How Females Choose Their Mates

Females often prefer to mate with the most flamboyant males. Their choice may be based on a complex interaction between instinct and imitation

by Lee Alan Dugatkin and Jean-Guy J. Godin

Picture a man who has a way with the ladies, and a character not unlike James Bond may spring to mind. He's clever, classy, fearless and flashy—characteristics that are almost universally appealing to the opposite sex. Throw in the powerful sports car, and you have a nearly irresistible combination.

That females often flock to the most ostentatious males is not a phenomenon unique to humans. In many different species, successful males—those that sire the most offspring—are often larger or more brightly colored or "show off" with more vigorous courtship displays.

Females tend to be the choosier sex when it comes to selecting a mate, partly because males can produce millions of sperm, whereas females' eggs are few and far between. Thus, females may be more selective because they have more invested in each gamete and in the resulting offspring. And because the availability of eggs is a limiting factor in reproductive success, males tend to compete for female attention and not vice versa.

Charles Darwin was the first to propose that competition for mates plays an important role in reproductive success—a process he dubbed sexual selection. In *The Descent of Man, and Selection in Relation to Sex,* published in 1871, Darwin hypothesized that any trait that gives a male mating and fertilization advantages will evolve in a population because males with such traits will produce more offspring than their competitors. Assuming the trait is heritable, offspring expressing the beneficial trait will, in turn, achieve greater reproductive success than their competitors, and so on, through future generations. Further, Darwin proposed that some of these traits may have evolved because they attract the attention of females.

The idea that females are discriminating and can actively choose with whom to mate was controversial from its inception—perhaps because male-male battles can be quite spectacular. Males may fight amongst themselves, occasionally in dramatic battles to the death, to gain mating privileges with females. In comparison, female choice is generally much more subtle.

Finding Mr. Right

Over the past 25 years, a considerable body of scientific evidence in support of female choice has accumulated. Females actively choose their mates in a large variety of species—particularly ones in which males are less aggressive and display individual differences in secondary sexual characteristics, such as ornamental plumage or courtship displays. Nevertheless, how and why females select their partners and how mating preferences have evolved remain hotly debated issues among evolutionary biologists.

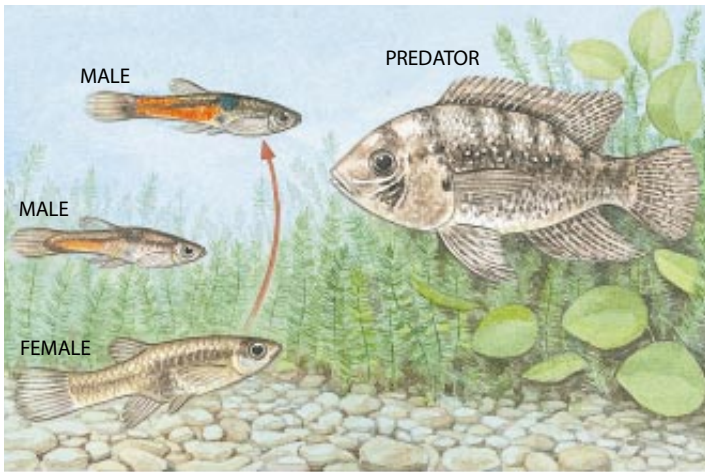
A choosy female faces two general tasks in selecting a mate. First, she must search for and locate a male. This task can be difficult if the population is sparse or if the danger of predators prevents her from spending a good deal of time searching for a suitable mate. Once she has encountered a male, the female must then decide whether to accept or reject him as a mate. The decision often involves some shopping around. In cer-

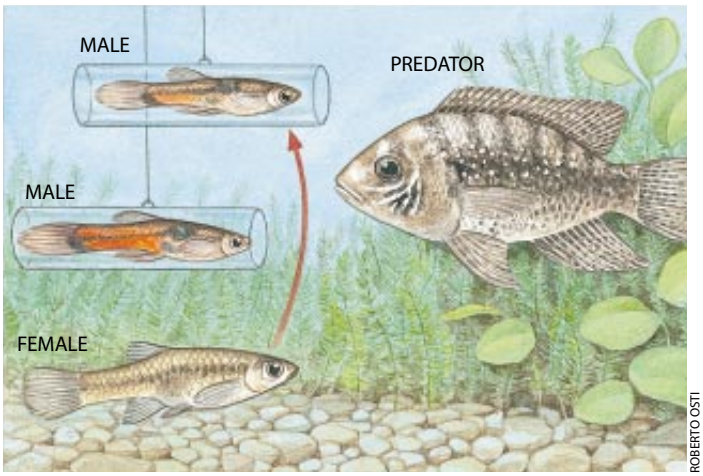
FEMALE TRINIDADIAN GUPPIES do the choosing when it comes to selecting a mate. Generally speaking, female guppies prefer males that are brighter or more orange in color (*upper right*). But even guppies are prone to social pressure. If, for example, an older female appears to fancy a drabber male, a young female may ignore her instincts and choose to copy her elder's mate selection (*lower left*).

tain mating systems, females may encounter a group of available males and can compare them on the spot. For example, in early spring, male sage grouse (*Centrocercus urophasianus*) aggregate "cheek-to-jowl" in temporary communal mating arenas called leks, where they strut their stuff for the females. A female typically observes the displays of a number of males, apparently comparing them before mating with one lucky suitor. She then leaves the lek to nest and raise her brood elsewhere. Of all the potential mates on a lek, a few preferred males receive the bulk of the female attention.

But males are not always conveniently displayed like chocolates in a sampler box. More commonly, females encounter males one at a time. Comparing males in this case is presumably a more challenging cognitive task, as it involves remembering the characteristics of an individual that is no longer in sight. Studies have shown that females can rank the characteristics of sequentially presented males. Theo C. M. Bakker and Manfred Milinski of the University of Bern in Switzerland found that female three-spined sticklebacks (*Gaster-*

ROBERTO OSTI





ROBERTO OSTI

MALE GUPPIES inspect predators; female guppies inspect the males. When a predator—such as the cichlid pictured here—approaches a school of guppies, a pair of males often swims over to inspect the potential threat. Such bold behavior may be attractive to females, which tend to choose as a mate the suitor that swims closest to the predator (*left*). Although the bravest males are often the most colorful, females will choose a less flashy contender if he appears to be more courageous than his inspection partner (*right*). In the laboratory, custom-made containers allow the authors to position the males.

osteus aculeatus) will tailor their mate choice to the relative attractiveness of the present and previously encountered males. Females were more likely to show interest in a male if his red nuptial coloring was brighter than the previous male's and more likely to reject a suitor whose coloring was less bright than his predecessor's.

Whether a female chooses her mate from among a dozen dancing grouse or between a pair of crimson fish, she generally selects the most conspicuous contender. Empirical evidence indicates that females commonly prefer male traits that most strongly stimulate their senses. (This evidence has recently been reviewed by Malte Andersson of the University of Göteborg in Sweden and by Michael J. Ryan of the University of Texas at Austin and Anne C. Keddy-Hector of Austin Community College.) For example, when given a choice, female green tree frogs (*Hyla cinerea*) are preferentially attracted to males that call the loudest and most frequently; female guppies (*Poecilia reticulata*) to the most brightly colored males; and female mallards (*Anas platyrhynchos*) to males that court them most frequently. Because of such preferences, males have typically evolved exaggerated secondary sexual traits to attract the opposite sex.

Why Be Choosy?

Even though evidence indicates that females can actively choose their mates, the question of why females discriminate, rather than mate at random, remains largely unresolved. How did female choice originate and evolve? What are its benefits and costs to individual females?

In some cases, females may favor mating with a male that is loud or brightly colored simply because he is easy to locate. Reducing the amount of time it takes to find a mate may reduce a female's risk of being killed by a predator. But for many species, mate choice is probably more complex. For many birds and mammals, natural selection appears to favor females who choose mates that provide them with some direct benefit that will increase their fecundity, their survival or the survival of their offspring. Such benefits might include food, a safe haven or even the prospect of fewer parasites.

In a long-term study of the barn swallow (*Hirundo rustica*), Anders P. Møller of the CNRS in Paris observed that females prefer to mate with males possessing elongated tail feathers. As it turns out, the long-tailed males are infected with fewer bloodsucking mites than their short-tailed counterparts. Because these parasites can jump from bird to bird, females that mate with long-tailed males benefit by avoiding infection and by producing greater numbers of healthier chicks than females that mate with shorter-tailed males. Unfortunately, because selecting a mate that offers direct benefits seems so obvious, few studies have tested this evolutionary model in a rigorous way.

When males provide no obvious resources, such as food or protection, females may choose to mate with the males that appear to have the best genes. How do they know which males have good genes? And why don't males just cheat by faking the traits associated with such genes? In 1975 Amotz Zahavi of the University of Tel Aviv in Israel suggested that females assess only those traits that are honest indicators of male fitness—a hypothesis known as the handicap principle. Honest indicators, which are "costly" to produce and maintain, should be associated with the most vigorous males.

While studying antipredator behavior in the Trinidadian guppy, we recently obtained some evidence that is consistent with the handicap principle. When a predatory fish nears a school of guppies, males, often in pairs, cautiously approach the potential threat to "inspect" it. Such risky behavior has been observed in many species, and behavioral ecologists have suggested that bold males may swim close to a predator to advertise their vigor to nearby females. In fact, laboratory studies have shown that when no females are present, no male guppy plays the hero by approaching the predator more often than his counterpart.

We hypothesized that boldness exhibited during predator inspection might be attractive to females because it should be a reliable indicator of fitness. Less vigorous guppies who tried to "fake" competence in predator inspection would likely be eaten. By using small, custom-built containers that allowed us to position males at different distances from a predator fish, we found that females indeed preferred the most intrepid males. Such courage appears to correlate with color: the males that swim

closest to the predator are usually the most colorful. Thus, in the wild, females may have evolved a preference for the flashier males because color is a proxy for boldness and fitness.

Once females have expressed a preference for a certain trait, a process called runaway selection can occur. The model, first brought to the attention of evolutionary biologists by Ronald Fisher in 1958, suggests that a male trait and the female preference for that trait coevolve. For example, females that prefer to mate with large males should produce large sons as well as daughters that show a preference for large males. Under certain conditions, this process can escalate, producing increasingly exaggerated male traits and stronger female preference for those traits.

A number of behavioral ecologists have found some evidence for runaway coevolution of orange body coloration in male guppies and of female preference for this male trait. But a more convincing example of runaway selection has recently been presented by Gerald S. Wilkinson and Paul Reillo of the University of Maryland in their study of the stalk-eyed fly (*Cyrtodiopsis dalmanni*). In this species, females generally prefer to mate with males possessing widely spaced eyes. By selectively breeding the flies for 13 generations, Wilkinson and Reillo generated one line of flies in which the males had large eyestalks and another line of shorter-stalked males. They found that females in each line preferred the male trait selected for in that line—that is, females from the large-stalk line preferred males with the longest stalks, and females from the short-stalk line preferred shorter-stalked males. Female preference thus coevolved with the selected male trait.

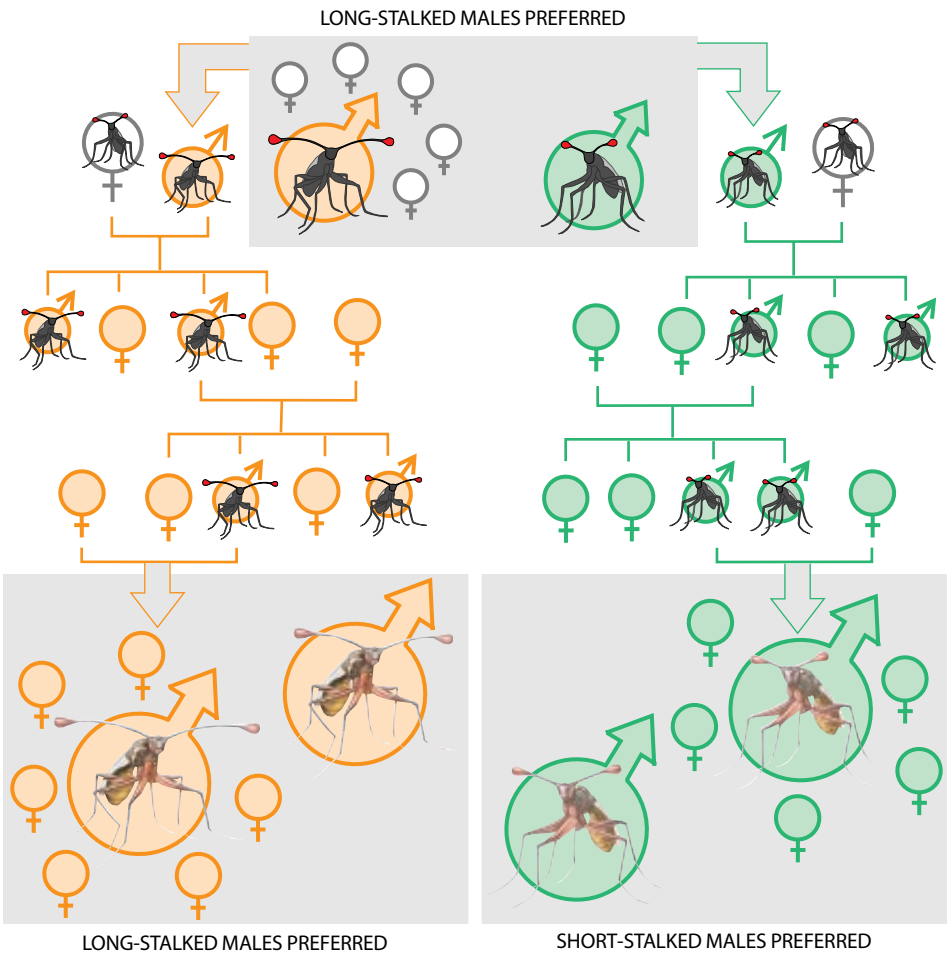
How do preferences about mate choice originate? In some cases, females may have a preexisting sensory bias for a certain trait, not because it represents anything but because it attracts attention—a hypothesis championed most prominently by Ryan and by John Endler of James Cook University in Australia. For example, female swordtails (*Xiphophorus helleri*) prefer males with long "swords" on their tail fins. And although males of a related species—the platyfish *Xiphophorus maculatus*—lack swords completely, Alexandra L. Basolo of the University of Nebraska found that when she attached artificial, plastic swords onto these naturally swordless males, female platyfish showed an immediate, strong and consistent preference for the males with the counterfeit swords. In other words, platyfish females harbored a preexisting bias for long swords, even though swords reveal nothing about the fitness of platyfish males.

These evolutionary models may be operating separately or in conjunction; it is difficult to untangle them experimentally. Female guppies, for instance, may be partial to orange males because bright coloring is a proxy for boldness or for good health (males with the brightest pigments are probably eating well). But the preference could have originated because females are more attuned to colors of a particular wavelength and then further evolved through a runaway mechanism.

All these models assume that female preference is genetically determined. Recent studies indicate, however, that social factors, such as imitation, also influence mate choice.

Copycat Birds and Fish

Some guys get all the girls. On a crowded grouse lek, for example, the top male may receive 80 percent of the mating opportunities. Is he simply irresistible? Or do females take one another's choices into account when selecting a mate? In the early 1990s a group of Scandinavian researchers, led



DRAWINGS BY ROBERTO OSTI; DIAGRAM BY JENNIFER C. CHRISTIANSEN

RUNAWAY SELECTION may shape mate preferences in stalk-eyed flies. Females of the species normally choose to mate with males that sport the longest stalks (*top center*). But when researchers used selective breeding techniques to generate two lines of flies—one in which males have long stalks (*left*), the other in which males' stalks are short (*right*)—they found that female preferences evolved along with male stalk length. Females from the long-stalk line were partial to males with longer stalks (*bottom left*), and females from the short-stalk line preferred shorter-stalked males (*bottom right*).

by Jacob Höglund and Arne Lundberg of Uppsala University and Rauno Alatalo of Jyväskylä University, initiated a detailed study of mate-choice copying in the black grouse (*Tetrao tetrix*). Using stuffed dummies to represent interested females, the researchers showed that female grouse mated preferentially with the male that appeared to have other females in his territory.

Why copy? Perhaps imitation teaches females what to look for in a male. In an extensive series of experiments on mate-choice copying in guppies, we determined that young females are more likely to copy the mate choice of older, more experienced females than vice versa. Further, copying may save time. Relying on the judgment of others may allow a female to assess a potential mate quickly and efficiently, leaving her more time to forage for food or hide from predators.

For species in which females copy, a fascinating question emerges: How much of female mate choice is based on instinct and how much on imitation? To tease apart the relative contributions of genetic and social factors involved in mate choice in guppies from the Paria River in Trinidad, one of us (Dugatkin) carried out a behavioral "titration" experiment. First, a female guppy was allowed to choose between two males that differed in the amount of orange that covered their bodies. As expected, females virtually always chose the more orange of a pair of males. Then a copying opportunity was staged, in which the test female was allowed to observe another female apparently choosing the less orange male as her putative mate.

Which male did she then choose for herself? Remember that the female's genetic predisposition is "pulling" her toward the more orange male, but social cues and the potential to copy are tugging her toward the drabber male. In the end, her choice depended on how much the males differed in coloration. When the paired males differed by small (12 percent) or moderate (25 percent) amounts of orange, the female consistently chose the less orange of the two. In this case, the female succumbed to peer pressure, her tendency to copy overriding her genetic preference for orange males. If, however, the males dif-

SEXUAL SELECTION comes in many styles. During mating season, male mule deer challenge their rivals to battle for the right to claim the available females. Male kangaroos also fight for their mates. But in species in which female choice is the main mode of sexual selection, males have evolved bold traits designed to attract the attention of females. Male peacocks show off by being spectacularly colored and meticulously groomed. Human males employ strategies that are somewhat less obvious.

ERWIN AND PEGGY BAUER *Bruce Coleman, Inc.*

DAVID C. FRITTS *Animals Animals*

M. AUSTERMAN *Animals Animals*

LARA JO REGAN *Gamma Liaison Network*

fered by a large amount (40 percent) of orange, the female ignored the seemingly bad advice and chose the more orange male, her genetic predisposition masking any copying effects.

It appears as if there exists in guppies a color threshold, below which social cues steer female mate choice and above which genetic factors predominate. Dugatkin is performing further experiments to assess whether copying behavior in guppies is itself heritable. Although imitation appears to be based on social cues, perhaps genes govern the likelihood that a female guppy will engage in copying behavior.

Sadie Hawkins Day

Although people are more complex than guppies and grouse, some of the same mate-choice rules may apply to human dating games. According to popular wisdom, it is human females who are the choosier sex when it comes to selecting a mate. As a species, humans meet the criteria for female choice: men, for the most part, will avoid fighting to the death for the hand of a young maiden. And females can distinguish between various males on the basis of differences in their characteristics: some men are brasher, some are brighter and some have bigger bank accounts.

Women may even engage in mate-choice copying. After all, imitation is important in many types of human learning. To determine whether copying plays a role in how women rate a man's attractiveness, Dugatkin is currently collaborating with social psychologists Michael Cunningham and Duane Lundy of the University of Louisville. Although their results are preliminary, they find that women are more likely to express an interest in going out with a man if they are told that other women also find him attractive.

Of course, evolutionary theory will never be able to explain fully singles bars, personal ads or cyber-romance. Even for animals, it appears that the benefits and costs of being choosy when selecting a mate differ for different species, in different environments and sometimes at different times of day. In any case, if animals as simple as guppies can consider the opinions of their peers when choosing a mate, imagine how complex the cues must be that guide humans in their search for the perfect mate. SA

What Females Want

MALE TRAIT	FEMALE PREFERENCE	SPECIES
Call (song)	Greater intensity Greater frequency Longer duration Greater complexity Larger repertoire	Meadow katydid American toad Green tree frog Tungara frog Song sparrow
Courtship display	Greater frequency	Sage grouse
Body size	Larger size	Convict-cichlid fish
Tail	Longer tail Greater tail height Greater number of "eyespots"	Barn swallow Crested newt Peacock
Comb	Larger comb	Red jungle fowl
Bower	More decorated bowers	Satin bowerbird
Breast stripe	Larger stripe size	Great titmouse
Body color	Greater brightness Greater area of orange	House finch Guppy

JENNIFER C. CHRISTIANSEN

The Authors

LEE ALAN DUGATKIN and JEAN-GUY J. GODIN first joined forces in Trinidad, where they became fascinated by the mating behavior of guppies. An evolutionary biologist, Dugatkin has been an assistant professor of biology at the University of Louisville since 1995. He received his Ph.D. in biology from the State University of New York at Binghamton in 1991. His research interests include the evolution of cooperation and altruism and the interaction of genetic and social factors in shaping behavior. Godin, a behavioral ecologist, is professor of biology at Mount Allison University in New Brunswick, Canada, where he has been on the faculty since 1981. He received his doctorate in zoology from the University of British Columbia and has been a visiting fellow at the University of Oxford. His research focuses on the behavioral ecology of antipredator, foraging and mating decisions in animals.

Further Reading

SEXUAL SELECTION. M. Andersson. Princeton University Press, 1994.

INTERFACE BETWEEN CULTURALLY BASED PREFERENCES AND GENETIC PREFERENCES: FEMALE MATE CHOICE IN *POECILIA RETICULATA.* L. A. Dugatkin in *Proceedings of the National Academy of Sciences USA*, Vol. 93, No. 7, pages 2770–2773; April 2, 1996.

FEMALE MATING PREFERENCE FOR BOLD MALES IN THE GUPPY, *POECILIA RETICULATA.* J.-G. J. Godin and L. A. Dugatkin in *Proceedings of the National Academy of Sciences USA,* Vol. 93, No. 19, pages 10262–10267; September 17, 1996.

SEX, COLOR AND MATE CHOICE IN GUPPIES. Anne E. Houde. Princeton University Press, 1997.

SEXUAL SELECTION AND MATE CHOICE. M. Ryan in *Behavioural Ecology: An Evolutionary Approach*. Fourth edition. Edited by J. R. Krebs and N. B. Davies. Blackwell Science, 1997.