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FEATURE

The Myth of Sexual Selection

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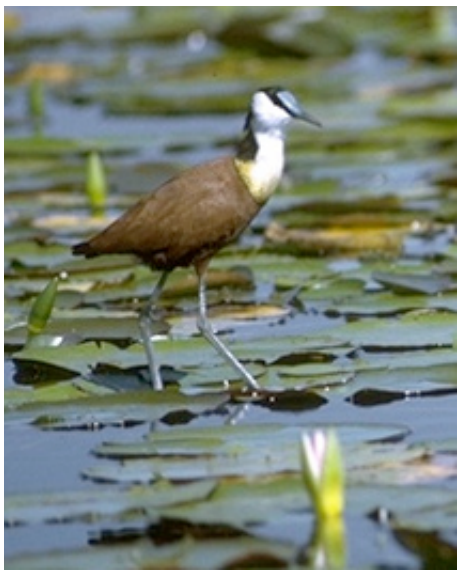
Males of almost all animals have stronger passions than females," and "The female. . . with the rarest of exceptions is less eager than the male...she is coy." Darwin wrote these words 130 years ago, in his book *The Descent of Man and Selection in Relation to Sex*. He theorized that these male/female 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."



Females wear the pants in plenty of species. Female African jacanas dominate the smaller, meeker males and brawl with one another to collect male harems. Males build nests and raise young, including eggs and nestlings that they did not sire, without female help.

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Today, Darwin's scientific descendants still repeat these stereotypes. For example, population geneticist Jerry Coyne of the University of Chicago asserts: "Males, who can produce many offspring with only minimal investment, spread their genes most effectively by mating promiscuously. . . Female reproductive output is far more constrained by the metabolic costs of producing eggs or offspring, and thus a female's interests are served more by mate quality than by mate quantity." (*The Times Literary Supplement*, July 30, 2004.)

Meanwhile, on the popular front, Elle magazine confides that "males fighting for females is the elastic in the jockstrap of evolution, therefore women are hardwired to 'size up' and appreciate male competition" (Ask E. Jean, *Elle*, Feb. 2005).

Clearly, the idea that males and females conform to rigid gender profiles still dominates sex role discussions. According to this model, passionate males with cheap sperm pursue coy females with expensive eggs. Females look for males with the best genes, whereas males want to fertilize as many females as possible. Genetically superior males distinguish themselves as the winners of male-male combat, as with jousting elk, or by having the most expensive and beautiful ornaments, as among peacocks. These male and female profiles, together with the cheap sperm/expensive egg rationale, comprise what biologists call "sexual-selection theory." Throughout nature, it would seem, delicate

discerning damsels welcome horny handsome warriors to bed.

This is rubbish.

If you examine the millions of plant and animal species in the world, you find countless exceptions to this theory. Although biologists are often familiar with these individual examples, many are reluctant to confront the implications of the big picture.

To begin with, sexual-selection advocates presume that there is one male gender and one female gender for each species. In reality, this male-female binary is rarer than you might think.

Most fungi and green algae, comprising many tens of thousands of species, have only one sex; all individuals produce the same size gametes. Higher plants typically make both sizes of gametes, called pollen and ovules, at the same time, usually within a single flower. Even animals blur the sexual binary. Barnacles, mollusks, and starfish are usually hermaphroditic, producing both sizes of gametes simultaneously. Among vertebrates, perhaps 30 percent of the fish species on a coral reef start out as males, and end up as females, or vice versa, or are both male and female at the same time.

In biology, an animal's sex is defined by the size of its gametes, or sex cells. Females make big gametes, or eggs, while males make small gametes, sperm or pollen. The biggest mistake being made in biology today is extrapolating the gender definition for gametes out to the whole-organism level, where it often breaks down.

Sexual identity is not about having a Y chromosome. That's only a mammal thing, and doesn't even apply to all mammals. Male and female mole-voles, for example, don't bother with any sex-chromosomal differences. In turtles, crocodiles, and some lizards, the temperature at which the egg is reared determines whether it will turn into a male or a female. Among birds, females, not males, possess the special sex chromosome. It's called a W, not a Y.

For many species of fish, frogs, lizards, and birds, multiple kinds of males and females occur. I term these differences biological genders. Each gender not only looks distinct but follows a different breeding strategy and life history.

For example, there are two male genders among the plainfin midshipman fish of San Francisco Bay. The large-gender males defend territories and guard the eggs laid in them. When ready to mate, a male emits a low humming sound for as long as 15 minutes. If he's lucky, a female may respond to this by entering the territory and laying eggs. Over the breeding season, up to five or six females may deposit their eggs for him to fertilize and guard.

The second, silent type of male midshipman is smaller, has a different shape, and is a different color than the large males. It matures early, doesn't defend territories, and mates by darting in to fertilize eggs laid in a large male's territory. Large males and small males represent very different developmental programs expressing different suites of genes.

Pacific coho salmon also have two types of males. "Jacks" spend two years in the ocean before returning to streams to breed, while "hooknoses" spend an extra year at sea growing larger and more powerful. Jacks are small and cryptically colored, while hooknoses grow a pronounced, curved snout and are brightly colored.

Hooknose males are better at fighting for positions near breeding females than jacks, and wind up with the most fertilizations. But jacks still father some fry by darting in under egg-laying females. Being able to breed a year earlier, and avoiding the hazards of another year at sea, compensates for the jack's disadvantages in the breeding pools.

The side-blotched lizard of California follows an even more complex mating system. This lizard has three male genders and two female genders, each a characteristic color. Orange-throated males are aggressive and ultradominant, with high-testosterone levels. They defend territories large enough to overlap the home ranges of several females. Blue-throated males are less aggressive and juiced with less testosterone. Their small territories overlap with only one female, whom they guard. Yellow-throated males don't defend territories at all, cluster around the territories of the orange males, and mate with females in their vicinity.

Orange-throated females, like their male counterparts, are very territorial, and defend large personal territories. Their clutches consist of many small eggs. Yellow-throated females lay fewer eggs per batch, but each is fairly large. Yellow-throated females, like their male counterparts, are more tolerant of one another, and have smaller territories. So Darwin was wrong to claim that all males match one behavior pattern and females another.

Among species with just two genders, the sexes can play roles completely opposite to those that sexual-selection imagines. Among these creatures, coy, drab males are pursued by passionate, showy females. Well-studied examples include mormon crickets, bush crickets, and katydids; the two-spotted goby, and North-Sea pipefish (relatives of seahorses); and among birds, the wattled jacana, red-necked phalarope, and spotted sandpiper.

Sexual selection theory also teaches that because eggs are larger and more expensive to produce, females must conserve this resource by playing hard to get. Conversely, because sperm are small and easy to manufacture, males can spread them around with little loss on investment. But in fact, sperm are not cheap. The relevant comparison is not between individual sperm and egg, but between ejaculate and egg. An ejaculate often has a million sperm whereas an individual egg is often a million times as large as an individual sperm, making the mating investment of both male and female about the same. As a result, in many species a mating for a male may be just as costly as for a female, even when there is no male investment in raising the offspring.

Supporting the equal costs idea are ever-lengthening lists of species where males choose their mates as carefully as females select theirs. Known as "partial sex-role reversal," this phenomenon has been documented in over 50 species of insects spanning 11 orders. Even among the Drosophila fruit flies studied by population geneticists, reviews of scientific literature cite five species where males choose females as much as females choose males.

Partial sex-role reversal isn't limited to invertebrates alone. Primatologist Meredith Small writes in *Female Choices: Sexual Behavior of Female Primates* (Cornell University Press, 1993), "Non-human primates show us what many single women in America know—sometimes it's very hard to get a date." Female rhesus monkeys, lion-tail macaques, and baboons may offer sex to males, yet males regularly refuse. Female lion-tail macaques initiate almost 70 percent of sexual encounters but only 59 percent of those solicitations end in mounts.

According to sexual-selection theory, more sex is always better for males. Males who mate whenever the opportunity presents itself, and make their own opportunities when possible, will sire more progeny. Mammals seem to follow this pattern. About 90 percent of mammal species are polygynous, with one male servicing many females.

However, monogamy not only exists, but is quite common. Fully 90 percent of bird species are economically monogamous--a male and female bird cooperate in raising the eggs together in their nest. Often

some of those eggs are sired by neighboring males, and females deposit some eggs in adjacent nests, so that parental relationships are distributed in neighborhoods. Thus, in birds economic monogamy often occurs without reproductive monogamy. Turning to monogamous mammals, males contribute to parental care by building a den, burrow, or lodge, defending the family's feeding territory, feeding his mate when she's nursing, and carrying the young around the way humans drive their kids to after-school soccer. Although not as common as in birds, mammalian monogamy does happen. Most wild canines, as well as 15 percent of primates, are faithful to a single mating partner. Monogamy too contradicts sexual selection.

Sexual selection views mating as solely for conception. But the point of mating is not usually to make babies; it usually serves a social function. Mating occurs too often relative to number of offspring produced to be solely for conception. The intimacy of sex strengthens relationships between adults, defuses social tensions, and helps keep groups together, as in our closest living relative the bonobo. Strong social bonds help ensure males and females will work well as a team to protect and raise young.

Same-gender sex can promote friendships as well, helping to explain why homosexual sex has been observed in more than 300 species of vertebrates as a regular component of social interactions.

So far as is known, the reproductive social behavior of tens of thousands of species departs from sexual-selection norms. You might think that these examples ought to prompt some to reexamine the argument. Yet proponents such as Jerry Coyne claim this account is "focusing entirely on exceptions" while "ignoring the much larger number of species that do conform to sexual selection theory." In fact, we have no idea how many species conform; the reproductive social behaviors of most have not been studied.

I suggest that we replace sexual-selection theory with a new approach that I call social selection theory. I argue that reproductive social behavior, including mate choice and family organization, can be completely explained by focusing solely on the direct ecological benefits each individual obtains from the interactions it has with others. Indirect genetic benefits can be ignored; they don't realistically factor into mating decisions at all.

Social selection theory proposes that every animal has a time budget for its social interactions. Each animal interacts with others in ways that improve the number of offspring he or she can successfully rear. Animals may pursue their most beneficial course by acting independently or by acting together in teams, but usually in teams. From a group's many instantaneous decisions as to whom to associate with and what actions to perform with one another, a unique social system emerges for each species in each ecological situation.

In social selection, cooperation is purchased when animals barter for control of reproductive opportunities. One morph of fish, say the large controller-gender of blue-gill sunfish, is programmed to breed after five years. The fish may die during this time, but if he survives, he will be big enough to control territory in which females lay eggs. This fish can offer fertilization of the eggs laid in his territory as a payment to smaller, shorter-lived cooperator morphs. Cooperators provide services such as helping to attract female visitors to a territory or keeping the territory clean, while the big controller rebuffs neighboring large males.

This kind of bartering and team play is the subject of cooperative game theory, a branch of mathematics with theorems tracing to John Nash (the Princeton economist made famous in the recent movie "A Beautiful Mind"). Cooperative game theory also predicts the emergence of cooperative coalitions. Family structures such as monogamy, polygyny,

and polyandry can be considered the outcomes of a cooperative game. Players weigh the direct benefits they can obtain while making choices about whom to associate with. Achieving cooperative solutions requires coordinated actions and staying in close contact. Same-sex sexuality and intimacies such as grooming and tongue-touching evolved to help animals stay in touch with each other's condition and intentions. This knowledge helps them work together as a team.

In social selection, the expensive tail on a peacock does not seduce a peahen. Instead, that tail is primarily a badge that earns the peacock membership in male power-holding cliques. In social selection, secondary sex characteristics like the peacock's tail are more important for same-sex power dynamics than for between-sex romance. Such traits are used to secure admission to resource-controlling coalitions and must be expensive to ensure exclusivity. They are not signs of genetic quality advertised to females. Such traits may indeed connote physiological health and good condition, but this indicates a male's ability to offer direct benefits to a female rather than his genetic quality. She should choose a male displaying good condition not because he has high quality genes, but because she will be able to raise more, not "better," offspring by mating with him.

Instead of judging a male by his genes, females look for how much he can directly contribute to the survival and provisioning of young. For example, lion cubs are often killed when a new male takes over the pride. Their mothers may mate with the new ruler to give him a share of the paternity, and thereby reduce the likelihood that he will commit infanticide. Female peacock wrasses choose to lay eggs in the territory of a male whom they assess as likely to stay and guard the eggs rather than swim away for bigger egg masses somewhere else. Such immediate benefits of avoiding mortality to the young far outweigh any possible advantages from superior genes. Nor do females always consider male-male combat the best indicator of a superior mate. In sand gobies from Scandinavia, experiments show that females preferred males who protect eggs from predators, not males that jousted with other males and won. Animals are primarily concerned with the number of offspring successfully reared, not with the genetic characteristics of those offspring.

To a naturalist, the failure of sexual- selection to describe and explain animal behavior is reason enough to reject it at this time. But the stakes are even higher. Sexual selection is not innocent. It promotes a view of nature as violent and deceitful, emphasizing male-male combat and war between the sexes. It licenses male promiscuity. It views female choice of mates as a broom to clean the gene pool of males with bad genes. It persecutes diverse expressions of gender identity and sexuality. Social scientists and the popular media uncritically reproduce its myths.

To be clear, the scientific truth, or lack of it, of sexual selection is logically independent of its social implications. Yet, the ethical wrongs issuing from sexual selection's narrative require holding it to the highest standards of scientific rigor. It fails. After 130 years, sexual selection is still not confirmed and I suggest it never will be.

Once scientists start looking through the lens of social-selection, animal behaviors become much easier to understand, and many of the apparent contradictions fall away. Instead of trying to shore up Darwin's sinking theory of sexual selection, we should be improving our understanding of gender and sexuality, because friendship, love, and sex are important.

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