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Multivariate male traits misalign with multivariate female preferences in the swordtail fish, *Xiphophorus birchmanni*

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Mate choice represents the outcome of a complex decision that is most often based on the integration of information on multiple traits expressed by potential mates. Multiple traits, however, can show phenotypic correlations, which may coincide with, or oppose, female preference for individual traits. Thus, if multivariate preferences are misaligned with trait covariation, variation in single traits can persist because of weakened net sexual selection. Male swordtails, *Xiphophorus birchmanni*, show positive covariation among three sexually dimorphic visual traits: body size, vertical bars and dorsal fin size. Using synthetic video animations, we isolated each trait and found that females preferred males with large bodies and vertical bars, but small dorsal fins, thus conflicting with male trait covariation. We then tested females using live wild-caught males and found that females preferred smaller dorsal fins on larger males. We suggest that multivariate discordance between traits and preferences results in weak sexual selection on male visual traits, and may help explain the maintenance of variation in sexually dimorphic phenotypes.

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Across taxa, females use multiple cues to assess and select mates. While it is possible that multiple male traits are relics of past selection and have no effect or a negative effect on current fitness (Holland & Rice 1998), considerable research has shown that mate choice using multiple cues can increase both male and female fitness (reviewed in Candolin 2003). In some cases, female preference for multiple traits may align with covariation in male traits, such that mate choice effectively selects on a unitary signal complex (Møller & Pomiankowski 1993; Johnstone 1997). Multiple cues, however, do not always work together; each cue may convey different information, which in some cases may elicit conflicting behaviours from a receiver. In some species, for example, the traits used in signal recognition and those used in intraspecific mate choice may differ (Pfennig 1998). In the pygmy swordtail fish, *Xiphophorus pygmaeus*, females prefer large males, putting them at risk of mating with sympatric heterospecifics (Morris et al. 1996). These females, however, use chemical cues to discriminate against heterospecific mates (Hankison & Morris 2003). Moreover, multiple cues may convey different aspects of quality and/or appeal to

multiple receivers (Andersson et al. 2002). In the red-collared widowbird, *Euplectes ardens*, for example, males display long tails to attract females, and red collars to deter competitors (Pryke et al. 2001). Multiple receivers may also be the target in varying environments or social conditions: different females may weight the importance of particular signals differently (Wedekind 1992), or female preferences may change over time (Moore & Moore 2001; Coleman et al. 2004; Morris et al. 2006).

The multivariate nature of female preferences, as highlighted above, suggests that female preference functions may fail to map onto variation in male traits (Kirkpatrick et al. 2006; Engeszer et al. 2008), thereby weakening the overall effect of selection via mate choice. In at least one case, the direction of sexual selection is nearly orthogonal to the prevailing axis of male trait variation. Van Homrigh et al. (2007) showed that sexual selection, via female preference, for combinations of cuticular hydrocarbons in *Drosophila serrata* is oriented at 88° away from male trait variation. Therefore, net sexual selection is weak despite abundant variation in individual sexually selected traits.

Multivariate mismatches between senders and receivers are likely to be quite common. Both proximate and ultimate constraints differ sharply between display traits and mating biases. For example, many animals use colourful stripes as visual signals. The production of these stripes depends on the dispersion of pigment cells as well as the ultrastructure of those cells. The evaluation of

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stripes by receivers, on the other hand, depends on the expression of cone pigments, the tuning of spatial frequency filters, and the assignment of valence in the visual system (Rosenthal 2007). Natural selection, meanwhile, can favour increased sensitivity in females, but more modest traits in males (Endler 1983). In many systems, females show preferences for trait values outside the range of extant variation in conspecific males (Ryan & Wilczynski 1988; Ryan & Keddy-Hector 1992; Macias Gracia & Ramirez 2005). All these factors suggest that there are likely to be marked differences between the topologies of multidimensional male traits and those of multidimensional female preferences.

In the swordtail fish, *X. birchmanni*, the large, sail-like dorsal fin of males is an intrasexual aggressive signal. Females, however, prefer males with small dorsal fins (Fisher & Rosenthal 2007). Dorsal fin size is positively correlated with body size (Rosenthal et al. 2003), and females in other swordtail species show strong preferences for large body size (Ryan & Wagner 1987; Rosenthal & Evans 1998). In this study, we measured phenotypic correlations among wild-caught *X. birchmanni* males for dorsal fin size, body size, and vertical bar size and number. Vertical bars are known to be under sexual selection via mate choice in other swordtail species (*X. multilineatus*: Morris et al. 1995; *X. continens*: Morris et al. 2005). We then used computer-generated animations to independently decouple these correlated aspects of male signal complexes, allowing us to determine female mating preferences for individual traits. This assay also allowed us to compare the strength of preference for each trait. Our results suggest that females have the greatest preference for large male body size. Consequently, we addressed how preferences for large body size and small dorsal fins jointly determine overall preferences for males expressing natural covariation in these two traits. We predicted that the most attractive males should be males with small dorsal fins for their body size (i.e. males with negative residuals on the allometric slope of dorsal fin size).

METHODS

Animal Collection and Housing

Xiphophorus birchmanni males and females were wild-caught adults collected from the Río Garces, Hidalgo, Mexico. Sexually mature females were isolated from males for at least 3 weeks before testing and were housed in well-planted, single-species 40-litre aquaria. Animals were maintained on a 12:12 h light:dark cycle and were fed TetraMin flakes (Tetra Werke, Melle, Germany), brine shrimp, bloodworms and mysids. All fish were fed the same diet to control for diet-dependent variation in mate choice (Fisher & Rosenthal 2006).

Morphometrics

To quantify natural covariation in focal traits (body size, vertical bars, dorsal fin size) we measured live wild-caught males ($N = 24$) following the procedure described in Rosenthal et al. (2003). Mature males were identified by the presence of a fully developed gonopodium. We placed each male on a laminated sheet of graph paper and took a digital photograph of the male's right and left sides. Males not retained for the behavioural experiments were then released at point of capture. We used the UTHSCSA ImageTool program (University of Texas Health Sciences Center, San Antonio, TX, U.S.A.) for morphometrics. Scale was standardized using the graph paper as background. For each fish, we measured four traits known to be important in sexual signalling (Morris et al. 1995; Rosenthal et al. 2003): standard length (snout to hypural plate), dorsal fin width (anterior to posterior

insertion of dorsal fin), the number of vertical bars and the total pigment area in the bars. Dorsal fin width is highly correlated with dorsal fin height in swordtails (Rosenthal et al. 2003) and, therefore, is a robust measure of overall fin size. Measurements were taken for each side of the body and either averaged (standard length and dorsal width) or summed (bar number and bar pigment area, since bars can vary by side) for use in analyses. We then compared each of these trait values using a two-tailed Spearman's rank correlation. Finally, we performed partial correlations on the dorsal width, bar number and pigment area while controlling for standard length.

Preference Tests with Animated Stimuli

We used synthetic computer animations of males to test female preference for large body size and vertical bars. The base animated stimulus was identical to the one used in previous studies (Fisher & Rosenthal 2006; Fisher et al. 2006; Wong & Rosenthal 2006). The animation was generated using mean trait values for wild-caught *X. birchmanni* males in standard length and depth, and dorsal fin height; a representative male was used to generate body texture and vertical bars. Quantitative analysis of *X. birchmanni* courtship interactions revealed that males perform a simple, conserved courtship display similar to the lateral display described for *X. nigrensis* (Ryan et al. 1992). Animations showed males repeatedly swimming onscreen, performing this courtship behaviour, and then swimming offscreen.

Preference tests were conducted in an aquarium (51 × 28 × 33 cm), with two 35 cm IBM CRT monitors positioned on opposite ends of the aquarium to deliver the animated sequences. We conducted separate experiments testing preferences for each trait. In each experiment, we simultaneously tested preference for the unmodified mean *X. birchmanni* animation versus the same stimulus with one of the signal components reduced. Respectively, we reduced body size to 75% of the original (mean) value and removed the vertical bars; these modified stimuli represent phenotypic traits seen in mature males at the low end of natural variation.

The playback procedure was identical to that used in previous simultaneous-choice studies using animated stimuli (Rosenthal et al. 2002; Fisher et al. 2006; Wong & Rosenthal 2006). Females ($N = 15$) were acclimatized for 10 min, then presented with 10 min of monochromatic screen, followed by simultaneous presentation of the 300 s test stimulus. Subjects were then presented with another 10 min of monochromatic screen followed by the same set of 300 s test stimuli, now switched between monitors to control for any side biases. The side from which a given stimulus was first displayed was also alternated between trials. Female preferences were estimated by measuring association time: the amount of time the female spent within 10 cm of the stimulus. Association time is widely used in studies of mate choice in fishes, and is the standard measure of mating preferences in poeciliids, including swordtails (see Wong et al. 2005, and references therein). In a closely related species, *X. nigrensis*, association time in laboratory trials is a strong predictor of observed mate choices in the wild (Ryan et al. 1992), and is a consistent, repeatable measure of female preference (Cummings & Mollaghan 2006). Females that spent more than 90% of the total time in any one section of the aquarium were defined as unresponsive and were excluded from analysis.

We then compared the total time that each female associated with the mean trait value stimulus versus the modified stimulus (reduced body size or removed bars) using a paired two-tailed *t* test. Then, to test the relative strength of preference for body

size and bars, we compared each female's net preference for size (association time with large male stimulus minus time with small stimulus) to her net preference for bars (association time with barred stimulus minus time with unbarred stimulus) using a paired two-tailed *t* test. In the latter test, two females were removed from the analysis because they showed a side bias in one of the trials.

Preference Tests with Live Males

To test female preference for visual traits of live males, nine wild-caught females and nine wild-caught males were selected from the laboratory colony. The individuals selected for experimentation directly represent the range and mean of natural phenotypic variation, which was determined earlier in this study (see *Morphometrics* above). In simultaneous choice tests, we measured each female's association time with each of the live stimulus males versus the animated standardized mean *X. birchmanni* male stimulus used above, for a total of 81 choice tests.

The experimental set-up involved an aquarium (51 × 28 × 33 cm) housing the focal female, with a double pane (to prevent transfer of odour cues) of UV-transmitting Plexiglas (Rhöm Plexiglas GS2458) placed at 20 cm from one end to house the live male, and a 35 cm IBM CRT monitor positioned on the opposite end of the aquarium, connected to a central computer (Dell OptiPlex GX260) to deliver an animated *X. birchmanni* stimulus. The positions of the live male and the video stimulus were alternated between the right and left side of the aquarium to control for side biases. Both the focal female and the stimulus male were acclimatized for 5 min before the start of a trial. During this time, the monitor was set to display a monochromatic screen, and a sheet of paper of the same colour was inserted between the panes of Plexiglas to prevent the fish from seeing and interacting with one another. When the trial began, we gently lifted the paper, using a pulley system to avoid disturbing the fish, as the monitor began to play an animated stimulus of a *X. birchmanni* male. Live males were presented to females in random order to control for order effects. The time that the female spent associating with live and animated males was recorded for 5 min. A female was deemed to be associating with a particular stimulus if she was within 10 cm of either the monitor or the live male compartment. To evaluate whether females responded differently to live and computer-animated stimuli, we compared the mean response of females to live *X. birchmanni* males versus the computer-animated reference stimulus representing average male traits. To test for order effects, we performed a linear regression on stimulus order and female association time, and found no order effects ($R^2 = 0.053$). As a control, we also tested an additional 20 females on a single randomly selected live heterospecific male *X. malinche* and the animated stimulus of *X. birchmanni* (female *X. birchmanni* show a significant preference for visual cues of conspecific males over *X. malinche* males: Fisher et al. 2006; Wong & Rosenthal 2006). Methods were identical to those stated above for live *X. birchmanni* males. Paired two-tailed *t* tests were used for both of the above comparisons.

To test the prediction that the most attractive males should be males with small dorsal fins for their body size, we first conducted a linear regression of dorsal fin width on standard length for stimulus males used in the preference trials. We then used a one-tailed Spearman's rank correlation to test the a priori hypothesis that females would prefer males with proportionately shorter dorsal fins. Specifically, we evaluated the relationship between mean net female preference (time spent with live exemplar minus time spent with animated reference stimulus) and the residual of dorsal fin width on standard length.

RESULTS

Morphometrics

Standard length, dorsal fin width and bar pigment area of *X. birchmanni* were all strongly positively correlated ($N = 24$; Table 1, Fig. 1). The partial correlations showed a significant positive correlation between dorsal fin width and total bar area even when controlling for standard length ($r = 0.554$, $N = 24$, $P = 0.006$). Again, controlling for standard length, we found a positive correlation between average bar number and total bar area ($r = 0.604$, $N = 24$, $P = 0.002$), but not for dorsal fin width and average bar number ($r = 0.196$, $N = 24$, $P = 0.368$). Thus, the positive interaction between dorsal fin width and average bar number can be attributed to their correlations with standard length.

Preference Tests with Animated Stimuli

In the female preference tests for animated male stimuli, subjects preferentially associated with the large male stimulus over the smaller male stimulus (paired two-tailed *t* test: $t_{14} = 7.067$, $P < 0.001$; Fig. 2) and the barred stimulus over the nonbarred stimulus ($t_{14} = 3.204$, $P = 0.006$; Fig. 2). When comparing the net preference for large body size to bars, we found that the strength of preference for body size was significantly greater (paired two-tailed *t* test: $t_{12} = 2.751$, $P = 0.017$).

Preference Tests with Live Males

In female choice tests with live male stimuli, females associated significantly more with males displaying a proportionately small dorsal fin for their body size (Spearman rank correlation: $r_s = -0.633$, $N = 9$, $P < 0.05$; Fig. 3). Overall, females showed no preference for the live male stimuli over the animated stimulus representing mean trait values for wild-caught conspecific males (paired two-tailed *t* test: $t_{71} = 0.67$, $P = 0.50$); however, females strongly preferred the animation over a live heterospecific male, *X. malinche* (mean ± SE association time: conspecific: 198.86 ± 6.46 s; heterospecific: 73.79 ± 5.95 s; paired two-tailed *t* test: $t_{19} = 2.53$, $P = 0.020$).

DISCUSSION

Our results suggest that female *X. birchmanni* show contrary preferences for allometrically related traits. Although dorsal fin size covaried positively with body size and vertical bar expression in wild-caught males, females preferred large, barred males with small dorsal fins. The net effect of these trait preferences was weak net intersexual selection, since preference was directed away from the prevailing axis of male trait variation. In other words, the attractiveness of large bodies was counterbalanced by unappealing large dorsal fins, and vice versa.

Like most *Xiphophorus* species, we found that *X. birchmanni* females retained broadly shared female preferences for larger body size (Ryan & Wagner 1987; Ryan et al. 1990; Morris et al. 1996) and

Table 1

Spearman rank correlation (r_s) among morphometric variables from wild-caught adult male *X. birchmanni* ($N = 24$)

	Standard length	Dorsal width	Bar area
Dorsal width	0.9157**	—	—
Bar area	0.7989**	0.8461**	—
Bar number	0.6385*	0.6804*	0.8647**

* $P < 0.001$; ** $P < 0.0001$.

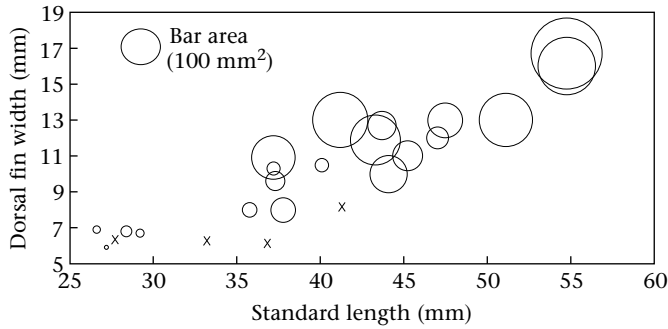


Figure 1. Relationship between standard length, dorsal fin width and total area of bars on wild-caught adult male *X. birchmanni*. 'X' indicates males that displayed no bars.

vertical bars (Morris et al. 2007). However, female *X. birchmanni* in our study differed from most swordtail species in that they preferred males with less elaborate fins. Wong & Rosenthal (2006) found that females strongly prefer males without conspicuous 'sword' elongations of the caudal fin, a reversal of the ancestral preference for swords (Basolo 1995). Similarly, Fisher & Rosenthal (2007) also found that females prefer shorter dorsal fins. These diametrically opposed preferences for more conspicuous bodies and bars and less conspicuous fins present a puzzle, particularly in light of the fact that female preferences tend to be directionally biased in favour of greater sensory stimulation (Ryan & Keddy-Hector 1992). Both small dorsal fins and shorter swords elicit reduced visual stimulation at a gross sensory level (Rowland 1995), suggesting that the valence (attractive or unattractive) assigned to stimuli is not a simple function of stimulus salience.

Data on female mating preferences in numerous other swordtail species indicate that preferences for large bodies and longer swords are ancestral to *Xiphophorus* (Basolo 1998; Rosenthal & Evans 1998). In an earlier paper (Fisher & Rosenthal 2007), we suggested two alternative explanations for female preferences for small dorsal fins: (1) selection may favour females that avoid the more aggressive, high-finned males; (2) preference for small dorsal fins may be an incidental consequence of disdain for swords, a general evaluative bias against fin elongations (swords, an elongation of the caudal fin, and large dorsal fins) may have arisen at some point in the *X. birchmanni* lineage. Wong & Rosenthal (2006) speculated that

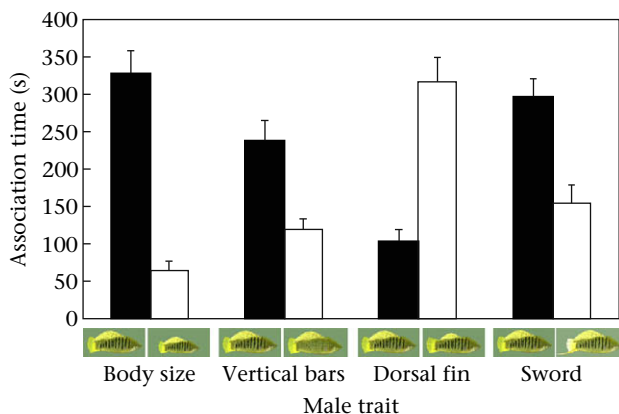


Figure 2. Mean \pm SE female association time for animated stimuli of conspecific males ($N = 15$). In each set of trials, females were shown a stimulus representing the unmodified mean trait values of wild-caught *X. birchmanni* males (■) and the same stimulus with one of the signal components modified (□): body size was reduced to 75% of mean, vertical bars were removed, dorsal fin was reduced to 66% of mean (Fisher & Rosenthal 2007), or a sword was added (Wong & Rosenthal 2006). Still images of the corresponding animated stimuli are shown below each bar.

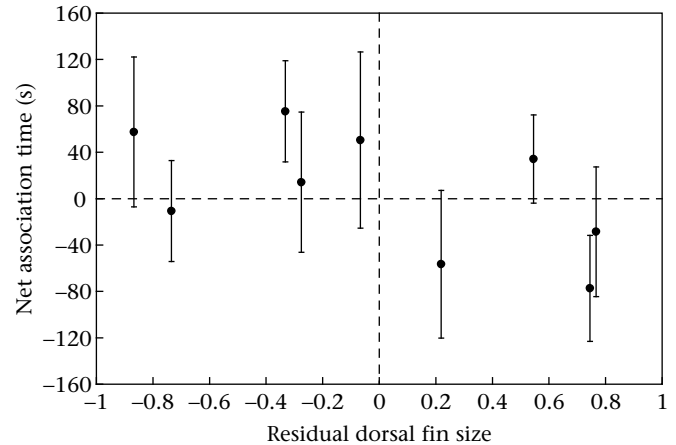


Figure 3. Mean \pm SE female net preference for live males versus the male's relative dorsal fin size (linear regression residual of dorsal fin width on standard length). Female preference is shown as net association time (the time that females associated with a live male stimulus minus the time that they associated with the animated male stimulus); each point represents the mean behaviour of all females tested on each male ($N_{\text{females}} = 9$, $N_{\text{males}} = 9$). The residual dorsal fin width represents the proportional size of a male's dorsal fin for his body length; thus, -1 represents a male with a small dorsal fin for his size, and $+1$ represents a large fin on a small fish.

female disdain for swords, in turn, may have evolved as a mechanism for avoiding hybridization with sworded congeners (*X. malinche* and *X. cortezi*; Rauchenberger et al. 1990). Multiple examples of reduction or loss of sword preference (Basolo 1998; Rosenthal et al. 2002; Wong & Rosenthal 2006) suggest that female preferences for large size and fin elaboration can evolve independently.

The greater strength of female preference for large male body size in our study relative to that for male stimuli with vertical bars suggests that female preference for bars is relatively weak in *X. birchmanni*. This finding is consistent with the results of Morris et al.'s (2007) study, in which female *X. birchmanni* did not respond to computer-animated males varying in the presence or absence of vertical bars. However, in Morris et al.'s (2007) study, the strength of female response was compared using an outgroup taxon, *X. variatus*, which the authors indicate may not be sensitive enough to reveal a weak preference for bars.

In this study we tested *X. birchmanni* females on two types of complex visual signals: synthetic animations of courting males, which allowed us to manipulate individual signal parameters independently, and live males behind a clear partition, which allowed us to sample natural variation in multivariate visual signals. Several authors (D'eath & Dawkins 1996; Fleishman & Endler 2000; Zeil 2000) have pointed out important deficiencies of video playback relative to natural stimuli. Our results suggest, however, that females perceived live and animated males comparably. Males drawn from a sample of live, wild-caught *X. birchmanni* were, on average, no more attractive to females than the animated stimulus representing mean values for sexually selected traits, as measured by association time in the laboratory. The animated *X. birchmanni* was, in turn, substantially more attractive to females than were live *X. malinche* males. In terms of mate choice within and among species, therefore, females make comparable choices with live and virtual males.

There are numerous examples of females preferring supernormal trait values not found in conspecific males (Ryan & Wagner 1987; Basolo 1990; Parsons et al. 1993; Burley & Symanski 1998). Our study suggests that even when female preferences for individual traits favour naturally occurring phenotypes, multivariate female preferences may favour multivariate trait combinations that

are unlikely to occur in conspecific males. If males expressing some novel trait combinations have a mating advantage, this may explain the success of F_2 or later hybrids in natural hybrid zones between *X. birchmanni* and *X. malinche*, which has a smaller dorsal fin. Hybrids show substantially lower phenotypic correlations among sexually dimorphic traits (Rosenthal et al. 2003), and some hybrid phenotypes are more attractive to females of the parental species than are conspecific males (G.G.R., unpublished data). Some hybrid males may thus enjoy higher mating success by virtue of breaking undesirable correlations among traits.

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