

Sexual Selection and Sensory Exploitation

In a recent review, Michael J. Ryan states (1, p. 1999) that, in females of many species, "receiver biases result in 'preexisting preferences,' and males that evolve traits that exploit these preexisting preferences are favored by sexual selection." The idea is that, if females hear some sounds (for example, those of predators) or see some colors (for example, those of foods) better than others, then these sensory biases may "incidentally" affect their choice of mates.

In support of his "sensory exploitation" hypothesis, Ryan cites experiments in which females exhibited preferences for phenotypic attributes that were not possessed by conspecific males. However, such preferences might have originated, and be maintained, by the advantages of choosing conspecific males of superior quality, rather than being phylogenetic "baggage" left over from discriminations in contexts other than mating, as Ryan suggests.

For example, female *Physalaemus coloradorum* frogs prefer artificial conspecific calls preceded (2) or followed (3) by low-pitched sounds, including the "chucks" of a congeneric species or even white noise. This may occur because, in the wild, females prefer males of the same species that give low-pitched calls (4), indicative of the male's size, age, and viability. Similarly, female *Xiphophorus helleri* swordtail fish prefer sworded males over unsworded males of similar size (5), but recently it was discovered that they prefer large males without swords over normal-sized males with swords (6). Thus, brightly colored tail ornaments apparently help advertise size (7). Female *X. variatus* platyfish (in which males lack swords) also choose males with bright, enlarged tails, even including tails elongated with ersatz *X. helleri* swords (8). Again, this may simply reflect a preference for large mates.

In these cases, and others mentioned by Ryan (for example, tufts of feathers on auklets and fuzzy forelegs on wolf spiders), females' choices may reveal open-ended preferences for elaborations of characters indicative of male quality, rather than specific preferences that were presumed to have evolved in ancestral species for nonmating contexts. In mate-choice experiments that used manipulated characters of heterospecific males (2-5), females' preferences were described as biases for specific traits that conspecific males did not possess—but, in every case, females may instead have exhibited a generalizable preference for higher-quality

conspecific males (6,7).

Female preferences and male traits can coevolve rapidly (9), especially when females are penalized reproductively (for example, through reduced survival or mating success of females or their offspring) for mating with males exhibiting an "exploiting" stimulus. Indeed, only if initial sensory biases by chance resulted in optimal mate choices would such coevolution *not* occur (7). However, given the negative connotations of the word "exploited," it is inappropriate to use this term to describe circumstances in which females prefer male traits that increase female fitness.

In light of mounting evidence that females' mate choices yield direct (10) and indirect benefits (that is, good genes; 11), Ryan's conclusion (1) that female mating preferences are "incidental consequences rather than evolved functions" of females' neural circuitry is premature at best.

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Response: My review (1) was an attempt to integrate neural mechanisms and evolutionary history with studies of current fitness in order to understand female mating preferenc-

es. I disagree with the criticisms of Sherman and Reeve made here and elsewhere (2) of my approach.

First, I do not agree with the interpretations of other studies made by Sherman and Reeve concerning sensory exploitation. Their statement that preference for large swords in swordtails and platyfish might be derived from a preference for large body size is consistent with the sensory exploitation prediction that specific traits can exploit more general biases, and is cited by the authors of that study (see 6 in the comment) as such. The statement that large size in swordtails is a good indicator of viability seems incorrect because most the variation in size is correlated with allelic variation at the Y-linked P locus, and this variation is in genetic equilibrium, as males of different size-genotypes have equivalent lifetime fitness (3). Furthermore, growth of swords is metabolically cheaper for males than is growth of overall body size, which suggests that sword length and body size are unlikely to be equally accurate indicators of a quality such as viability (4).

Also, I do not agree that female frogs of the species *P. coloradorum* "prefer artificial conspecific calls preceded or followed by low-pitched sounds, including the 'chucks' of a congeneric species or even white noise." My colleagues and I have tested *P. coloradorum* only with their conspecific call (the whine) followed by a heterospecific (*P. pustulosus*) chuck (5). The heterospecific chuck has more than 90% of its energy above 1500 Hz. In *P. pustulosus*, a whine followed by a synthetic chuck with only the energy above 1500 Hz present results in preferential phonotaxis as compared with a whine only, while a whine with a chuck with only the energy below 1500 Hz present does not elicit preferential phonotaxis (2, 5). Thus, adding a chuck to the *P. coloradorum* call adds a higher, not a lower, dominant frequency than the conspecific whine. The preexisting preference for chucks exhibited by *P. coloradorum*, therefore, cannot be explained by adaptive mate choice for larger males producing lower-frequency calls, as suggested by Sherman and Reeve.

Investigations of the neural basis of call preference, however, do provide insights into the origin of this preexisting preference (5). The whine in both species is processed by the hearing organ that is most sensitive to low-frequency sound, the amphibian papilla. In *P. pustulosus* the chuck is processed by the hearing organ that is most sensitive to high-frequency sound, the basilar papilla. The shared preference for chucks between species in which chucks do (*P. pustulosus*) and do not (*P. coloradorum*) exist derives from similar tuning properties of the high-frequency-sensitive basilar papilla in both species (5).

Second, Sherman and Reeve propose the

false dichotomy of female preferences being either an adaptive trait or "phylogenetic baggage." Understanding neural and cognitive mechanisms underlying female mate preference, however, complements other approaches to explaining sexual selection (for example, 1, 6). For example, adaptive mate choice theory would not itself predict that moths would use ultrasonics to signal to females, but knowledge that the moth's sensory system evolved in response to bat predation explains why sexual selection, even selection for "good genes," can now act in this sensory channel (1). There are strong clade-specific patterns in signal diversity, and the consensus seems to be that "the efficacy based perspective [how signals are matched to receiver biases] has proved more successful in accounting for the diversity of natural signal form. . . . Animal signals, in other words, must be both efficient [elicit responses] and reliable [indicate the quality of the sender], but it is the former condition that places the greatest constraint on their design" (7). Their statement of my conclusion is taken out of context, with the result it reinforces this false dichotomy of traits being either adaptive or phylogenetic baggage. In my review, I tried to emphasize the compatibility rather than the exclusivity of these two approaches.

Third, Sherman and Reeve state that only if sensory biases result in adaptive mate choice would they not be replaced during natural selection over generations. This is a possibility, but not an exclusive one; in pygmy swordtails, population variation in an an-

cestral preference for large size might result from such a process (8), but in other cases ancestral preferences are retained without a clearly adaptive function (9). Counter to the statement by Sherman and Reeve, female preference can be maladaptive and lead to species extinction, as in the case of cichlid fishes in Lake Victoria (10).

Finally, Sherman and Reeve object to the term "exploitation" to describe the male's use of a given signal because, they argue, female preferences that persist over generations are necessarily adaptive. But our use of the term is consistent with English usage ["the action of turning to account for selfish purposes, using for one's own profit" (11)], and is used similarly in other types of animal behavior studies, such as when the calls of parasitic cuckoos exploit the feeding response of hosts (12) or orchids exploit the mate location strategies of insects (13). In most of these cases, the exploited response might be maladaptive in one context, but still exhibit an overall fitness advantage. Neither general usage nor specific treatments suggest that the response being exploited need result in an overall, lifetime fitness decrement to the receiver of the signal.

I maintain that many of the response biases associated with female mate preferences do not result from selection for adaptive mate choice, that they can be important in directing the evolution of sexually selected signals, and that they cannot be fully understood without reference to past evolutionary history and

neural and cognitive mechanisms. Although the "good genes" hypothesis (see reference 11 in the comment) would predict that a signal should be reliable, it does not predict the phenotypic form the signal should take.

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