the showy nuptial plumage of wild birds to the showy plumage that breeders had established, by artificial selection, in many varieties of ornamental poultry.)

In male combat, Darwin's second form of sexual selection, males fight other males, and the winners gain a monopoly over the females. The females don't make choices. The males fight among themselves, often with weapons such as horns, antlers, hooves, or teeth, and the successful males sire all or most of the offspring that constitute the next generation. The fighting can be quite spectacular. We have all seen films showing male combat in deer, bighorn sheep, and other animals. Roughgarden presented a pair of fighting bull elk as an example of something thought to be selected by the females because of its putative eugenical effect. Although some later authors attempted to put that sort of spin on it, Darwin treated it as an effort to monopolize the opportunity to mate pure and simple. The females are not in a good position to make that kind of choice even if it is to their advantage. Roughgarden has handed us a travesty of sexual selection theory and used it as a straw-man.

The notion that a peacock's tail is chosen as a sign of genetical superiority has been maintained by some authors, but Darwin did not know about genes, and he did not explain female choice in terms of eugenics either. His explanation was that the stronger the stimulus, the more attractive it is to the females. Recent studies have supported that view, by showing that the preference for the stimuli was already present before the exaggerated ornaments evolved. Both explanations might be true, however, and it is difficult to decide between them.

Sexual selection, whether by female choice or by male combat, is conceptually distinct from natural selection, but each mode's relative contribution is hard to evaluate. Consider a case involving female choice. As Darwin recognized, a female may find a particular male attractive for some reason other than his bright colors, his jaunty crest, or his big tail; she may choose him because he appears to be healthy and highly vigorous. This would make him a fortunate choice if he is going to have to contribute in some way to the welfare of the pair's offspring—say, by protecting them from predators or by obtaining food for them. But a male's good health and great vigor are also advantageous to him as he tries to cope with his environment and to survive on a daily basis. In other words, his good health and great vigor affect his capacity to meet the requirements of natural selection, regardless of whether they impress any females. Thus, even if she selects a mate because he is vigorous, that is natural, not sexual, selection.

To establish the fact that sexual selection does in fact occur, we need to be able to separate its effects from those of natural selection. Sometimes we can do this, because there are some species in which we can see “pure” sexual selection—sexual selection that operates alone and doesn’t overlap with natural selection. We can then compare that species with other, related species, in which sexual selection does not occur, or at least is less intense.

One species that offers us an opportunity to see sexual selection in its pure form is the northern elephant seal (*Mirounga angustirostris*). During their breeding season, elephant seals crowd themselves into rookeries where the females give birth to offspring that were conceived a year earlier, during the previous breeding season, while the males fight with each other to monopolize the females, mate with them, and sire the offspring that will be born a year hence. The females nurse the young seals that they have just delivered, but the males do not care for the young at all, nor do the males do any courting. The biggest males devote themselves entirely to fighting for territories, to controlling females, and to defending their territories and their females from other big males.

Under these conditions, the males experience intense, purely sexual selection by combat. They don’t have to get food for themselves as they don’t eat during the breeding season, they don’t have to defend offspring, and they don’t have to cope with predators (while they are on land, they are beyond the reach of any predators that are big enough and strong enough to threaten them).

Now look at the effects of this sexual selection. The males may weigh as much as 5,000 pounds while the females typically weigh less than 2,000. This extreme difference in size between males and females is due entirely to sexual selection by male combat, and it is there for all of us to see, even if Roughgarden imagines that sexual selection is merely a “myth.”

A similar pattern, with the males much larger than females, occurs in other pinniped species. Sea lions display a breeding regime similar to that of the elephant seal, complete with tightly packed rookeries and continual fighting among the males for territories and females. We do not find any comparable dimorphism in pinnipeds that do not display such a regime. In the Hawaiian monk seal, for example, males and females are of approximately equal size. It is this kind of comparison that provides the compelling evidence in favor of Darwin’s theory.

My own interest in sexual selection arose many years ago while working on my book *The Triumph of the Darwinian Method* (University of California Press, 1969). A review of the literature convinced me that Darwin’s theory of sexual selection had not been properly understood and had languished in neglect, and that many reproductive phenomena needed to be reinvestigated. My understanding of Darwin’s thinking allowed me to solve the puzzle of sequential hermaphroditism.

An hermaphrodite is an organism that can function both as a male and as a female, either at the same time or at different times. An organism that functions in both roles at the same time is called a simultaneous hermaphrodite. An organism that functions first as a member of one sex and later as a member of the other sex is called a sequential hermaphrodite.

There are two kinds of sequential hermaphroditism. In protandrous hermaphroditism, an individual spends a part of its life as a male and then becomes a female. A protogynous hermaphrodite is an individual that spends a part of its life as a female and then becomes a male.

The reproductive regimes of coral reef fishes often revolve around

protogynous hermaphroditism. Here is a simplified description of one such regime that occurs in certain species of wrasses. These animals begin their reproductive lives by functioning only as females, though they possess both male and female sex organs. The females living in any particular place constitute a harem that is controlled and defended by one male, who is typically far larger than the females. The females in the harem form a hierarchy, with one female—usually the largest—dominating all the others. This arrangement remains stable until the reigning male is devoured by a predator or is otherwise removed from the scene. When that happens, the dominant female quickly changes sex and becomes the new reigning male.

In certain other species of wrasse, some of the females—as they become older and bigger—turn into males and go roaming in search of a territory in which they can assume the role of reigning male.

To explain life histories such as these, I proposed what I called the size-advantage model of sequential hermaphroditism: "If a small animal (or a young one) can reproduce more effectively as a member of one sex, while a large animal (or an older one) can reproduce more easily as a member of the other sex, then it becomes advantageous for an individual to switch gender as it grows and ages."

A protogynous wrasse reproduces as a female while small and young because this is the only way in which this individual can reproduce at all: though she carries the sexual equipment of both sexes, she is too small to claim and hold the position of a reigning male. But when she grows large enough to function as a reigning male, she can greatly increase her reproductive output by doing exactly that. Consider: If she continues to function as a female, she will continue to have only one mating partner. But if she can herself become a reigning male, she (turned he) will win a big reproductive payoff.

I proposed the size-advantage model in a paper published in 1969, and I expanded on it in my book *The Economy of Nature and the Evolution of Sex* (University of California Press, 1974). The neglect of sexual selection came to an abrupt end, and the size advantage model was soon confirmed and extended. The theory bore unexpected fruit when applied to a wide range of organisms, including flowering plants. It even explains such phenomena as the little males in some gastropods that scramble to find a female, then become females themselves. Yet Roughgarden asserts in her article, "After 130 years, sexual selection is still not confirmed, and I suggest it never will be." In fact it has been confirmed time and time again.

In general, males specialize in getting the sexes together, whereas the females specialize in provisioning the next generation with resources. Sometimes this leads to males that are larger than females, but this is exceptional, and generally happens where there is sexual selection by male combat. Where the mode of competition between males is a matter of getting to the females first, the males tend to be smaller, as happens in some barnacles, certain deep sea fishes and quite a range of other animals. Indeed, male/female dimorphism of eggs and sperm, with the latter being much smaller, is perhaps a better way to conceptualize the differences between males and females than what we see in species with large and combative males. Such facts quite reasonably can be used to disabuse us of our prejudices and misconceptions. But this raises a second problem with Roughgarden's article: it gives no indication of the author's ulterior motivations for writing it.

At the age of 51, Jonathan Roughgarden had himself transformed into Joan Roughgarden, and in 2004 published a popular book entitled *Nature's Rainbow* (University of California Press). It was a work of self-justification, in which a personal agenda was overtly discussed. Had Roughgarden simply argued that there is more to reproductive

strategies than just male combat and female choice, and presented some reinterpretations of the data, there would have been no reason to respond. But here we have an effort to discredit perfectly good science. To suggest, on the grounds that it may not explain everything, that sexual selection or any other scientific theory is wrong, is an offense against elementary logic and common sense. In claiming that sexual selection is false, Roughgarden has created her own mythology.

Whether selection theory in general or sexual selection theory in particular might be improved upon is not an issue. We have a much better understanding of sexual selection now than we did 35 years ago for the very reason that scientists have been actively questioning received views and proposing alternatives. Honest seekers after truth do not want to suppress controversy. But they also do not want to see the issues misrepresented.

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