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Alexandra Basolo

University of Nebraska - Lincoln, basolo@unl.edu

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## THE PHYLOGENETIC DISTRIBUTION OF A FEMALE PREFERENCE

ALEXANDRA L. BASOLO

Nebraska Behavioral Biology Group, University of Nebraska, Lincoln, Nebraska 68510, USA;  
E-mail: basolo@niko.unl.edu

**Abstract.**—Robust phylogenetic information can be instrumental to the study of the evolution of female mating preferences and preferred male traits. In this paper, the evolution of a preexisting female bias favoring a sword in male swordtail fish and the evolution of the sword, a complex character, are used to demonstrate how the evolution of mating preferences and preferred traits can be examined in a phylogenetic context. Phylogenetic information suggests that a preference for a sword arose prior to the evolution of the sword in the genus *Xiphophorus* and that the sword was adaptive at its origin. A phylogenetic approach to the study of female preferences and male traits can also be informative when used in conjunction with mate choice theory in making predictions about evolutionary changes in an initial bias, both prior to the appearance of the male trait it favors and subsequent to the appearance of the trait. [Mate choice; female preference; preexisting biases; *Priapella*; swordtail; sword; *Xiphophorus*.]

The study of the evolution of mating preferences is an area of much contention. Until relatively recently, there was disagreement over the importance of female mate choice. In the past 15 years, however, many studies have shown that females exhibit mating preferences and that these mating preferences can have an important effect on male mating success. Many models have been proposed to explain the evolution of female preferences; these models can be assigned to one of five primary categories: direct benefits (Trivers, 1972; Halliday, 1978; Thornhill and Alcock, 1983; Kirkpatrick and Ryan, 1991), good genes (Williams, 1966; Zahavi, 1977; Hamilton and Zuk, 1982; Andersson, 1986; Pomiankowski, 1988), Fisherian processes (Fisher, 1930; Lande, 1981; Kirkpatrick, 1982), correlated effects (Darwin, 1871; Lande and Arnold, 1985; Halliday and Arnold, 1987; Arnold and Halliday, 1992), and preexisting biases (Barlow, 1977; West-Eberhard, 1984; Kirkpatrick, 1987a; West-Eberhard et al., 1987; Endler and McLellan, 1988; Basolo, 1990b, 1995b; Kirkpatrick and Ryan, 1991). Direct benefits models suggest that females receive a benefit from mating with a certain male. For example, they may receive a resource directly or they may gain access to a resource for either themselves or their offspring. Good genes models suggest that female preferences evolve under selection for females to mate with males

who have genotypes of higher viability. Fisherian processes models stress the importance of linkage disequilibrium between the female preference and the sexually selected trait; the preference evolves as a correlated response to male trait evolution. Correlated effects models suggest that female preferences evolve as a correlated result of male preference evolution. That is, males have a preference for a trait in females, the genetic basis of the preference in males is shared with females or is correlated for some other reason, there is no significant cost to the expression of this preference in females, and thus a female preference for the trait in males evolves as a correlated effect of evolution of the male preference for the trait in females.

Models stressing the importance of good genes, correlated effects, Fisherian processes, and some cases of direct benefits require genetic variation in the preference and some component of male fitness, and they predict coevolution of the preference and trait. Little experimental data have been produced that support one of these coevolutionary models to the exclusion of the others. None of these models predict the evolution of a preference prior to a trait (although any of them could result in preferences for traits not yet present). The fifth model, the preexisting bias model, suggests that there are female biases resulting from evolutionary processes independent

of sexual selection on the specific trait under study and present prior to the appearance of that male trait. (By convention, mating preferences are presented in terms of females and preferred traits are presented in terms of males, but the ideas are interchangeable regardless of sex.)

A unique prediction of a preexisting bias model is that the preference appeared prior to the origin of the trait. This prediction can only be tested using the comparative method, and to implement the comparative method good phylogenetic information is essential. In this paper, the importance of robust phylogenetic information to the study of the evolution of female preferences and preferred male traits is demonstrated. First, I discuss the preexisting bias model of sexual selection in terms of both female preference and male trait evolution. Second, I discuss the use of phylogenetic information to test a hypothesis of sexual selection, using my own work on swordtail fish as an example. Third, I discuss how phylogenetic information can be utilized to generate new hypotheses once we know the phylogenetic distribution of a preference and trait; specifically, how new hypotheses can be formulated about how a preexisting bias should differ between lineages in which the male trait has and has not arisen.

#### PREEXISTING BIASES

##### *Sexual Selection*

The idea of preexisting biases affecting the direction of selection is not new, but it has recently been formalized. Barlow (1977) suggested that signals should evolve to forms that are best perceived by the receiver. West-Eberhard (1984) suggested that sensory traps can be used by a signaler to capitalize on receiver response that has been selected in another context. Kirkpatrick (1987a, 1987b) suggested that intrinsic biases affect female perception and can affect the direction of male trait evolution. Endler and McLellan (1988) considered how the environment and sensory properties of the receiver affect signal reception and used the term "sensory drive"

to describe how their interaction might affect the direction of selection. Ryan (1990) suggested that male traits may arise that capitalize on biases in the female sensory system, using the term "sensory exploitation." Basolo (1990b) proposed a critical test using phylogenetic information and a stepwise approach for testing preexisting biases models and suggested a broadening of the category of biases to include higher levels of integration and information processing.

Preexisting biases can evolve for a number of reasons (Basolo, 1990b, 1995a, 1995b), but regardless of the origin of the bias, preexisting bias models postulate that a male trait can arise and be favored by a previously established bias. However, further evolution of the bias may occur following its origin, and after the male trait arises and is selected by the preexisting bias, other sources of sexual selection, e.g., good genes, direct benefits, correlated effects, Fisherian processes, and other preexisting biases, may act in conjunction with the existing bias to further elaborate or modify the preference. In addition, the initial bias can be changed as a result of natural selection or other sources of evolutionary change.

A clear demonstration that a preexisting bias has played a role in the evolution of a male trait requires that three criteria be met: (1) females prefer a conspecific male trait, (2) the absence of the male trait is the ancestral state within a group, and (3) in a species possessing the ancestral state for the male trait, females prefer the male trait even though it was not generally present in the evolutionary history of the species. To adequately test a preexisting bias model, a robust phylogenetic hypothesis is essential.

##### *Adaptive Male Trait Evolution*

Mate choice models address the evolution of mating preferences, but they also make predictions concerning the evolution of male traits. In the case of preexisting biases, male traits that arise and increase in frequency because of a preexisting bias are always by definition adaptive in the

context of mating. Using phylogenetic information, it is possible to determine when a female bias arose. At any time after the appearance of a bias, an "adaptive field" for a male trait exists; that is, mate choice will favor the male trait if it arises. Mutations that occur at low frequencies and result in new male traits may be lost before selection can ever act on them or before selection can have a maintaining effect. However, when an adaptive field in the form of a preexisting bias exists for this new variant, there is a higher likelihood that the trait will increase in frequency. If there is no counterbalancing selection, the preexisting bias will result in an increase in the frequency of the male trait (predictions concerning the fate of the male trait if it arose prior to the origin of the bias favoring it are not considered here). Armed with phylogenetic information, one can make predictions concerning the direction of selection, should the appropriate male trait arise. Therefore, although female preferences based on preexisting biases may or may not have an adaptive origin, in a sexual selection context the male traits selected by such biases are undeniably adaptive at their origin.

#### *Bases of Biases*

Preexisting biases can exist at any level along the signal reception and processing continuum from stimulation of a peripheral sensory system to actual synthesis of input from sensory systems, including higher level integration and cognitive processing. The possible bases for an initial bias are numerous; a subset of the possibilities are presented here. First, the basis of a preexisting bias may be as simple as preference for rare, novel traits (but see Basolo, 1990b). Second, preferences for one male trait may have a pleiotropic effect, resulting in selection on a different male trait (Ryan, 1990). Third, females may show stronger mating responses to males with more conspicuous traits simply because males with these traits are easier to detect. Fourth, evolutionary change in an established preference could result in a new bias or preference. The plasticity of a pref-

erence has been investigated theoretically with a model of visual recognition (Arak and Enquist, 1993; Enquist and Arak, 1993); simulations of a neural network model demonstrate that in some cases a response to certain patterns not previously encountered can be stronger than a response to patterns that were initially selected to elicit a response. These unexpected biases may evolve concealed and nonfunctioning until a trait arises that is recognized and selected by them. The degree of similarity or dissimilarity of a male trait among lineages resulting from the same initial preference, or from an altered form of the initial bias, would depend on available variation, the influence of other sources of selection, and genetic drift.

Preexisting biases can be defined by biases in the sensory system, which have been shaped by natural selection, sexual selection in another context, or other sources of evolutionary change or by a combination of these. To establish that a bias is specifically a sensory bias, a fourth criterion must also be met: it must be established that there is a bias in a specific sensory modality that is predictive of the direction of sexual selection (Basolo, 1995a). To my knowledge, these four criteria have been met in only one case. Ryan et al. (1990) found that *Physalaemus pustulosus* and *P. coloradorum* share basilar papillae with peak sensitivity at 2,200 Hz, which phylogenetic evidence suggests is the ancestral condition. *Physalaemus coloradorum* males do not produce calls at this frequency, but *P. pustulosus* males produce chucks that appear to have evolved to "exploit" this bias in the peripheral auditory system. Based on the phylogenetic information available for female peak sensitivity, one would predict that females of both species may prefer male calls near 2,200 Hz over calls at other frequencies. Ryan and Rand (data published and discussed by Kirkpatrick and Ryan, 1991) found that *P. coloradorum* females prefer synthetic calls with an added chuck. With these combined results, the four criteria supporting a sensory basis to a bias are satisfied. However, one must be careful when

specifically invoking a sensory bias as the basis of a preference. Sensory biases have been targeted as the basis of a bias in two other situations (Clark and Uetz, 1992; Proctor, 1992). Both appear to involve male exploitation of female prey detection mechanisms. Whereas a specific sensory bias at the peripheral sensory level may explain the results in these additional studies, such as was found for the *Physalaemus* complex, it may be that a bias involving a search image would involve higher order processing. Higher level biases may involve reception and integration of neural signals from several to many peripheral sensory sources. Because the level of a bias may be difficult to establish directly, caution should be exercised when assigning a basis to a bias; the bias may be more complex than stimulation of several neurons at the peripheral sensory system level.

#### DEMONSTRATING A PREEXISTING BIAS IN POECILIID FISHES

##### *Background on Xiphophorus and Priapella*

The genus *Xiphophorus* is a group of freshwater, livebearing fish (Poeciliidae), which has historically been divided into two groups, the unsworded platyfish and the swordtails, most species of which possess a sword. The sword does not develop until sexual maturity, at which time rays at the lower margin of the caudal fin in males begin to elongate and acquire pigmentation. The proposed sister genus of *Xiphophorus* is *Priapella* (Rosen, 1979), which consists of five described species, all of which lack a sword.

##### *Nature of the Sword*

The term "sword" has been used by different investigators to describe different structures but was originally used by Heckel (1848) to describe the lower caudal appendage of the green swordtail, *Xiphophorus helleri*. This species is a member of the southern swordtail group, all members of which have a complex sword consisting of a number of component characters. Most species in the second group of swordtails, traditionally called the northern swordtails, also have a complex sword.

The character states for nine caudal fin and sword characters for the genus *Xiphophorus* are presented in Table 1 (based on Rosen, 1979; Kallman and Bao, 1987; Rauchenberger et al., 1990; Basolo, 1991, pers. obs.). One component of the sword is elongation of a specific set of rays (Rauchenberger et al., 1990; Basolo, 1995a) at the base of the caudal fin (E), ranging in length from 0.6 to 1.0 times the body length (standard length). A second component, lower black stripe (L), consisting of melanophore coloration extending from the proximal base of the sword to the distal tip along the ventral margin of the rays, occurs in 12 species of swordtails. A character found in some populations of the southern platyfish, *X. maculatus*, resembles the proximal third of this lower black stripe. A third component of the sword, the proximal portion of the upper melanophore stripe, is derived from the character grave spot (G: a black caudal fin pigment pattern that is sex limited in some species but not in others), which is shared by 13 of the 14 swordtail species, although its expression is reduced in 2 species (*X. birchmanni* and *X. continens*; Rauchenberger et al., 1990). In the 11 swordtails that have an upper black stripe, the grave spot gives rise to the proximal portion of the stripe (PU: proximal upper stripe) in 7 species, and in the remaining 4 species the grave spot gives rise to the proximal portion of the stripe, which continues to develop distally to the tip of the sword (PU plus MDU: midway to distal upper stripe). Of the seven species in which the grave spot gives rise only to the proximal portion of the upper stripe, one is in the southern swordtail group (*X. clemenciae*) and the other six are in the northern swordtail group. Of these seven species of swordtails, five always have a distal upper stripe, which develops from the distal tip of the sword proximally (DMU: distal to midway upper) and meets the proximal portion of the stripe midway, and two species occasionally have DMU (*X. nigrensis*, *X. multilineatus*). A final sword component consists of orange, yellow, and/or green coloration (C) situated between the two melanophore stripes. This coloration con-

TABLE 1. Twenty-three described species of *Xiphophorus* with character states for nine caudal fin and sword characters. + = presence of the character; ca = carotenoid coloration; pt = pterin coloration. - = absence of the character but does not indicate whether or not character has been secondarily lost; ? = no available information because species has not been tested. An asterisk indicates that character state is obscured by presence of E. States in parentheses indicate that a species is polymorphic for that character.

Species	Characters <sup>a</sup>								
	p	P	E	C	G	L	PU	MDU	DMU
<b>Platyfish</b>									
<i>meyeri</i>	?	-	-	-	-	-	-	-	-
<i>couchianus</i>	-	-	-	-	-	-	-	-	-
<i>gordoni</i>	-	-	-	-	-	-	-	-	-
<i>maculatus</i>	+	-	-	-	-	- <sup>b</sup>	-	-	-
<i>milleri</i>	+	-	-	-	-	-	-	-	-
<i>variatus</i>	-	-	-	-	-	-	-	-	-
<i>evelynae</i>	?	-	-	-	-	-	-	-	-
<i>xiphidium</i>	+	+	-	-	-	-	-	-	-
<i>andersi</i>	+	+	-	-	-	-	-	-	-
<b>Swordtails</b>									
<b>Northern</b>									
<i>nigrensis</i>	*	*	+	(+ca)	+	+	+	-	(+)
<i>multilineatus</i>	*	*	+	(+ca)	+	+	+	-	(+)
<i>pygmaeus</i>	*	(+)	-	(+ca)	-	-	-	-	-
<i>cortezi</i>	*	*	+	(+ca)	+	+	+	-	+
<i>malinche</i>	*	*	+	(+ca)	+	+	+	-	+
<i>birchmanni</i>	*	(+)	-	(+ca)	(+)	(+)	-	-	-
<i>continens</i>	*	-	-	-	(+)	-	-	-	-
<i>nezahualcoyotl</i>	*	*	+	(+ca)	+	+	+	-	+
<i>montezumae</i>	*	*	+	(+ca/pt)	+	+	+	-	+
<b>Southern</b>									
<i>clemenciae</i>	*	*	+	+ca	+	+	+	-	+
<i>alvarezii</i>	*	*	+	(+ca/pt)	+	+	+	+	-
PMH <sup>c</sup>	*	*	+	+ca/pt	+	+	+	+	-
<i>signum</i>	*	*	+	+pt	+	+	+	+	-
<i>helleri</i>	*	*	+	(+ca/pt)	+	+	+	+	-

<sup>a</sup> p = genetic ability to express protrusion, unexpressed unless hormonally induced; P = expressed protrusion; E = elongation; C = yellow, green, and/or orange coloration; G = grave spot; L = lower melanophore stripe; PU = proximal upper melanophore stripe; MDU = distal upper melanophore stripe, developing from midway to distal tip of sword; DMU = distal upper melanophore stripe, developing from distal tip of sword proximally.

<sup>b</sup> A color pattern resembling the proximal 1/3 to 1/2 of L is expressed in some males and females. Whether this partial stripe is homologous to L is unknown.

<sup>c</sup> Designation given by Rosen (1979:361) to a swordtail species in the southern clade, "clearly allied to *helleri* and *signum* . . . possibly a separate entity from *helleri*."

sists of a central field of pterin and/or carotenoid pigments (Kallman and Bao, 1987). The wealth of information available for the genus *Xiphophorus* indicates that the sword is a composite trait, consisting of a set of distinct component characters (some of which may not yet be designated). (The branching patterns of the rays constituting the swords differ between the northern and southern swordtails, which may indicate that the character E is a composite character itself. This difference would suggest that there are two independent

branching patterns, but it could also indicate that one branching pattern is ancestral and the other evolved from it.)

The term "sword" has been used to describe structures in other genera (e.g., in fish hobbyist publications to describe caudal fin extensions in guppies, *Poecilia reticulata*) that do not appear to be homologous to the sword found in swordtails, based on caudal rays counts, branching patterns, ontogeny, and the position of color pigments (Rauchenberger et al., 1990; Basolo, unpubl. data).

Within *Xiphophorus*, the term "sword" has also been used to describe a short, unpigmented protrusion (P) found naturally in two species of platyfish and to describe a short, unpigmented protrusion that can be hormonally induced (*p*) in two other species (Gordon et al., 1943; Zander and Dzwillow, 1969). In his revision of the genus *Xiphophorus*, Rosen (1979) referred to the structure P as a caudal appendage (described as the prolongation of the ventral-most principal caudal fin rays in adult males) and used the term sword within quotation marks for describing this short prolongation, indicating it was not a true sword. Such a structure is also seen occasionally in two of the three swordtails lacking a sword (*X. birchmanni*, *X. pygmaeus*). This structure is never seen in the other swordtail lacking a sword, *X. continens*. In this paper, P is considered a possible ancestral state for the sword component character E but is not equivalent to the complex sword. For this paper, a structure consisting of characters  $\bar{E}$ , L, C, PU, and either MDU or DMU is defined as a sword.

#### Preference for the Sword in Swordtails

To address the first criterion of the pre-existing bias model, I examined female preference for sword length in the green swordtail, *X. helleri*, a species in which males possess swords that vary in length. Females preferred conspecific males with longer swords to those with shorter swords (Basolo, 1990a). The sword is thus a target of female choice in this sworded species.

#### Evolutionary History of the Sword

Sexual selection arising from a preexisting bias requires that the origin of the preference precede the origin of the male trait. To address the second criterion of the pre-existing biases model, phylogenetic information must be assessed to establish the evolutionary history of the sword.

Four phylogenies have now been proposed for *Xiphophorus*, three of which are depicted in Figure 1. One is a composite phylogeny (Fig. 1a), constructed by impos-

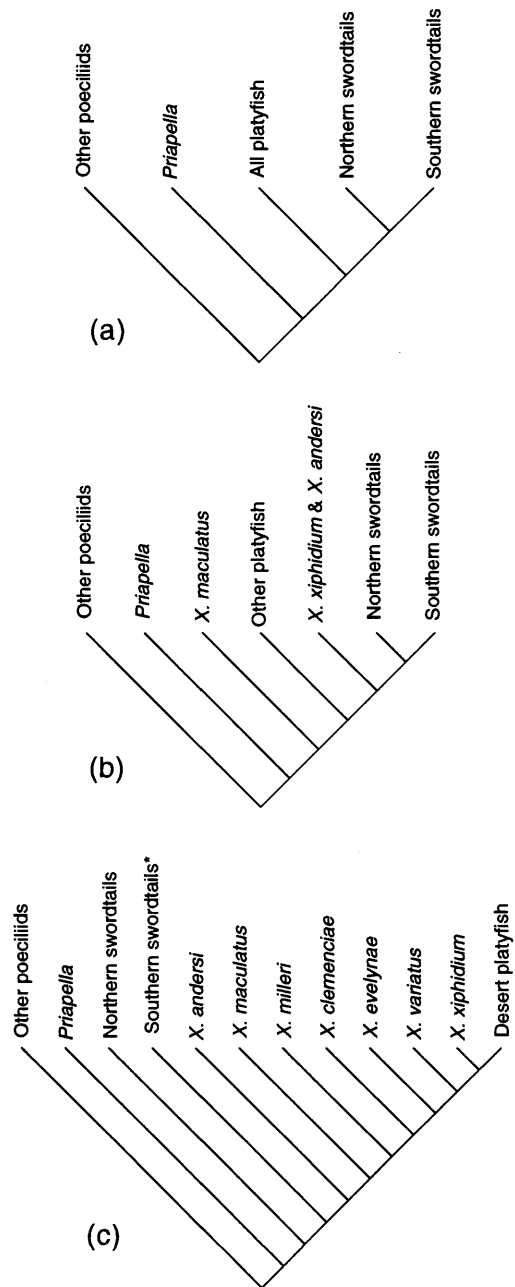


FIGURE 1. Three phylogenies showing proposed relationships of *Xiphophorus* and other poeciliids. (a) Composite phylogeny based on biochemical, genetic, and morphological characters, with biogeographic considerations (Rosen, 1979; Rauchenberger et al., 1990). (b) Phylogeny based on morphological and behavioral data (Haas, 1993). (c) Phylogeny based on molecular evidence (Meyer et al., 1994). \* = all southern swordtails except *X. clemenciae*.

ing Rauchenberger et al.'s (1990) phylogeny at the appropriate node of Rosen's (1979) phylogeny (consolidated by Basolo, 1991). This phylogeny, the culmination of nearly 50 years of work by a number of researchers (Gordon, 1947; Rosen and Gordon, 1953; Atz, 1962; Miller and Minckley, 1963; Rosen and Bailey, 1963; Kallman and Atz, 1966; Kallman, 1971, 1975, 1989; Rosen, 1979; Borowsky, 1984; Morizot and Siciliano, 1984; Rauchenberger et al., 1990), was derived using biochemical and genetic hybridization data and a suite of morphological characters, with biogeographic considerations. This phylogeny suggests that swordtails are a monophyletic group and that the components constituting a sword appeared progressively, with a completely assembled sword appearing relatively late in the evolutionary history of the group (Basolo, 1991, 1995a). The Rosen/Rauchenberger et al. composite phylogeny in its entirety, representing the relationships of 22 of the 23 described species of *Xiphophorus* (the platyfish *X. andersi* is not represented) is shown in Figure 2a, with the character states of sword components depicted. Rauchenberger et al. (1990) listed the lower melanophore stripe component of the sword (L) as a character that unites the two swordtail clades: the northern and the southern swordtails. However, the ontogeny of sword development suggests that the evolution of the upper melanophore stripe is not straightforward. Of the 14 species of described swordtails, 3 do not have an upper stripe (*X. pygmaeus*, *X. birchmanni*, *X. continens*). However, two of these three species have a grave spot (G). The proximal portion of the upper stripe (PU) appears to be a synapomorphy of the northern and southern swordtails, but the condition for the distal portion of the upper black coloration is not clear. DMU appears to be the primitive condition because it is shared by one species each from the southern and northern swordtail clades, whereas the upper stripe portion MDU may be the derived condition for the remaining four species in the southern swordtail clade. Available information for sword coloration (C) (Kallman and Bao,

1987; Rauchenberger et al., 1990) suggests that this character is shared between the two swordtail groups. Regarding the sword, Rauchenberger et al. (1990:21) concluded that the distribution of the character long sword (involving character E but not character P) "is most parsimoniously interpreted as a synapomorphy uniting the northern and southern swordtail groups." However, they conceded that the form of the long sword in the northern swordtails may not be homologous to the form of the long sword in the southern swordtails and that these two "evolved in parallel from a common ancestor with a gene pool that permitted the evolution of a long sword" (Rauchenberger et al., 1990:21). Therefore, although parsimony suggests that the northern and southern swordtails are united by the general development of long pigmented swords in males, Rauchenberger et al. allowed that there is evidence concerning the shape of the sword and differences in the development of the upper melanophore stripe between the two groups of swordtails that indicates that the sword may not be homologous for all components. Some evidence suggests that the sword may have evolved further after the divergence of the northern and southern swordtails clades (primarily the differences in the development of the upper black distal portion of sword coloration and the branching pattern of the most elongated rays of the sword). Nonetheless, the southern and northern swordtails are united as a monophyletic group, and they share the presence of a sword composed of elongation (E), the lower black melanophore stripe (L), an interior field of coloration (C), and the proximal portion of the upper black stripe (PU). Using parsimony, the composite phylogeny suggests that swordlessness is the ancestral state, because the platyfish and the sister genus *Priapella* lack a long pigmented sword. In addition, *Priapella* species lack character P, which is found in the platyfish *X. andersi* and *X. xiphidium*. Therefore, this character likely arose after the divergence of *Xiphophorus* and *Priapella*. From the distribution, character P and the genetic ability to



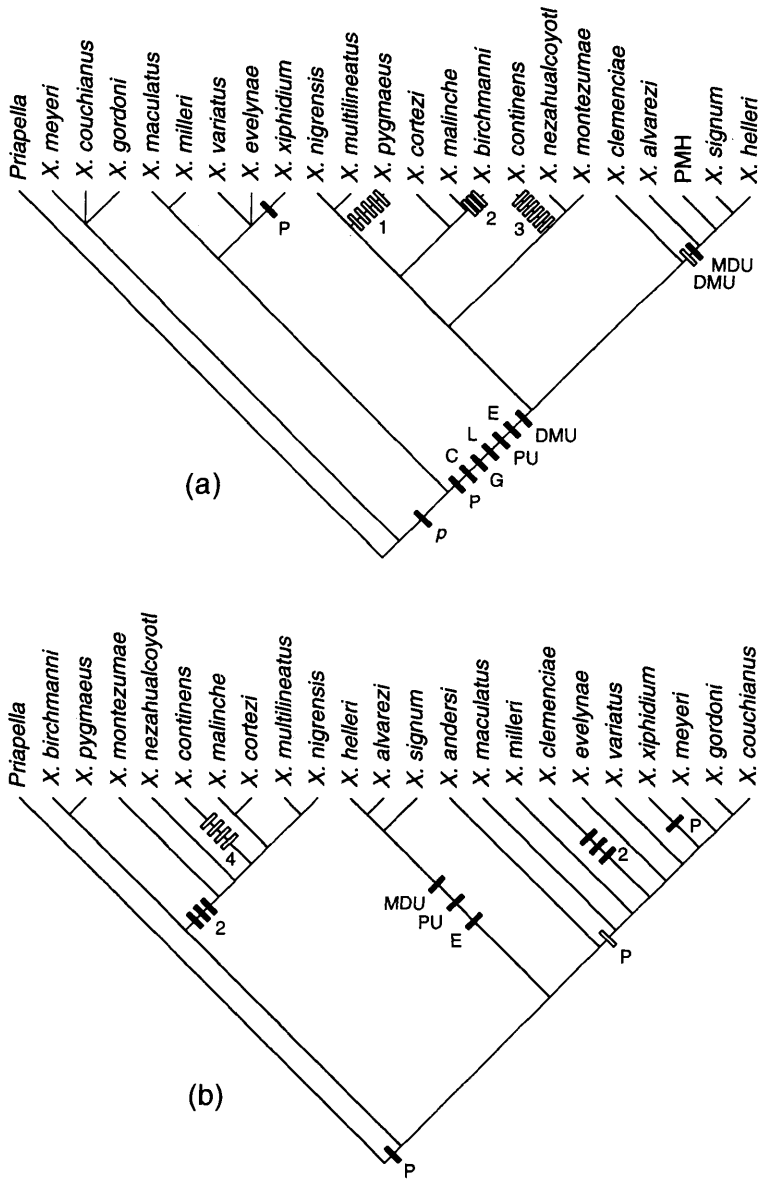


FIGURE 2. Two proposed *Xiphophorus* phylogenies with caudal fin characters and sword component characters mapped onto two proposed phylogenies. 1 = characters PU, G, E, DMU, L; 2 = characters PU, E, DMU; 3 = characters PU, C, E, DMU, P, L; 4 = characters E, P, PU, DMU. ■ = gain of character; □ = loss of character. (a) Rosen (1979)/Rauchenberger et al. (1990) composite phylogeny. (b) Meyer et al. (1994) phylogeny, with G, C, and L not depicted because interpretation of character appearance is equivocal.

express this character (character *p* = unexpressed genetic ability to produce a protrusion; some female and male *X. maculatus* and *X. milleri* that do not normally have a protrusion develop one with hormone

treatment, whereas *X. variatus*, *X. couchianus*, and *X. gordonii* do not) appear to have arisen after the divergence of the desert platyfish from the rest of *Xiphophorus*. *Xiphophorus continens* has secondarily lost

character P along with all component characters constituting a sword. For the swordtails *X. birchmanni* and *X. pygmaeus*, character P ( $\leq 5$  mm prolongation) and the color components of the sword (L, PU, C) are occasionally expressed and thus appear either to be in the state of evolutionary loss or to have reached some equilibrium state at which they are maintained at a low frequency.

A second phylogeny based on courtship behavioral traits and morphological traits differs in its placement of several species (Haas 1993; Fig. 1b); the southern platyfish *X. maculatus* is placed basal to the rest of the genus and the platyfish *X. xiphidium* and *X. andersi* are grouped together. Despite these differences, the sword still appears to be a derived composite character within *Xiphophorus*, arising after the divergence of the platyfish and the swordtails. This phylogeny suggests that P arose after the divergence of the swordtails and the two platyfish species *X. andersi* and *X. xiphidium* from the rest of the platyfish. Based on this phylogeny, there are two equally parsimonious explanations for character *p*: (1) *p* is a primitive character for the genus *Xiphophorus* and has been secondarily lost by both *X. variatus* and the desert platyfish or (2) *p* has arisen three separate times.

In a third phylogeny (Meyer et al., 1994; Fig. 1c) based on partial sequences from three genes, the swordtails are not a monophyletic group and the platyfish are placed within the swordtails (data for the swordtail PMH [see Table 1] were not included in this analysis). Meyer et al. (1994) used their phylogeny to investigate male caudal fin elaboration in *Xiphophorus*. In their analysis, they called different structures a sword: not only those structures consisting of E, C, L, PU, and either MDU or DMU but also those defined here as P. With these two different criteria for a sword, they concluded that a sword is ancestral for the genus *Xiphophorus*, and the distribution of the character states based on this phylogeny (Fig. 2b) suggests that a sword defined as such has been gained three times and lost once. (However, Meyer et al. omitted the

present state for *X. continens*, which is the lack of P and of any other sword characters; their conclusion should have been three gains and two losses.) In essence, however, their analysis suggests only that character P likely is ancestral for the genus *Xiphophorus* (see also Wiens and Morris, 1996) and has been lost once and regained at least twice within *Xiphophorus*. To investigate the evolution of the sword using this phylogeny, characters E, C, L, PU, MDU, and DMU must be considered; based on the distribution of E, PU, MDU, and DMU, the most-parsimonious conclusion is that these characters are not ancestral to but have multiple origins within the genus *Xiphophorus*. The conclusions for characters C, L, and G based on this phylogeny are equivocal. There are three equally parsimonious interpretations for G, each involving four evolutionary events; two suggest that G is a derived condition within *Xiphophorus* and one suggests that G is ancestral for *Xiphophorus*. There are three equally parsimonious interpretations for L, each involving five evolutionary events; two suggest that L is a derived character for *Xiphophorus* and one suggests that L is ancestral for *Xiphophorus*. There are two equally parsimonious interpretations for C, each involving four evolutionary events; one suggests that C is derived within *Xiphophorus* and the other suggests that C is ancestral for *Xiphophorus*. Therefore, based on this phylogeny, the distribution of four sword components suggests that a composite sword is not ancestral to the genus. In addition, the most-parsimonious analysis of the distribution of E, PU, DMU, and MDU suggests that none of these sword components have occurred in any platyfish lineage.

In another phylogenetic treatment of *Xiphophorus*, Borowsky et al. (1995) used arbitrarily primed polymerase chain reaction (AP-PCR) data to investigate the relationships of 14 of the 23 known species of *Xiphophorus* to produce an unrooted tree. They converted both the Rosen/Rauch-berger et al. composite phylogeny (Fig. 2a) and the molecular phylogeny based on three genes (Fig. 2b; Meyer et al., 1994) to

unrooted trees and compared each to the unrooted tree they generated; they concluded that their tree was "very consistent" with the composite phylogeny and "less so" with the three-gene molecular phylogeny. Because this AP-PCR molecular phylogeny is unrooted, its utility in determining the evolution of the sword components as such is poor and will not be discussed further in this context.

The evidence that a preexisting bias has played a role in the evolution of the sword in the genus *Xiphophorus*, as well as any investigation on the origin and subsequent change in the bias, critically depends on the phylogeny. Problems with conflicting phylogenies at one taxonomic level, however, may be circumvented by examining the character states in outgroups to obtain a clearer picture of character evolution. Members of *Priapella*, the proposed sister genus of *Xiphophorus*, lack any sword component and lack the caudal fin characters G and P. In addition, composite swords are not known to occur in any other species of poeciliid fishes. Some traits similar to sword components are found in other species, but their structure, rarity, and scattered phylogenetic distribution indicate that they are homoplastic rather than homologous characters. Thus, the sword appears to be a derived structure that arose after the divergence of *Priapella* and *Xiphophorus*. Consequently, by referring to phylogenetic relationships outside of the genus *Xiphophorus*, the second criterion for the preexisting biases model is satisfied and in full agreement with all proposed phylogenies; parsimony suggests that the absence of the sword is the ancestral condition for the *Priapella/Xiphophorus* group (Rosen, 1979; Meyer et al., 1994).

#### Evolutionary History of the Preference Favoring a Sword

Sexual selection arising from a preexisting bias requires that the origin of the preference precede the origin of the male trait. To address the third criterion of the preexisting bias model, I tested sword preferences of female platyfish and female

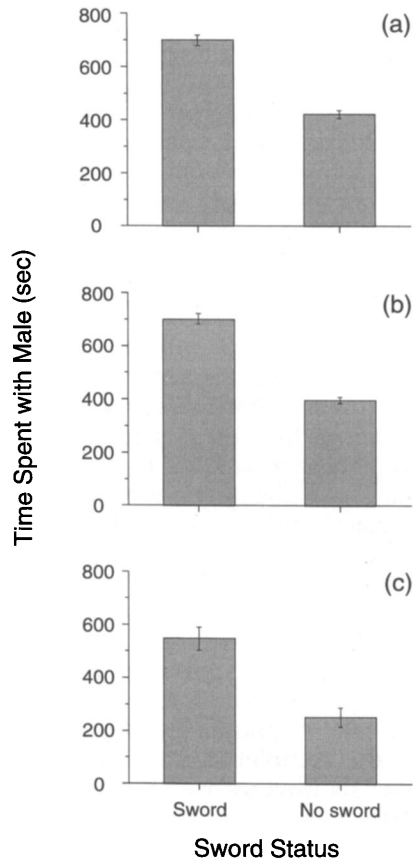


FIGURE 3. Preference for conspecific males with artificial swords for three species. (a) *Xiphophorus maculatus* (six of six females preferred conspecific males with artificial swords; two-tailed binomial test,  $P = 0.03$ ). (b) *Xiphophorus variatus* (six of six females preferred conspecific males with artificial swords; two-tailed binomial test,  $P = 0.03$ ). (c) *Priapella olmecae* (13 of 14 females preferred conspecific males with artificial swords; two-tailed binomial test,  $P < 0.01$ ). [This comparison is for illustrative purposes. Because experimental methodology varied, the data may not be strictly comparable.]

*Priapella* to assess the evolutionary history of the preference favoring a sword.

Preference for conspecific males with swords was found in two species of platyfish, the southern platyfish, *X. maculatus* (Basolo, 1990a; Fig. 3a), and the variable platyfish, *X. variatus* (Basolo, 1990c, 1995b; Fig. 3b), despite the absence of a sword in both species (this result has been verified for *X. variatus* by Haines and Gould [1994]). In these choice tests, the character

state of males was manipulated by surgically attaching artificial swords to males. To control for surgery and swimming effects, paired males each received a lower caudal extension, but one test male received a complete sword consisting of elongation, a lower stripe, a complete upper stripe, and interior yellow coloration, and the other received a clear attachment of equal length. This clear attachment simulates absence of a sword but controls for surgery effects and the influence of the attachments on swimming and courtship behavior. The results for these two platyfish species satisfy the third criterion of the preexisting bias model for the composite phylogeny and the phylogeny based on morphological and behavioral traits (Figs. 1a, 2a, 1b) but not for the three-gene molecular phylogeny (Meyer et al., 1994) when the presence of P is considered as the presence of a sword (Figs. 1c, 2b). Considering the first two phylogenies, it appears that a preference for a sword arose in the ancestor of platyfish and swordtails, whereas the completed composite sword arose after the divergence of platyfish and swordtails.

Although the three-gene molecular phylogeny suggests an alternative scenario for male sword evolution when the presence of character P is considered as presence of a sword, it sheds no light on the evolution of the preference for a sword. This phylogeny suggests that a "sword" evolved in the ancestor of platyfish and swordtails, after the divergence of *Priapella* and *Xiphophorus*. However, it does not distinguish between the two possible hypotheses for the relative time of origin of the preference: (1) the preference evolved simultaneously with the sword or (2) the preference evolved prior to the origin of the sword. Based on this molecular phylogeny, it is impossible to accept one of these hypotheses to the exclusion of the other. Thus, although the molecular phylogeny provides support for an alternate hypothesis for the evolutionary history of a "sword," it provides no support for any of the five models for the evolution of the preference favoring a sword.

The sword appears to have evolved either subsequent to the divergence of platyfish and swordtails (Figs. 1a, 1b) or in the common ancestor of platyfish and swordtails when P is scored as presence of a sword (Fig. 1c). When P is assumed to be a sword (Meyer et al., 1994), the critical test of the preexisting bias model to explain preference favoring a sword therefore involves testing preferences of females in outgroups to *Xiphophorus*. Considering *Priapella* as the closest relative to *Xiphophorus*, three hypotheses can be generated concerning the distribution of a preference favoring a sword: (1) a homologous preference is shared by *Priapella* and *Xiphophorus*, (2) *Priapella* lacks a preference favoring a sword, and (3) *Priapella* has a preference favoring a sword, but this preference is not homologous to that found in *Xiphophorus*.

The conflict generated by the conclusions drawn from the three-gene molecular phylogeny and the other proposed phylogenies can be resolved by determining the character state for the character sword preference for the proposed sister genus *Priapella*. Preference tests were conducted to determine whether *P. olmecae* females preferred conspecific males with artificial swords to conspecific males without swords. Like female platyfish, female *P. olmecae* preferred conspecific males with artificial swords to males without artificial swords (Fig. 3c; see also Basolo, 1995b). These results suggest that a preference favoring a sword is an ancestral condition shared by the sister taxa *Priapella* and *Xiphophorus*, and this conclusion is consistent with all three of the proposed rooted phylogenies (Fig. 1). Regardless of relationships within *Xiphophorus*, these results suggest that the preference favoring a sword evolved prior to the origin of the sword itself. A less parsimonious explanation for the presence of a shared preference in the four species tested is that the preference favoring a sword has evolved several times. However, this interpretation requires at least two independent evolutionary events: the evolution of a preference in the *Xiphophorus* clade and the evolution of a similar preference in the

*Priapella* clade. A preexisting bias hypothesis, in which a single evolutionary event accounts for a shared preference, is a more parsimonious explanation. Whether the ancestral bias resulting in the demonstrated preference favoring a sword in the two species of platyfish and *Priapella* is specific for a sword or for something else has yet to be addressed.

By referring to phylogenetic relationships outside of the genus *Xiphophorus*, resolution of the problem presented by the differing phylogenies is attained. *Priapella* and *Xiphophorus* share the ancestral condition of sword preference, and the sword arose later, after the appearance of the preference. With the combined phylogenetic evidence, the three criteria to support a preexisting bias model for the evolution of a preference for a sword are satisfied. In addition, phylogenetic information indicates that there was an "adaptive field" for the sword when it appeared.

#### TESTING OTHER HYPOTHESES IN A PHYLOGENETIC CONTEXT

The data suggest that a preexisting bias has played a role in the establishment of a sword preference and in the subsequent evolution of the sword: (1) female green swordtails prefer conspecific males with longer swords, (2) the sword is either a shared derived character of swordtails or a shared derived character of *Xiphophorus*, and (3) a preference favoring a sword is a shared primitive state for *Xiphophorus* and *Priapella*. This knowledge of the phylogenetic distribution of the preference and the sword allows us to propose and test additional hypotheses concerning the evolutionary history of the preference favoring a sword.

The existence of a preexisting bias does not necessarily preclude a role for other processes in the evolution of a mating preference. For example, a preexisting bias may select for a male trait once it arises, but as the male traits evolves, other processes may subsequently modify the preference, depending on the nature of genetic variation in the female bias and the fitness consequences of such variation. Once a pre-

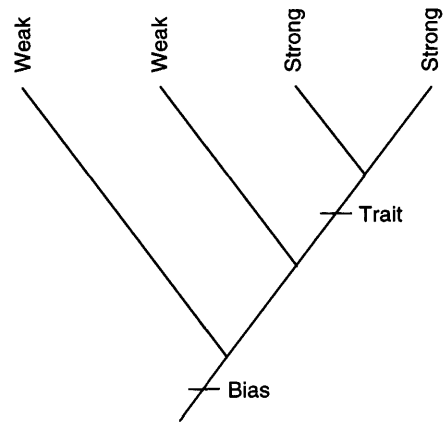


FIGURE 4. Hypothetical distribution for the strength of a female preference (bias) prior to the appearance of a male trait and after the male trait has arisen if there has been coevolution of the preference and the trait.

existing bias has been documented, it then becomes possible to use a phylogenetic approach to test whether other processes have modified the bias after the origin of the male trait favored by the bias. Given a phylogeny, robust inferences about when the bias arose in relation to when the male trait arose can be made, and we can make predictions about how the preference may vary among taxa. If other processes have modified a preference after the origin of the trait, the strength of the preference could either be stronger or weaker in taxa in which males possess the trait than in taxa exhibiting the primitive conditions of the presence of the female bias and the absence of the male trait.

For poeciliid fishes, Fisherian processes, good genes models, and some direct benefits models predict that the strength of the preference favoring a sword should be greater in species with swords than in species with the preference but without swords in their evolutionary history (Fig. 4). These coevolutionary hypotheses would thus predict that the strength of the preference favoring the sword will be greater in swordtails than in *Priapella*. Alternatively, if there is a cost associated with expressing the preference or if the trait and preference become genetically linked and

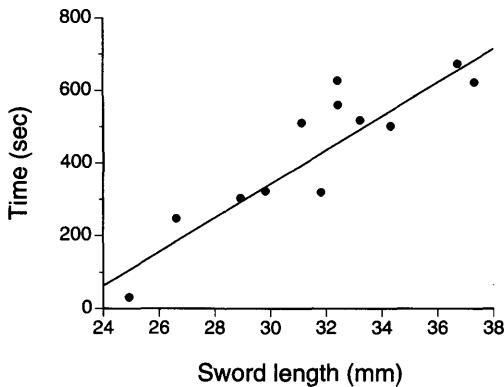


FIGURE 5. Strength of female preference for sword length in *Priapella olmecae* (from Basolo, 1995b). The amount of time females spent in courtship was significantly correlated with male sword length ( $n = 12$ ,  $r = 0.9$ ,  $P < 0.001$ ).

there is a cost to expressing the trait, the bias in *Priapella* could be stronger than that in *Xiphophorus*. One way to quantify the strength of a female preference is to determine the preference function (Wagner et al., 1995), which describes variation in the strength of a female's response in relation to expression of the male trait. The steeper the slope of the preference function, the more strongly females prefer greater values of the trait.

Based on one or a combination of the coevolutionary models, we might predict that the preference functions based on male sword length would be stronger in swordtails than in *Priapella*. I examined the relationship between male sword length and the amount of time females spent in courtship with sworded males in *P. olmecae* by attaching artificial swords to conspecific males. Females were tested using a single stimulus design; in these choice tests, a single male and a companion female were presented to each test female. Individual females were randomly assigned males of variable sword lengths, and each test female and male were only used once. In these tests, the sword preference in *P. olmecae* was positively correlated with sword length; as sword length increased, the strength of the preference increased (Fig. 5 [from Basolo, 1995b]). These results illus-

trate that in *P. olmecae*, an unsworded genus, the preference favoring a sword is an increasing function of sword length.

#### PREDICTIONS

Once the strength of a preference is determined for a group lacking the favored trait, this preference function can be used to investigate how the preference has changed since the trait appeared. In the case of *Xiphophorus*, female preference functions in swordtails such as *X. helleri* can be determined. If the bias has not been modified subsequent to the divergence of *Priapella* and *Xiphophorus*, the preference function in *Priapella* and in swordtails should not differ. However, if evolutionary processes have influenced preference evolution after the divergence of *Priapella* and *Xiphophorus*, we would predict that the preference function in *Xiphophorus* will differ from that in *Priapella*.

In addition, once a preference has been found in a group lacking the male trait, the strength of the preference can be compared with that in more distantly related groups. From such analyses, information can be obtained concerning bias origin and changes in the strength of the preference prior to trait evolution. With phylogenetic inference concerning the distribution of the preference and the strength of the preference, we can determine whether the initial bias has changed since its origin. Thus, phylogenetic information concerning the strength of a preference can be important in examining the origin of a bias and in examining changes in an initial bias. If such changes are found, phylogenetic information may also be useful in generating hypotheses concerning why such changes may have occurred.

#### Possible Costs of Preference Expression

Numerous costs could be associated with expression of a preference for a male trait. If the degree of preference expression is positively correlated with search cost (time and/or energy involved in finding a preferred mate), then searching for a male with a preferred trait would be costly to the female. In addition, searching could in-

crease predation risk, if females with the preference take longer to find mates and thus expose themselves to a greater predation risk than do females who do not have the preference.

If females with a bias favoring a male trait are more likely to mate with males with the trait once it has arisen, this will lead to a genetic correlation between the trait and the preference. If the preference is open ended, i.e., if females with the bias prefer the most extreme variation of the traits (in the case of swordtails, longer and more colorful swords), and if the trait is costly, then the bias may decrease in strength as an indirect result.

The examples given here are just several of the possible ways in which expression of a preference could carry a cost. By using phylogenetic information about the strength of the preference in sworded and unsworded species, we can determine whether changes in a bias occur prior to the appearance of the male trait it favors, as neural network simulations suggest (Enquist and Arak, 1993), and whether changes occur after the male trait arises, as suggested by both coevolutionary models and models in which there is a cost associated with preference expression.

#### *Examining the Bases of Bias*

The *Xiphophorus* group appears to be an excellent example of the accumulation over time of a suite of characters resulting in an elaborate male trait: the genetic ability to produce a short protrusion arose but was not expressed, ability was followed by actual protrusion expression, and expression was then followed by elongation of varying degree with several types of pigmentary coloration. By examining the appearance of the different components of the sword along with variation in the strength of the preference among taxa, one can examine whether the preference was strengthened with each additional component and if and to what degree each of the sword components contributes to the preference favoring a sword in swordtail species. For example, the initial bias may have favored fin elongation. Once a mutation arose in-

roducing coloration to the fin elongation, a preference for coloration may have evolved that strengthened the overall preference for the sword (this is one of numerous possible scenarios). By comparing female preference functions across taxa for various sword components, it may be possible to determine if some components of the preference coevolved with the sword components they favor. In this way, the comparative method presents the potential to track the historical pathway of change in components of female preferences and male traits.

Whether the preference for the composite sword is general for a structure lacking one or several of the components of a complete sword is not known. Likewise, whether or not this preference will favor character P (called a sword by other researchers; Meyer et al., 1994) is also unknown.

#### PREEXISTING BIASES AND THE ADAPTIVE EVOLUTION OF THE SWORD

Robust phylogenetic information can provide information about the adaptive value of a male trait when it arises. Although this point seems obvious, in light of current criticism concerning the usefulness of using phylogenies to test hypotheses of adaptation (Reeve and Sherman, 1993; Frumhoff and Reeve, 1994), a brief discussion relative to sword evolution seems appropriate.

For the genus *Xiphophorus*, phylogenetic information suggests that the evolution of the sword was a result of adaptive selection in the form of female mate choice. Phylogenetic hypotheses suggest that the preference favoring a sword arose before the sword itself appeared. Thus, although it is not known whether the ancestral preference for a sword arose via adaptive processes, nonadaptive processes, or a combination of the two, it does appear that sword evolution was adaptive and thus that the sword is an adaptation in a sexual selection context.

Frumhoff and Reeve (1994) identified a number of difficulties in using phylogenies to test hypotheses of adaptation. The fol-

lowing are addressed here, using the evolution of the sword as an example: (1) the danger of using parsimony, (2) the problem of homoplasies and parallel evolution of similar traits in related taxa, (3) physiological constraints on character evolution, (4) the original versus current function of the character under consideration, and (5) the appropriateness of using phylogenies to test hypotheses of adaptation when the selective environment is not expected to have remained invariant.

First, a danger in using parsimony is that a character that is gained and then repeatedly lost and regained may be incorrectly determined to be a single gain when it is present in an extant group. In the case of the sword, this danger is decreased because we are considering a composite character. That is, the sword is not a single character; it consists of component characters that appear to have accumulated over time. Although other poeciliids have traits that resemble components of the sword, it is unlikely that these are homologous to sword components, and no other poeciliid has a complete sword. However, in one species of swordtail all sword components appear to have been lost, and in two additional species several sword components appear to have been secondarily lost. In the case of the preference, it is not known whether the preference for the sword found in four poeciliid species thus far is homologous or not.

Second, Frumhoff and Reeve (1994) expressed concern about the possibility of parallel evolution producing homoplastic but similar traits. However, preexisting biases are expected to favor the independent evolution of similar traits in different groups. Although a number of lineages may share a preexisting bias for a male trait, these different lineages are not expected to experience identical mutations. Thus, although the genetic blueprint for the male trait is not expected to be the same in most cases, the selective pressure via the preexisting bias is expected to be similar. In this way, male traits that resemble one another but are not homologous may be very common when they are a re-

sult of the same preexisting bias and in fact may be an identifying characteristic of male trait evolution in closely related species when a preexisting bias is involved.

Third, although in many cases male traits may be physiologically constrained to evolve down one pathway, this does not seem to be the case for at least some components of the sword. In the case of the upper melanophore stripe, there appears to be at least two separate pathways to the expression of the distal portion of this stripe. In the case of yellow, orange, and/or green coloration layered between the two melanophore stripes, there is variation both within and across swordtail species in the pigment-cell composition of this layer (Kallman and Bao, 1987; Basolo, pers. obs.).

Fourth, the statement that "reconstructed phylogenies cannot reliably be used . . . to determine whether a character originally spread in ancestral populations through natural selection for its current function" (Frumhoff and Reeve, 1994:172) does not appear to be true when considering the evolution of male traits via preexisting biases (using the same assumption as Frumhoff and Reeve used, the reconstructed phylogeny closely corresponds to the true phylogeny). If the condition exists in which a species has both the trait and preference for the trait and a closely related species lacks the male trait but shares the ancestral condition of the preference, then there is good inferential support that the trait spread at least in part through sexual selection for its current function (mating success).

Fifth, in the case of preexisting biases, we are considering the association of a male trait and a selective component of the biotic environment, i.e., females of the same species. Although the original environment, i.e., the ancestral females, may have had the preference at a frequency of  $<1$  and there may have been variation in the strength of the preference, demonstration of the preference in current females of both a species with the male trait and a sister species lacking the male trait (ancestral state) is strong evidence that the male



trait has evolved as an adaptation. In the case of the sword, even if sword preference has changed in frequency or strength over evolutionary time, the direction of the preference, i.e., for males with swords, has not changed.

Consequently, although female preferences based on a preexisting bias favoring a sword may or may not have an adaptive origin, the condition at the origin of the sword was undeniably adaptive for this male trait. Thus, in the case of preexisting biases, we have a general model to establish that a male trait spread at least in part for an adaptive function. In the *Xiphophorus* group, a source of selection favoring a trait was present prior to the trait itself and a male trait subsequently arose and capitalized on this preexisting bias. Such adaptive selection driven by preexisting biases in females may also explain the evolution of male traits in frogs (Ryan et al., 1990), jumping spiders (Clark and Uetz, 1992), water mites (Proctor, 1992), and Uganda kob (Deutsch, 1994).

#### CONCLUSIONS

The results presented here confirm the idea that a preexisting bias resulting in the preference favoring a sword is a primitive character for *Xiphophorus* or some larger unsworded group of fishes and thus likely played an important role in the evolution of the sword in this genus. As these results illustrate, knowledge about phylogenetic relationships can allow us to test hypotheses that would otherwise be difficult, if not impossible, to test. In addition, knowledge of phylogenetic distribution of traits may suggest new testable hypotheses. Without knowing that the preference is a shared ancestral trait for the *Xiphophorus/Priapella* complex, whereas the sword is a derived trait for *Xiphophorus*, we would not think to investigate how the preference might have changed since the origin of the male trait.

Caution is needed when using the comparative method to attribute a female preference to a preexisting bias model. Unless a robust phylogeny is available, female preferences may be incorrectly categorized

as preexisting biases. These apparent preexisting biases may actually be residual or retained primitive preferences (Basolo, 1995a), as appears to be the case in at least one study (Ryan and Wagner, 1987) in which preferences for male traits were shown in species that had secondarily lost the trait. However, knowledge of both the phylogeny and the distribution of a preference and trait can allow discrimination of true and apparent preexisting biases.

Once a residual preference has been detected, it is possible to test whether the loss of the trait has been accompanied by a reduction in the strength of the preference, as would be predicted by a number of models of sexual selection. For example, coevolutionary models suggest that with the loss of a trait, there would be a corresponding decrease in the strength of the preference. Alternatively, selection may have caused reduction in the preference, which in turn could result in the loss of the trait. For example, for *Xiphophorus*, the phylogenies suggest that some components of the sword have been secondarily lost. In such cases, we can ask whether the preference has weakened with the loss of sword components.

There are numerous ways in which knowledge of trait distribution obtained from robust phylogenetic inferences can be useful in generating new hypotheses. In the case of preexisting biases, knowledge concerning the evolution of the sword in swordtails allows for hypotheses to be tested concerning the evolution of the preference favoring the sword. By referring to the phylogeny, hypotheses can be generated and tested concerning the origin of the preference, changes in the preference over evolutionary time, what specific male traits the bias has influenced in different lineages, and whether the bias has changed since the appearance of the sword.

#### ACKNOWLEDGMENTS

I thank J. Endler, K. Kallman, D. Leger, and W. E. Wagner, Jr., for helpful conversations on the ideas presented here, W. E. Wagner, Jr., for input on experimental design and for constructive criticism of this manu-

script, and D. Cannatella, J. Losos, D. McLennan, and an anonymous reviewer for their critical reviews of this manuscript. This work was supported by NIMH National Research Individual Service Award F32-MH10089, an Animal Behavior Society Research grant, NIMH B-START award MH55288-01, and NSF RPG 9509211.

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Received 15 September 1995; accepted 1 May 1996

Associate Editor: Jonathan Losos