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Shared Preferences by Predators and Females for Male Ornaments in Swordtails

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ABSTRACT: Sexually dimorphic traits in many mate recognition systems have evolved in response to preexisting female biases. These biases are often quite general in form and are likely to be shared by predators, thereby imposing a cost on male trait expression. The Mexican tetra *Astyanax mexicanus* (Pisces: Characidae), a visual predator of swordtail fishes, exhibits the same visual preferences for male body size morphs as do females. Furthermore, tetras in populations where swordtails are absent prefer males with sword ornaments over males with swords removed. The predator preference is thus likely to have arisen prior to contact with fishes bearing the ornament, as has also been suggested for mating preferences for swords.

Keywords: sexual selection, visual signals, predation, Poeciliidae, *Xiphophorus*.

Sexual selection often favors conspicuous traits, an advantage counterbalanced by the fact that predators are often preferentially attracted to sexual ornaments (Endler 1980, 1983; reviewed in Zuk and Kolluru 1998). Such attraction can arise in at least two ways. Predator sensitivity can coevolve with the display trait, a phenomenon particularly well documented with acoustic cues (e.g., Tuttle and Ryan 1981; Wagner 1996).

Conspicuousness to receivers, however, need not arise through a coevolutionary process (Basolo 1990*b*; Endler 1992; Burley and Symanski 1998; Ryan 1998). Biases to-

ward particular cues may arise from selection in another context (e.g., Proctor 1991) or emerge from other perceptual tasks (Enquist and Arak 1993). There are numerous instances of such preexisting preferences in the context of mating (Ryan 1998). In such cases, conspicuous male traits have evolved in response to latent biases in females.

Preexisting preferences can also manifest themselves in predators, although this has rarely been demonstrated. Sparrowhawks are more likely to prey on great tits artificially supplied with bright red markings, even though these ornaments are not normally present in the species (Götmark and Olsson 1997). For visual traits, it is particularly likely that any preexisting female biases will be shared with predators. An increase in conspicuousness almost always involves an increase in brightness, size, or contrast with the background (Ryan and Keddy-Hector 1992; Andersson 1994). Visual predators of displaying animals are particularly likely to share many features of visual perception with their prey. Similar environmental light conditions will select for similar perceptual traits. If predators are to detect unornamented individuals of the prey species, these must be within the range of their spatial frequency sensitivity and detectable, at least to some degree, from the background. These attributes make it likely that any trait that is conspicuous to potential mates will also be conspicuous to predators. While conspicuous visual traits are likely to carry increased predation risk, there are only a handful of studies where this has been demonstrated (Zuk and Kolluru 1998; see Moodie 1972; Haas 1976; Endler 1978, 1983; Slagsvold et al. 1995). Few, if any, of these can differentiate between preexisting bias and a coevolutionary scenario where predator perception of prey has evolved in response to prey signals.

This study focuses on two related traits in male swordtails (Poeciliidae: *Xiphophorus*). Males have evolved swords—colored elongations of the caudal fin with contrasting components—in response to a preexisting preference on the part of females (Basolo 1990*b*, 1995*b*). Preferences for swords are found in swordless platyfish (Basolo 1990*b*) and *Priapella olmecae* (Basolo 1995*b*), which diverged from swordtails prior to the origin of the sword.

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This preference appears to reflect a more general bias for large apparent size: the preference of female *Xiphophorus helleri* for swords is abolished when the size of a swordless male is augmented to match that of a male with a sword (Rosenthal and Evans 1998).

The preference for body size is broadly shared as well. In the northern swordtails *Xiphophorus multilineatus* and *Xiphophorus nigrensis*, most variation in male body size can be explained by variation at the *P* locus on the Y chromosome. Small males reach sexual maturity earlier, are slender bodied, and lack conspicuous courtship displays. Large and intermediate males mature later, have robust bodies, and perform elaborate displays to potential mates (Ryan and Causey 1989; Zimmerer and Kallman 1989). Female northern swordtails *X. multilineatus*, *X. nigrensis*, and some populations of *Xiphophorus pygmaeus* all show preferences for large body size classes (Ryan and Wagner 1987; Ryan et al. 1990). Female *X. nigrensis* show preferences for large and intermediate males over small males but not between large and intermediate males (Ryan et al. 1990). Female preference for body size is likely an ancestral trait as well, widely present in poeciliids and other taxa (Rosenthal and Evans 1998). Both the presence of swords and the length of swords are correlated with genotype: intermediate and large males tend to express longer swords and are more likely to express swords (Rosenthal 2000).

A visual preference for large size is widespread in many ethological contexts (Staddon 1975; Ryan and Keddy-Hector 1992) and may arise from the fact that large objects stimulate a larger area of the retina (Rowland 1989). Predators are often size selective, preferring larger prey (Wilbur 1988), although there are few studies addressing the basis of this preference. In one case, bluegill sunfish preferred daphnia of larger apparent size (independent of actual size; O'Brien et al. 1976). These factors suggest that visual predators of swordtails may share with their prey an ancient preference for large size, manifesting itself as a bias for both large males and males with swords.

Northern swordtails are restricted to small, shallow streams with a low diversity of diurnally active animals that are potential visual predators. The eleotrid fish *Gobiomorus dormitor* is present at very low densities in a small subset of northern swordtail populations; gut content analyses reveal that these fishes prey on fishes and aquatic insects (Rosenthal 2000). Cichlid fishes, including *Herichthys* ("*Cichlasoma*") *labridens* and *Herichthys carpintes*, co-occur with every northern swordtail species. Gut content analyses of *H. labridens* from the Río Choy, where they co-occur with *X. nigrensis*, indicate that fishes are only an occasional prey item, with snails forming the majority of the diet (G. G. Rosenthal, T. Y. F. Martinez, M.

J. Stephens, F. J. G. de Leon, and M. J. Ryan, unpublished data).

The Mexican tetra *Astyanax mexicanus* co-occurs with every northern swordtail species except *Xiphophorus malinche*. The natural range of the species extends across the Atlantic slope from the Río Grande (Río Bravo del Norte) drainage, through the Río Pánuco basin, and south to the Río Cazonés and upland Río Papaloapan systems (Miller and Smith 1986). They are sympatric with northern swordtails in the Río Pánuco and nearby internal drainages. The Sierra Tamaulipas, formed during the Eocene, and >1,000 km separate *A. mexicanus* in the Río Grande drainage from conspecifics and swordtails in the Río Pánuco drainage.

Astyanax mexicanus is opportunistic and omnivorous, with a broad diet including algae, aquatic insects, benthic invertebrates, and fishes (Birkhead 1980). In swordtail habitat, *A. mexicanus* form shoals ranging from tens to thousands of individuals (Rosenthal 2000). Fishes comprise approximately 10%–15% of identifiable gut content volume of Mexican tetras in the Río Choy, where they co-occur with *X. nigrensis*. Because *A. mexicanus* take small bites out of prey items, individual food items in the gut of *A. mexicanus* were not identifiable to species (Rosenthal 2000). Experimental exposure of swordtails to tetras in seminatural enclosures results in loss of swords in approximately 50% of males. In addition, tetras are highly aggressive and may injure swordtails in the course of agonistic interactions (Rosenthal 2000). Tetras are therefore likely to be an important agent of natural selection on visual traits in swordtails.

We examined the body size preference of *A. mexicanus* from a population sympatric with swordtails. We subsequently examined the sword preference of *A. mexicanus* from two populations: one sympatric with swordtails and one unlikely to have encountered swordtails in its evolutionary history.

Methods

We performed experiments assaying the preferences of Mexican tetras for male swordtail morphology using the following general procedure. Male *Xiphophorus multilineatus* were collected from the Río Coy, Río Pánuco drainage, San Luis Potosí, Mexico. Animals were maintained on a 14L:10D light cycle and fed TetraMin flake food daily. Tetras were deprived of food for 24 h prior to testing. Visual preferences were assayed using methods similar to those used for measuring female association in swordtails (Ryan and Wagner 1987; Ryan et al. 1990; Baer et al. 1995). We used a 60 × 30-cm aquarium filled to a depth of 20 cm and divided along its length by glass dividers into two flanking sections 15 cm wide and a central section 30 cm wide. Animals were allowed to acclimatize for 15 min prior

Table 1: *Xiphophorus multilineatus* males used in preference experiments

Stimulus fish	Standard length (mm)	Sword extension length (mm)	Number of stimulus fish
Conspecific versus heterospecific—Nacimiento Río Huichihuayán and Waller Creek <i>Astyanax mexicanus</i> :			
<i>X. multilineatus</i>	34.6 ± 4.1	10.5 ± 7.1	5
<i>A. mexicanus</i>	40.4 ± 12.1		12
Body size morph preference—Río Choy <i>A. mexicanus</i> (sympatric):			
Large	32.5 ± 2.4	3.5 ± 2.4	12
Intermediate	29.3 ± 1.4	3.8 ± 2.0	10
Small	23.2 ± 1.3	1.6 ± 1.2	10
Sword preference—Nacimiento Río Huichihuayán <i>A. mexicanus</i> (sympatric):			
Sword	32.2 ± 2.7	5.1 ± 3.4	5
No sword	32.1 ± 1.8	0	5
Sword preference—Waller Creek <i>A. mexicanus</i> (allopatric):			
Sword	37.0 ± 2.7	14.9 ± 3.2	10
No sword	37.2 ± 2.5	0	10

Note: Stimulus fish are *X. multilineatus* males unless otherwise noted. Values are mean ± standard deviation. For “sword/no sword” experiments, values reflect sword length after manipulation.

to testing, with opaque sheets of Plexiglas covering the dividers and thus removing visual cues for both stimuli and subjects. An individual tetra was placed in the center section, and the swordtails were used as stimuli in the flanking sections. These dividers were then lifted, and the orientation of *Astyanax mexicanus* (left or right) was recorded for 3 min using a computer event-recording program. Orientation was operationally defined as the heading of the tetra’s snout; a heading within the 90° arc centered along the aquarium’s lengthwise axis was scored as a preference, while a heading in the 90° arc toward or away from the observer was recorded as neutral. Pilot tests showed that tetras spent the majority of the time in the central section, leaving it only for rapid attacks directed at the stimulus males. Tetras also habituated to the stimuli after 5 min, making it unfeasible to use attack rate as a response measure. We therefore used orientation toward a stimulus as our measure of preference. After this 3-min period, the stimulus fish were switched to control for side biases, after which we repeated the acclimatization and testing periods. We alternated the side of first presentation, such that the larger, or sworded, male was initially on the left side in every other trial. Although male *X. multilineatus* used as stimulus exemplars were reused within experiments (see below), we used a new set of both stimulus exemplars and subject *A. mexicanus* for each experiment.

Experiment 1

We sought to test whether tetras’ preferences for certain swordtail phenotypes reflected assessment in the context

of predation or a more general shoaling response. We presented six tetras from Waller Creek and six tetras from the Río Huichihuayán with a choice between a sworded *X. multilineatus* and an *A. mexicanus* from the same population, approximately matched for total length. We used a new *A. mexicanus* as a stimulus in each trial; three male *X. multilineatus* were used in two trials each, and two were used in three trials (table 1). Data from the two populations were pooled for statistical analyses.

Experiment 2

We tested tetras to determine whether they exhibited the same preferences for body size classes as female swordtails. *Astyanax mexicanus* were collected from the Río Choy, Río Pánuco drainage, San Luis Potosí, Mexico, where they are sympatric with *Xiphophorus nigrensis*, the sister species of *X. multilineatus* (Rauchenberger et al. 1990), which exhibits a body size polymorphism (Ryan and Causey 1989) and sword and body shape characteristics similar to *X. multilineatus*. Prior to the start of testing, male *X. multilineatus* were sorted by body size class (Zimmerer and Kallman 1989) into separate aquaria. For each tetra tested, we used a trio of *X. multilineatus* males from each phenotypic size class: small (<26 mm), intermediate (26–31 mm), and large (>31 mm). Each individual male was thus used in two tests with the same female; for example, the same large male was used in both the large-versus-small comparison and in the large-versus-intermediate comparison. Large and intermediate males tend to have longer swords than small males in nature; the large and inter-

mediate males in our sample had significantly longer swords than the small males (table 1; Mann-Whitney $U = 49$, $P < .01$). We tested three pairwise preferences: large versus small, large versus intermediate, and intermediate versus small. Because of permit restrictions, we were unable to use a distinct stimulus swordtail for each tetra. We used a total of 12 large males and 10 each of small and intermediate males. *Xiphophorus multilineatus* males were each used in sets of trials for two different females; four intermediate and three small males were used in trials for three subjects (table 1). To control for order effects, we systematically rotated the order of presentation of the three body size class comparisons. After testing, we measured the standard length (snout to hypural plate) and sword extension length (distance from the intersection of a line perpendicular to the axis of the ventral-most unextended caudal ray and crossing its tip with the ventral margin of the caudal fin to the tip of the longest caudal ray) of each male. Morphometrics for each stimulus class are given in table 1. All statistical tests were two tailed.

Experiment 3

We tested tetra preferences for male swords, first with a population sympatric with swordtails and then with an allopatric population that had not encountered swordtails in its recent evolutionary history. The sympatric population was from the Nacimiento of the Río Huichihuayán, Río Pánuco drainage, San Luis Potosí, where *A. mexicanus* co-occurs with the swordtails *Xiphophorus cortezi* and *Xiphophorus pygmaeus*; the latter has secondarily lost the sword. The allopatric population was the result of introductions of *A. mexicanus* from the Rio Grande drainage, Texas (Birkhead 1980). Neither the Colorado River nor Rio Grande drainages contain *Xiphophorus*.

We selected pairs of large *X. multilineatus* that were closely matched for body size and clipped off the sword extension (Basolo 1995a) of one individual. Fin clipping is a standard method of identifying fish or obtaining tissue samples from live individuals and is considered “a recommended procedure for many studies” (American Society of Ichthyologists and Herpetologists 1988). To control for any effects of manipulation, we clipped the sword of the sworded male 0.5–1 mm from the distal end of the sword. This procedure provided a control for any effects of manipulating the sword on male behavior. Since only a limited subset of *X. multilineatus* could be closely matched for body size, we reused *X. multilineatus* across treatments (table 1). We conducted two sets of tests: one on *A. mexicanus* from the Nacimiento Río Huichihuayán population, followed by tests on the Waller Creek population. We used a different set of male *X. multilineatus* for tests on each population. For the Waller Creek *A. mexi-*

canus, each male *X. multilineatus* stimulus pair was used for two different subjects (10 stimulus pairs total). For the tests on the Nacimiento Río Huichihuayán population, three male pairs were used twice, and two were used three times (table 1). We used two-tailed statistical tests for the first set of trials. Since the results of the first set of trials gave us a clear a priori prediction, statistical tests on the second set of trials were one tailed.

Results

Tetras oriented significantly more to *Xiphophorus multilineatus* males than to similarly sized conspecifics (fig. 1; mean response to *X. multilineatus*, 137 ± 16 s [mean \pm SE]; mean response to *Astyanax mexicanus*, 82 ± 15 s; Wilcoxon signed-ranks test, $N = 12$, $Z = -2.04$, $P < .05$). Tetras significantly preferred large to small *X. multilineatus* males (fig. 2A; Wilcoxon signed-ranks test, $N = 23$, $Z = -3.06$, $P < .002$) and intermediate to small males (fig. 2B; $N = 23$, $Z = -2.77$, $P < .01$) but did not show a preference between large and intermediate males (fig. 2C; $N = 24$, $Z = -0.06$, $P = .95$). Tetras in both the sympatric and allopatric populations significantly preferred the males with swords over their size-matched, manipulated, swordless counterparts (Nacimiento Río Huichihuayán, fig. 3A: $N = 12$, $Z = -2.20$, $P < .02$; Waller Creek, fig. 3B: $N = 20$, $Z = -1.76$, $P < .05$). There was no significant difference in response between populations (Mann-Whitney U -test statistic = 123, $N = 32$, $P = .91$).

Discussion

The visual preferences of Mexican tetras for male swordtail traits are markedly similar to the preferences of females. While these preferences do not necessarily predict the probability of attack, they do indicate the extent to which

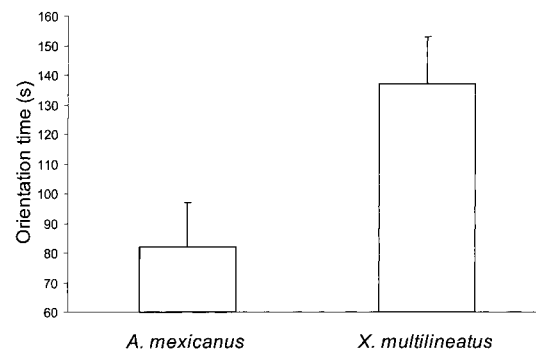


Figure 1: Orientation time (s; mean \pm SE) of *Astyanax mexicanus* with conspecific males versus *Xiphophorus multilineatus* males.

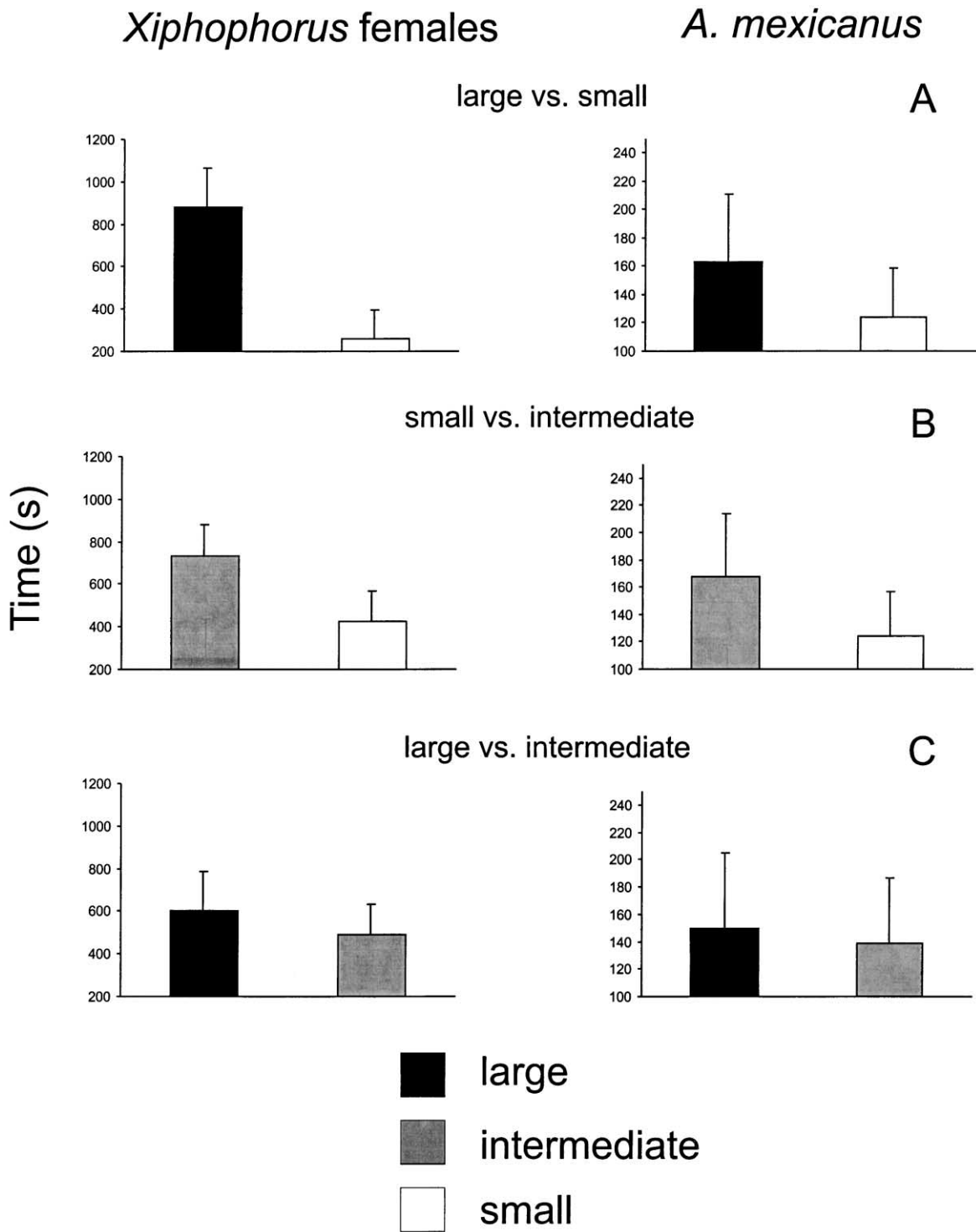


Figure 2: Association time (s; mean \pm SE) of female *Xiphophorus nigrensis* with conspecific males (after Ryan et al. 1990) and orientation time (s) of *Astyanax mexicanus* to *Xiphophorus multilineatus* males. Each row shows responses of female swordtails and tetras to the same male swordtail pairs: (A) large versus small, (B) intermediate versus small, and (C) large versus intermediate.

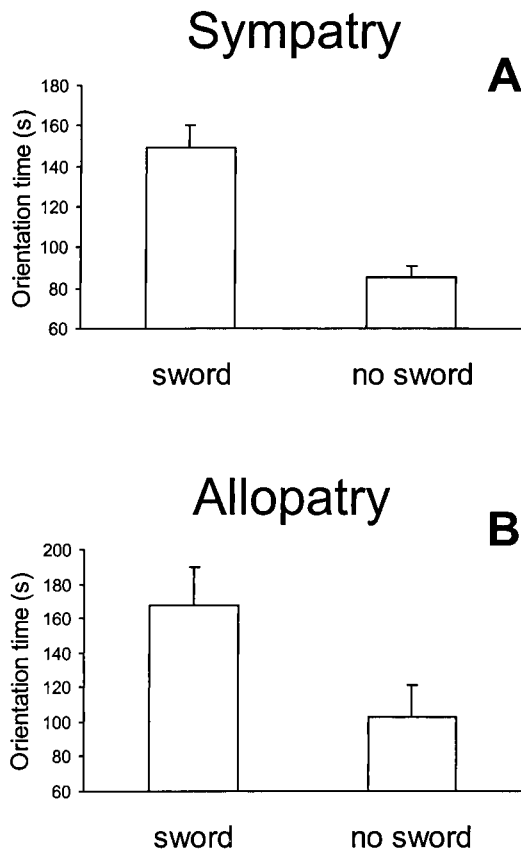


Figure 3: Orientation time (s; mean \pm SE) to *Xiphophorus multilineatus* males of *Astyanax mexicanus* from (A) the Nacimiento of the Río Huichihuayán, Río Pánuco system, and (B) Waller Creek, Colorado River system.

predators detect and attend to different phenotypes, a necessary first step in a predator-prey encounter (Endler 1991a). The significant preference of tetras for swordtails over similarly sized conspecifics, moreover, indicates that the preference is more specific than an inclination to shoal with other fishes and is likely to reflect a predation-specific response.

Ryan et al. (1990) suggested that females were attending primarily to the presence of courtship in intermediate and large males. Since males were not courting in this study, the predator preference is likely due to the greater aspect ratio and ornamentation of the large and intermediate males. The congruence of *Astyanax mexicanus* responses with those of female *Xiphophorus* suggests that predator preferences are influenced by factors other than gross size: large and intermediate males are similarly ornamented but differ in size, yet we were unable to detect a preference between the morphs. As with previous studies of preference for body size morphs (Ryan et al. 1990), we did not

attempt to control for sword length in experiments presenting *A. mexicanus* with different *P* genotypes, so this preference may in part be due to the fact that the intermediate and large males were, on average, expressing longer swords.

It is unclear whether predator preference plays a role in maintaining the genetic polymorphism in body size. Equal fitnesses of body size morphs can be explained by differences in maturation schedules and mating success alone, without assuming differences in postmaturation mortality (Ryan et al. 1992). While large males are more conspicuous to predators, they also have greater swimming endurance (Ryan 1988) and are likely to be faster swimmers. These factors may offset the conspicuousness cost of increased body size.

The presence or absence of a sword ornament elicited a preference from tetras in both populations. The need to size match stimulus males in these experiments limited the number of male exemplar pairs we could use, especially for the Río Huichihuayán population. Tetras exhibited consistent responses to all male stimulus pairs, however, which suggests that the effect of manipulating sword length was not obscured by random variation in other male traits. Tetras from the Río Huichihuayán are sympatric with *Xiphophorus cortezi*, which expresses a conspicuous sword, and *Xiphophorus pygmaeus*, in which the sword has been secondarily lost. Río Huichihuayán tetras exhibited preferences strikingly similar to those of allopatric *A. mexicanus* in the Río Grande drainage, which have likely been separated from swordtail habitat by the Sierra Tamaulipas, and >1,000 km, since the Eocene (Rauchenberger et al. 1990). The substantial natural barriers between the Waller Creek population and *A. mexicanus* populations currently in sympatry with swordtails make it extremely unlikely that current gene flow is maintaining visual preferences in tetras. We cannot exclude the possibility that ancestors of the Waller Creek tetras may have occurred in sympatry with a swordtail ancestor and that the observed preference for swords is a vestige of a coevolutionary process. Nevertheless, the preference is quite ancient and has not been maintained due to selection for detecting swordtails. *Astyanax mexicanus* thus appear to share a preexisting bias for swords along with swordtails (Basolo 1990a), platyfishes (Basolo 1990b), and *Priapella* (the sister taxon of *Xiphophorus*; Basolo 1995b). Such a bias could reflect a broad, relatively low-level preference for large body size (Rosenthal and Evans 1998).

Patterns of sword expression across the northern swordtails are associated with predation risk; in populations with high densities of *A. mexicanus*, only the largest males express prominent swords (Rosenthal 2000). The conspicuousness of swords to predators may account for this pattern. Swords are metabolically inexpensive to produce

compared with increased body size (Basolo 1998) and may have evolved as a less costly means of mimicking large apparent size (Rosenthal and Evans 1998). This advantage is offset by the increased predation cost of the sword (Rosenthal 2000).

Predation is also likely to have shaped the evolution of the sword as a visual signal. Evidence from other systems suggests that visual signals can evolve to minimize the risk of detection by predators while remaining conspicuous to conspecifics. The arthropod predators of guppies (*Poecilia reticulata*) and the poeciliid *Phalloceros caudimaculatus* are relatively insensitive to red, while some fish predators of guppies are insensitive to blue and ultraviolet (Endler 1982, 1991*b*). Males in *P. reticulata* (Endler 1991*b*) and *P. caudimaculatus* (Endler 1982) populations with arthropod predators have evolved red and orange markings, while guppy populations with fish predators have evolved blue and ultraviolet ornaments (Endler 1991*b*). This minimizes the contrast of the markings with background body color from a predator's point of view while maintaining contrast for conspecific receivers.

Comparative evidence suggests that the internal contrast of swords may respond to predation as well. The sword of a southern swordtail, *Xiphophorus helleri*, is characterized by a central stripe of orange yellow carotenoid pigments flanked by black melanin on the dorsal and ventral margins. *Xiphophorus malinche*, a northern swordtail in allopatry from *A. mexicanus*, expresses a similar sword. The swords of other northern swordtails, all in sympatry with *A. mexicanus* (*Xiphophorus nigrensis*, *X. cortezi*, *Xiphophorus nezahualcoytl*, *Xiphophorus montezumae*, and the *Xiphophorus multilineatus* used in this study), tend to lack colors conspicuous to the human eye. Ultraviolet imaging and spectroradiometry reveal that the swords of *X. nigrensis* reflect primarily in the ultraviolet. *Astyanax mexicanus*, like humans, lacks sensitivity in the ultraviolet; the color properties of the sword may thus have evolved to minimize conspicuousness to predators (G. G. Rosenthal, M. E. Cummings, and M. J. Ryan, unpublished data). Unlike body markings, however, swords are viewed against a variety of natural backgrounds. This limits the opportunity for privacy; even if internal contrast is minimized, the sword is likely to remain visible to predators as a dark object.

The Waller Creek population of tetras has no current experience and no recent evolutionary contact with swordtails. The sword is thus a novel, relatively conspicuous feature of the tetras' prey regime. Theory makes diametrically opposed predictions about how predators should respond to novel, conspicuous prey. By definition, more conspicuous prey are more likely to be detected, which could increase predation rate (Curio 1976; O'Brien et al. 1976). Alternatively, novel phenotypes may be at lower

risk of predation. Predators may avoid unfamiliar prey items that may be associated with aposematic or aversive stimuli (Götmark and Olsson 1997). Predation may be apostatic, with prey phenotypes at high frequencies taken disproportionately more often (Allen and Clarke 1968). Götmark (1994) found that stuffed blackbirds (*Turdus merula*) bearing novel red wing patches were less likely to be attacked than unornamented males.

If the visual preferences demonstrated here are an indication of predation risk, sworded males should suffer higher predation rates than nonsworded males, even at low frequencies. Aposematism generally takes the form of bright, high-contrast color patterns (Bradbury and Vehrencamp 1998) rather than morphological ornamentation, which may explain the apparent lack of hesitation in *A. mexicanus* vis-à-vis these novel prey.

Astyanax mexicanus lack fin elongation or other morphological ornamentation, so it is unlikely that sexual selection within tetras is maintaining their visual biases. Rather, the preferences of *A. mexicanus* for swords and body size reflect the broad nature of the conspicuousness of these traits. Given an appropriate background and viewing distance, an increase in sword length or body size will result in an increased probability of detection by a receiver. Other ornaments that have evolved in response to preexisting biases, such as chucks in túngara frogs (Ryan and Rand 1993) and feather ornaments in auklets (Jones and Hunter 1998), are similarly broadcasting signals that are likely to be readily detectable to a wide array of receivers. Such signals may therefore carry a built-in cost of increased conspicuousness to eavesdroppers such as predators.

Darwin ([1871] 1936) attributed the attraction of conspicuous traits for female animals to an "aesthetic sense" shared with humans. Recent work has refined this aesthetic in terms of emergent biases for complex or exaggerated stimuli (Ryan 1990; Enquist and Arak 1993; Burley and Symanski 1998) or widespread directional biases in mating preferences (Ryan and Keddy-Hector 1992). Darwin ([1871] 1936, p. 467) postulated that "the taste for the beautiful is confined ... to the attractions of the opposite sex." Our results suggest that this is not the case. Latent aesthetics can be widely shared and expressed in a variety of contexts, and, at least in the case of *A. mexicanus*, the term "taste" need not be metaphorical.

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