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Evolutionary change in a receiver bias: a comparison of female preference functions

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Female poeciliid fishes of the sister genera *Xiphophorus* and *Priapella* share a preference for males with swords, despite phylogenetic information suggesting that swords arose in *Xiphophorus* after the divergence of the two genera. This study examines the strength of sword and body-size preferences in a representative of both genera. A comparison of the preference functions reveals that the strength of the preference favouring a sword in *P. olmecae* is significantly stronger than that in *X. helleri*. This result demonstrates that the pre-existing bias is not evolutionarily fixed, and that there has been change in the bias favouring the sword, in either the *Priapella* lineage, or the *Xiphophorus* lineage, or in both. Although females in both species prefer conspecific males with swords, only *X. helleri* females also demonstrate a body-size preference. The preference functions for body size and sword length for *X. helleri* are not significantly different, whereas in *P. olmecae* the preference function for sword length is significantly stronger than for body size. These combined results indicate that an ancestral bias for body size cannot alone explain the pre-existing bias favouring a sword in *P. olmecae*.

Keywords: preference function; pre-existing receiver biases; sexual selection; mate choice; poeciliids

1. INTRODUCTION

One model for the evolution of mating preferences proposes that biases are established prior to the appearance of traits in the opposite sex and that these pre-existing receiver biases can play a role in the evolution of traits in the opposite sex (West-Eberhard 1984; Kirkpatrick 1987a,b; Endler & McClellan 1988; Basolo 1990a, 1995a,b, 1996; Ryan 1990; Ryan & Rand 1990; Christy 1995; Hurd *et al.* 1995; Dawkins & Guilford 1996; for a review, see Endler & Basolo (1998)). It suggests that there are biases present in the information processing system resulting from evolutionary mechanisms that are independent of intersexual selection on the specific trait under study, and that these biases can play a subsequent role in sexual selection. Such pre-existing receiver biases can function in female and/or male choice, but by convention, here the term will be used in reference to female preferences. Biases can be at the level of the peripheral nervous system or at the higher level of processing and integration. A bias may be specific for a trait, it may be general in nature but presently favour a specific trait, and/or it may be specific for one or more components of a complex trait. The establishment of a role of a pre-existing bias in the evolution of a male trait via female choice does not preclude a role for other mate-choice mechanisms as sources of selection on either preference or trait evolution.

Although phylogenetic evidence has proven useful in the detection of pre-existing biases (Basolo 1990a, 1995a,b; Ryan *et al.* 1990a; Clark & Uetz 1992; Proctor 1992; Ryan & Rand 1993), the evolutionary processes that have resulted in the establishment of these biases are not well characterized. To understand why biases have

evolved, it is first necessary to understand the nature of such biases. One approach to understanding the origin and evolution of pre-existing biases is to investigate possible base(s) of such biases. There are a number of ways to study possible bases to biases, including examining the neural mechanisms resulting in a bias, or determining the types of traits that stimulate a bias. The former approach provides direct information about the mechanistic bases of a bias, whereas the latter attempts to define the bias by identifying the types of traits that stimulate it. To date, two studies have tested possible underlying bases to receiver biases. Ryan *et al.* (1990a) investigated the frequency sensitivity of the hearing apparatus in females in the genus *Physalaemus*, and found that a peripheral sensory bias correctly predicted a female preference based on male calling behaviour. Basolo (1990a, 1995b) found preferences for both a sword, a composite male trait in swordtail fish, as well as for a single component of the sword, in an unsworded relative of swordtails, *Xiphophorus maculatus*, suggesting that this single component may contribute to the preference favouring a sword.

One system in which the role of pre-existing biases in the evolution of female preferences and male traits has been studied is a group of live-bearing fish, the poeciliids (Rosen & Bailey 1963). This group includes a tribe in which some species of a single genus, *Xiphophorus*, possess a sexually dimorphic male trait, the sword. The sword is a composite trait consisting of a number of components: upper black stripe, lower black stripe, internal carotenoid and/or pterin stripe coloration, and elongation of certain ventral caudal-fin rays. Most swordtail species possess at least two components (see Basolo (1996) for component variation). The sword in the green swordtail, *X. helleri*,

consists of all four components. Female green swordtails prefer conspecific males with longer swords to conspecific males with shorter swords (Basolo 1990b). Based on morphological data, *Priapella* was proposed as the sister genus of *Xiphophorus* (Rosen 1979; this hypothesis has been corroborated with molecular data from Meyer *et al.* (1994)). Based on caudal-fin ray counts, fin branching patterns and coloration, neither *Priapella* nor other poeciliids possess a structure that is homologous to the sword (Basolo 1995b). By testing *P. olmecae*, it was determined that females prefer conspecific males with swords, and thus that the preference favouring a sword is a shared character for these two genera (Basolo 1995b). Based on phylogenetic information and the combined results from female choice tests, it appears that a bias favouring a sword arose prior to the divergence of the *Xiphophorus*–*Priapella* clade, whereas the sword arose within the genus *Xiphophorus*.

Although past studies suggest that the bias favouring a sword arose before the sword itself, most of these studies provide little information about either variation between taxa in the strength of the bias or about the cause of the bias. Sherman & Wolfenbarger (1995) suggested that biases are fixed, but this need not be the case (Basolo 1990a; Basolo & Endler 1995). In addition, little is known about the nature of biases. Numerous possible bases for a bias exist: (i) a general bias for conspicuous or colourful traits; (ii) a bias for novel male traits (but see Basolo (1990a) for restrictions); (iii) a bias favoured by natural or sexual selection which the sword or sword components stimulate (e.g. a preference for body length favours long swords); and (iv) sensory architectures favoured by selection that have correlated consequences, as has been suggested by simulations of neural network models (Arak & Enquist 1993; Enquist & Arak 1993). These are but a subset of possible bases for initial biases and none of the possible bases are mutually exclusive. Selection on a trait may be a result of one or several biases acting in concert with other sources of selection, which may act to modify an initial bias (Basolo 1995a).

Using the comparative method, it may be possible to determine whether an ancestral bias for body size has had a correlated effect resulting in the bias favouring a sword. To support the idea that the sword bias results from an ancestral preference for larger males (Basolo 1990a; Ryan 1990), it must be shown that both *Priapella* and *Xiphophorus* share a body-size preference. Previous results have demonstrated a preference for body size in three swordtail species (Ryan & Wagner 1987; Ryan *et al.* 1990b; Basolo 1998). Thus, it is possible that an ancestral bias for larger body size in the *Xiphophorus*–*Priapella* clade could, as a by-product, favour the evolution of the sword, if the sword increases perceived male length in the horizontal plane. Rosenthal & Evans (1998) suggest that in green swordtails, preferences for body size and sword length do not differ, but whether an ancestral body-size preference can explain the ancestral sword bias is unknown. To understand if the sword bias is merely an extension of an ancestral bias for overall length in the horizontal plane, one needs to determine the nature of both the sword preference and the body size (here measured as standard length) preference within *Xiphophorus*, as well as in a sister taxon.

In this paper, the absolute preference functions for standard length and sword length are examined in *X. helleri* and *P. olmecae* to determine whether a preference for standard length is a possible basis of the bias favouring a sword in the *Xiphophorus*–*Priapella* clade and whether there has been evolutionary change in the bias after its origin. Absolute preference functions measure female response to trait variance presented in isolation (Wagner 1998). Previous work investigating relative sword preferences in *X. helleri* (Basolo 1990b) and absolute preference functions in *P. olmecae* (Basolo 1995b) suggests that in both species, the sword preference is an increasing function of sword length. However, the effect of standard length on female response was not controlled in these experiments. First, I compare the strength of the sword preferences in *X. helleri* and *P. olmecae*. If the preference for the two species do not differ, this would suggest that there has been no evolutionary change in the bias favouring the sword since the divergence of the two genera. If the strength of the sword preferences is found to differ, this would suggest that there has been evolutionary change in the bias favouring a sword. Second, I compare the sword and standard-length preferences within *X. helleri* and *P. olmecae*. If a preference for standard length is the basis of the bias favouring the sword, we would predict that sword length and standard length would be equally important to females; a unit increase in sword length should have the same effect on female response as a unit increase in standard length, if the preference function for sword length is a result of the preference for standard length. This result would suggest that an ancestral bias for standard length could explain the presence of a sword preference in both species. However, if the sword-length preference is stronger than the standard-length preference, particularly in *P. olmecae*, this would suggest that a standard-length preference cannot, by itself, explain the bias favouring a sword.

2. MATERIALS AND METHODS

X. helleri and *P. olmecae* are live-bearing fish found in freshwater streams and rivers in Mexico and Belize. *X. helleri* test subjects were first-generation offspring of fish collected from Savannah Stream, near mile marker 28, Western Highway, Belize. *P. olmecae* test subjects were first-generation offspring of fish collected from Rio Palma, Vera Cruz, Mexico. The fish were maintained in the laboratory and fed three times daily with shrimp nauplii, liver paste and fish flakes. Each species was raised in communal juvenile tanks until individuals approached sexual maturation. At this time, males were removed to communal same-sex tanks.

A preference favouring a sword has been established for both *X. helleri* and *P. olmecae* using a simultaneous stimulus design, in which a female is presented with two males that differ in a single trait. However, Wagner (1998) has argued that when measuring the strength of a preference, a single-male rather than a two-male choice design is the preferred method. Using this method, an absolute preference function is derived by measuring the variation in female response with variation in male trait value across tests. Here, a single-male design was used in which males varied across tests in standard length and sword length, female response was measured as the time spent attending to a single male, and the response times for multiple females were compared across tests.

The general methods and test apparatus to assay female preference have been described previously (Basolo 1995a). An abbreviated description follows. A test female was placed in the centre section of the test tank. A male with an artificial sword was placed in either a left- or right-hand section of the tank formed by polarizing filter-plate dividers. Across tests, the side in which males were placed first was altered. A juvenile conspecific was placed in the section at the opposite end of the test tank from the male to control for the possibility of schooling behaviour confounding the preference measure. After an acclimatization period of 10 min, the amount of time a virgin female spent attending to a sworded male, defined as interacting with or watching the male within a distance of three body lengths, was recorded for a 10-min trial period. The female was placed in the centre section for a second acclimatization period of 10 min and the male and juvenile were switched from one side to the other; a second trial period of 10 min followed. The two trials constituted a single test. The amount of time each female spent attending to the male for the two trials was summed and this sum was compared across tests. Because male sword length and standard length varied across tests for each species, the relationship between the amount of time females spent with sworded males, and male sword and standard lengths could be assessed.

Mature males were measured for standard length (distance from the anterior tip of the mouth to the insertion of the caudal-fin rays, just posterior to the caudal vein) and each received a surgically attached artificial sword ranging from 70–130% of their standard length (method described in Basolo (1990a, 1995a,b)). Ten male *X. helleri* ranging in standard length from 33.2 to 46.4 mm ($\bar{x}=40.3$ mm) received artificial swords ranging from 31.8 to 47.0 mm ($\bar{x}=38.2$ mm). Fifteen male *P. olmecae* ranging in standard length from 27.8 to 37.9 mm ($\bar{x}=31.7$ mm) received artificial swords ranging from 25.1 to 37.5 mm ($\bar{x}=31.6$ mm). Males of different standard lengths were haphazardly assigned swords of varying length, such that there was no correlation between sword and standard length (*X. helleri*, $n=10$, $r=-0.13$, $p=0.71$; *P. olmecae*, $n=15$, $r=0.18$, $p=0.53$). This assignment method maintained both the range of sword lengths and the ratios of sword to standard length measured for green swordtail populations in the field (A. L. Basolo and W. E. Wagner Jr, unpublished data). As the range in standard length of *P. olmecae* males is lower than that of *X. helleri*, the range in artificial sword lengths was also lower. However, the ratio of artificial sword length to standard length (*X. helleri*, $\bar{x}=0.96$, s.e.=0.05, range=0.73–1.23; *P. olmecae*, $\bar{x}=1.0$, s.e.=0.03, range=0.70–1.28) did not differ for the two species (t -test, d.f.=23, $t=0.73$, $p=0.48$). Artificial swords consisted of four components naturally present in green swordtails: ray elongation, upper and lower melanophore stripes, and yellow internal coloration. For *X. helleri*, the extension portion of natural swords was surgically removed and artificial swords were overlaid on the natural sword coloration of the caudal fin. Males were given a 5–7 day recuperative period before conducting female choice tests. Tests were conducted between 08.00 and 12.00. Variation among males in courtship behaviour was not quantified. However, during the tests, normal intersexual behaviour was observed (Basolo 1990b, 1995b) and each male actively interacted with the test female. No female or male was used in more than one test.

The amount of time females spent with males of varying sword and standard lengths was compared across males both within and between species. First, I examined the independent effects of sword length and standard length on female response

for each species using multiple regression. The partial regression coefficients were used to estimate female preference functions for each trait. To determine the relative importance of sword and standard lengths for each species, the partial regression coefficients were compared by restricting the parameter estimates in SAS (1989) using a Lagrangian parameter for each restriction (Pringle & Raynor 1971). Second, I compared the preference functions for standard length between *X. helleri* and *P. olmecae* using ANCOVA. In this analysis, the effect of sword length on female response was adjusted before analysis using the partial regression coefficient for sword length. For example, when comparing the standard-length preference functions between *X. helleri* and *P. olmecae*, the effect of sword length (SWL) on female response was controlled separately for each species using the relation: $\text{time}_{\text{adj}} = \text{time}_{\text{obs}} \pm \beta_{\text{SWL}} (\bar{x}_{\text{SWL}} - \text{SWL})$, where β_{SWL} is the partial regression coefficient of sword length on female response. In this analysis, a significant interaction between species and standard length indicates a significant difference in the standard-length preference functions of the two species. Third, I compared the preference functions for sword length between *X. helleri* and *P. olmecae* in the same manner as the comparison of standard-length preference functions.

3. RESULTS

A multiple regression showed that in *X. helleri* there was a significant combined effect of standard length and sword length on female response ($F_{2,7}=22.47$, $p=0.001$); together, sword and standard lengths explained 86.5% of the variation in the time females spent attending to males. Controlling for the effect of sword length on female response, the time female *X. helleri* spent attending to males was positively correlated with standard length; females spent more time with larger males than smaller males (partial regression coefficient, $\beta=18.54$, s.e.=3.79; two-tailed $t=4.89$, $p=0.002$; figure 1a). Controlling for the effect of standard length, the time female *X. helleri* spent attending to males was positively correlated with sword length; females spent more time with longer-sworded males than shorter-sworded males (partial regression coefficient, $\beta=15.05$, s.e.=2.89; two-tailed $t=5.2$, $p=0.001$; figure 1b). The relative importance of standard length and sword length was examined by comparing the partial regression coefficients (i.e. the slopes of the preference functions). For *X. helleri*, the difference between the partial regression coefficients for standard and sword lengths was not significant ($t=0.81$, $p=0.44$); there was thus, no difference between the preference functions for standard length and for sword length in this species.

A multiple regression showed that in *P. olmecae* there was a significant combined effect of standard length and sword length on female response ($F_{2,12}=16.43$, $p<0.001$); together, sword and standard length explained 73.3% of the variation in the time females spent attending to males. However, controlling for the effect of sword length on females response, the time female *P. olmecae* spent attending to males was not correlated with standard length; females did not spend more time with larger males than with smaller males (partial regression coefficient, $\beta=-7.05$, s.e.=12.26; two-tailed $t=-0.58$, $p=0.58$; figure 1c). Controlling for the effect of standard length, the time females spent attending to males was

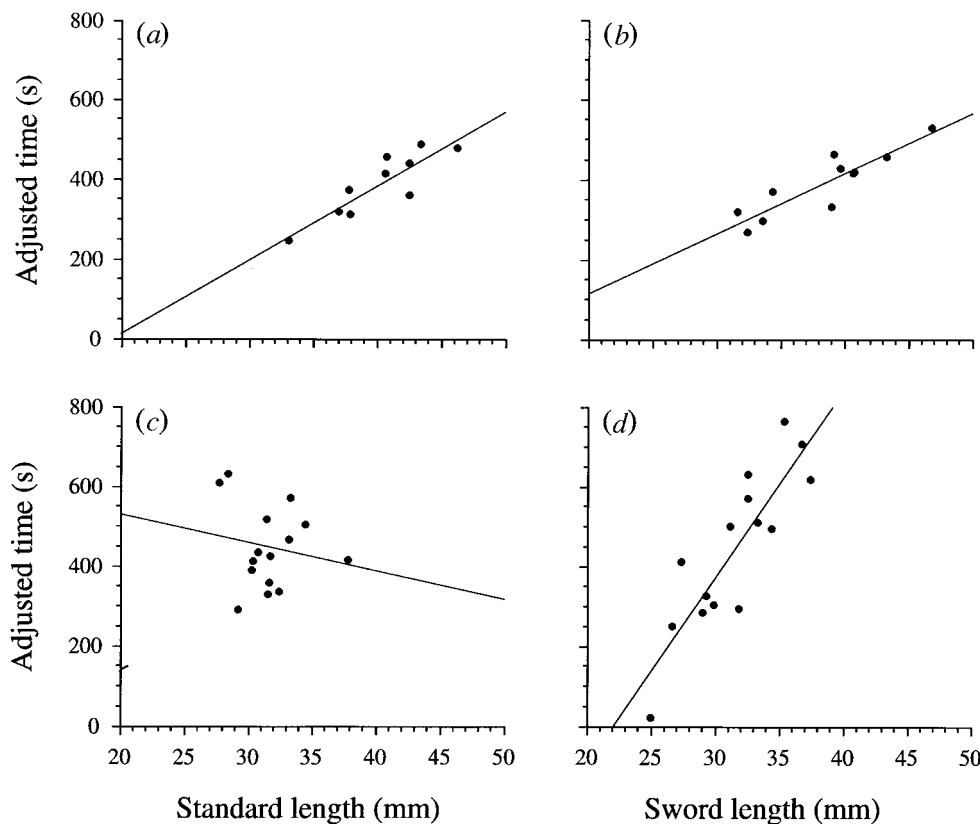


Figure 1. Female preference functions for standard length and sword length in two poeciliids. (a) Preference for standard length, controlling for sword length in *X. helleri*. (b) Preference for sword length, controlling for standard length in *X. helleri*. (c) Preference for standard length, controlling for sword length in *P. olmecae*. (d) Preference for sword length, controlling for standard length in *P. olmecae*.

positively correlated with sword length; females spent more time with longer-sworded males than shorter-sworded males (partial regression coefficient, $\beta=46.95$, s.e.=8.37; two-tailed $t=5.6$, $p<0.001$; figure 1d). For *P. olmecae*, the difference between the partial regression coefficients for standard and sword lengths was significant ($t=2.45$, $p=0.029$); thus there is a significant difference between the preference functions for standard length and sword length in this unsworded species. The female response to sword length is significantly stronger than that to standard length.

ANCOVA was used to compare the standard-length preferences of *X. helleri* and *P. olmecae*. In this comparison, the effect of sword length on female response was controlled for each species. There was a significant interaction between standard length and species ($F_{1,21}=5.17$, $p=0.026$), indicating a difference in the slopes of the standard-length preference functions between the two species. The standard-length preference was significantly stronger in *X. helleri* than in *P. olmecae* (figure 1a,c).

ANCOVA was used to compare the sword length preferences of *X. helleri* and *P. olmecae*. In this comparison, the effect of standard length on female response was controlled for each species. There was a significant interaction between sword length and species ($F_{1,21}=6.95$, $p=0.015$), indicating a difference in the slopes of the sword-length preference functions between the two species. The sword-length preference was significantly stronger in the historically unsworded species, *P. olmecae*, than in the sworded species, *X. helleri* (figure 1d,b).

4. DISCUSSION

Coevolutionary models for the evolution of female preferences, such as Fisherian-processes models, good-

genes models, and some direct-benefits models, suggest that the strength of a preference will increase subsequent to the origin of a male trait, as a result of either a genetic correlation between the preference and the male trait, or a genetic correlation between the preference and male fitness (Lande 1981; Kirkpatrick 1982; Pomiankowski 1988). If the sword preference in *P. olmecae* represents the ancestral state of the bias, and such coevolutionary processes occurred after the origin of the sword, one would predict that the sword preference function would be stronger in *X. helleri* than in *P. olmecae*. However, this is not the case; the preference for sword length is greater in *P. olmecae* than in *X. helleri* (figure 1d,b). This result is interesting for several reasons. First, if *P. olmecae* represents the ancestral state of the bias, then it appears that a preference for a sword in the green swordtail has actually weakened since the divergence of *Priapella* and *Xiphophorus*. A decrease in the strength of a preference could result from: (i) genetic drift; (ii) a cost associated with preference expression (e.g. Holland & Rice 1998); (iii) a cost associated with sword expression, once the trait was established and genetically correlated with the preference; and (iv) selection on the bias via intrasexual selection, natural selection or intersexual selection in another context. However, the finding that the strength of the bias favouring a sword is presently weaker in *X. helleri* than in *P. olmecae* does not necessarily rule out the role of one of the coevolutionary processes as important in shaping the present preference function in *X. helleri*. It could be that, initially, the genes for the preference and the sword became linked in *Xiphophorus* and the preference and trait coevolved; thus, the strength of the preference would have initially increased with the degree of sword expression. Subsequently, the strength of the

preference could have decreased for one or a combination of the four reasons given above. In this case, the preference in swordtails would have initially experienced positive selection, followed by negative selection to reach its present state, rather than solely negative selection since the divergence of *Priapella* and *Xiphophorus*.

Whether *P. olmecae* or *X. helleri* more closely represents the ancestral bias favouring the sword, it is clear that there has been change in the bias since the divergence of the two genera. If *P. olmecae* represents the ancestral state of the bias, the results suggest that the strength of the preference weakened in *Xiphophorus* after the divergence of *Priapella* and *Xiphophorus*. If *X. helleri* represents the ancestral state of the bias, the results suggest that the strength of the preference bias has strengthened in *Priapella*. But regardless of the ancestral condition for the bias, the results for *P. olmecae* and *X. helleri* demonstrate that pre-existing biases are not necessarily evolutionarily fixed. Evidence of no difference in the strength of a bias across taxa would suggest either an absence of genetic variation for the bias or strong selection on the bias in another context. If a shared ancestral bias is fixed, we would not expect coevolution of trait and preference, and therefore, there would be no modification in the preference as a result of trait evolution. If the bias for the sword were the result of a fixed sensory bias, there should be no measurable difference between the strength of the preference in the two species tested. However, the results suggest that there was genetic variation for the bias favouring the sword in the ancestor of the two taxa and they thus reject the hypothesis that the pre-existing bias favouring a sword is historically fixed for the *Xiphophorus*–*Priapella* clade.

It is not possible to determine from this work whether the bias favouring a sword in *P. olmecae* and in this species of *Xiphophorus* have the same evolutionary origin; parsimony, however, would suggest that the shared bias has a common basis. Although it is clear that there has been change in the sword bias since the divergence of *Priapella* and *Xiphophorus*, the change may not have occurred in the *Xiphophorus* clade. Without information on the sword preferences of other poeciliids, it is not possible to determine whether the preference function found in *P. olmecae* represents the ancestral state of the bias. One possibility is that the preference function for *P. olmecae* is not typical of other species of poeciliids possessing the primitive state for the male trait; it may be that other species of poeciliids would show a weaker preference than *P. olmecae*. In addition, the population of *X. helleri* tested may be neither typical of other *X. helleri* populations nor typical of other swordtail species. It may be that other populations of swordtails would show a preference equal to or stronger than that of *P. olmecae*. Therefore, there may have been change in one or both of the lineages tested. To clarify the evolutionary history of the bias, a measure of the bias in more distantly related taxa and in more swordtail populations is necessary.

If a preference for standard length is the basis of the sword bias, sword and standard lengths should be equally important; the preference for standard length should predict the response for sword length. This is clearly not the case for *P. olmecae*, as this species demonstrates a strong sword preference, yet no preference for standard

length was detected. Only in *X. helleri* did both standard length and sword length have a significant effect on the time females spent attending to males, although it is not known whether the preference for larger males was in part due to a trait correlated with body size. However, a bias for standard length does not appear to explain the preference favouring a sword in *P. olmecae* (see Basolo (1990a, 1996) for possible alternative bases for the sword bias). Using manipulated video stimuli, and a simultaneous presentation design, Rosenthal & Evans (1998) found that female *X. helleri* do not discriminate between a sworded male stimuli 70.0 mm in total length (standard plus sword length) and an enlarged, unsworded male stimuli 83.0 mm in total length (standard plus caudal length). From these results, they concluded that a general preference for large size could explain the preference for a sword. Based solely on the *X. helleri* data presented herein, the same conclusion could be drawn. However, the available phylogenetic evidence combined with the results for *P. olmecae* suggests that a bias for large body size cannot alone explain the sword bias in this sister genus.

Although a preference for body size cannot explain the sword bias in *P. olmecae*, it is not clear whether the ancestor of *P. olmecae* and *X. helleri* possessed a preference based on body size. It is possible that the ancestral state was the presence of a body-size preference, and that this preference was secondarily lost in *Priapella* after the divergence of these two genera. Alternatively, a standard-length preference may have arisen in *Xiphophorus*. Information about the preference functions for both standard-length and sword length in more distantly-related taxa could be used to address this issue. It is clear, however, that a body-size preference is not necessary for the expression of a strong sword bias. As a result, the sword bias does not appear to be the correlated consequence of a body-size preference.

5. CONCLUSIONS

The present study adds to our growing understanding of pre-existing receiver biases as a general model for the evolution of female preferences and male traits, and it provides several insights into the nature of the bias favouring a sword. Here it is established that such biases are not necessarily genetically fixed, and that such biases do evolve. Although, in the case of the sword bias it is not clear whether the change occurred before sword evolution, during sword evolution, or in the *Priapella* lineage. In addition, the results suggest that the comparative method is essential when investigating biases. Here the data for the green swordtail cannot reject the hypothesis that a preference for overall length in the horizontal plane has led to a sword preference. However, the evidence that the sister taxa *P. olmecae* shares a sword bias but has a standard-length bias that is significantly weaker suggests that a bias for overall length cannot explain the present sword preference in this sister genus. Numerous questions remain to be answered concerning the nature of the bias favouring a sword and how pre-existing biases evolve in general. Further research investigating the nature of the bias favouring a sword, in a variety of sworded and unsworded species, should produce a more accurate characterization of the state of the bias both

before and after sword evolution, as well as add to the growing base of knowledge concerning bias and trait evolution.

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