Male Swords and Female Preferences

A. L. Basolo tests the hypothesis that, in the swordless platyfish, *Xiphophorus maculatus*, female mate choice arises from a preexisting sensory bias (*1*). Basolo shows that females exhibit a mating preference for males with an attached, artificial, colored sword when given a choice between these males and males with an artificial, transparent sword as a control. Because swordlessness is the ancestral state of the *Xiphophorus* clade, Basolo argues that the results of her experiment indicate that female preference for swords predates the evolution of the sword and concludes that coevolutionary models of sexual selection are inadequate. Basolo provides no direct evidence in support of a preexisting female sensory bias, but rejects the coevolutionary hypotheses of mate-choice evolution.

Female platyfish may have exhibited a preference for artificially sworded males because these males were novel (*2*). The appropriate control for this possibility would be males with some other shapes attached that do not resemble any marking on males, a blue triangle, for example. If females prefer males with a triangle to those without, then females are clearly attracted to novel males. If this test shows that females are not attracted to novel males, then it would be necessary to demonstrate that females are attracted to the sword per se and not the context in which the sword is displayed. This is an important distinction, because the sensory-bias hypothesis implicitly assumes that it is the character alone, not its context, that attracts the females. Such an experiment could be done by attaching a sword to areas other than the lower edge of the caudal fin.

The most convincing support for the sensory-bias hypothesis would come from a demonstration that males show a mating preference for females bearing swords. This counterintuitive prediction derives from the hypothesis that a female sensory bias evolves in response to some environmental stimulus. Basolo gives the example that females may have evolved a search image for a favorite food and then preferred to mate with males that sported an appendage resembling this food. In such a scenario, males would be just as likely to evolve the sensory bias, as they are also subject to selection to detect food. The prediction that males prefer females with swords should be tested with a swordless species whose females exhibit a sword preference, as the swords of sworded species may be used by males as an indicator of gender (*3*). Even if males preferred females with swords, female swords would not be expected to have evolved, as sworded females are not likely to have experienced a mating advantage. This is because female gestation in these live-bearing species probably means that females are the limiting sex.

Is the sensory-bias hypothesis tenable? One must ask why a female might want to mate with a male associated with something that looks good to eat. It cannot be argued that males with swords are more easily detected by females because of limits to female visual perception; *X. maculatus* males and males of the sworded species *X. helleri* both perform complex courtship displays at very close range to females (*3, 4*). Perhaps some constraint on the development of neural circuitry causes females to court attractive objects even though they provide no information about mate type or quality. As pointed out by Basolo, this is not the same as a novel-male effect, as such a hypothesis does not explain the fixation of sword genes in a population. Nevertheless, natural selection would likely favor a strategy of informed mate choice over arbitrary mate choice. Further tests of the sensory-bias hypothesis would be useful, but the premise of the hypothesis must first be carefully examined.

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If, as Basolo asserts, the ancestral state of *X. helleri* and *X. maculatus* is swordlessness, this provides evidence that the female bias for sworded males predated the evolution of the sword itself. We propose, however, that the common ancestor of these two species was sworded. Swords develop in *X. maculatus* and in other apparently swordless species within this genus (*1*) through treatment with testosterone. "Sword genes" appear to be present, but not expressed. Thus, there is no evidence to suggest that the female preference for sworded males predated the appearance of the swords.

If females of both species exhibit a preference, and males of both species are able to produce swords, why are swords only expressed in *X. helleri*? We suggest that there is a difference in how the two species balance the costs of natural selection and the benefits of sexual selection. For example, swords may entail a stronger survival disadvantage for *X. maculatus* because of higher predation risk, or the mating system of *X. helleri* may allow for greater variance in male mating success.

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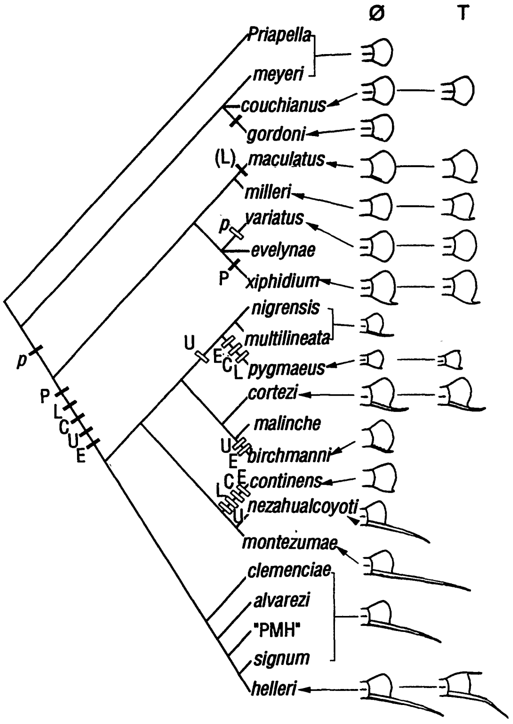
Response: The conclusion that female preference resulting in selection for a sword existed before the sword itself is critically dependent on the evolutionary history of female preference and the male trait. Winquist *et al.* question the phylogenetic inference that swordlessness is the ancestral state in the genus *Xiphophorus*. Of five species of platyfish treated with methyltestosterone (*1, 2*), two developed protrusions (Fig. 1). The gene that produces a short, uncolored protrusion appears to be a shared, derived character of one platyfish clade and the swordtail clade.

Evidence for the evolution of a short, uncolored protrusion early in the history of *Xiphophorus* does not necessarily reject the preexisting bias hypotheses for the evolution of the sword. As defined in my paper, the sword consists of "a colored extension of the lower margin of the caudal fin." Elongation results from the lengthening of rays at the distal base of the caudal fin, and pigmentation varies among the swordtails (Fig. 1). The phylogenetic distribution of traits suggests that the evolution of the sword occurred progressively (Fig. 1). The most primitive clade of platyfish does not demonstrate the genetic ability to express a protrusion, but one species expresses lower caudal "stippling." The other clade of platyfish expresses a range of conditions; one species

Fig. 1. This composite phylogeny of *Xiphophorus* incorporates those of Rosen (*3*) and of Rauchenberger *et al.* (*4*). The platyfish *X. meyeri* is in the *X. couchianus/gordoni* complex (*5*), and the platyfish *X. andersi* is not represented because phylogenetic analysis has not been published. *Priapella* is the sister group to *Xiphophorus* (*3, 6*). The before (∅) and after (T) hormone treatment drawings are taken from Zander and Dzwillo (*2*). Not all species have been tested. The normal (∅) caudal fins and swords depicted are taken from published descriptions and photos or modeled after fish in my laboratory. The normal caudal fin of *X. evelynae* is similar to that of *X. variatus*. The sword of *X. malinche* is similar to that of *X. cortezi*. Unexpressed protrusion-producing gene, *p*; expressed protrusion (defined as 0.0 to 0.3 × the length of the caudal fin), P; elongation of the rays at the base of the caudal fin (defined as 0.7 to 6.0 × the length of caudal fin), E; lower caudal black stripe, L; upper caudal black stripe, U; green, yellow, or orange stripe coloration at base of caudal fin, C. Closed ticks on the cladogram represent character gains; open ticks represent character losses; ( ) designates characters that are expressed by some individuals in a species. The gains and losses given for U represent one of two equally parsimonious possibilities.



cannot express a protrusion, two can be induced to express a protrusion, and another has a naturally occurring protrusion. In addition, one species is polymorphic for a short, black caudal stripe. Six species in the next clade, the northern swordtails, have swords elaborate in length and pigmentation, similar to the artificial swords that were attached to *X. maculatus* males. Of the remaining three species of northern swordtails, *X. birchmanni* has secondarily lost the sword (although many males have coloration at the base of the caudal fin) and *X. continens* and *X. pygmaeus* have secondarily lost a long, colored sword but can express a protrusion of 1 to 3 mm. The final members of the genus, the southern swordtails, all possess a long, colored sword.

It appears that the genetic ability to produce a protrusion at the base of the distal tip of the caudal fin arose within the genus *Xiphophorus* between the two clades of platyfish and that a sword consisting of elongated caudal fin rays and coloration is a shared, derived character of the swordtails. It is less parsimonious to posit that swords were present in the ancestors of *Xiphophorus* and were later lost through natural selection (although selection may account for the loss of both coloration and elongation in *X. continens* and *X. pygmaeus*). The strongest test of the preexisting bias hypothesis would be to measure the sword preferences of platyfish from the *couchianus-meyeri* clade and from the closest relative of *Xiphophorus* in which no component of the sword is exhibited.

Da Silva states that my work "provides no direct evidence in support of a preexisting female sensory bias. . . ." However, I did not specifically address a sensory bias model, but rather tested the hypothesis that preexistng biases in the female information processing system could have resulted in selection of the sword when it arose in the swordtails. I discussed several possible sources of the initial bias, including a preference for novelty and biases in the sensory system or cognitive system or both. The results reject the coevolutionary hypothesis for the evolution of female choice; the phylogenetic distribution of the preference and the trait suggests that a preference for the sword arose before the sword itself.

The test of novelty proposed by da Silva (attaching a blue triangle to males) would not distinguish between a preexisting preference for novelty per se and a more general bias for conspicuousness. The preexisting bias model does not "implicitly assume . . . that it is the character alone . . . that attracts the female," as stated by da Silva. If the basis for the preexisting bias is preference for conspicuousness, then any trait that made the male more conspicuous would be favored.

Da Silva suggests that "the most convincing support for the sensory-bias hypothesis would come from a demonstration that males show a mating preference for females bearing swords." Although such a preference might suggest that selection has acted similarly on both males and females, the absence of evidence for such a preference would not reject the preexisting bias hypothesis. For example, a preference by females for large males could favor the sword because it increases perceived body size. One could not necessarily assume that males would share a similar preference for large females.

Da Silva states that "it cannot be argued that males with swords are more easily detected by females because of limits to female visual perception. . . ." However, the sword may increase sensory input in a number of ways. Its form may cause more horizontal detectors to fire, or the intensity of coloration may cause the stimulation of more visual cones. Thus, a bias that results in more (or less) stimulation of the peripheral nervous system could result in a demonstrated preference. More generally, the preexisting bias may be for larger or more conspicuous males.

Da Silva appears to object to the possibility of arbitrary mating preferences that is implied by preexising bias models. However, these models do not imply that female preferences have been established through nonadaptive mechanisms. In the majority of cases, these biases are most likely shaped by selection in another context, with pleitropic consequences for mate choice.

Finally, it is important to stress that preexisting biases need not be specific. A preexisting bias that results in a preference for a specific male trait does not imply that the initial bias is specific. Nor need a preexisting bias be the sole explanation for the fixation of a trait. Rather, preexisting biases may determine the direction of evolution and, at any point, act in conjunction with other sources of selection to drive characters to a high frequency or fixation.

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