

# Sex roles, ornaments, and evolutionary explanation

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**M**ales are competitive, sexually indiscriminate, and pushy, whereas females are passive, choosy, and coy. This familiar generalization about the sexual behavior of animals and humans is grossly overstated and potentially misleading, yet has its roots in empirical observation of at least some species. One of the triumphs of modern sociobiology (1, 2) is that evolutionary theory can explain why the sexes differ in their behavior along these lines in so many cases. To state the generalization more accurately, it is frequently, if not usually, the case that for every receptive female in the mating pool of a population, there is more than one male ready to inseminate her. This typical imbalance in the operational sex ratio (OSR; ref. 3) in turn stems from the basic facts of reproductive physiology: sperm are small and cheap, whereas the time and energy burdens of egg production, gestation, and parental care typically fall more heavily on females with the result that fewer females than males are available in the mating pool at any given time (4). Consequently, competing *inter alia* often benefits males most strongly, whereas being discriminating in mate choice often benefits females most strongly, leading to an evolutionary process of sexual selection expected to result in the evolution of secondary sexual traits in males: weapons that help them win in competition with one another and ornaments that help them win the attentions of females.

The appeal of this evolutionary explanation lies in part with its simple scientific validity, but in part with its consistency with long-standing, deep-seated cultural stereotypes about the roles of men and women. Most likely, our cultural stereotypes about human gender roles stem from the same biological bases that shape sex roles in other species. This cultural bias, in turn, and the very human tendency to see the world in terms of stereotypes, has tended to distort and obscure our view of the full richness of the conceptual framework explaining the evolution of sexual behavior and secondary sexual characters (5). A paper by Trond Amundsen and Elisabet Forsgren in this issue of PNAS (6) makes a significant contribution toward a more complete perspective on sex roles and their consequences for sexual selection. Their work with two-spotted gobies (*Gobiusculus*

*flavescens*) shows that males can be discriminating in mate choice and implies that this discrimination may lead to the evolution of ornamentation in females.

Overly simplistic notions of stereotypical or “normal” sex roles for males and females and attendant patterns of morphological dimorphism have been refined on a number of fronts in recent years. Studies of cryptic female choice (7), especially in insects, dispel the notion that females are passive recipients of the sperm of competing males. Instead, females of a number of species have been shown to be capable of discriminating among the sperm of different males once inseminated, allowing active mate choice to occur even if females are unable to exercise preferences before mating. Studies of fully role-reversed species provide exceptions that prove the rule for sex role theory more generally. In pipefishes, for example, biological constraints limit the reproductive capabilities of males relative to females so that the OSR becomes female-rather than male-biased (8, 9). In such role-reversed species, females are competitive, more highly ornamented (Fig. 1), and actively court males, whereas males are choosy in mate choice. The theory, then, can be extended to predict both “normal” and reversed sex roles from prevailing OSR, rather than focusing explanations on male-competitive, female-choosy sex roles (although this may be the more common occurrence).

A further lack of generality in sex role theory lies in the common but unnecessary assumption that *either* females choose and males compete (most commonly) *or* males choose and females compete (less commonly) and that therefore *either* males *or* females evolve ornaments and weapons. As a result, male mate choice is rarely studied in species in which females show strong mating preferences based on conspicuous ornaments of males. Guppies (*Poecilia reticulata*; Fig. 2), for example, have been the subject of intensive studies of color pattern evolution in males and mate choice evolution in females (10), but work on mate choice by males in this species, which is easily observable, has lagged far behind. A more complete view of sex roles and sexual selection is to realize that either sex may be expected to



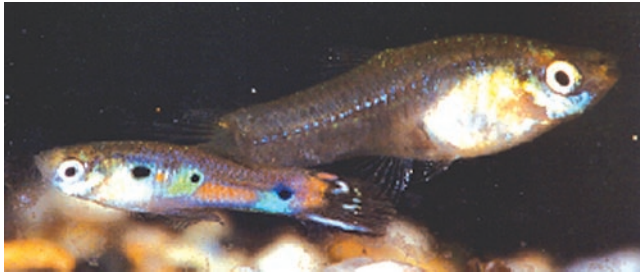
**Fig. 1.** Female pipefish *Syngnathus typhle* showing blue ornamentation. (Photograph by Ola Jennersten.)

exercise discrimination in mating given that the potential for mating repeatedly is not unlimited, that females vary in quality, and thus that the relative degree of mating competition and mating discrimination in each sex will affect the evolutionary outcome with regard to sex roles and the evolution of secondary sexual characteristics (11–14). In most cases, however, male mate choice appears to be based on variation in female fecundity or reproductive state and is easily explained. Amundsen and Forsgren’s work illustrates the broader concept of sex roles and sexual selection far more dramatically by demonstrating male mate choice based on a seemingly ornamental characteristic of females in a species that does not seem to have behavioral role reversal.

Two-spotted gobies appear at first to fit sex role stereotypes as usually conceived quite well. Males are larger than females,

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**Fig. 2.** Male (Lower) and female (Upper) guppies. Guppies provide an example of “normal” sex roles in which males are ornamented, compete among one another, and court females. (Photograph by Jonathan Weiland.)

competitively defend nest sites, court females to attract them to the nest, and show conspicuous breeding coloration. Like a number of other species, including the well studied three-spined stickleback (*Gasterosteus aculeatus*), male two-spotted gobies care for the eggs of several females. Female two-spotted gobies exhibit breeding coloration, which, in part, mirrors the male coloration, but more drably, but also includes orange-red pigment spots in the belly region that overlies the ripe eggs (Fig. 3). The presence of female breeding coloration is not itself unusual among fishes and is usually presumed to be a direct cue of the female’s reproductive state. Male sticklebacks, in fact, do discriminate among females based on the presence of breeding coloration (15), which appears to be a direct cue of readiness to spawn. Amundsen and Forsgren questioned the assumption that female coloration is either a correlated expression of male ornaments (16) or a

direct cue of reproductive state and instead wondered whether the orange-red coloration in two-spotted gobies could be a sexually selected ornament in its own right. This alternative hypothesis was prompted by the observation that the orange-red coloration varied considerably, even among individuals at similar stages of egg development—in other words, the coloration did not seem to be simply correlated with reproductive state. The study’s prediction, then, was that male gobies should show mating discrimination based on the ornamental coloration itself, independent of reproductive state.

Amundsen and Forsgren used a standard assay for mate choice, placing females that differed in the characteristic of interest in the end chambers of an aquarium divided into three sections and recording the behavior of males in the center chamber. In the first experiment, the test pairs of females showed natural variation in breeding coloration and were matched for body length. As



**Fig. 3.** Male (Lower) and female (Upper) two-spotted gobies. Whereas males of this species are ornamented, compete among one another, and court females, females also show ornamentation in their yellow-red belly coloration. [Reproduced with permission from ref. 6 (copyright 2001, PNAS).]

predicted, males showed the greatest sexual interest in the more highly ornamented females, but this experiment did not fully separate out possible effects of reproductive state—i.e., egg maturation. The second experiment more fully controlled for this by directly manipulating coloration with permanent marker in pairs of females matched for both body length and body mass. Matching for both length and mass ensures that the two females have a similar degree of belly roundness or enlargement due to egg development. Again, males preferred the more conspicuously ornamented females.

This experiment is simple, and its design and results are similar to a long line of previous studies of female mate choice (17) and a few studies of male mate choice. But because this was a study of male mate choice and because the female characteristic studied was an ornamental trait that varies independently of fecundity and reproductive state, the implications are surprising and novel. All similar experiments showing female preference based on male ornaments imply, albeit indirectly, that the ornament is likely to have evolved by sexual selection resulting from the female mating preference. The novel implication here is that the female ornament, too, has evolved by sexual selection, but this time resulting from male mate choice.

Not only is this the first time that male mate choice has been implicated in the evolution of a female ornament, but Amundsen and Forsgren’s results bring stereotyped ideas of sex roles into question. Is this a really unusual case? Or is ornament evolution in females generally overlooked? Perhaps both. It appears that the ecological circumstances of two-spotted goby populations may make sexual selection on female ornaments more likely than in other species. Over the course of the breeding season, as males fill their nests with eggs and care for them, the composition of the mating pool shifts to a point where the OSR becomes strongly female-biased and there is a surplus of females with eggs ready to fertilize. This female-biased OSR sets up the potential for males to discriminate among females and hence for sexual selection on female traits—but the potential benefit of discriminating is not known. Is this an unusual situation? We do not know, although the evolution of costly ornaments in females may often be limited by the greater evolutionary benefits of greater fecundity (12). On the other hand, it may be that the role of sexual selection in the evolution of secondary sexual traits of females has often been overlooked except in role-reversed species. One notable exception is the suggestion that male mate choice has played a role in the evolution of secondary sexual traits, such as breast size and waist-to-hip ratio in human females (18).

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