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.

Jack da Silva
Department of Biology, McGill University, Montreal, Quebec, H3A 1B1, Canada

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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.

S. Todd Winquist
Daniel M. Weary
Alastair J. Inman
D. James Mountjoy
Elizabeth A. Krebs
Department of Biology, McGill University, Montreal, Quebec, H3A 1B1, Canada

REFERENCES


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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
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